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The relation of fungal communities to wood microclimate in a mountain spruce forest

Václav Pouska [a, *], Petr Macek [b], Lucie Zíbarová [c]

[a] Faculty of Forestry and Wood Sciences, Czech University of Life Sciences Prague, Kamýcká 129, 16521 Praha 6 – Suchdol, Czech Republic
[b] Faculty of Science, University of South Bohemia, Branišovská 31, 37005 České Budějovice, Czech Republic
[c] Resslova 26, 40001 Ústí nad Labem, Czech Republic

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ABSTRACT

Microclimatic conditions influence fungal growth, yet accurate descriptions of the relationships between the occurrence of fungi and microclimate (especially temperature) are lacking for dead wood in natural conditions. Here, we studied the occurrence of fungal fruit bodies on 2 m long segments of both standing and lying trunks of Norway spruce (*Picea abies*). The fungal assemblages were associated with properties of the segments related to the progression in wood decay, causes of tree death, and temperature and moisture conditions. Fluctuations in the temperature of wood decreased with increasing water content, and both water content and temperature stability increased with diameter and with the progression in wood decay. Red-listed species differed in their relations to both wood and microclimate parameters, which highlights the importance of the simultaneous presence of various wood types for the occurrence of rare and threatened species.

1. Introduction

The process of wood decay is reflected in the composition of fungal communities in individual lying trunks (Renvall, 1995; Høiland and Bendiksen, 1997; Heilmann-Clausen, 2001; Pouska et al., 2011; Rajala et al., 2011, 2012; Heilmann-Clausen et al., 2014). Species composition is also related to the decay rate of wood and is influenced by external microclimatic conditions (Heilmann-Clausen, 2001), as well as being interconnected with the way the tree died (Renvall, 1995; Pouska et al., 2011; Ottosson et al., 2015). In addition to the stage of decay, several other related characteristics have been demonstrated to be important for species composition on lying trunks (i.e. logs), such as the cover by bark (Renvall, 1995; Kubartová et al., 2012), contact with the ground (Lindblad, 1998; Rajala et al., 2012) and moisture (Fukasawa et al., 2009; Rajala et al., 2011, 2012). The occurrence of fungal species is influenced by the properties of the wood they occupy, but fungal activity is in turn the main driver of decay, changing the chemical composition and structure of wood (e.g. Rypáček, 1957; Stokland et al., 2012) and, under aerobic conditions, producing water, carbon dioxide and heat (Rypáček, 1957; Boddy, 1983a,b; Bjurman and Wadsö, 2000).

In Norway spruce, the size of logs is an important determinant of species composition (e.g. Lindblad, 1998; Rajala et al., 2011, 2012), and large logs are very important for the occurrence of certain species (Bader et al., 1995; Høiland and Bendiksen, 1997; Stokland and Larsson, 2011). Junninen and Komonen (2011) concluded that the threshold diameter critical for polypore species richness is 20–30 cm, above which the sporocarps of species demanding large-diameter trunks start to appear. Although some fungal species prefer the fine wood of spruce, most also form sporocarps on coarse wood (Allmér, 2005). It is unlikely that fine woody debris (diameter 5–9 cm) can substitute coarse woody debris in managed spruce forests where red-listed species are concerned (Kruys and Jonsson, 1999).

There are several explanations for the importance of trunk size on fungal community assembly. Larger trunks persist longer in

* Corresponding author.
E-mail address: vaclav.pouska@yahoo.com (V. Pouska).

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particular stages of decay (Harmon et al., 1986), which is important for many rare species that seem to depend on the slow decay process (Renvall, 1995), and for species that disperse mainly through spores, because these species have a greater chance of landing on a trunk in a suitable stage of decay due to a longer 'window of opportunity' (Stokland et al., 2012). Furthermore, the greater surface area of large trunks can collect more spores, which may be particularly important for rare species with low population densities and spore deposition (Bader et al., 1995; Jönsson et al., 2008). On the other hand, small trunks may not provide a sufficient amount of substrate for the sporocarp production of some species (Stokland and Kauserud, 2004). It is also hypothesised that increasing diameter influences species composition through the stabilisation of microclimatic conditions (Griffith and Boddy, 1991; Renvall, 1995). Microclimatic conditions include mainly variations in temperature and the content of water, oxygen and carbon dioxide in wood, which have all been reported to have an influence on the growth of fungi (Rypáček, 1957; Boddy, 1983b,c; Harmon et al., 1986; Bjurman and Wadsö, 2000; Hendry et al., 2002), resulting in various outcomes of interspecific interactions (Boddy, 2000; Carlsson et al., 2014). For example, competitive fungi are rather sensitive to environmental stress, and both drought and heat stress may decrease their competitiveness and hence cause shifts in the dynamics of competitive interactions (Crowther et al., 2014).

Fluctuations in environmental conditions can facilitate species coexistence (e.g. Chesson and Huntly, 1997); for instance, fluctuating temperature can maintain the diversity of wood decay fungi in artificial communities (Toljander et al., 2006). On the other hand, excessive microclimatic fluctuations result in reduced fungal growth (e.g. Rypáček, 1957; Jensen, 1969; Viitanen, 1997; Bjurman and Wadsö, 2000). Therefore, it is important to investigate the role of fluctuation intensity in wood of various sizes on the growth of fungi under natural conditions. Although morphological characteristics of trunks and characteristics influencing conditions in wood, such as solar radiation and canopy cover, have been investigated in relation to fungal species composition (e.g. Bässler et al., 2010), studies on internal conditions in trunks and their relation to the occurrence of fungi are largely lacking.

The scarcity of suitable wood in conventionally managed forests and the isolation of old-growth stands are the main causes for the rarity of many species of wood-inhabiting fungi (e.g. Bader et al., 1995; Stokland and Kauserud, 2004; Abrego and Salcedo, 2013; Nordén et al., 2013). Our study site in the Bohemian Forest is one of the areas where a variety of dead wood is abundant, supporting a high diversity of fungi (Bässler et al., 2012).

In this study, we repeatedly investigated the occurrence of fungal sporocarps on 2 m long segments on both standing and lying trunks of Norway spruce (*Picea abies*), and related this to biotic and abiotic characteristics of the segments. Besides characteristics known to have an influence on fungal assemblages, we investigated microclimatic conditions within trunks as potential characteristics further explaining fungal occurrence. We hypothesised that the thickness of trunks influences the fungal species composition, namely through the variance of temperature and moisture conditions. We expected that large trunks would have more stable conditions than small ones, and such stability would likely support the occurrence of rare species, hence shaping the fungal species assembly.

2. Materials and methods

2.1. Study area

The study was conducted in a mountain spruce forest in the Bohemian Forest (Šumava) of the Czech Republic, on the northern slope of the mountain Trojmezná (Bayerischer Plöckenstein; 48°46′19″N, 13°49′37″E). The bedrock is coarse-grained granite. Average annual precipitation is 1100 mm; average annual air temperature is 3 °C; average annual number of frost days is greater than 200; average dates of the first and last snow cover are 20th October and 10th May, respectively (Tolasz et al., 2007). However, July 2013 and the period from December 2013 to April 2014 were about 3 °C warmer than the long-term normal from 1961 to 1990 (meteorological station Churáňov, 1117 m a.s.l.). On the basis of our measurements, average air temperature 15 cm above the soil surface from July to October 2013 was 10.3 °C (range −4.1 °C to 35.1 °C; Supplementary data 1). Precipitation from 13th June to 21st October 2013 was 400 mm which corresponds to the long-term normal (Tolasz et al., 2007).

The forest is disturbed old-growth dominated by *P. abies* trees that are the source of various types of dead wood in all decay stages. The majority of trees at the site were recruited between the years 1750 and 1870 (Svoboda et al., 2012). However, a bark beetle outbreak was exacerbated by a windstorm in 2007 and by 2008 most of the canopy trees were dead. Currently, living trees are present mainly as a variably tall and dense regeneration of *P. abies* and *Sorbus aucuparia*. In addition, the field-layer vegetation shades the studied trunks to a various degree, and is dominated by *Athyrium distentifolium*, *Luzula sylvatica*, *Calamagrostis villosa*, *Avenella flexuosa* and *Vaccinium myrtillus*.

2.2. Trunks and their characteristics

Dead trunks of spruce (30 snags and 68 fallen logs) were selected so that a wide range of diameters and all available decay stages were represented. Two-metre long trunk segments were then established to record the occurrence of fungi together with their characteristics including microclimatic measurements. Characteristics of the segments are listed in Tables 1 and 2. Segments on standing snags had their lower edges just above the roots, and segments on lying logs were either in the middle of their length (in most cases), or sometimes in their thicker sections in order to include the largest diameters in logs (no segments included breaks). The causes of tree death (bark beetles, butt rot, competition, wind and unascertained) were also recorded for each trunk, and their probabilities were combined using fuzzy coding (for details see Pouska et al., 2011).

Temperature characteristics (Table 2) were recorded, at 15 min intervals from 14th June to 21st October 2013, in 38 segments (i.e. trunks) in the sub-surface layer of wood (5 cm deep) using Pt100 resistance thermometers connected to data loggers (MINILOG-T6, Fiedler AMS, České Budějovice, Czech Republic). Thermometers were mostly placed on the northern side of segments to avoid direct exposure to the sun. Holes for thermometers were drilled using a borer with a diameter of 10 mm; the remaining space around cables was filled with rubber and hole openings were sealed with silicone adhesive.

2.3. Sampling of fungi

Inventories of fungal sporocarps on segments of trunks except branches were carried out from July to October 2013 (the majority of segments were visited at least four times although one snag and seven logs were visited three times) and in June 2014 (all segments visited). Dead sporocarps were omitted. Records (presence data) from all visits were pooled. We attempted to identify all sporocarps to species but we did not include *Athelia* spp. (due to unclear trophic modes), *Galerina* spp. (due to uncertain identification), mycorrhizal and mycoparasitic fungi, and some tiny ascomycetes (e.g. *Actidium hysterioides*) because they could be easily overlooked.