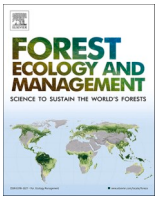
Forest Ecology and Management 568 (2024) 122148

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco



Significance of *Heterobasidion* species among wood decay fungi in northern peatland forests

Tuula Piri, Eeva J. Vainio *

Natural Resources Institute Finland, Latokartanonkaari 9, Helsinki 00790, Finland

ARTICLE INFO

Keywords:
Peat soil
Root rot
Heterobasidion sp.
Armillaria sp.
Competitiveness
Continuous cover forestry
Picea abies
Pinus sylvestris

ABSTRACT

In Nordic countries, Heterobasidion root rot is known as a widespread and severe disease affecting conifer trees on mineral soils, while our understanding of its occurrence in peatland forests is more limited. This study investigated the prevalence of *Heterobasidion parviporum* and *H. annosum*, along with common coexisting fungi in disease centers, in six Norway spruce-dominated and two Scots pine-dominated drained peatland forests in southern Finland. Among the 590 trees examined, *Heterobasidion* species were the most common fungi responsible for root rot in both spruce and pine stands. In mature spruce stands, *Heterobasidion* sp. had infected an average of 5.4 trees per hectare, and in pine stands, 4.5 trees per hectare. However, our results showed that compared to mineral soils in the same region, *Heterobasidion* sp. was neither as frequent nor as dominant in Norway spruce stands on peat soil. Furthermore, the absence of large multi-tree *Heterobasidion* genets in peatland forests indicated restricted progression of *Heterobasidion* infections. Instead of *Heterobasidion* sp., *Armillaria* sp. was the predominant decay fungus in three spruce stands and one pine stand, while *Resinicium bicolor* was dominant in one spruce stand. Interestingly, *Armillaria cepistipes*, less pathogenic than *A. borealis* and rarely causing decay on spruce on mineral soil, was the most common *Armillaria* species at peatland sites. Further *in-vitro*-tests revealed that certain fungal isolates from the disease centers were highly competitive against *H. parviporum*. These isolates included both basidiomycetes, such as *Stereum sanquinolentum* and *Amylostereum aerolatum*, as well as the ascomycetes, *Acocoryne* sp., *Leptodontidium elatius*, and *Rutstroemia calopus*. Our findings led us to speculate that the competitive ability of *Heterobasidion* sp. against coexisting fungi might be lower in peatland conditions compared to mineral soils. Moreover, the potential risks and benefits of continuous cover forestry (CCF) regarding Heterobasidion root rot are discussed. Considering the relatively low prevalence of the pathogen in peatland forests and the more beneficial environmental effects of CCF compared to clear-cut-based rotation forestry, CCF appears to be a viable management option in spruce-dominated stands on drained peat soil. However, to ensure the health of peatland forests in the future, controlling Heterobasidion root rot is as crucial on peatland as it is on mineral sites.

1. Introduction

In Finland, continuous cover forestry (CCF) is recommended as a preferred forest management approach for peatland sites. In comparison to the conventional even-aged silvicultural system with clearcutting, CCF results in reduced greenhouse gas emissions, positive effects on groundwater levels and water quality, as well as decreased silvicultural costs (Nieminen et al., 2018; Saarinen et al., 2020; Lehtonen et al., 2023; Laudon and Hasselquist, 2023). However, these numerous advantages of CCF can only be fully realized when the forest is healthy and in good growing condition.

One of the most significant threats to the health of conifer forests in the Northern Hemisphere is Heterobasidion root rot. In Finland, the causal agents responsible for Heterobasidion root rot in living conifer trees are *Heterobasidion parviporum* Niemelä & Korhonen and *H. annosum* sensu stricto (Fr.) Bref. In Norway spruce stands, Heterobasidion root rot is mainly caused by *H. parviporum*, while in Scots pine stands the causal agent is *H. annosum* (Korhonen, 1978a; Korhonen and Piri, 1994). For Finnish forestry, the annual economic losses caused by Heterobasidion root and butt rot due to decreased timber value are estimated to be around 51 million euros; if reduced growth of infected trees and indirect costs due to changing the tree species to a less

* Corresponding author.
E-mail address: eeva.vainio@luke.fi (E.J. Vainio).

https://doi.org/10.1016/j.foreco.2024.122148
Received 27 May 2024; Received in revised form 5 July 2024; Accepted 7 July 2024
Available online 17 July 2024

productive one are included, the annual losses could exceed 80 million euros (Hantula et al., 2023).

Heterobasidion spp. infect an initially healthy stand by means of airborne spores, which colonize freshly cut conifer stumps and, to a lesser extent, wounded roots, and deep logging injuries near to root collar of spruce trees. Subsequently, the fungus spreads from the stump roots or roots of the injured tree via root contacts to healthy roots of neighboring trees within the same or the next tree generation (Redfern and Stenlid, 1998; Stenlid and Redfern, 1998). If the susceptible tree species cannot be replaced with a resistant one, there is a risk that Heterobasidion root rot will develop into a chronic disease of the site (Piri and Valkonen, 2013). For sites infested by *H. parviporum*, the most resistant tree species are deciduous trees and Scots pine, while for sites infested *H. annosum*, only deciduous trees exhibit resistance (Korhonen, 1978a). Unlike rotational forest management based on clear cutting, changing the tree species is not a feasible option within CCF management. This limitation complicates disease control once the pathogen has entered the forest stand (Piri and Valkonen, 2013). Therefore, there is a need to investigate both the current situation as well as alternative approaches for controlling the disease in peatland forests.

Compared to forests growing on mineral soils, our understanding of the epidemiology of Heterobasidion root rot in peatland forests is much more limited. A recent study conducted in southern Finland demonstrated that both Norway spruce and Scots pine stumps are highly susceptible to *Heterobasidion* spore infection on drained peatland (Piri et al., 2023). However, beneath the ground, the conditions for the pathogen might be less favorable. Lindberg and Johansson (1991) reported that infection of *H. parviporum* through bark wounds of Norway spruce roots was less frequent on peat soil compared to mineral soil. Similarly, British experiments have shown that the long-term survival of *H. annosum* in Sitka spruce stumps was poorer, the mycelial spread of the fungus from stumps to the adjacent trees less common, and the infected roots less seriously damaged in peat than mineral soils (Redfern et al., 2010). On the other hand, a recent Latvian study focusing on the identification of *Heterobasidion* genets in peatland forests revealed that almost 70 % of Norway spruces suffering from Heterobasidion root rot were infected vegetatively through root contacts. This suggests that mycelial spread can play a significant role in disease spreading in peat soils as well (Gaitnieks et al., 2022).

So far, the incidence of Heterobasidion root rot in northern peatland forests is poorly known. Furthermore, our understanding of the behavior of *Heterobasidion* species within peatland conditions, particularly when susceptible tree species are growing continuously, is restricted. Similarly, more information is needed on other wood decay fungi that might contribute to tree decline at peatland sites. Besides *Heterobasidion* species, other pathogens causing noticeable conifer damages in boreal forests are *Armillaria* spp. and *Stereum sanguinolentum* (Alb. & Schw. ex Fr.) Fr. (Hallaksela, 1984; Piri et al., 1990; Solheim, 2006). In the case of *Armillaria* spp., vegetative spread is mainly based on resistant mycelial cords called rhizomorphs, and low soil pH, high soil organic matter content (peat soils), and high soil moisture have been suggested to favor their formation (Redfern, 1973; Kubiak et al., 2017). Moreover, the non-optimal nutrient balance of peatland soils may enhance the spread of *Armillaria* spp. by predisposing the trees to stress and weakening their defenses, making them more susceptible to *Armillaria* infection (Kubiak et al., 2017). In turn, *S. sanguinolentum* infection is typically initiated via root and stem wounds (Vasiliauskas, 1998; Mäkinen et al., 2007), and therefore might be expected to become more common due to CCF where root and stem damages easily occur during selective felling (Fjeld and Granhus, 1998; Modig et al., 2012).

Numerous fungal species have shown capable of acting as antagonists against *Heterobasidion* spp. (see Holdenrieder and Greig, 1998; Woodward et al., 1998: Appendix II for a thorough list of laboratory experiments and field observations), but thus far only the saprotroph fungus *Phlebiopsis gigantea* (Fr.) Jül. has been registered as a biocontrol against the disease and is commonly used in practical forestry (Pratt et al., 2000). Although stump treatment with *P. gigantea* has generally been found to be highly successful on mineral soil when conducted properly (e.g., Korhonen et al., 1994; Rönnberg and Cleary, 2012; Kenigsvalde et al., 2016), its efficacy in controlling *Heterobasidion* sp. on drained peatland has proven to be more unsteady, likely due to different environmental conditions (Piri et al., 2023). To develop biological control in peatland forests, more information is required regarding the competitive abilities between *Heterobasidion* species and other fungi adapted to peatland conditions.

The aim of this study was: i) to elucidate the role of *Heterobasidion* species as a decay fungus in northern peatland forests by examining their prevalence in comparison to other decay fungi, and ii) to evaluate the progression of Heterobasidion root rot by investigating the mycelial spread of the pathogen in the root systems of spruce and pine trees, iii) to identify other fungi than *Heterobasidion* spp. colonizing living trees in disease centers, and iv) assess the capability of these fungi to act as antagonists against *H. parviporum*.

2. Material and methods

2.1. Experimental stands

The study was carried out in six Norway spruce-dominated and two Scots pine-dominated stands on drained peatland in the southern part of Finland. According to the Finnish site type classification system (Laine et al., 2018), the sites represent (from more fertile to less fertile): herb rich spruce forest (Rhtkg), *Vaccinium myrtillus* spruce and pine forests (Mtkg), and *Vaccinium vitis-idea* pine forest (Ptkg). Acidity of the soils, measured as pH in water suspension, was typical for Finnish peatland, varying from 3.6 to 4.1 (Silfverberg and Huikari, 1985; Westman and Laiho, 2003). The thickness of the peat layer varied from 0.5 to more than 2 m. Five stands were recently subjected to selection cutting with the goal of creating an uneven-aged stand structure, while two stands were subjected to clear cutting, and one stand (Lapinjärvi) was left unharvested (Table 1). Therefore, most of the stands had freshly cut stumps suitable for estimating the causative agent of decay in the living trees (not representing secondary saprotrophic growth).

The drainage history of the study areas is not precisely documented. Based on available information, in Pöytyä, Multia and Tammela, the pristine mire was drained for forestry in the 1930s, in Janakkala in the 1940s, and in Suonenjoki, Asikkala, and Lapinjärvi at the turn of the 1950s and 1960s. Subsequently, ditch network maintenance operations (including ditch cleaning and/or complementary ditching) were carried out in Pöytyä 1964–66 and 1993 (summer ditching), in Asikkala 2021 (Feb/Mar), and in Tammela in the early 1970s. In Janakkala, the ditch network was supplemented by digging additional drains in the early 1960s. Unfortunately, no information is available about ditch network maintenance in Multia, Suonenjoki, and Lapinjärvi.

The nutrient status of the experimental stands was not defined in this study. However, information from the pine stand in Pöytyä included the results of a needle analysis conducted in 2018 as a part of previous investigation, revealing a nutrient imbalance, i.e., high nitrogen but low potassium and phosphorus contents (data not shown).

2.2. Establishment of study plots and sampling of trees and stumps for decay fungi

Initially, the experimental stand was systematically examined for signs indicative of *Heterobasidion* infection, including decayed stumps, dead or windfall trees, trees with sparse crowns, stunted height growth, exudation of resin on the stem, and the presence of fruit bodies (Greig, 1998). Trees and fresh stumps suspected of *Heterobasidion* infection were marked with fiber tape for sampling. The standing trees were sampled using an increment borer, extracting 2–4 wood cores from the base of the trunk and one core near the root collars of 3–4 main roots. From freshly cut stumps, a sample disc was sawn with a chainsaw from the stump base

Table 1
Location and characteristics of the study sites.

Study area	Location	Stand area, ha	Stand age	Tree species	No. of investigated stumps/trees	Diameter at stump height, cm	Forest site type[a]	Peat depth, m	Soil pH	Forest manag. strategy[c]
Pöytyä	60°49.10' 22°25.56'	3.2	85–140	pine	61	29	Ptkg/Mtkg	>2	NA[b]	RF
Multia	62°32.43' 24°34.44'	1.0	80–150	pine/ spruce	46	37	Mtkg	0.6–1	NA	CCF
Suonenjoki	62°33.66' 27°14.90'	3.3	67–112	spruce	63	31	Mtkg	0.5	3.9	CCF
Asikkala I	61°10.99' 25°16.13'	5.0	100	spruce	47	31	Rhtkg/ Mtkg	>1	3.6	RF
Asikkala II	61°10.88' 25°15.62'	3.7	95	spruce	100	25	Rhtkg/ Mtkg	>1	3.7	CCF
Tammela	60°38.46' 23°57.60'	8.5	70/45	spruce	126	23	Mtkg	1.5–2	4.1	CCF
Janakkala	61°0.75' 24°44.59'	2.5	90	spruce	83	28	Rhtkg	>1	3.9	CCF
Lapinjärvi	60°39.71' 26°6.86'	0.7	70	spruce	64	32	Mtkg	0.7–1	4.0	RF

[a] Forest site types: Ptkg = *Vaccinium vitis-idea* pine forest, Mtkg = *Vaccinium myrtillus* spruce and pine forests, Rhtkg = herb rich spruce forest
[b] data not available
[c] Forest management strategy: RF = continuous-cover forest management, CCF = clear-cut-based rotation forest management

just above the ground and near the root collars of the main roots. Additionally, spruce undergrowth (1–2 m high) found in pine-dominated sample plots in Multia, as well as spruce-dominated plots in Tammela, were felled and sampled by taking disks from above the ground level. The collected sample disks were placed in separate paper bags and stored at +4 °C for further processing.

After confirming the trees and stumps infected by *Heterobasidion* sp. (see the next chapter for details), a study plot was established around each of them. The number of study plots (*Heterobasidion* disease centers) ranged from 0 to 13 among the experimental forests (Table 3). Sampling proceeded from the center point (tree or stump infected by *Heterobasidion*) outwards until at least two trees/stumps were found to be healthy. All trees and stump on the plots were mapped, measured (diameter at stump height) and sampled as described above. The area of the sampling plots varied from approximately 80 to 1960 m^2. *Heterobasidion* infections were found in all experimental stands except in Janakkala.

2.3. Identification of isolated fungi

In the laboratory, the core samples were cultured on 2 % malt extract agar (MEA), and fungal mycelia growing from the wood samples were isolated. The disks samples were washed, incubated, and sampled for fungal mycelium, following the procedures described earlier (Piri et al., 2021). The resulting pure cultures were identified using a combination of morphological and molecular methods. Alongside the morphological characterization of *Heterobasidion* sp. and *Armillaria* sp. (Hallaksela, 1984), 77 isolated mycelia were subjected to molecular analysis. Of these, 59 mycelia were analyzed by ITS rDNA analysis. The highly variable ITS1 and ITS2 regions and the conserved 5.8 S rDNA between them were amplified by PCR using primers ITS1F (Gardes and Bruns, 1993) and ITS4 (White et al., 1990) annealing to the small and large subunit rDNA -encoding sequences of the ribosomal gene cluster. DreamTaq DNA polymerase (Thermo Fisher Scientific) was used for the PCR as instructed by the manufacturer. The amplification products were sent to Macrogen Europe for purification and sequence analysis in both directions, and the obtained sequences were trimmed and aligned using Geneious R10, analyzed against the GenBank and UNITE databases and assigned to species according to their similarity with annotated sequences. In addition, 18 isolates morphologically identified as *Armillaria* spp. were analyzed by sequence analysis of the Intergenic Spacer 1 (IGS-1) region of the nuclear ribosomal gene cluster amplified with primers O-1 and LR12R as described earlier (Veldman et al., 1981; Duchesne and Anderson, 1990; Anderson and Stasovski, 1992). This region is suitable for determining the species identity of closely related *Armillaria* species such as *A. cepistipes* Velenovský and *A. lutea* Gillet, as well as *A. borealis* Marxmüller & Korhonen and *A. ostoyae* (Romagnesi) Henrik.

To determine the frequency of secondary infections (mycelial spread through root contacts) in relation to primary spore infections, the number and size of the *Heterobasidion* genets were identified with the aid of somatic incompatibility tests (Stenlid, 1985). Thereafter, a representative from each genet was identified at the species level by pairing tests based on their ability to heterokaryotize homokaryotic tester strains of *H. annosum* s.s. and *H. parviporum* (Korhonen, 1978a).

2.4. Dual culture tests

To assess the competitiveness of *H. parviporum*, *in vitro* dual culture tests were conducted to examine the interactions between *H. parviporum,* and other fungi isolated in disease centers. In total, 11 fungi (17 strains) were included in the tests, comprising two commonly occurring basidiomycetes. Additionally, the most frequently isolated ascomycete (*Ascocoryne* sp.), as well as five fast-growing ascomycetes and one fast-growing zygomycete, were tested. Each fungal strain was paired with five different genotypes of *H. parviporum*, isolated during the current study from spruces in the Asikkala and Tammela experiments. The detailed list of the fungal isolates subjected to testing is provided in Table 5.

All fungal cultures for dual culture tests were grown on Petri dishes containing 2 % w/v malt-extract agar (MEA) for two weeks. Thereafter, a mycelial plug with a diameter of 0.5 cm was removed from the margin of an actively growing colony of *H. parviporum* and the test fungus. The plugs were simultaneously placed on opposite sides of a 9-cm diameter Petri dish containing 2 % MEA. Dual cultures with two plugs from the same fungal strain (self-pairing) were used as a control. All dual cultures were prepared in triplicate, resulting in a total of 277 dual cultures, including controls. The dishes were incubated in the dark at +20 +/- 2 °C and kept in polythene bags to prevent drying out. The competitiveness between *H. parviporum* and tested fungi was observed at 7-day intervals for a period of up to 4–6 weeks, i.e., until the fungal colonies had filled the plate and no further alternation in the interaction between the fungal colonies was observed.

Interactions between *H. parviporum* and the tested fungi were assessed as follows:

- *H. parviporum* has ceased growth and is partially or completely overgrown by the test fungus (strong biocontrol potential, signified with + symbol in Table 5).
- Neither species is capable of dominance over the other, and a thin mycelium-free inhibition zone (deadlock) approximately 1–2 mm is seen between the fungal colonies (moderate biocontrol potential, signified with 0 symbol in Table 5).
- The test fungus has ceased growth and is partially or completely overgrown by *H. parviporum* (low biocontrol potential, signified with - symbol in Table 5).
- Mutually intermingling; both fungi grow into one another without any macroscopic signs of interaction (only self-pairings used as controls).

No attempt was made to quantify these observations.

After conducting the dual cultures test at +20 °C, an additional test was carried out at +15 °C for six fungal species (consisting of 10 strains). These fungal species have shown inhibition of growth and/or partially or completely overgrowth of *H. parviporum* mycelium (interactions 0 and +) at +20 °C. The mode of interactions at +15 °C was evaluated using the same method as in the test conducted at +20 °C, with the exception that the final assessment was made after a three-month incubation period.

2.5. Statistical analysis

A Spearman's rank-order correlation, which is suitable for small samples that do not meet the assumption of normality, was used to assess the relationships between the frequency of trees infected by *Heterobasidion* sp. and other basidiomycetes, as well as the most common ascomycete (*Ascocoryne* sp.) found in disease centers. These correlations (between trees infected by *Heterobasidion* sp. and other basidiomycetes as well as between trees infected by *Heterobasidion* sp. and *Ascocoryne* sp.) were also calculated separately for the frequency of trees primarily infected by *Heterobasidion* spores and those secondarily infected by *Heterobasidion* mycelium. Additionally, correlations between the frequency of the trees infected by *Heterobasidion* sp. or *Armillaria* sp. and factors such as stand age, site fertility, and depth of the peat layer were examined using the same method. The significant level for all tests was set at $p \leq 0.05$. The analyses were carried out using the SPSS statistical package (SPSS Version 20.0 for Windows; SPSS Inc., Chicago, IL, USA).

3. Results

3.1. Fungi isolated from the decay centers

A total of 452 spruces (199 stumps of freshly felled trees and 253 standing or windthrown trees) and 138 pines (136 stumps and 2 standing trees) were sampled for decay. The proportion of trees visually classified as decayed averaged 55.3 % for spruce and 33.3 % for pine. No decay was found in the understory of spruce trees (Multia and Tammela experiments only). The total number of trees suffering from decay per hectare varied among all study stands from 4.8 to 44.3 (mean 14.9). In spruce-dominated stands, the number of decayed trees averaged 16.4, and in pine-dominated stands, it averaged 8.4 per hectare.

Among the spruce stands, *H. parviporum* was the causal agent of decay in 21.2 % of mature trees and stumps displaying visible decay or discoloration. Following *H. parviporum*, the next frequently isolated decay fungus was *Armillaria* sp. (*A. borealis* or *A. cepistipes*) occurring in 18.4 % of cases. In Suonenjoki and Multia, *Armillaria* sp. was the predominant decay fungus in spruce trees, and in Asikkala I, *Armillaria* sp. was as prevalent as *H. parviporum*. Only two of the 18 *Armillaria* isolates subjected to molecular analysis were isolates of *A. borealis*, both originating from the Lapinjärvi site. All the remaining ones were *A. cepistipes* (3 isolates from Lapinjärvi, 3 from Suonenjoki, 2 from Multia, 5 from Asikkala, and 3 from Janakkala).

In addition to *Heterobasidion* and *Armillaria* species, 13 other basidiomycetes isolated from decayed wood were identified based on morphological or molecular characterization. Most of the basidiomycetes were common inhabitants of decaying conifer wood and clearly distinguishable from their relatives based on ITS sequence information. Some species known to prefer broadleaved trees (*Hypholoma lateritium, Trametes hirsuta)* have been reported also earlier from Norway spruce wood (Arhipova et al., 2011; Szczepkowski et al., 2022). The third most common fungus causing decay in Norway spruce was *Resinicium bicolor* (Alb.& Schw. ex Fr.) Parm. (11.6 %). In Janakkala, where no Heterobasidion root rot was found, *R. bicolor* was the most frequently isolated fungus from Norway spruce. Other fungi isolated from more than one spruce tree included *Fomitopsis pinicola* Fr. (Karst.) (12 isolates, 4.8 %), *Stereum sanguinolentum* (10 isolates, 4 %), and *Bjerkandera adusta* (Willd.) P. Karst. (3 isolates, 1.2 %). In the pine-dominated stand, *H. annosum* was the dominant species isolated from 61.3 % of decayed pines. The second most common was *Armillaria* sp. with 12.2 % (Table 2).

In addition to wood-decaying basidiomycetes, several non-pathogenic fungi, primarily ascomycetes, were isolated from spruce wood. The most frequently encountered was *Ascocoryne* sp., isolated 33 times. Other taxa, including primarily blue-staining fungi, dark septate endophytes and nectriaceous fungi such as *Cadophora/Phialophora* spp., *Cosmospora* sp., *Cytospora* sp., *Graphilbum* sp., *Grosmannia piceaperda* and *Ophiostoma piceae/flexuosum* were detected with low frequency (in total 9 isolates). Additionally, a zygomycete species, *Umbelopsis* sp., was isolated from two trees. It should be noted that for the ophiostomatoid fungi (e.g., species of *Graphilbum, Grossmannia, Ophiostoma*), taxonomical assignment beyond the genus level is often not possible based on ITS sequences alone (Linnakoski et al., 2016; de Beer et al., 2022), and therefore the taxonomic assignments reported here (supplementary Table S1) are informative at the genus rather than species level.

It's worth noting that all trees and stumps exhibiting visible decay or discoloration did not yield any fungal mycelium, or the isolation attempts were unsuccessful, and the specific causal agent could not be determined. In cases where no fungal growth occurred, discoloration was likely attributed to bacterial colonization or reaction wood following an old injury (Isomäki and Kallio, 1974; Hallaksela and Salkinoja-Salonen, 1992). In a total of 25.9 % of spruces and 5.1 % of pines, visually classified as decayed, the causative agent could not be identified.

The GenBank accession numbers (OR807764-OR807822) and results of BlastN analyses of ITS rDNA sequences against the GenBank and UNITE databases are listed in detail in Supplementary Table 1, and the GenBank accession numbers of *Armillaria* spp. IGS rDNA sequences are PP620461-PP620478. In the case of *Armillaria*, vegetative isolates are diploid, which was reflected as nucleotide polymorphisms in some of the IGS sequences at sites known to possess intraspecies variation in *A. cepistipes* based on earlier research (Anderson and Stasovski, 1992). These nucleotide positions were marked with ambiguity nucleotide characters following the IUPAC nucleotide code nomenclature.

3.2. Prevalence and extent of Heterobasidion infections

In the seven experimental stands where Heterobasidion root rot was observed, the density of *Heterobasidion* disease centers per hectare ranged from 0.3 to 5.7, and the number of *Heterobasidion* infected trees and stumps varied from 1.2 to 20 per hectare. On average, there were 5.4 infected trees per hectare in spruce-dominated stands and 4.5 in pine-dominated stands (Table 3).

The maximum distance between pines infected by the same *H. annosum* genotype was 9.5 m in Pöytyä and 15 m in Multia. Despite the areal span of the genets, the number of trees infected by the same *H. annosum* genotype was low, with a maximum of two trees, and 81.8 % of genets in pine stands were single-tree genets. The average size of *Heterobasidion* genets in pine stands was 1.28 trees.

Table 2
Number of identified fungi in spruce and pine trees among study sites.

Fungal species	Experimental stand							
	Pöytyä	Multia	Suonenjoki	Asikkala I	Asikkala II	Tammela	Janakkala	Lapinjärvi
Basidiomycetes								
Amylostereum areolatum					1			
Armillaria sp.		2/5*	13	6	6	6	6	7
Bjerkandera adusta					1		2	
Calocera viscosa				1				
Fomitopsis pinicola			1		8			3
H. annosum	19*	2*						
H. parviporum		1	4	6	13	15		14
Hypholoma lateritium					1			
Lentinus substrictus			1					
Peniophora sp.						1		
Phanerochaete laevis							1	
Phlebiopsis gigantea						1		
Phlebiopsis sp.	10*							
Resinicium bicolor			2	4	5	4	13	1
Stereum sanquinolentum		1		1	5	1	1	1
Trametes hirsuta						1		
Xylodon asperus				1				
Unknown	2*	0	7	5	18	12	27	5
Ascomycetes								
Ascocoryne sp.		10	12	1 / 1*	6		1	3
Cosmospora sp.					1			
Cytospora sp.			1					
Graphilbum sp.					1			
Grosmannia piceaperda						1		
Hypocrea pachybasioides/Trichoderma polysporum				1				
Leptodontidium trabinellum					1			
Neobulgaria premnophila		1					2	
Ophiostoma piceae/flexuosum						1		
Penicillium glaucoalbidum			1					
Phialophora/Cadophora sp.				1	2			
Rutstroemia calopus					1			
Trichoderma polysporum					1			
Umbelopsis sp.			1					

* isolated from pine

Table 3
Incidence of *Heterobasidion* infections and structure of genets.

Stand	Tree species	No. of *Het* disease centers	No. of *Het* inf. trees/stumps	No. of disease centers per ha	No. of *Het* inf. trees/ stumps per ha	Mean (max) size of genet, number of trees	Max. distance of mycelial spread, m
Pöytyä	pine	13	19	4.06	5.9	1.05 (2)	9.5
Multia	pine/ spruce	2*	3	2	3	1.5 (2)	15
Suonenjoki	spruce	1	4	0.3	1.2	4 (4)	6.5
Asikkala I	spruce	5	7	0.8	1.4	1.16 (2)	2
Asikkala II	spruce	8	11	2.2	3.0	1.8 (3)	5.7
Tammela	spruce	8	12	0.9	1.4	1.1 (2)	2.5
Janakkala	spruce	0	0	0	0	-	-
Lapinjärvi	spruce	4	14	5.7	20	1.55 (4)	7.3

* 1 pine and 1 spruce

In spruce-dominated stands, the longest distance between trees infected by the same fungal genotype was 7.3 m, and the highest number of trees within the same *Heterobasidion* genet was four (with a mean of 1.87 trees). Half of the genets in spruce stands consisted of only one tree.

Heterobasidion fruit bodies were not found in any experimental stand.

In spruce stands, strong negative correlations were observed between the proportion and number of trees infected by *H. parviporum* and the proportion of trees infected by other decay fungi in disease centers. Also, the correlations were negative between the number and size of *Heterobasidion* genets and the proportion of trees infected by other decay fungi. The strongest negative correlation was found between the number of *Heterobasidion* genets in disease centers and the proportion of trees infected by *Armillaria* or *R. bicolor* ($r_s = -.710$, $p = .000$) (Table 4). In contrast, no significant correlation was observed between the occurrences of *Ascocoryne* sp. and *Heterobasidion* sp. in disease centers, nor between incidence of *Heterobasidion* or *Armillaria* infection and soil pH, depth of the peat layer, and stand age.

3.3. Outcomes of dual cultures

In vitro on MEA plates at +20 °C, the growth of *H. parviporum* mycelium was inhibited by the basidiomycetes *Resinicium bicolor*, *Stereum sanquinolenteum*, *Amylostereum areolatum* (Fr.) Boid., and *Fomitopsis pinicola*. The most competitive ascomycete was *Rutstroemia calopus* (syn. *R. bolaris*), which partially grew over and replaced *H. parviporum*. Additionally, the fast-growing *Leptodontidium elatius*, *Ascocoryne cylichnium*, and *Calocera viscosa* showed competitiveness against *H. parviporum* (Table 5). *Cadophora fastigiata, Xylodon asperus*, and *Umbelopsis* sp., which were overgrown by *H. parviporum*, as well as a very slow-growing strain of *A. cylichnium* and *Calocera viscosa*, were not

Table 4
Spearman's rho correlation coefficients and significance (2-tailed) between occurrence of *Heterobasidion parviporum* (*Het.*) and *Armillaria* sp. (*Arm.*), *Resinicium bicolor* (*Res.*), *Arm.* and *Res.* combined, all basidiomycetes combined, and *Ascocoryne* sp. (*Asc.*) in disease centers.

	Het. %	No. of *Het.* isolates	No. of *Het.* genets	Mean size of genets	*Arm.* %	*Res.* %	*Arm.* and *Res.* %	Basidiomyctes %	No. of *Asc.* isolates
Het. % of all spruces	1000								
No of *Het.* isolates	**,805**** 0000	1000							
No of *Het.* genets	**,798**** 0000	**,911**** 0000	1000						
Mean size of genets	**,783**** 0000	**,913**** 0000	**,776**** 0000	1000					
Arm. % of all spruces	**-,603**** 0001	**-,516**** 0005	**-,608**** 0001	**-,544**** 0003	1000				
Res. % of all spruces	-0293 0131	-0168 0391	-0264 0175	-0177 0367	0198 0313	1000			
Arm. and *Res.* % of all spruces	**-,687**** 0000	**-,596**** 0001	**-,710**** 0000	**-,614**** 0001	**,849**** 0000	**,589**** 0001	1000		
All basidiomycetes % of all spruces	**-,647**** 0000	**-,498**** 0007	**-,582**** 0001	**-,550**** 0002	**,736**** 0000	**,596**** 0001	**,902**** 0000	1000	
No of *Asc.* Isolates	0005 0979	0083 0674	-0183 0352	-0041 0836	0182 0354	0058 0771	0064 0747	0051 0795	1000

N=28
Significant correlations are highlighted in bold.

Table 5
Interactions between *H. parviporum* and the test fungi at inoculation temperatures of +20 and +15 °C.

	Interaction at +20 °C/+15 °C				
	Het 1	Het 2	Het 3	Het 4	Het 5
Basidiomycetes					
Amylostereum areolatum	0/0	0/0	0/0	0/0	0/+
Fomitopsis pinicola	0/0	0/0	0/+	0/-	0/0
Resinicium bicolor	0/-	0/0	0/0	0/0	0/0
Resinicium bicolor	0/-	0/0	0/0	0/0	0/0
Resinicium bicolor	0/n	n/0	0/0	0/0	0/0
Resinicium bicolor	0/-	n/-	0/-	0/0	0/0
Resinicium bicolor	0/-	0/0	0/0	0/0	0/0
Stereum sanguinolentum	0/0	0/0	0/0	0/0	0/0
Stereum sanguinolentum	0/0	0/0	0/0	0/0	0/0
Ascomycetes					
Ascocoryne cylichnium	-/+	-/+	-/+	n/+	-/n
Ascocoryne cylichnium	0/n	0/n	0/n	0/n	0/n
Cadophora fastigiata	-/n	0/n	-/n	-/n	-/n
Calocera viscosa	0/n	0/n	0/n	0/n	0/n
Leptodontidium elatius	0/+	0/+	0/+	0/+	0/+
Rutstroemia calopus	+/+	+/0	+/0	+/0	+/0
Umbelopsis sp.	-/n	-/n	-/n	0/n	-/n
Xylodon asperus	-/n	-/n	-/n	-/n	-/n

0: neither species is capable of dominance over the other and a thin zone of uncolonized agar (c. 1–2 mm) is seen between the fungal colonies (deadlock).
+: *H. parviporum* has ceased growth and it is partially/completely overgrown by the test fungus.
-: the test fungus is partially or completely overgrown by *H. parviporum*.
n: not tested.

included in further testing at +15 °C.

After a three-month incubation period at +15 °C, differences between fungal strains of the same species became more evident. In interaction with *R. bicolor*, four *R. bicolor* strains halted the mycelial growth of four out of five *Heterobasidion* strains, while one *R. bicolor* strain proved to be a weak competitor and was overgrown by three out of five *Heterobasidion* strains. *F. pinicola* (only one strain tested) proved to be an effective competitor against four *Heterobasidion* strains but was overgrown by one strain. Both *S. sanquinolentum*, and *A. aerolatum* (only one strain of each), inhibited the growth of all *Heterobasidion* strains. Additionally, the three tested ascomycetes *R. calopus*, *L. elatius* and *A. cylichnium* were capable of either stopping or overgrowing all *Heterobasidion* strains (Table 5). In general, hyphal extension rates were slower at +15 than at +20 °C for all tested species, with the exception of the fast-growing *L. elatius*, which was the only tested fungus that exhibited faster growth than *Heterobasidion* strains and completely covered the entire Petri disc at the end of the dual test at +15 °C.

During the first seven days, the growth rate of *H. parviporum* strains averaged 3.3 mm per day (range 3.1 – 3.6) and 1.34 mm (1 – 1.5) at temperatures of +20 and +15 °C, respectively. After two weeks, the growth rate of *H. parviporum* strains decreased at +20 °C averaging 2.2 mm per day (range 2.2 – 2.3) and increased at +15 °C averaging 3.5 mm per day (2.6 – 3.8).

4. Discussion

4.1. Prevalence of Heterobasidion sp. in peatland forests

In the present study, *Heterobasidion* species were the most common decay causing agents both on Norway spruce and Scots pine. They were found to be the primary cause of decay in half of the stands investigated (of both spruce and pine stands). However, when compared to spruce stands on mineral soil in the same region in southern Finland, *Heterobasidion* sp. did not exhibit the same dominance on peat soil. In this study, an average 21 % of decayed spruces were infected by *Heterobasidion* sp. In contrast, on mineral soil sites, Hallaksela (1984) found 47 % and Piri et al. (1990) found 56 % of decayed spruces at final cuttings to be infected by *Heterobasidion* sp. In material collected in the National Forest Inventory consisting of 40–160-year-old spruces the corresponding percentage was 38 % (Hallaksela, 1984). Similarly, the incidence of *Heterobasidion* root rot, averaging 4.1 infected spruce trees per hectare in this study, was clearly lower than the average of 43 infected trees per hectare observed in mature spruce-dominated stands on mineral soil in the same region of Finland (Piri et al., 1990). Thus, our results are consistent with previous findings indicating that the damage caused by Heterobasidion root rot to spruce forests is less severe on peat soil than on mineral soil (Stenlid and Redfern, 1998; Mattila and Nuutinen, 2007; Redfern et al., 2010; Arhipova et al., 2011). In contrast, Kaarna-Vuorinen (2000) reported slightly higher butt-rot frequency on drained peatland than on moist or dryish mineral soils but lower than on herb-rich mineral soils among spruce final cutting areas in southeastern Finland. However, this study only analyzed total decay frequency by soil types without a separate examination for Heterobasidion root rot.

In Latvia, where peat soils are generally more fertile and alkaline than in Finland, serious damage caused by Heterobasidion root rot has been documented in individual spruce stands (Gaitnieks et al., 2016; Brūna et al., 2019; Gaitnieks et al., 2022). In the present study, the

experimental sites were relatively homogeneous in terms of site fertility, with seven out of eight sites primarily representing moderately fertile site types. The only exception was a site classified as a higher fertile herb-rich peatland forest type in Janakkala, where no *Heterobasidion* infections occurred. Therefore, further research is necessary to explore the potential relationship between site fertility and the occurrence of Heterobasidion root rot in northern peatland forests.

In contrast to the Latvian study, which reported abundant *Heterobasidion* fruit bodies in spruce forests on peatland (Gaitnieks et al., 2021), no fruit bodies were found in our experimental stands. The probable explanation for their absence is the scarcity of fertile herb-rich site types with abundant field flora that maintain sufficient moisture for fruit body development. Moreover, old stumps with an advanced stage of Heterobasidion root rot, which are most suitable for fruit body development, did not occur on our study sites due to the short disease history.

The prevalence of Heterobasidion root rot in Scots pine forests growing on mineral soil in Finland and other Nordic countries is currently poorly known. Significant damage has, however, been reported in individual pine stands (Wang et al., 2014; Piri et al., 2021), and Heterobasidion root rot might be much more common in boreal pine forests than currently recognized (Youssef et al., 2023). Although limited data prevent conclusive comparations of disease prevalence between mineral and peat soils, our study highlights that even when growing on peat soil, pine forests are not safe from Heterobasidion root rot.

4.2. Primary infections by Heterobasidion spores

In both spruce and pine stands, infected trees were commonly situated near ditches, suggesting that ditching operations (including supplement and improvement ditching as well as cleaning of old ditches) may have created entry points for *Heterobasidion* sp. through broken roots. In addition to root injuries, conifer stumps created in summer cuttings are potential targets for *Heterobasidion* infection in peat soil (Piri et al., 2023). Until recently, summer cuttings in peatland forests have, however, been infrequent due to the poor load-bearing capacity of unfrozen peat soil, and the role of stumps in the spread of the disease has likely been minimal. However, logging activities in peatland forests during periods of *Heterobasidion* spore production (when the daily mean temperature is consistently above +5° C) are increasing due to advanced logging and driving machines that can operate more effectively on soft soils. In a response to increasing risk of *Heterobasidion* spore infections, stump treatment to prevent the spread of Heterobasidion root rot into peatland forests is mandated in the southern part of Finland for both spruce and pine stands.

4.3. Mycelial spread of Heterobasidion sp.

In this study, the average size of *Heterobasidion* genets, determined by the number of infected trees and reflecting the rate of mycelial spread of the fungus across root contacts and grafts from infected to healthy trees, was 1.7 trees in spruce stands, which is only slightly smaller than in northern spruce forests on mineral soil, averaging 1.8 trees at the end of the rotation (Stenlid, 1987; Piri et al., 1990). However, the large genets with ten or more trees which are not uncommon on mineral soil (Stenlid, 1985; Piri et al., 1990, Piri and Korhonen, 2008; Piri and Valkonen, 2013), were not observed in the present study.

The mycelial extension of *H. annosum* in Scots pine forests on mineral soil has been little studied in the Nordic countries. On mineral soil in southern Finland, the largest *Heterobasidion* genet identified in a pine stand with a long disease history consisted of 17 infected trees, with an average of 3.2 trees (Piri et al., 2021). In the present study, the genets (19 genets in two stands) were smaller with on average of 1.1 pines and a maximum of two trees.

The absence of large genets in both spruce and pine stands on peat soil can be attributed to several factors. Firstly, the history of Heterobasidion root rot affecting peatland forests is shorter compared to the upland forests on mineral soil. Most peatland forests in Finland, including the experimental stands in this study, represent the first post-drainage tree generation that could have been exposed to *Heterobasidion* spore infection. As a result, multi-infections originating from old *Heterobasidion* genets of previous tree generations are exceptional. Secondly, the unfavorable conditions of peat soil for mycelial extension of *Heterobasidion* species may contribute to the smaller size of fungal genets. Previous studies have indicated that the mycelial spread of *Heterobasidion* is more difficult in peat soil than in mineral soil. In Britain, the mycelial spread of *H. annosum* from inoculated Sitka spruce stumps to adjacent trees was less frequent on peat soil, as compared to mineral soil (Redfern, 1984, 1998). However, it is important to note that in a pine stand, remarkably long distances of up to 15 m between two trees infected by the same fungal genotype was observed. This suggests that the frequency of roots, which transfer the *Heterobasidion* infection, rather than the growth rate of the fungus, may be limited in peat soil. Thirdly, the coexistence of competing fungi in disease centers, e.g., *Armillaria* sp. and *R. bicolor*, may hinder the transfer of *Heterobasidion* mycelium through root contacts.

4.4. Other fungal species identified in disease centers

After *Heterobasidion* species, *Armillaria* spp. were the second most common decay fungi, infecting 18 % of all decayed spruces in disease centers and being the dominant species in half of the experimental stands. In comparison to upland mineral sites in southern Finland, where 8 % and 3 % of root rot infections on Norway spruce was caused by *Armillaria* sp. (Piri et al., 1990; Hallaksela, 1984), the frequency of *Armillaria* sp. was higher in the present study. Since *Armillaria* spp. can grow freely through the soil with the aid of rhizomorphs and adapt to harsh environments, these fungi might have an advantage when competing for the same niches with other decay fungi, including *Heterobasidion* sp., in acid and occasionally wet peat soil.

Trees suffering from a nutrient imbalance can give an advantage to *Armillaria* species, which are considered weak pathogens that rarely cause disease in unstressed, vigorous trees (Guillaumin et al., 1993; Kubiak et al., 2017). In boreal peatland forests, the availability of nitrogen for trees typically improves after drainage, whilst there can be a severe lack of other nutrients, such as potassium, boron and zinc (Kaunisto and Paavilainen, 1988). However, Armillaria root rot did not occur in the experimental stand in Pöytyä, where the pines suffered from severe potassium and slight phosphorus deficiencies, while nitrogen was abundant. Instead, the incidence of Heterobasidion root rot in Pöytyä was the second highest among the experimental stands. Unfortunately, nutrient data (needle analyses) are not available for other stands. This single case shows, however, that nutrient imbalance does not necessarily predispose Scots pines to *Armillaria* infection.

An interesting finding is that *A. cepistipes* was the predominant *Armillaria* species causing decay in conifers on peatland. In boreal mineral soil, *A. cepistipes* is not considered to be a major conifer pathogen, although it occurs commonly in coarse woody debris of broad-leaved trees. In turn, *A. borealis* is the most common *Armillaria* species in southern Finland (Korhonen, 1978b) and is considered to be the main *Armillaria* species causing disease in Norway spruce (Piri et al., 1990; Piri, 1996; Keča and Solheim, 2011) but was only rarely found from the peatland sites in this study (molecularly identified from only the Lapinjärvi forest site). One factor that might explain the relative commonness of *A. cepistipes* on peatland soils is its high tendency to produce rhizomorphs (Redfern and Filip, 1991).

The third most frequently isolated basidiomycete was a saprotrophic, cord-forming *R. bicolor* that was isolated from 12 % of the decayed spruces. *R. bicolor* is a common stump colonizer and in central Sweden, it was found in 40 % of 8- to 10-year-old spruce stumps (Kirby et al., 1990). In addition, Hallaksela (1984) discovered that *R. bicolor* acted as

a causal agent of butt rot in 2 % of decayed spruce trees in Finland, indicating its potential pathogenicity. The fungus was also found to exhibit slight pathogenicity on Norway spruce and Scots pine seedlings (Holmer and Stenlid, 1997). Although *R. bicolor* was not an effective competitor against *Heterobasidion* on malt agar medium (25 % of *R. bicolor* cultures were overgrown by *H. parviporum* at +15 °C), previous studies have demonstrated that *R. bicolor* is more aggressive on woody substrates, where it can outcompete other species, including *Heterobasidion* sp. (Holmer and Stenlid, 1993, 1996; Woods et al., 2005; Woods et al., 2006). In our study, *R. bicolor* was the most frequently isolated fungus in the Janakkala experimental stand, where no *Heterobasidion* infections were found.

Although our result indicates that *A. cepistipes* might be a more significant pathogen in boreal peatland forests than on mineral sites, it might also act, together with *A. borealis* and *R. bicolor*, as an antagonist limiting the spread of Heterobasidion root rot in peatland forests. Both *Armillaria* sp. and *R. bicolor* have the ability to penetrate the soil and infect roots externally. Since they primarily colonize the outer tissues of roots, it is possible that they could hinder the transfer of *Heterobasidion* sp. from an infected root to a healthy root through root contact (Greig, 1962; Morrison and Johnsson, 1978; Shaw and Loopstra, 1988). Indeed, several early studies reporting mostly field observations provide circumstantial evidence of *Armillaria* acting antagonistically towards *Heterobasidion* (Holdenrieder and Greig, 1998; Appendix II in Woodward et al., 1998 and the references therein). The negative correlation observed in our study between the co-occurrence of *Armillaria* sp. and *R. bicolor*, and the frequency of *Heterobasidion* infections and the number and size of *Heterobasidion* genets, supports this hypothesis.

On the contrary, *A. aerolatum* and *S. sanquinolentum*, which were competitive basidiomycetes against *H. parviporum* in the *vitro*-tests, have not proven to be strong competitors in a natural growth environment. In Sitka spruce stumps co-inoculated with *H. annosum* and *S. sanquinolentum*, *S. sanquinolentum* did not limit growth of *H. annosum* but instead increased its colonization (Woods et al., 2006). Although both *S. sanquinolentum* and *A. aerolatum* are known as wound pathogens (Vasiliauskas, 2001), in the present study, *H. parviporum* was the most frequent pathogen in the spruce trees near the ditches that obviously have been damaged during digging operations. Previously, a negative correlation has been observed between the presence of *S. sanquinolentum* and *H. annosum* s.l. in spruce trees wounded by bark peeling by moose in Sweden (Vasiliauskas et al., 1996). Further studies carried out in live standing spruce trees are necessary to better understand the competitive dynamics between the wound pathogens and *Heterobasidion* sp. especially on drained peatlands, where root injuries due to digging operations and peat subsidence are common.

Overall, ascomycetes demonstrated greater competitiveness than basidiomycetes against *H. parviporum* in the dual culture tests. Species such as *Ascocoryne* sp., *Leptodontidium elatius*, and *Rutstroemia calopus* partially or completely overgrew *H. parviporum* on malt agar medium. *Ascocoryne* isolates have earlier been tested for antagonistic properties against *Heterobasidion* species on Norway spruce wood and the effect was found to be strain-specific (Ricard, 1970; Delatour and Sylvestre-Guinot, 1978; Etheridge and Craig, 1973, bilayer technique). *Ascocoryne* spp. do not cause decay and have been isolated from the heart wood of healthy-looking spruces (Roll-Hansen and Roll-Hansen, 1979; Müller and Hallaksela, 2000). Interestingly, *Ascocoryne* sp. has been found together with *Heterobasidion* sp. in the same decay column in spruce trees (Hallaksela, 1984). In a Latvian study, instead, a significant negative co-occurrence between the genera *Heterobasidion* and *Ascocoryne* was found in Norway spruce stands on mineral soil (Klavina et al., 2023). In our material, *Ascocoryne* sp. did not occur together with *Heterobasidion* in the same tree. On the other hand, there was no correlation between the occurrences of *Ascocoryne* sp. and *Heterobasidion* sp. in disease centers either.

Both *L. elatius* and *R. calopus* are dark septate endophytes of which *L. elatius* has been detected earlier in Norway spruce stumps in Sweden (Kubart et al., 2016) and in both stumps and living spruce trees in Latvia (Arhipova et al., 2011), while *R. calopus* is common in various habitats and occurs on different types of organic compounds. *R. calopus* has been recently patented as a biostimulant capable of promoting and increasing the growth and development of agricultural crop plants under stress conditions (Huertas et al., 2024). However, these species have to our knowledge not been tested for antagonism against *Heterobasidion* sp., whereas the related *Leptodontidium beauverioides* was found to be non-effective (Falk, 1987). In the present study, these endophytes were isolated from freshly cut spruce stumps, suggesting that they may also occupy the same niche as *Heterobasidion* sp. Fungal endophytes form a highly diverse group of fungi, and some of them can protect the host through direct interaction with pathogens or indirect enhancement of plant defense. In previous studies, endophytes like *Cryptosporiopsis ericae*, *Phialocephala sphaeroides*, *Rhytismatales* sp., *Acephala* sp., and *Paraphaeosphaeria neglecta* have been found to inhibit the growth of *H. parviporum in vitro* (Terhonen et al., 2014; Wen et al., 2022; Durodola et al., 2023). The first four of the above-mentioned endophytes were isolated from fine roots of Norway spruce on drained peatland. Although the endophytes, especially in peat soils, are poorly known, and their role in the disease dynamic of *Heterobasidion* spp. is insufficiently understood, some of them may have potential in controlling Heterobasidion root rot, as noted by Terhonen et al. (2014), and this is also supported by the results obtained in the present study.

It should be noted that in 26 % of spruce trees and 5 % of pine trees, the causal agent of root rot or discoloration could not be identified. Future studies utilizing molecular markers to determine fungal diversity, followed by principal component analysis would allow a thorough comparison of the fungal communities at mineral soil sites and peatland forests.

4.5. CCF management and Heterobasidion root rot on drained peatland

Currently, the transformation of even-aged stands into CCF is underway in Finnish peatland forests. This process spans several decades, and the experimental stands, where cutting aimed at CCF was conducted, are still in the early stages of this transition. Consequently, our study does not provide a direct answer regarding the long-term effects of CCF management on the spread and incidence of Heterobasidion root rot in peatland forests. Nevertheless, our study indicates that, at present, Heterobasidion root rot is not as prevalent on peatland as it is in the same region on mineral soil. The absence of large *Heterobasidion* genets on peat soils, along with healthy understory spruces in disease centers, also support earlier observations suggesting that the transfer of the *Heterobasidion* mycelium from one root system to another might be less common in peat than in mineral soils (Redfern, 1984, 1998). Additionally, taking into account the advantages of CCF management over clear-cut based forest management, such as better opportunities to reduce greenhouse gas emissions and maintain the forest carbon sink (Nieminen et al., 2018; Lehtonen et al., 2023), CCF can be considered a feasible forest management alternative in drained peatland forests.

To ensure the health of peatland forests in the future, it is crucial to protect the stand from primary infections by *Heterobasidion* spores. This involves winter logging, stump treatment during summer logging, and restricting ditch network maintenance operations to the cold season of the year. In CCF management, the need for ditch cleaning is reduced because the continuous tree cover helps to maintain the groundwater table at an acceptable level for wood production (Leppä et al., 2020, Laudon and Hasselquist, 2023). This may have positive effects on tree health, as undisturbed soil lowers the risk of *Heterobasidion* infections through root damage. On the other hand, the risk of the disease spreading through logging injuries is high in spruce stands due to peat subsidence and superficial root system. For this reason, winter logging is a better option than summer logging especially in stands subjected to CCF management with frequently recurring harvestings.

Moreover, forest management practices that promote diverse tree

species composition with deciduous trees help maintain a high fungal diversity, contributing to the natural prevention of *Heterobasidion* sp. in peatland forests (Johansson and Marklund, 1980). Birches, especially downy birch (*Betula pubescens*) that thrives on poor boreal peatland sites and often is the first pioneer species after drainage, are important for diversity, even though the economic value of downy birch is low (Hynynen et al., 2010). Birch and pine mixture also hinder the mycelial spread of *H. parviporum* in spruce stands (Piri et al., 1990). Maintaining these light-demanding tree species in CCF, where shading of overstory trees favor the regeneration of more shade-tolerant Norway spruce, is, however, challenging (Laudon and Hasselquist, 2023). In addition, it should be taken into account that species of *Armillaria* are efficient in colonizing coarse woody debris of broadleaved trees (including birch), which are known to serve an infection route to conifers (Simard et al., 2005). Based on the common occurrence of *A. cepistipes* in the current study, there is a need to investigate its clonal spread from hardwood trees and debris into living conifers, and its potential to act as a conifer pathogen at boreal peatland sites.

In conclusion, our results suggest that *Heterobasidion* sp. is not as frequent and not as dominant agent causing root and butt rot in Norway spruce stands on peat soil compared to mineral soil in the same region. Instead, certain basidiomycetes, such as *Armillaria* spp. (particularly *A. cepistipes*) and *Resinicium bicolor*, were found to be more prevalent on peat than on mineral soil. Although more detailed information on the competitiveness of both pathogenic and non-pathogenic fungi *in vivo* conditions in peatland forests is needed, our results indicate that the coexisting fungi might have a positive effect by reducing the dominance of *H. parviporum* in Norway spruce stands. Moreover, further research is necessary to monitor the progression of Heterobasidion root rot in peatland forests in the long run. Considering the current health condition of peatland forests, the prerequisites for practicing CCF in the distribution area of Heterobasidion root rot are generally better on peat than on mineral soils. To ensure the health of peatland forests it is imperative that control of Heterobasidion root rot has the highest priority in all logging operations.

CRediT authorship contribution statement

Tuula Piri: Writing – original draft, Methodology, Investigation, Formal analysis, Conceptualization. **Eeva J. Vainio:** Writing – review & editing, Methodology, Investigation.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgments

The authors wish to thank Ari Rajala, Minna Oksanen and Juha Puranen for help with the field and laboratory work.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2024.122148.

References

Anderson, J.B., Stasovski, E., 1992. Molecular phylogeny of northern hemisphere species of *Armillaria*. Mycologia 84 (4), 505–516. https://doi.org/10.1080/00275514.1992.12026170.

Arhipova, N., Gaitnieks, T., Donis, J., Stenlid, J., Vasaitis, R., 2011. Butt rot incidence, causal fungi, and related yield loss in *Picea abies* stands of Latvia. Can. J. For. Res. 41, 2337–2345. https://doi.org/10.1139/x11-141.

de Beer, Z.W., Procter, M., Wingfield, M.J., Marincowitz, S., Duong, T.A., 2022. Generic boundaries in the *Ophiostomatales* reconsidered and revised. Stud. Mycol. 101, n57–120. https://doi.org/10.3114/sim.2022.101.02.

Brūna, L., B, Kļaviņa, D., Korhonen, K., Zaļuma, A., Burņeviča, N., Gaitnieks, T., 2019. Effect of soil properties on the spread of Heterobasidion root rot. : Proc. Latv. Acad. Sci. Sect. B. Nat., Exact., Appl. Sci. 73 (6), 466–471. https://doi.org/10.2478/prolas-2019-007.

Delatour, C., Sylvestre-Guinot, G., 1978. Microflore interne des tissus ligneux de l'épicéa commun sur pied. *II. – Etude in vitro de la microflore naturelle*. Annls Sci. 35, 285–298.

Duchesne, L.C., Anderson, J.B., 1990. Location and direction of transcription of the 5S rRNA gene in *Armillaria*. Mycol. Res. 94, 266–269. https://doi.org/10.1016/S0953-7562(09)80626-6.

Durodola, B., Blumenstein, K., Akinbobola, A., Kolehmainen, A., Chano, V., Gailing, O., Terhonen, E., 2023. Beyond the surface: exploring the mycobiome of Norway spruce under drought stress and with *Heterobasidion parviporum*. BMC Microbiol. 23, 350. https://doi.org/10.1186/s12866-023-03099-y.

Etheridge, D.E., Craig, H.M., 1973. A bilayer plate technique to detect broad-spectrum antagonism in microorganisms and its application to wood-inhabiting fungi. Can. J. Microbiol. 19 (11), 1455–1458. https://doi.org/10.1139/m73-236. PMID: 4768835.

Falk, E., 1987. Untersuchungen zum Einfluß von Rhizosphärenorganismen der Fichte (*Picea abies* L. H. Karst.) auf den Rotfäuleerreger *Fomes annosus* (Fr.) R. Karst sowie die Identifikation von Gliotoxin als Stoffwechselprodukt von *Penicillium spinolosum* Thom. Bibl. Mycol. III, 170.

Fjeld, D., Granhus, A., 1998. Injuries after selection harvesting in multi-stored spruce stands – The Influence of operating systems and harvest intensity. J. For. Eng. 9 (2), 33–40. https://doi.org/10.1080/08435243.1998.10702716.

Gaitnieks, T., Klavina, D., Muiznieks, I., Pennanen, T., Velmala, S., Vasaitis, R., Menkis, A., 2016. Impact of Heterobasidion root-rot in fine root morphology and associated fungi in *Picea abies* stands on peat soils. Mycorrhiza 26 (5), 465–473. https://doi.org/10.1007/s00572-016-0685-4.

Gaitnieks, T., Bruna, L., Zaluma, A., Burnevica, N., Klavina, D., Legzdina, L., Jansons, J., Piri, T., 2021. Development of *Heterobasidion* spp. fruit bodies on decayed *Picea abies*. For. Ecol. Manag. 482, 118835 https://doi.org/10.1016/j.foreco.2020.118835.

Gaitnieks, T., Silbauma, L., Muižnieks, I., Zaļuma, A., Kļaviņa, D., Burņeviča, N., Grosberga, M., Lazdiņš, A., Piri, T., 2022. Spread of *Heterobasidion* genotypes in Norway spruce stands on drained peat soil in Latvia. Can. J. For. Res. 52 (4), 499–510. https://doi.org/10.1139/cjfr-2021-0309.

Gardes, M., Bruns, T.D., 1993. ITS primers with enhanced specificity for basidiomycetes-application to the identification of mycorrhizae and rusts. Mol. Ecol. 2 (2), 113–118. https://doi.org/10.1111/j.1365-294X.1993.tb00005.x.

Greig, B.J.W., 1962. *Fomes annosus* (Fr.) Cke. and other root-rotting fungi in conifers on ex-hardwood sites. Forestry 35, 164–182.

Greig, B.J.W., 1998. Field recognition and diagnosis of *Heterobasidion annosum*. In: Woodward, S., Stenlid, J., Karjalainen, R., Hüttermann, A. (Eds.), *Heterobasidion annosum*: Biology, Ecology, Impact and Control. CAB International, London, pp. 35–41.

Guillaumin, J.J., Mohammed, C., Anselmi, N., Courtecuisse, R., Gregory, S.C., Holdenrieder, O., Intini, M., Lung, B., Marxüller, H., Morrison, D., Rishbeth, J., Termorshuizen, A.J., Tirró, A., van Dam, B., 1993. Geographical distribution and ecology of the *Armillaria* species in western Europe. Eur. J. For. Pathol. 23, 321–341. https://doi.org/10.1111/j.1439-0329.1993.tb00814.x.

Hallaksela, A.-M., Salkinoja-Salonen, M., 1992. Bacteria inhabiting artificially inoculated xylem of *Picea abies*. Scand. J. For. Res. 7 (1-4), 165–175. https://doi.org/10.1080/02827589209382709.

Hallaksela, A.-M., 1984. Causal agents of butt-rot in Norway spruce in Southern Finland. Silva Fenn. 18 (3), 237–243.

Hantula, J., Ahtikoski, A., Honkaniemi, J., Huitu, O., Härkönen, M., Kaitera, J., Koivula, M., Korhonen, K.T., Lindén, A., Lintunen, J., Luoranen, J., Matala, J., Melin, M., Nikula, A., Peltoniemi, M., Piri, T., Räsänen, T., Sorsa, J.-A., Sandström, M., Uusivuori, J., Ylioja, T., 2023. Metsätuhojen kokonaisvaltainen arviointi: METKOKA-hankkeen loppuraportti. Luonnonvarakeskus, Luonnonvara- ja biotalouden tutkimus 46/2023. http://urn.fi/URN:ISBN:978-952-380-688-7 [In Finnish].

Holdenrieder, O., Greig, B.J.W., 1998. Biological methods of control. In: Woodward, S., Stenlid, J., Karjalainen, R., Hüttermann, A., A. (Eds.), In *Heterobasidion annosum*: Biology, Ecology, Impact and Control. London CAB International, Wallingford, UK, pp. 235–258.

Holmer, L., Stenlid, J., 1993. The importance of inoculum size for the competitive ability of wood decomposing fungi. FEMS Microbiol. Ecol. 12, 169–176. https://doi.org/10.1111/j.1574-6941.1993.tb00029.x.

Holmer, L., Stenlid, J., 1996. Diffuse competition for heterogeneous substrate in soil among six species of wood-decomposing basidiomycetes. Oecologia 106, 531–538. https://doi.org/10.1007/BF00329712.

Holmer, L., Stenlid, J., 1997. *Resinicium bicolor*; a potential biological control agent for *Heterobasidion annosum*. Eur. J. For. Pathol. 27, 159–172. https://doi.org/10.1111/j.1439-0329.1997.tb00857.x.

Huertas, V., Jiménez, A., Diánez, F., Chelhaoui, R., Santos, M., 2024. Importance of dark septate endophytes in agriculture in the face of climate change. J. Fungi 10 (5), 329. https://doi.org/10.3390/jof10050329.

Hynynen, J., Niemistö, P., Viherä-Aarnio, A., Brunner, A., Hein, S., Velling, P., 2010. Silviculture of birch (*Betula pendula* Roth and *Betula pubescens* Ehrh.) in northern Europe. Forestry 83, 103–119. https://doi.org/10.1093/forestry/cpp035.

Isomäki, A., Kallio, T., 1974. Consequences of injury caused by timber harvesting machines on the growth and decay of spruce (*Picea abies* (L.) Karst.). Acta For. Fenn. 136, 25.

Johansson, M., Marklund, E., 1980. Antagonists of *Fomes annosus* in the rhizosphere of grey alder (*Alnus incana*) and Norway spruce (*Picea abies*). Eur. J. For. Pathol. 10 (7), 385–395. https://doi.org/10.1111/j.1439-0329.1980.tb00056.x.

Kaarna-Vuorinen, L., 2000. Kuusen (*Picea abies* (L.) Karst.) lahoisuus, sen taloudelliset vaikutukset ja syyt Kaakkois-Suomen päätehakkuissa. Rot frequency and ensuing economic losses, and the cause of butt rot in final fellings in Norway spruce (*Picea abies* (L.) Karst.) stands in south-eastern Finland. Hels. Yliop. Mets. Ekon. Laitok. Julk 8, 82.

Kaunisto, S., Paavilainen, E., 1988. Nutrient stores in old drainage areas and growth of stands. Commun. Inst. Forst Fenn. 145, 39.

Keča, N., Solheim, H., 2011. Ecology and distribution of *Armillaria* species in Norway. For. Pathol. 41, 120–132. https://doi.org/10.1111/j.1439-0329.2010.00644.x.

Kenigsvalde, K., Brauners, I., Korhonen, K., Zaļuma, A., Mihailova, A., Gaitnieks, T., 2016. Evaluation of the biological control agent Rotstop in controlling the infection of spruce and pine stumps by *Heterobasidion* in Latvia. Scand. J. For. Res. *31* (3), 254–261. https://doi.org/10.1080/02827581.2015.1085081.

Kirby, J.J.H., Stenlid, J., Holdenrieder, O., 1990. Population structure and responses to disturbance of the basidiomycete *Resinicium bicolor*. Oecologia 85, 178–184. https://doi.org/10.1007/BF00319399.

Klavina, D., Tedersoo, L., Agan, A., Zaluma, A., Bitenieks, K., Polmanis, K., Daugaviete, M., Gaitnieks, T., Drenkhan, R., 2023. Effect of stand thinning, former land use and individual tree parameters on wood inhabiting fungal community composition in young living Norway spruce. Fungal Ecol. 65 (2023), 101281 https://doi.org/10.1016/j.funeco.2023.101281.

Korhonen, K., 1978b. Interfertility and clonal size in the *Armillaria mellea* complex. Karstenia 18, 31–42.

Korhonen, K., 1978a. Intersterility groups of *Heterobasidion annosum*. Commun. Inst. For. Fenn. 94, 1–25.

Korhonen, K., Piri, T., 1994. The main hosts and distribution of the S and P groups of *Heterobasidion annosum* in Finland. In: Johansson, M., Stenlid, J. (Eds.), Proceedings of the 8th Int. Conf. on Root and Butt Rots, Sweden and Finland. Swedish University of Agricultural Sciences, Uppsala, Sweden, pp. 260–267. ISBN 91- 576-4803-4.

Korhonen, K., Lipponen, K., Bendz, M., Johansson, M., Ryen, I., Venn, K., Seiskari, P., Niemi, M., 1994. Control of *Heterobasidion annosum* by stump treatment with 'Rotstop', a new commercial formulation of *Phlebiopsis gigantea*. In: Johansson, M., Stenlid, J. (Eds.), Proceedings of the 8th international IUFRO Conference on Root and Butt Rots. Swedish University of Agricultural Sciences, Wik, Sweden and Haikko, Finland, pp. 675–685.

Kubart, A., Vasaitis, R., Stenlid, J., Dahlberg, A., 2016. Fungal communities in Norway spruce stumps along a latitudinal gradient in Sweden. For. Ecol. Manag. 371, 50–58. https://doi.org/10.1016/j.foreco.2015.12.017.

Kubiak, K., Żółciak, A., Damszel, M., Lech, P., Sierota, Z., 2017. *Armillaria* pathogenesis under climate changes. Forests 8 (4), 100. https://doi.org/10.3390/f8040100.

Laine, J., Vasander, H., Hotanen, J.-P., Nousiainen, H., Saarinen, M., Penttilä, T., 2018. Suotyypit ja turvekankaat – kasvupaikkaopas. Metsäkust. Oy 160.

Laudon, H., Hasselquist, E.M., 2023. Applying continuous-cover forestry on drained boreal peatlands; water regulation, biodiversity, climate benefits and remaining uncertainties. Trees, For. People 11 (2023), 100363. https://doi.org/10.1016/j.tfp.2022.100363.

Lehtonen, A., Eyvindson, K., Härkönen, K., Leppä, K., Salmivaara, A., Peltoniemi, M., Salminen, O., Sarkkola, S., Launiainen, S., Ojanen, P., Räty, M., Mäkipää, R., 2023. Potential of continuous cover forestry on drained peatlands to increase the carbon sink in Finland. Sci. Rep. 13, 15510 https://doi.org/10.1038/s41598-023-42315-7.

Leppä, K., Hökkä, H., Laiho, R., Launiainen, S., Lehtonen, A., Mäkipää, R., Peltoniemi, M., Saarinen, M., Sarkkola, S., Nieminen, M., 2020. Selection cuttings as a tool to control water table level in boreal drained peatland forests. Front. Earth Sci. 8, 576510 https://doi.org/10.3389/feart.2020.576510.

Lindberg, M., Johansson, M., 1991. Growth of *Heterobasidion annosum* through bark of *Picea abies*. Eur. J. For. Pathol. 21, 377–388. https://doi.org/10.1111/j.1439-0329.1991.tb00775.x.

Linnakoski, R., Jankowiak, R., Villari, C., Kirisits, T., Solheim, H., de Beer, Z.W., Wingfield, M.J., 2016. The *Ophiostoma clavatum* species complex: a newly defined group in the *Ophiostomatales* including three novel taxa. Antonie Van. Leeuwenhoek 109, 987–1018. https://doi.org/10.1007/s10482-016-0700-y.

Mäkinen, H., Hallaksela, A.-M., Isomäki, A., 2007. Increment and decay in Norway spruce and Scots pine after artificial logging damage. Can. J. For. Res. 37, 2130–2141. https://doi.org/10.1139/X07-087.

Mattila, U., Nuutinen, T., 2007. Assessing the incidence of butt rot in Norway spruce in southern Finland. Silva Fenn. 41, 29–43. https://doi.org/10.14214/sf.473.

Modig, E., Magnusson, B., Valinger, E., Cedergren, J., Lundqvist, L., 2012. Damage to residual stand caused by mechanized selection harvest in uneven-aged *Picea abies* dominated stands. Silva Fenn. 46 (2), 267–274. https://doi.org/10.14214/sf.442.

Morrison, D.J., Johnsson, A.L.S., 1978. Stump colonization and spread of *Fomes annosus* five years after thinning. Can. J. For. Res. 8, 177–180. https://doi.org/10.1139/x78-028.

Müller, M.M., Hallaksela, A.M., 2000. Fungal diversity in Norway spruce: a case study. Mycol. Res. 104, 1139–1145. https://doi.org/10.1017/S0953756200003105.

Nieminen, M., Hökkä, H., Laiho, R., Juutinen, A., Ahtikoski, A., Pearson, M., Kojola, S., Sarkkola, S., Launiainen, S., Valkonen, S., Penttilä, T., Lohila, A., Saarinen, M., Haahti, K., Mäkipää, R., Miettinen, J., Ollikainen, M., 2018. Could continuous cover forestry be an economically and environmentally feasible management option on drained boreal peatlands? For. Ecol. Manag. 424, 78–84. https://doi.org/10.1016/j.foreco.2018.04.046.

Piri, T., 1996. The spreading of the S type of *Heterobasidion annosum* from Norway spruce stumps to the subsequent tree stand. Eur. J. For. Pathol. 26, 193–204. https://doi.org/10.1111/j.1439-0329.1996.tb00839.x.

Piri, T., Korhonen, K., 2008. The effect of winter thinning on the spread of *Heterobasidion parviporum* in Norway spruce stands. Can. J. For. Res. 38, 2589–2595. https://doi.org/10.1139/X08-103.

Piri, T., Valkonen, S., 2013. Incidence and spread of Heterobasidion root rot in uneven-aged Norway spruce stands. Can. J. For. Res. 43, 872–877. https://doi.org/10.1139/cjfr-2013-0052.

Piri, T., Korhonen, K., Sairanen, A., 1990. Occurrence of *Heterobasidion annosum* in pure and mixed spruce stands in southern Finland. Scand. J. For. Res. 5, 113–125. https://doi.org/10.1080/02827589009382598.

Piri, T., Vainio, E.J., Nuorteva, H., Hantula, J., 2021. High seedling mortality of Scots pine caused by *Heterobasidion annosum* s.s. Forests 12, 1289. https://doi.org/10.3390/f12091289.

Piri, T., Saarinen, M., Hamberg, L., Hantula, J., Gaitnieks, T., 2023. Efficacy of biological and chemical control agents against *Heterobasidion* spore infections of Norway spruce and Scots pine stumps on drained peatland. J. Fungi 9 (3), 346. https://doi.org/10.3390/jof9030346.

Pratt, J.E., Niemi, M., Sierota, Z.H., 2000. Comparison of three products based on *Phlebiopsis gigantea* for the control of Heterobasidion annosum in Europe. Biocontrol Sci. Technol. 10, 467–477. https://doi.org/10.1080/09583150050115052.

Redfern, D.B., 1973. Growth and behaviour of *Armillaria mellea* rhizomorphs in soil. Trans. Br. Mycol. Soc. 61, 569–581. https://doi.org/10.1016/S0007-1536(73)80126-3.

Redfern, D.B., 1984. Factors affecting spread of *Heterobasidion annosum* in plantations. In: Kile, G.A. (Ed.), In Proceedings of the Sixth International Conference on Root and Butt Rots of Forest Trees. CSIRO, Melbourne, Australia, pp. 104–114.

Redfern, D.B., 1998. The effect of soil on root infection and spread by *Heterobasidion annosum*. In: Delatour, C., Guillaumin, J.J., Lung-Escarmant, B., Marcais, B. (Eds.), Root and Butt Rots of Forest Trees (9th International Conference on Root and Butt Rots). Les Colloques No. 89. INRA Editions, Paris, France, pp. 267–273.

Redfern, D.B., Filip, G.M., 1991. Inoculum and infection. In: Shaw III, C.G., Kile, G.A. (Eds.), Armillaria Root Disease. Forest Service United States Department of Agriculture, Washington, D.C., pp. 48–61

Redfern, D.B., Stenlid, J., 1998. Spore dispersal and infection. In: Woodward, S., Stenlid, J., Karjalainen, R., Hüttermann, A., A. (Eds.), In *Heterobasidion annosum*: Biology, Ecology, Impact and Control. London CAB International, Wallingford, UK, pp. 105–124.

Redfern, D.B., Pratt, J.E., Hendry, S.J., Low, J.D., 2010. Development of a policy and strategy for controlling infection by *Heterobasidion annosum* in British forests: a review of supporting research. Forestry 83 (2), 207–218. https://doi.org/10.1093/forestry/cpq005.

Ricard, J.L., 1970. Biological Control of *Fomes annosus* in Norway spruce (*Picea abies*) with immunizing commensals. Stud. For. Suec. 84, 50. ⟨https://res.slu.se/id/publ/125265⟩.

Roll-Hansen, F., Roll-Hansen, H., 1979. Microflora of sound-looking wood in *Picea abies* stems. Eur. J. For. Pathol. 9 (5), 308–316. https://doi.org/10.1111/j.1439-0329.1979.tb00693.x.

Rönnberg, J., Cleary, M.R., 2012. Presence of *Heterobasidion* infections in Norway spruce stumps 6 years after treatment with *Phlebiopsis gigantea*. For. Pathol. 42 (2), 144–149. https://doi.org/10.1111/j.1439-0329.2011.00731.x.

Saarinen, M., Valkonen, S., Sarkkola, S., Nieminen, M., Penttilä, T., Laiho, R., 2020. Jatkuvapeitteisen metsänkasvatuksen mahdollisuudet ojitetuilla turvemailla. Metsätieteen aikakauskirja 2020, 10372. https://doi.org/10.14214/ma.10372.

Shaw III, C.G., Loopstra, E.M., 1988. Identification and pathogenicity of some Alaskan isolates of *Armillaria*. Phytopathology 78, 971–974. https://doi.org/10.1094/Phyto-78-971.

Silfverberg, K., Huikari, O., 1985. Tuhkalannoitus metsäojitetuilla turvemailla. Abstract: wood-ash fertilization on drained peatlands. Folia For. 633, 25.

Simard, S.W., Hagerman, S.M., Sachs, D.L., Heineman, J.L., Mather, W.J., 2005. Conifer growth, *Armillaria ostoyae* root disease, and plant diversity responses to broadleaf competition reduction in mixed forests of southern interior British Columbia. Can. J. For. Res. 35, 843–859. https://doi.org/10.1139/x05-010.

Solheim, H., 2006. White rot fungi in living Norway spruce trees at high elevation in southern Norway with notes on gross characteristics of the rot. Aktuelt fra Skogforsk 1, 5–12. ⟨https://hdl.handle.net/11250/2673959⟩.

Stenlid, J., 1985. Population structure of *Heterobasidion annosum* as determined by somatic incompatibility, sexual incompatibility, and isoenzyme patterns. Can. J. Bot. 63, 2268–2273. https://doi.org/10.1139/b85-322.

Stenlid, J., 1987. Controlling and predicting the spread of *Heterobasidion annosum* from infected stumps and trees of *Picea abies*. Scand. J. For. Res. 2 (1-4), 187–198. https://doi.org/10.1080/02827588709382457.

Stenlid, J., Redfern, D.B., 1998. Spread within the tree and stand. In: Woodward, S., Stenlid, J., Karjalainen, R., Hüttermann, A. (Eds.), *Heterobasidion annosum*: Biology, Ecology, Impact and Control. London CAB International, Wallingford, UK, pp. 125–141.

Szczepkowski, A., Kowalczuk, W., Sikora, K., Damszel, M., Sierota, Z., 2022. Fungi occurring in Norway spruce wood decayed by *Heterobasidion parviporum* in Puszcza

Borecka stands (northeastern Poland). Forests 13 (2), 229. https://doi.org/10.3390/f13020229.

Terhonen, E., Keriö, S., Sun, H., Asiegbu, F., 2014. Endophytic fungi of Norway spruce roots in boreal pristine mire, drained peatland and mineral soil and their inhibitory effect on *Heterobasidion parviporum in vitro*. Fungal Ecol. 9, 17–26. https://doi.org/10.1016/j.funeco.2014.01.003.

Vasiliauskas, R., 1998. Five basidiomycetes in living stems of *Picea abies*, associated with 7-25 year-old wounds. Balt. For. 1, 29–35.

Vasiliauskas, R., 2001. Damage to trees due to forestry operations and its pathological significance in temperate forests: a literature review. Forestry 74, 319–336. https://doi.org/10.1093/forestry/74.4.319.

Vasiliauskas, R., Stenlid, J., Johansson, M., 1996. Fungi in bark peeling wounds of *Picea abies* in central Sweden. Eur. J. For. Pathol. 26, 285–296. https://doi.org/10.1111/j.1439-0329.1996.tb01074.x.

Veldman, G.M., Klootwijk, J., de Regt, V.C., Planta, R.J., Branlant, C., Krol, A., Ebel, J.P., 1981. The primary and secondary structure of yeast 26S rRNA. Nucleic Acids Res. 9, 6935–6952. https://doi.org/10.1093/nar/9.24.6935.

Wang, L.-Y., Zhang, J., Drobyshev, I., Cleary, M., Rönnberg, J., 2014. Incidence and impact of root infection by *Heterobasidion* spp., and the justification for preventative silvicultural measures on Scots pine trees: a case study in southern Sweden. For. Ecol. Manag. 315, 153–159. https://doi.org/10.1016/j.foreco.2013.12.023.

Wen, Z., Terhonen, E., Asiegbu, F.O., 2022. The dark septate endophyte *Phialocephala sphaeroides* confers growth fitness benefits and mitigates pathogenic effects of *Heterobasidion* on Norway spruce. Tree Physiol. *42* (4), 891–906. https://doi.org/10.1093/treephys/tpab147.

Westman, C.J., Laiho, R., 2003. Nutrient dynamics of drained peatland forests. Biogeochemistry 63, 269–298. https://doi.org/10.1023/A:1023348806857.

White, T.J., Bruns, T., Lee, S.J.W.T., Taylor, J., 1990. Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. PCR Protoc.: a Guide Methods Appl. 18 (1), 315–322.

Woods, C.M., Woodward, S., Redfern, D.B., 2005. In vitro interactions in artificial and wood-based media between fungi colonizing stumps of Sitka spruce. For. Pathol. 35, 213–229. https://doi.org/10.1111/j.1439-0329.2005.00403.x.

Woods, C.M., Woodward, S., Pinard, M.A., Redfern, D.B., 2006. Colonization of Sitka spruce stumps by decay-causing hymenomycetes in paired inoculations. Mycol. Res. 110 (7), 854–868. https://doi.org/10.1016/j.mycres.2006.02.007.

Woodward, S., Stenlid, J., Karjalainen, R., Hüttermann, A. (Eds.), 1998. *Heterobasidion annosum*: Biology, Ecology, Impact and Control. CAB International, Wallingford.

Youssef, K., Dambrauskaite, M., Witzell, J., Rönnberg, J., 2023. Survey study reveals high prevalence of Heterobasidion root rot infection in Scots pine (*Pinus sylvestris*) stands established on seemingly low-risk sites. Forests 14 (5), 1018. https://doi.org/10.3390/f14051018.