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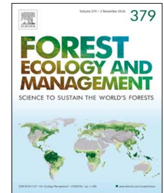

Fungal diversity and potential tree pathogens in decaying logs and stumps

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ABSTRACT

Different types of dead wood in forest ecosystems contribute to an increase of habitats for decomposer fungi. This may have a positive effect on fungal diversity but may also increase habitats for tree pathogens. In this study we investigate the fungal diversity and composition via high-throughput sequencing in decaying stumps and logs (three years after cutting) of two tree species (*Larix kaempferi* and *Quercus rubra*) in a forest site.

Fungal diversity and composition in decaying wood was different between tree species, between stumps and logs of the same tree species, and between sapwood and heartwood. When different wood sources were combined, fungal species diversity increased. This indicates that different wood sources contribute to fungal diversity and, therefore, species conservation in forests.

Potential fungal tree pathogens were found in *L. kaempferi* stumps and logs, whereas their occurrence was generally less in *Q. rubra* wood sources. No clear difference was found in the relative abundance of potential fungal tree pathogens between stumps and logs, but some potential tree pathogens were only found in either stumps or logs. This indicates that both logs and stumps can be habitats for potential fungal tree pathogens, and each wood type seems to harbor different fungal tree pathogens.

In conclusion, forest management practices that aim at maintaining different types of dead wood seem to positively affect fungal diversity, but may additionally increase the risk of survival of potential tree pathogens. This potential risk seems to depend on the tree species.

1. Introduction

Natural forests harbor a high amount of dead wood, including branches, snags and stumps. These different types of dead wood represent a range of habitats for organisms, such as fungi, bacteria and invertebrates (Cornelissen et al., 2012). In Europe, forests are largely managed and it was estimated that the volume of dead wood is reduced tremendously (90–98%) as compared to natural forests (Siitonen, 2001). Such a reduction in available habitats has a negative effect on the diversity of species depending on dead wood (Penttilä et al., 2004; Ódor et al., 2006). It has been suggested that the presence of large dead logs and the continuous supply of new dead wood is important to protect fungal biodiversity in managed forests (Heilmann-Claussen and Christensen, 2003). Nowadays, nature conservation organizations in Europe are creating, maintaining and managing dead wood habitats to improve the condition of the forest ecosystem (Natura, 2000). The increase in volume of dead wood might, however, also increase habitats for tree pathogens as some tree pathogens are able to survive in large dead roots and stumps (Garbelotto, 2004). The dilemma between maintaining different types of dead wood to increase fungal diversity and the potential increase in tree pathogens can be challenging in forest management practices.

Not only the amount, but also the size and type of dead wood are influencing the number of fungal species (Lassauce et al., 2011; Junninen and Komonen, 2011). Fungal species number (based on identification of sporocarps (fungal fruiting bodies) increased with increasing dead tree size (Heilmann-Clausen and Christensen, 2004). Large logs are able to maintain more stable microclimatic conditions required by some specialized species (Stokland and Kauserud, 2004). However, also branches with a small diameter are important to support fungal species diversity, likely because they have a high surface area per volume, thereby supporting more sporocarps compared to large logs (Heilmann-Clausen and Christensen, 2003; Nordén et al., 2004). Also variation in wood traits within trees can influence fungal community composition and decay rates (Van der Wal et al., 2015). For instance, different fungal communities were found in heartwood and sapwood within the same tree species after one year of wood decay (Van der Wal et al., 2016). Besides size and variation in wood traits within dead wood, also the position of the wood is affecting fungal diversity. Logs are laying horizontally on the soil, while stumps are standing vertically

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consequently affecting microclimate conditions and colonization opportunities of fungi spreading via soil, air and tree roots. Based on screening of sporocarps, it was found that the number of species was higher on logs than on stumps (Lindhe et al., 2004). So far, most of the studies investigating the effect of different wood types on fungal species diversity were based on sporocarp inventories, making the contribution of fungi in the hidden life stages to fungal species diversity less clear (Ovaskainen et al., 2013).

Based on the above-mentioned differences in fungal community composition between different types of dead wood, it appears that saprotrophic fungi do prefer a certain habitat (Van der Wal et al., 2013). Wood-inhabiting fungi have developed specific adaptations to utilize different dead wood qualities, which depends on the tree species, wood type (sapwood, heartwood, bark, roots), diameter of the wood and its stage of decomposition (Abrego and Salcedo, 2013). For instance, it has been found that heartwood of oaks (*Quercus* spp.) showed a strong decomposition resistance (van der Wal et al., 2015). This is probably due to the presence of organic toxic compounds in oak heartwood, selecting for specialized heartwood-rotting fungi.

In forests, several wood-inhabiting fungi are major pathogens of trees. Affected wood is not suitable anymore for timber production, causing serious economic losses in commercial forestry (Tura et al., 2016). For example, *Heterobasidion annosum* and *Armillaria mellea* are some of the most severe tree pathogens worldwide. The control of these diseases is primarily a matter of prevention. A common practice is to remove infected trees and clean the cut place by removing the remaining stumps and wood fragments to prevent colonization of neighboring trees via infected stumps. However, this method can be rather inefficient if the tree pathogen is able to survive in infected roots and may also decrease overall fungal diversity in the forest by removing their habitats. An alternative method is the use of aggressive saprotrophs as biological control agents of pathogenic wood decay fungi (Boddy, 2000). The best known example is to treat conifer stumps with spores of *Phlebiopsis gigantea* to prevent establishment of the pathogen *H. annosum* (Holdenrieder and Greig, 1998; Vainio et al., 2005).

In this study, we hypothesize that fungal diversity and composition is different between (1) stumps and logs, (2) tree species and (3) sapwood and heartwood. Because of these differences, we expect that the presence of different wood types will contribute to higher fungal diversity, and therefore fungal species conservation. Secondly, we hypothesize that the relative abundance of tree pathogens is higher in stumps than in logs. Thus, although an increase in overall fungal diversity may be accomplished by the presence of stumps, it may also increase the risk of spread of tree pathogens to neighboring trees. To identify total fungal diversity we will use high-throughput sequencing.

2. Material and methods

2.1. Research site and experimental design

We have established a field experiment in a forest located at the Schovenhorst estate in the Veluwe region, in the central part of the Netherlands (52.25N, 5.63E) in February 2012. See for a detailed description of the field site and the experimental design van der Wal et al. (2016). Briefly, the plot (± 150 × 150 m) is a relatively light-open *Larix kaempferi* (Lambert) Carrière stand with low understory dominated by the grass *Deschampsia flexuosa*, mosses and patches of bilberry (*Vaccinium myrtillus*). In this forest, eight individual needle-leaved trees of *Larix kaempferi* (subsequently referred to as *Larix*) and eight broad-leaved trees of *Quercus rubra L.* (subsequently referred to as *Quercus*) were cut in 2012. From each individual tree, 18 sections of 30 cm length were sampled using a chainsaw. In addition, two 2-cm thick discs at the bottom and at the upper side of the stem were sawn out for determination of tree diameter and width of heartwood and sapwood. Next, from each disc a wedge-shaped piece was separated into bark, sapwood and heartwood (Fig. 1A). Sapwood and heartwood were analyzed for initial wood moisture content, wood density and composition of wood-inhabiting fungal communities (van der Wal et al., 2016). Logs were randomized per tree species and thin branches were cut off. For each tree species, 16 subplots (2 × 2 m) were created, each subplot hosting 9 logs (Fig. 1C, D). Logs within subplots were placed 50 cm apart and subplots were at least 15 m apart.

2.2. Sampling of logs and stumps

After three years of incubation, in February 2015, one log from each subplot was randomly chosen and taken to the lab for analyses. From the middle part of each log, a disc of 2 cm thickness was collected with a chainsaw. Next, for each disc, two wedge-shaped pieces representing as much as possible all fungal decay patterns (e.g. interaction zones, type of wood decay) present in the whole disc were cut out and separated into sapwood, heartwood and, if still present, bark. One piece was collected from the part of the log that had been in contact with the soil, the other piece was collected from the upper side (Fig. 1B). Wood of the wedge-shaped pieces were used for determination of wood moisture content and wood density. We thus collected 32 discs from the logs, and from these discs 64 wedge-shaped pieces were collected (one from the soil side, one from the upper side). In addition, from the remaining part of every disc (32 in total), sawdust samples were taken from sapwood and heartwood and these were used for DNA analyses (see below), ending up in total with 64 sawdust samples (32 heartwood and 32 sapwood). Wood samples were stored in plastic bags at −20 °C until analyses.

In February 2015, we also collected a 2-cm thick disc (1 cm below the cut surface) from stumps of the trees that had been cut for the experiment (8 *Larix* stumps, 8 *Quercus* stumps, Fig. 1E) and discs were treated in the same way as discs sampled from the logs (see Table S1 for the number of samples from logs and stumps).

Here, we will present the results after three years of wood decay in logs (laying horizontally), and in stumps (standing vertically) that were incubated in the same forest under the same climatic conditions.

2.3. Wood density, mass loss and moisture content analyses

Volumes of sapwood and heartwood were calculated using Archimedes' volume displacement method. All samples were then oven dried at 70 °C for three days and the density of each segment was calculated as dry weight per unit volume (g/cm^3). Moisture content (%) was expressed on dry weight basis and calculated as ((mass wet wood - mass dry wood)/dry wood) ∗ 100%.

Densities of wood samples taken from the basal side and from the upper side of the stem for both *Larix* and *Quercus* were averaged to calculate the initial density for both wood types (heartwood and sapwood) in each tree. Next, mass loss for every wood type in each sample was calculated as ((density of wood type in corresponding tree at time of cutting – density of wood type at time of sampling)/density of wood type in corresponding tree at time of cutting) ∗ 100%.

2.4. Sample preparation

From each disc, sawdust samples were taken using an electric drill (bit diameter 8 mm) in the laboratory. Discs were drilled on a metal plate, and plate and drill bit were thoroughly sterilized with ethanol and water between samples. Sawdust from sapwood and heartwood was separately collected. At least 15 holes were drilled into both heartwood and sapwood. The resulting sawdust samples were pooled resulting in two samples per disc: one from heartwood and one from sapwood. Samples were stored at −20 °C until further analyses.

2.5. DNA extraction, amplification and sequencing

Sapwood and heartwood sawdust samples were frozen in liquid

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