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Influence of the substrate and ecosystem attributes on the decomposition rates of coarse woody debris in European boreal forests

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ABSTRACT

Narrowing the uncertainties in coarse woody debris (CWD) decomposition rates depending on the ecosystem and substrate attributes can improve our understanding of biodiversity patterns and carbon dynamics in forest ecosystems. We estimated decomposition rates of aboveground CWD, represented by fallen and leaning logs, stumps and snags >8 cm in diameter sampled at eight sites in European boreal forests. In total, 3491 CWD pieces were sampled. The chronosequence period covered a range up to 168 years. Single exponential decomposition (mass loss) rates (k) averaged 0.066, 0.032, 0.027, and 0.014 year^{-1} for aspen (*Populus tremula*) and birch (*Betula pendula*, *Betula pubescens*), fir (*Abies sibirica*) and spruce (*Picea abies*, *Picea obovata*), Scots pine (*Pinus sylvestris*) and Siberian pine (*Pinus sibirica*), respectively. At the regional-scale, the decomposition rate decreased with increasing difference between maximum and minimum temperatures. The CWD decomposition rate was greater on open fertile sites with moderate moisture compared to rates on poor dry or moist sites under closed tree canopies. CWD tree species played the primary role in decomposition at the CWD-piece scale. CWD position and tree mortality mode were rate-controlling mainly for decomposition of fir and spruce CWD. CWD size did not affect decomposition rates. Our results predict CWD decomposition rates as a function of climatic factors, site conditions, tree species, stem position and mode of tree mortality in European boreal forests at the scale of regions, forest stands and individual CWD pieces.

1. Introduction

The role of wood decomposition in forest ecosystems is comparable in magnitude to the role of the synthesis of organic matter. Decomposition rate controls energy flows, carbon and nutrient retention (Yatskov et al., 2003; Kudeyarov et al., 2007; Palviainen et al., 2010a,b) and influences the availability of coarse woody debris (CWD) for wood-dependent organisms (Berg et al., 1994).

The complexity of wood decomposition processes and their dependence on interrelated biotic and abiotic factors are widely recognized (Rayner and Boddy, 1988; Soloviev and Malysheva, 2004; Stokland et al., 2012). Decomposition factors include identity of the decomposing organisms and substrate characteristics (Boddy, 2001; Mackensen et al., 2003; Laiho and Prescott, 2004). The activity of decomposing organisms depends on controlling factors such as temperature, moisture, aeration, and substrate quality. While much has been written about CWD decomposition, less has been done to quantitatively estimate the relative importance of the rate-controlling factors (Weedon et al., 2009; Zell et al., 2009).

The decomposition rate-controlling factors *in situ* can be examined as ecosystem and substrate attributes. At the regional scale, climate is known to affect the decomposition rates. Environmental variables such as moisture and temperature have a profound effect on respiration (Rypaček, 1957; Stepanova and Mukhin, 1979; Herrmann and Bauhus, 2012). Laboratory tests indicate an increase in decomposition rate with temperature, followed by a sharp drop once the temperature exceeds an optimum value. The range between maximum and minimum temperatures may better explain the variation in wood decomposition rates as compared to mean temperature. Decomposing organisms are sensitive to low temperatures and temperature variations (Stepanova and Mukhin, 1979). Thus, their activity and wood decomposition rates may negatively depend on temperature range. At low levels of moisture, colonization by wood decaying fungi is slow. When water fully saturates a substrate, most decomposers are unable to respire due to the lack of oxygen. Based on those relationships, moisture and temperature of the substrate are used as parameters in CWD decomposition models (Yin, 1999; Karelin and Utkin, 2006; Zell et al., 2009; Tuomi et al., 2011). However, CWD decomposition rates as a function of

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climatic factors under different conditions and for different substrates were not examined yet.

At the forest stand scale, decomposition rates are influenced by forest canopy and site characteristics that may affect climatic parameters within the regional range of variability. *In situ* temperature and moisture of dead wood and their daily and seasonal fluctuations may depend on the site conditions and successional stage of an ecosystem. However, the reported decay rates take into account characteristics of forest stands only to some extent (Tarasov and Birdsey, 2001; Yatskov et al., 2003). The influence of forest type and successional stage of the forest stand on decomposition rates is theoretically assumed (Harmon, 2001). However, there are only few studies comparing wood decomposition rates in pristine vs. managed forests (Janisch et al., 2005; Jacobs and Work, 2012) and in closed canopy forests vs. clear-cut areas (Mäkinen et al., 2006; Shorohova et al., 2008a). Forest management may affect the wood decomposition rates by decreasing: (1) variation in stand density and consequently the temperature and moisture regimes; (2) CWD volumes and compositional diversity (Siitonen, 2001; Shorohova and Shorohov, 2001); and (3) decomposer community composition and diversity (Sippola and Renvall, 1999) and by decreasing wood bulk density through improving tree growth conditions (Polubojarinov, 1976). In addition, CWD volumes and compositional diversity may influence wood decomposition rates through providing ecological niches for community of decomposing organisms. High species diversity of decomposers is assumed to be positively related to their functioning, i.e. to wood decomposition rates (Jacobs and Work, 2012). When decomposition starts, less dense wood is more easily accessed and degraded by decomposers (Edman et al., 2006). Site conditions may also affect decomposition through moisture regimes. This relationship is assumed to be non-linear: in both excessively dry and wet sites, the decomposition process is slower compared to that on sites with moderate moisture. The successional stage may affect the decomposition rate indirectly through temperature and moisture regimes. In early successional open sites, the surface temperature is higher and the surface air humidity is lower and the evaporation demand on the substrate is higher compared to those under a closed forest canopy, which is the case in the late successional sites (Yin and Arp, 1993). Thus, the research is needed on interspecific differences in decomposition rates of logs, snags and stumps under different forest management and disturbances regime and growth conditions in European boreal forest.

At the scale of individual CWD pieces, the decomposition rate predictors may be substrate moisture, temperature, gaseous regime and chemical composition. Among substrate characteristics, the most commonly examined are tree species, CWD piece size and, in some studies, wood position (logs vs. stumps or snags) (Yatskov et al., 2003; Janisch et al., 2005; Angers et al., 2011). Deciduous tree species are widely found to have higher decomposition rates compared to coniferous species (Rayner and Boddy, 1988; Weedon et al., 2009). CWD size is assumed to affect decomposition rates directly by influencing substrate moisture, temperature, and aeration, and indirectly by influencing characteristics of the substrate itself. Decomposition rates for large-diameter logs are slower because the lower surface/volume ratio reduces access to decomposers and lowers rates of gas and water exchange in proportion to the volume of a log (Abbott and Crossley, 1982). In addition, an increasing portion of more slowly decomposable heartwood is found in bigger logs (Harmon et al., 1986). However, the effect of piece size on decomposition rates has been reported to be positive, negative or non-existent (Mackensen et al., 2003). Wood position may affect moisture through the distance of the substrate to the ground and differences in wood structure. The density of stump wood is greater than that of logs. Fallen logs decompose faster compared to snags (Yatskov et al., 2003), whereas the evidence about stump vs. log decomposition rates is contradictory. The elevation of CWD above the ground may increase the rate of moisture loss and thus hasten the rate of decomposition. In contrast, the higher density of stump wood may delay moisture loss and decomposition rate. Stumps have been reported to decompose at the same rate (Janisch et al., 2005; Shorohova et al., 2009) or faster (Tobin et al., 2007) compared to fallen logs. The potential role that the cause of tree mortality might have on decomposition rates has not yet been well studied.

In our study, we inventoried CWD and calculated the bulk density and mass loss associated with the decomposition of above-ground parts of logs, snags, and stumps. Our main objective was to examine the effects of ecosystem and substrate characteristics on decomposition rates.

At the regional scale, we hypothesized there would be positive effects of mean temperature and precipitation and negative effects of the temperature range on the decomposition rates of CWD. At the forest stand scale, we hypothesized accelerated decomposition rates with increasing site productivity, CWD volume and species and structural diversity. Decomposition rates were expected to be lower on dry and moist sites compared to sites with moderate moisture, and under closed canopies compared to open sites.

At the CWD piece scale, we hypothesized that (1) tree species would play a primary role in the decomposition rate of CWD; the decomposition rate would increase in the order: Siberian pine, Scots pine, spruce, fir, birch, aspen; (2) the effect of CWD piece size would be less useful for predicting rates of decomposition than other factors; (3) that substrate, position and tree mortality mode would play a secondary decomposition rate-controlling role; (4) decomposition rates would increase with the degree and time of CWD contact with the ground; i.e. in the order: snags, leaning logs (when trees died standing), leaning uprooted and broken trees, natural stumps, cut stumps, fallen logs when trees died standing, fallen logs when trees were uprooted, fallen logs when trees were broken.

2. Materials and methods

2.1. Study sites

The studies were carried out from 1997 to 2009 in a subset of eight sites located in Russia and Finland (Fig. 1 and Table 1). The Russian sites included Nature Park “Vepssky Forest” (VF1 and VF2), in the Saint-Petersburg region; Central Forest State Natural Biosphere Reserve (CFR) in the Tver region; 2 areas in Russian Karelia (K1 and K2); and sites in Ygyd-va National Park, Komi Republic (Komi). The Finnish sites are located in southern Finland (SF) and in Finnish Lapland (NF). The K1, K2 and NF sites belong to the northern-boreal, VF – to the middle-boreal and CFR and SF – to the southern boreal vegetation zones (Ahti et al., 1968; Kurnaev, 1973). The VF1 sites are pristine forests, located in the core area of the “Vepssky Forest” reserve. The inventory was made on permanent sample plots with known year of tree death for every sampled CWD (see Shorohova et al., 2008c for details). The VF2 sites are first time clear-felled forests, located in the reserve’s buffer zone and its vicinity. After clear-felling no site preparation was conducted; some uncut patches and large amounts of CWD were left. The CFR sites are pristine forests; inventories were made in the permanent sample plots and in temporary plots with known years of stand-replacing windthrows (Table 2). In the K1, K2 and Komi pristine forests, inventories were made on newly established permanent (K1) and temporary (K2 and Komi) sample plots. The SF and NF sites have a long history of forest use. Samples were collected across a chronosequence of clear-felled areas with prescribed burning on some sites and subsequent soil preparation