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Fungal wood decomposer activities influence community structures of myxomycetes and bryophytes on coarse woody debris

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ABSTRACT

Dead wood is an important habitat for forest organisms, and wood decay fungi are the principal agents determining the dead wood properties that influence the communities of organisms inhabiting dead wood. In this study, we investigated the effects of wood decomposer fungi on the communities of myxomycetes and bryophytes inhabiting decayed logs. On 196 pine logs, 72 species of fungi, 34 species and seven varieties of myxomycetes, and 16 species of bryophytes were identified. Although white rot was the dominant decay type in sapwood and heartwood, brown and soft rots were also prevalent, particularly in sapwood. Moreover, white rot and soft rot were positively and brown rot negatively correlated with wood pH. Ordination analyses clearly showed a succession of cryptogam species during log decomposition and showed significant correlations of communities with the pH, water content, and decay type of wood. These analyses indicate that fungal wood decomposer activities strongly influence the cryptogam communities on dead wood.

Introduction

Growing evidence shows that coarse woody debris (CWD) is crucial for maintaining forest biodiversity, including decomposers, such as fungi and bacteria; fungivores and bacterivores, such as amoebae and invertebrates; epiphytes, such as bryophytes, lichens, and vascular plants; and invertebrates and vertebrates that use such substrata as food sources or dwelling and hunting places (Bunnell and Houde, 2010; Stokland et al. 2012). The diversity of the community of such saproxylic organisms may result in a variety of trophic and non-trophic species interactions in forest ecosystems

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(Stokland et al. 2012). Revealing such interactions is important to completely understand integrated forest dynamics.

Fungi are dominant in CWD communities and play a central role in CWD decomposition (Rayner and Boddy, 1988). Obvious physicochemical changes during CWD decomposition include reduced bulk density, increased water content, accumulation of nutrients and acid-unhydrolyzable residues (formerly referred to as lignin), and reduced pH (Rayner and Boddy, 1988). Such dead wood properties have been classified into different decay types, such as white, brown, and soft rots according to the lignocellulose-decomposition capabilities of various fungal species. In addition, because the decomposition of lignocellulose is a key determinant of humus formation on the forest floor (Stevenson, 1982), decay types have marked effects on the species composition of detritus-dwelling organisms, such as bacteria (Jurgensen et al. 1989; Folman et al. 2008; Hoppe et al. 2014), fungi (Tedersoo et al. 2008; Lindner et al. 2011), invertebrates (Araya, 1993; Cornelius et al. 2002; Wardlaw et al. 2009), and plants that grow above the detritus communities (Bače et al. 2012; Fukasawa, 2012). Such effects could be recognized as indirect effects of fungi on detritus communities and plants, mediated by environmental changes in CWD. However, the effects are far less well understood for a variety of wood-inhabiting organisms.

Myxomycetes and bryophytes are taxonomically distinct groups of organisms with vastly different lifestyles. The former are eukaryotic amoebozoa preying on other microorganisms, and the latter are eukaryotic autotrophs, but both are frequent on CWD, and previous studies have shown clear compositional changes of their community compositions during the decay of CWD (McCullough, 1948; Muhle and LeBlanc, 1975; Söderström, 1988; McAlister, 1997; Heilmann-Clausen, 2001; Ódor and van Hees, 2004; Heilmann-Clausen et al. 2005; Ódor et al. 2006; Caruso and Rudolphi, 2009; Takahashi and Hada, 2009). They may also be functionally important for structuring CWD communities. Amoebae of myxomycetes are abundant in detritus and feed on bacteria, fungi, and plant residues (Stephenson et al. 2011). Such panphytophagous amoebae may have critical effects on nutrient mineralization and may affect the nutrition of other organisms (Schroter et al. 2003). Furthermore, mycophagy by invertebrates can stimulate or inhibit wood decomposition processes (A'Bear et al., 2014). Bryophytes are known to dramatically influence seedling establishment on log surfaces by facilitating seedling colonization by trapping seeds (Harmon, 1989), protecting them from vertebrate and invertebrate foragers (van Tooren, 1988), holding water (Iijima et al. 2006), and increasing nutrient availability (Sand-Jensen and Hammer, 2012). In contrast, they prevent seedling growth by shading (Delach and Kimmerer, 2002; Iijima and Shibuya, 2010) and allelopathic effects (Michel et al. 2011).

The establishment of tree seedlings on fallen trunks is an important regeneration process in forests (Harmon et al. 1986). Because tree regeneration may be strongly affected by detritus organisms on their regeneration substrata (Bardgett and Wardle, 2010), we used previously published data for tree seedlings on logs (Fukasawa, 2012) and re-analyzed them with cryptogam community data in this study. Although the effect of wood decay type on seedling establishment has already been reported (Bače et al. 2012; Fukasawa, 2012), we expect that tree seedlings also have some relationship with cryptogam species on logs.

In this study, we assessed the effects of wood decay by fungi on myxomycete and bryophyte communities on CWD by recording the occurrence patterns of fungal sporocarps, myxomycetes, and bryophytes on CWD and by analyzing their occurrence with CWD decay stages and decay types, particularly in the late stages of decomposition.

Materials and methods

Study site

The study site was located in the Higashiyamato Park (35°45′N, 139°26′E; 114–122 m a.s.l.), 40 km west of Tokyo, Japan. The mean annual temperature at the nearest meteorological station (Tokorozawa; 35°46′N, 139°25′E; 119 m a.s.l.) was 14.1 °C from 1979 to 2000. The mean monthly temperature ranged from 3.6 °C in Jan. to 25.5 °C in Aug. The mean annual precipitation was 1 443.9 mm and snow was rare (Japan Meteorological Agency 2011, http://www.data.jma.go.jp/obd/stats/etrn/index.php). The park area of 184 ha is surrounded by a residential district. The forest was an abandoned coppice of *Quercus serrata* and *Pinus densiflora* that had been thinned on a 20–25-yr cycle until the late 1970s. The park was established in 1979, and the most recent clearcut of this area (excluding *P. densiflora*) occurred from 1982 to 1986. Pine wilt disease caused widespread mortality of the dominant *P. densiflora* canopy from 1980s until the present. These tree deaths provided abundant quantities of woody substrata on the forest floor (Kato and Hayashi, 2006). The details of the present vegetation are described by Fukasawa (2012).

Data collection

Ten 10 × 10 m plots were randomly selected within a tract of approximately 1 ha on a gentle north-facing slope. All fallen logs of *P. densiflora* (diameter >10 cm) were numbered and classified into five subcategories, according to decay class (DC), using the criteria of Fukasawa (2012) as shown in Supplementary Table A1. To eliminate within-stem variation in DCs (Pyle and Brown, 1999), a stem section of approximately 2 m was selected from each CWD where DC was uniform. A

Table 1 – Results of generalized linear models for testing relationships between wood decay types and log variables

Variable	Sap			Heart			
	White	Brown	Soft	White	Brown	Soft	Sound
Diameter	1.20[c]	−1.02[b]	0.53	−0.19	−0.24	n.a.	0.66[a]
pH	1.16[c]	−1.33[c]	0.82[b]	0.48	−0.84[b]	n.a.	0.42
Water	0.57	−0.02	−0.10	0.27	−0.81[a]	n.a.	0.57

n.a. not applicable due to small sample size.
a $P < 0.1$.
b $P < 0.05$.
c $P < 0.01$.