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Decay dynamics of *Abies alba* and *Picea abies* deadwood in relation to environmental conditions

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ABSTRACT

In this study we analysed a dataset of 8661 logs of silver fir (*Abies alba* Mill.) and Norway spruce (*Picea abies* L., Karst) in mixed fir-spruce-beech stands in primeval and natural forests in four sites separated into the two macroclimatic categories according to mean annual temperature ("cold" and "warmer") and according to mean annual precipitation ("mesic" and "humid"). We used "Bayesian Survival Trajectory Analysis" on a more than 40-year long time series (1972–2015), focusing on differences in the residence time of deadwood in different macroclimatic categories and two DBH classes. We also evaluated two qualitative characteristics of the downed logs: mortality mode and log position during decomposition. We calculated residence time and the time needed to reach the advanced decay stage. Our analyses confirmed the influence temperature and precipitation on modelled residence time. The residence time for silver fir logs in the DBH class 55 + cm in the "cold" site was 106 years, while in the "warmer" sites was 78 years. The residence time in the "mesic" site was 57 years, while in the "humid" sites was 90 years. It took 81 years for Norway spruce logs in the DBH class 55 + cm to completely decompose in the "cold" site. Suspended logs 11 took years longer to decay than those in contact with the ground. The modelled residence time of logs on wet sites was the same as that of logs at sites unaffected by water. These results can be utilised in biodiversity oriented forest management, as well as in modelling future amounts of deadwood. In order to maintain the continuous presence of silver fir and Norway spruce deadwood for those organisms that depend on it, it is necessary to supply deadwood at least once every 25–40 years (depending on climatic category and DBH class). During this time, approximately 50% of logs become completely decomposed and 50% remain in the last decay stage.

1. Introduction

Silver fir (*Abies alba* Mill., hereafter "fir") and especially Norway spruce (*Picea abies* L., Karst., hereafter "spruce") are the dominant tree species at intermediate and high altitudes in European forests (San-Miguel-Ayanz et al., 2016). Increased amounts of deadwood are expected in forests because of more frequent disturbance events and the expansion of protected areas (Natura 2000, etc.). The lifespan and balance of carbon stored in deadwood are determined by the decay rate (as expressed by the rate of CO_2 respiration), and are mostly related to the activity of microorganisms, primarily fungi, that are capable of decomposing lignin and cellulose (Herrmann and Bauhus, 2013). In addition, wood-boring insects have been suggested as decay accelerators because of the galleries that they excavate in the wood (Rayner and Boddy, 1988; Zhong and Schowalter, 1989). The activity of these organisms in deadwood is mainly dependent on climatic variables (temperature, moisture, aeration) and substrate (tree species, decay stage, DBH of the log). Some studies have demonstrated that substrate variables have a more significant effect than climatic variables (Harmon et al., 1995). Other studies have shown that the rate of CO_2 respiration is mainly influenced by climatic variables (Mackensen et al., 2003). Studies have shown differences in decomposition rate between different tree species. For example, the decomposition rates of Norway spruce stems were somewhat lower than those of Scots pine (Mäkinen et al., 2006). Findings of Freschet et al. (2012) suggests differences in decay dynamics across wood species that arise from changing underlying wood decay processes (i.e., varying wood functional traits and decomposer community interactions). Increased deadwood diameter results in a smaller surface to volume ratio exposing a minimal portion of deadwood exterior to mechanical and biological colonization then decreases decomposition rate (Graham and Cromack, 1982; Stone et al., 1998). But other researches indicated that there is no significant relationship between deadwood diameter and decomposition rate especially towards to the big size deadwood (Mattson et al., 1987; Laiho and

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Prescott, 1999). In-situ analyses have shown that the decay rate in European beech (*Fagus sylvatica* L., hereafter "beech") and spruce increase with growing temperature and decreasing DBH, with an optimal annual precipitation of 1100–1300 mm (Zell et al., 2009). Although decomposition processes are generally positively related to the moisture content of the substrate, decomposition is retarded in saturated wood, where oxygen availability is limited and fungal growth obstructed (Rayner and Boddy, 1988).

Several studies have examined the substrate characteristics that influence residence time, i.e. average time during which the major part of the downed logs or deadwood mass completely decompose (Tarasov and Birdsey, 2001), for example the size of deadwood (DBH) and its status (log, snag, and stump) (Angers et al., 2011; Yatskov et al., 2003). The position of the log during decomposition can influence the wood moisture in relation to the amount of contact with the ground. Increasing water loss can limit the activity of decomposers (Shorohova and Kapitsa, 2014) and influence the composition of fungal communities (Rajala et al., 2012). Spruce logs in direct contact with the ground decay quicker than suspended logs (Næsset, 1999). The influence of log position on decomposition and mortality mode has also been demonstrated for Siberian fir (*Abies sibirica* Ledeb.) and spruce: logs in contact with the ground have a much shorter residence time than leaning logs or those that died standing (Shorohova and Kapitsa, 2014). Site conditions may also affect decomposition through moisture regimes; in both excessively dry and wet sites, the decomposition process is slower compared to that in sites with moderate moisture (Shorohova and Kapitsa, 2014).

The successional series of several organisms that inhabit deadwood are significantly determined by the decay stage. The highest number of fungus species can be found on downed spruce logs in the last decay stage (Lindblad, 1998; Rajala et al., 2011), while the highest species diversity of bryophytes on downed fir and spruce logs can be observed during the intermediate decay stage (Kruys et al., 1999; Söderström, 1988; Táborská et al., 2015). Advanced-decay deadwood volume also favours the local diversity of small mammals (Fauteux et al., 2013). The availability of large logs in advanced decay is known to affect many rare species of saproxylic beetles (Sverdrup-Thygeson, 2001).

A higher diversity of deadwood structures translates into a particularly diverse community of organisms, mainly fungi and arthropods (Martikainen et al., 2000). Gossner et al. (2013) concluded that the amount and quality of deadwood (diameter, decay stage) are the key parameters for saproxylic beetles in a European beech forest. Thus, knowledge on residence time and the duration of decay stages diversified according to various attributes (species, DBH, etc.) is important for the targeted management of forests in protected areas or for biodiversity-oriented forest management.

Wood-inhabiting fungi and other organisms living on deadwood are habitat-tracking specialists, depending on a continuous supply of deadwood (Halme et al., 2013). Because of the decay process a given habitat patch is only suitable for each species in a limited time window, and all species need to repeatedly colonize new suitable habitat patches to survive in the system (reviewed in Stokland and Siitonen, 2012). Increasing the amount of deadwood artificially clearly enhances the possibilities for polypores to thrive in forests; however, this does not seem to work as a quick solution for facilitating the populations of red-listed and rare polypores (Pesanen et al., 2014). As most red-listed polypores have shown to favour trees in the advanced decay stages (Junninen and Komonen, 2011), it may take several decades until the benefits of restoration for threatened species will be fully realized.

Many studies dealing with the residence time have been conducted in boreal spruce forests in northern Europe (e.g. Shorohova and Kapitsa, 2014; Tarasov and Birdsey, 2001) as well as in temperate mixed and spruce forests (e.g. Holeksa et al., 2008; Herrmann et al., 2015). However, only a few studies have evaluated the residence time of silver fir deadwood (for example Lombardi et al., 2008), and without assessing various macroclimatic conditions. In this paper we present research on the residence time of fir and spruce deadwood, focusing on how environmental conditions influence the residence time and the time needed to reach the advanced decay stage, which is of key importance in biodiversity conservation. We compared the silver fir and Norway spruce deadwood, the two main coniferous species in Central European temperate forests. We analysed a dataset of 3297 fir and 5364 spruce logs spanning 43 years in four sites of central European temperate forests separated into the two temperature categories ("cold" and "warmer") and two precipitation categories ("mesic" and "humid"). Our aim was to answer the following questions: (i) What are the differences in the residence time of downed fir logs that fell alive and their time needed to reach the advanced decay stage (the most important for biodiversity) in the climatically different sites, (ii) what are the differences in the residence time of downed fir logs that died as standing trees, (iii) what is the residence time of downed spruce logs that fell while alive and that died standing in one site, and (iv) what is the effect of log position during decomposition on the residence time of spruce.

2. Materials and methods

2.1. Study sites

The four study sites are located in three mountain ranges with different macroclimatic conditions: (i) Šumava Mts. (Boubín) – Hercynian fir-spruce-beech mixed forests, (ii) Novohradské hory Mts. (Žofín) – Hercynian beech dominated forests, and (iii) Moravskosleszké Beskydy and Javorníky Mts. (Salajka, Razula) – fir-beech mixed forests in the Western Carpathians. Table 1 shows details on mean annual temperature (hereafter "temperature"), mean annual precipitation (hereafter "precipitation") and other important data. Macroclimatic data were obtained from the climatic normal from 1981 to 2010 (CHMÚ, 2016).

Research was carried out in the Boubínský prales national nature reserve (48°59′N, 13°49′E), which includes one of the best preserved mountain old-growth forests in temperate Europe (altitude 925–1105 m a. s. l.), and has been officially protected since 1858 (Šebková et al., 2011; Vrška et al., 2012). *Picea abies* (L.) Karsten and *Fagus sylvatica* L. dominate in the tree layer with some *Abies alba* Mill. and other trees (*Acer pseudoplatanus* L., *Sorbus aucuparia* L., *Ulmus glabra* Huds.). Detailed descriptions of the stand structure and the development of species composition and diameter structure can be found in Šebková et al. (2011) and Vrška et al. (2012). In 2010, the proportions of downed logs by numbers that were eventually used in the evaluation were 67% spruce, 20% beech and 13% fir.

Žofínský prales national nature reserve (48°40′N, 14°42′E)

Table 1
Basic characteristics of the study sites. MAT – Mean annual temperature, MAP – Mean annual precipitation.

Site	Time since the last cutting	Size of site (ha)	No. of evaluated logs	Censuses	MAT (°C)	MAP (mm)	Temperature category	Precipitation category
Boubín	Never cut	46.62	6250	1972, 1996, 2010, 2015	4.9	1067	Cold	Humid
Žofín	Never cut[a]	74.20	718	1975, 1997, 2008, 2015	6.2	866	Warmer	Mesic
Razula	Since 1935	22.84	771	1972, 1995, 2009, 2014	6.5	1121	Warmer	Humid
Salajka	Since 1930	19.03	943	1974, 1994, 2007, 2014	6.2	1142	Warmer	Humid

[a] Partial removal of deadwood until 1882.