

Article

Persistence of Viable *Heterobasidion parviporum* Inoculum in Norway Spruce Root Fragments in Drained Peat Soils

Dārta Kļaviņa ^{1,*} , Lauma Silbauma ¹, Astra Zaļuma ¹ , Natālija Burneviča ¹, Madara Strelča ¹, Silvia Canna ² , Zane Striķe ¹, Guglielmo Gianni Lione ² , Jurgis Jansons ¹, Tālis Gaitnieks ¹ and Paolo Gonthier ² 

¹ Latvian State Forest Research Institute Silava, Rigas 111, LV-2169 Salaspils, Latvia; lauma.silbauma@silava.lv (L.S.); zalumaastra@gmail.com (A.Z.); natalija.burnevica@silava.lv (N.B.); strelca.ms@gmail.com (M.S.); zane.strike@silava.lv (Z.S.); jurgis.jansons@silava.lv (J.J.); talis.gaitnieks@silava.lv (T.G.)

² Department of Agricultural, Forest and Food Sciences (DISAFA), University of Torino, Largo Paolo Braccini 2, I-10095 Grugliasco, Italy; silvia.canna@unito.it (S.C.); guglielmo.lione@unito.it (G.G.L.); paolo.gonthier@unito.it (P.G.)

* Correspondence: darta.klavina@silava.lv

Abstract

Roots infected by the forest pathogen *Heterobasidion parviporum* that remain in the soil after tree harvesting may serve as a source of inoculum for root infection of new generations of trees, thereby perpetuating outbreaks over time. As drained peat soils are evolutionary novel yet common habitat for commercial *Picea abies* stands in Northern Europe, the experiment was conducted to assess the mid-term viability of *H. parviporum* mycelium in root deadwood. Persistence of viable mycelia of *H. parviporum* in relation to root fragment volume and exposure period was assessed over the seven-year period. Additionally, the potential of transmission of the pathogen from root fragments to conifer seedlings was assessed. The likelihood of finding viable *H. parviporum* inoculum in Norway spruce root fragments depended on the size of fragments, indicating a higher likelihood in larger fragments, and on the time since burial, showing a substantial reduction in viable inoculum after seven years. We also documented the low infection rate from the root fragments to nearby *Picea abies* seedlings. The obtained results indicate the necessity for the removal of larger root fragments during soil preparation in commercial Norway spruce stands on drained peat soils to reduce infection potential.

Keywords: *Heterobasidion* root rot; *Picea abies*; *Pinus sylvestris*; infection; root pathogens



Academic Editors: Young-Seuk Park and Salvatore Moricca

Received: 19 November 2025

Revised: 16 December 2025

Accepted: 17 December 2025

Published: 19 December 2025

Copyright: © 2025 by the authors.

Licensee MDPI, Basel, Switzerland.

This article is an open access article distributed under the terms and conditions of the [Creative Commons Attribution \(CC BY\)](https://creativecommons.org/licenses/by/4.0/) license.

1. Introduction

Root and butt rots caused by the fungal pathogens *Heterobasidion* spp. threaten European coniferous forests, particularly those composed of Norway spruce (*Picea abies* (L.) Karst.) and Scots pine (*Pinus sylvestris* L.), making it one of the most economically significant forest pathogens [1,2]. Among *Heterobasidion* species reported in Europe [1], the Norway spruce-associated *H. parviporum* Niemelä & Korhonen is widespread in both naturally regenerated and planted forests [3–5]. The majority of infections by *H. parviporum* result from the propagation of mycelium through root contacts from an infected stump or tree to a neighboring healthy one, even across tree generations, thereby perpetuating outbreaks over time [1,6,7]. One of the most effective methods to reduce the likelihood of root infection is stump removal, but even after it, root fragments remain in the soil, and those can be a potential source of inoculum [8,9]. Given such infection biology, the soil type plays

a significant role in the risk of infection and in disease transmission, with that being higher in mineral soils than in organic soils [10], possibly due to the faster growth of ectotrophic mycelium, which allows escaping active host defenses or lower competitiveness with other wood decay fungi [11,12]. In this regard, the common peat soil properties (high moisture and acidity in particular) are thought to limit the pathogen's growth and spread [10,12,13].

In Northern Europe, Norway spruce stands on drained peat soils are prospective for the timber industry [14]. Nevertheless, there are several indications of high root rot infection that might be related to both chemical and biological soil properties, differing from deep peat soils and mineral soils [12,15,16]. As a forest on drained peat soil is an evolutionary novel habitat, the biotic interactions between fungus and their host might be specific due to altered equilibria [16–18]. Hence, the body of knowledge on the extended survival of *Heterobasidion* spp. inoculate in residual root systems from mineral soils [6,19–25] might not be directly applicable to forests on drained peat soils. To our knowledge, there is no information on the survival and infection potential of *Heterobasidion parviporum* mycelium in host roots in drained peat soils, thus highlighting a knowledge gap.

In this study, we aimed to assess the viability of *H. parviporum* mycelium in Norway spruce root fragments in drained peat soils. Additionally, we aimed to assess the potential of transmission of the pathogen from root fragments to seedlings of *P. abies* and *Pinus sylvestris*. We hypothesize a reduced persistence of *Heterobasidion parviporum* mycelia and low infection transmission of the *H. parviporum* mycelia to the seedlings.

2. Materials and Methods

2.1. Experimental Design

In a Norway spruce stand in Latvia (WGS84 coordinates: 56.672479, 25.891165, forest type: *Myrtillosa* turf. mel. (drained forest on peat soil) according to K. Bušs [26], age: 46 years), where *Heterobasidion* spp. disease centers were detected before [15]. A total of 12 *P. abies* trees infected by *Heterobasidion* were selected and cut in May 2017. Selected trees were located in three different disease centers, comprising three, four and five infected trees, respectively. The root systems were fully excavated from the soil, divided into fragments and transported to the laboratory. Wood disks (2–3 cm thick) were taken from the surfaces of all stumps and roots for *Heterobasidion* spp. isolation, identification and genotyping. To confirm *Heterobasidion* spp. infection, wood disks were collected from both ends of the roots (distal end and branching point), rinsed under running tap water and incubated in a growth chamber (BINDER GmbH, Tuttlingen, Germany, model KBWF 720) at a temperature of +21 °C and a relative humidity of 80% for one week. Following incubation, the samples were inspected under a stereomicroscope (Leica M205C, Deerfield, IL, USA) for the presence of the typical conidiophores of *Heterobasidion* spp. Pieces of mycelium and conidiophores were transferred into Petri dishes filled with Hagem agar medium (5 g glucose, 0.5 g NH₄NO₃, 0.5 g MgSO₄ 7H₂O, 5 g malt extract, 20 g agar, 1000 mL distilled H₂O at pH 5.5) to obtain pure cultures, subsequently stored at +4 °C.

Identification at the species level of pure cultures was performed with molecular methods. DNA extraction was performed using CTAB method [5], followed by polymerase chain reaction (PCR) with species-specific primers for *H. annosum* (MJ-F and MJ-R) and *H. parviporum* (KJ-F and KJ-R) [27], the only two *Heterobasidion* species reported in Latvia and Northern Europe, and both known to infect *P. abies*. Genotyping was accomplished through somatic incompatibility tests by pairing isolates in all possible combinations, as previously described [6].

Root fragments harboring *Heterobasidion* spp. were divided into four volume classes: “50 cm³” (20–75 cm³), “100 cm³” (76–150 cm³), “200 cm³” (151–250 cm³), and “300 cm³” (251–350 cm³), resulting in 192, 180, 180 and 152 fragments of each class, respectively. Root

fragments were stored at +4 °C for a week to confirm the infection. When the pathogen was confirmed, root rot fragments (110, 337 and 252 from the three disease centers mentioned above) were used in the experiment (five fragments lost their origin mark).

To assess the survival of *Heterobasidion* spp. mycelium, the experiment was established in three closely located forest lands growing on drained peat soil in Olaine municipality, Olaine rural territory of Latvia (Table 1). In May 2017, to assess the potential of transmission of the pathogen from root fragments to seedlings, one-year-old *P. abies* and *P. sylvestris* seedlings were planted in the experimental plots. Each sample plot contained 23–28 seedlings (planting distance between seedlings was standardized: 1.5 to 2 m), with a total of 152 Norway spruce and 152 Scots pine seedlings distributed across 12 sample plots (4 plots per forest stand) (Table 1). In May 2017, infected root fragments were buried 10 cm deep in the soil, positioned parallel to the soil surface, near seedlings (5–10 cm away) on raised mounds prepared in peat soils, which is a technology that facilitates more even root development and architecture to all sides [28,29]. The number of fragments per seedling varied depending on fragment size: fragments of volume classes 100 cm³, 200 cm³, and 300 cm³ were placed in pairs opposite to each other, and root fragments of 50 cm³—in the four directions around the seedling. All root fragments and seedlings were individually marked, and coordinates for each sample plot were recorded to facilitate systematic assessment.

Table 1. Experimental plantings.

No.	Coordinates WGS84, Latitude	Coordinates WGS84, Longitude	Forest Type According to Bušs 1997 [26]	Area, ha	Soil pH, CaCl ₂	Number of Root Fragments Buried	Number of Scots Pines Planted	Number of Norway Spruces Planted
1	56.78031	23.82672	Oxalidosa turf. mel.	1.7	3.4	244	53	53
2	56.78015	23.83246	Oxalidosa turf. mel.	1.3	3.7	224	48	48
3	56.77718	23.85279	Myrtillosa turf. mel.	1.8	3.0	236	51	51

2.2. *Heterobasidion* spp. Mycelium Survival and Seedling Infection Analyses

Each sample plot was surveyed annually in late June or early July to assess the persistence of viable inoculum of *Heterobasidion* spp. in the buried root fragments and the health status of planted seedlings over seven consecutive years (2018–2024). In total, 674 root fragments during seven consecutive years were excavated.

Each year, after retrieval from the sample plots, within 24 h, root fragments were washed under running tap water, dried overnight at room temperature, and wood samples were cut out from root central sections to minimize potential contamination from soil-borne fungi. All obtained wood samples were flame-sterilized and placed on either Hagem agar medium in Petri dishes for fungal isolation. The Petri dishes were monitored every 2–3 days for mycelial growth. Any observed *Heterobasidion* spp. mycelium was subcultured and paired with reference cultures obtained during the experiment's initial setup using somatic incompatibility tests as described above [30], thus verifying whether the pathogen had survived in the fragments and retained the ability to infect neighboring conifer seedlings. From the excavated seedlings, three 1–2 cm thick wood disks were collected from the root collar upwards, debarked, washed under tap water and incubated in a growth chamber (BINDER GmbH, Germany, model KBWF 720, regime of +21 °C temperature and 80% humidity) for one week. Following incubation, the samples were inspected under a stereomicroscope (Leica M205C) for the presence of the typical conidiophores of *Heterobasidion* spp. Isolations were performed as described above. Somatic incompatibility tests were performed by pairing isolates obtained from seedlings with those retrieved from

the associated root fragments to confirm that isolates belonged to the same genotype and therefore that seedling infection originated from infected root fragments buried in the soil.

2.3. Statistical Analysis

To analyze the factors influencing the presence of *Heterobasidion* spp. mycelium, generalized linear mixed-effects models (GLMM) analyzed with the lme4 R package (function glmer with a binomial distribution) [31] were implemented. Models used in this study incorporated both fixed effects (root fragment volume and burial duration) and random effects (specific tree stumps, plots, subplots, and individual trees). While the random effects were not directly studied, their inclusion was essential for ensuring the accuracy and precision of the model. The general model form was:

$$\log(E(T)) = \beta_1 \times T + \beta_2 \times G + u(\text{Plot, Subplot, Tree}) + u(\text{Group, Stump})$$

where $\log(E(T))$ represents the logarithm of the predicted probability of *Heterobasidion* spp. presence, β_1 and β_2 are regression coefficients associated with fixed effects: root fragment volume (T : 50, 100, 200, 300 cm³) and time (G : 1–7 years) since burial in the soil. The terms $u(\text{Plot, Subplot, Tree})$ and $u(\text{Group, Stump})$ represent random effects accounting for variability across plots, subplots, individual trees, stump sampling groups and stumps. The significance of fixed effects was evaluated using the Type II analysis-of-variance table of the Wald Chi-square test (function Anova from the car package). The normality was checked based on graphical visualization of the model residuals. Data analysis was performed in R v.4.4.3 [32].

3. Results

All *Heterobasidion* spp. isolates obtained from the surface of stumps and roots of the 12 *P. abies* trees used in this study were identified as belonging to *H. parviporum*. Somatic incompatibility tests indicated that each of the disease centers was occupied by a different *H. parviporum* genotype.

3.1. Survival and Viability of *Heterobasidion* spp. Mycelium in Root Fragments

A total of 704 *H. parviporum*-infected Norway spruce root fragments were buried in the soil. After seven years, at the end of this study, 674 of these root fragments were retrieved, representing 95.7% of the initial number of fragments. The remaining 30 fragments (16 from the 50 cm³ size class, eight from the 100 cm³ class, five from the 200 cm³ class, and one from the 300 cm³ class) were not found.

The rate of survival of viable *H. parviporum* inoculum in roots of *P. abies* increased with fragment size: 6.62% for the 50 cm³ class, 9.59% for the 100 cm³ class, 12.26% for the 200 cm³ class, and 27.64% for the 300 cm³ class. Statistical modeling using GLMM confirmed that fragment volume is a significantly related factor to the mycelial survival ($p < 0.001$, $\chi^2 = 21.406$) (Table 2, Figure 1). Larger fragments demonstrated higher viability and a wider range of potential survival values (95% confidence interval).

Additionally, the exposure period of root fragments in the peat soil had a significant negative impact on the survival of mycelia. With a longer exposure period, the proportion of infected root fragments decreased. Generalized linear mixed-effects models results indicated that the burial duration was also a critical factor influencing survival rates ($p < 0.01$, $\chi^2 = 10.087$) (Figure 1). The predicted probabilities showed that longer burial periods reduced the likelihood of mycelial survival and narrowed the range of potential survival values (95% confidence interval).

Table 2. The summary statistics of the generalized linear mixed-effects model (GLMM). The estimated Chi-square values and *p*-values (ANOVA-like table) for the root volume and exposure period of root fragments on *Heterobasidion parviporum* mycelial survival, the variance of the random effects and the marginal R^2 values for the refined model are shown.

Variable	Chi-Square Value	<i>p</i> -Value
Year	10.1	0.002
Root fragment volume	21.4	<0.001
Random effects	variance	
Plot × Subplot × Seedling	0.193	-
Genotype × stump	0.342	-
Plot × Subplot	<0.001	-
Genotype	<0.001	-
Planting site	0.349	-
Model performance, marginal R^2	0.137	
Model performance, conditional R^2	0.320	

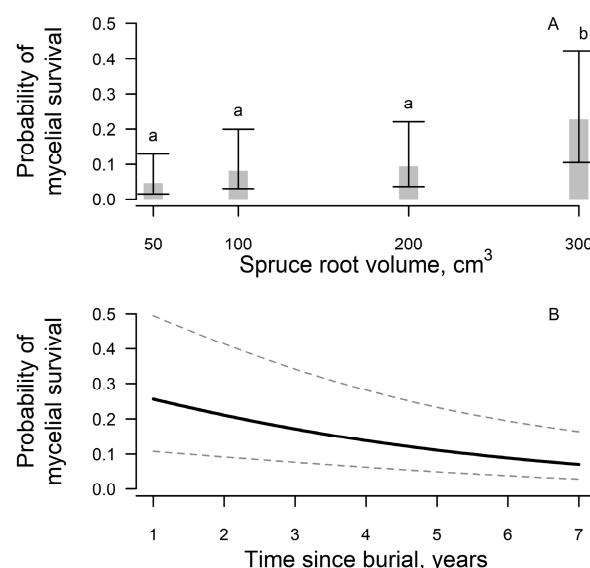


Figure 1. Probability of the survival of *Heterobasidion parviporum* mycelium in peat soils in Norway spruce root fragments of different size classes (50 to 300 cm³) (confidence interval (95%) shown by error bars; different letters indicate significant differences between groups at $\alpha = 0.05$) (A) and over a period of seven years (confidence interval (95%) shown by dotted lines) (B).

3.2. Seedlings Infection

Over the seven-year study period, 122 dead seedlings (70 Norway spruces and 48 Scots pines, mainly collected in the first and second year after the establishment of the experiment) were examined for the presence of *H. parviporum*. Among these, only one Norway spruce was found to be infected by the pathogen. This seedling was located near two 100 cm³ root fragments and it was collected in 2022, five years after establishing the experiment. Although no viable mycelium was detected in corresponding root fragments at the time of retrieval, somatic incompatibility tests confirmed that the infection originated from the buried fragments.

3.3. Influence of Environmental Factors on Mycelial Survival

The intraclass correlation coefficient (ICC) indicated that 21% of the total variability in mycelial survival could be attributed to the random effects included in the model (experimental plot, subplots, individual trees, stump groups and stump ID). Among the random effects ($\sigma^2 = 3.29$), the largest impact on mycelial survival was observed for the experimental plot ($\tau_{00} = 0.35$), the combined random effect of stump groups and stump ID ($\tau_{00} = 0.34$), and the combined random effect of individual trees, subplots, and experimental plot ($\tau_{00} = 0.19$).

When considering only the fixed effects (root fragment volume and burial duration), the GLMM model explained 13.7% of the total variance (R^2_m). However, when both fixed and random effects were included, the total variance (R^2_c) increased to 32.0%.

4. Discussion

Considering drained peat soils as evolutionary novel habitats for Norway spruce [14,16–18], the dependence of survival of *Heterobasidion parviporum* mycelia on the size of the root fragments was generally consistent with those of previous experiments conducted in mineral soils [9,25]. Accordingly, persistence of viable *H. parviporum* inoculum increased in larger Norway spruce root fragments compared to smaller ones ($p < 0.05$) (Figure 1). Larger root fragments (up to 350 cm³) left in the soil after harvesting can conserve viable pathogen inoculum over an extended period. The likelihood that this may happen with smaller root fragments (50 cm³) is much lower and could be considered negligible (Figure 1) due to increased competition with other fungi and/or decomposition [12,33].

In terms of the level of reduction in viable inoculum over time, our results slightly differed from previous studies conducted on mineral soils [25]. Although a reduction in viable inoculum after six years from burial was observed in both studies, the time did not have a significant effect on the probability of occurrence of *H. parviporum* in root fragments in mineral soils [25], while we identified as a significant factor in drained peat soils. As a comparison, while the incidence of root fragments carrying viable *H. parviporum* inoculum over time went from 39.6% after one year to 17.8% after six years in mineral soil [25], it went from 30.1% after one year to 9.7% after seven years in drained peat soil in this study. The previously studied range from mineral soils [25] are well within the predicted range in our study (Figure 1), indicating similar patterns on both studies. However, caution should be taken with this conclusion because part of the results is explained by *Heterobasidion* genotype or site-specific factors, as outlined by the random effect analysis in this study (Table 2). One *H. parviporum* genotype in buried wood fragments showed a better survival rate than others (Supplementary Material), possibly indicating that the persistence of the inoculum in wood depends on the pathogen genotype, similarly to other traits such as pathogenicity [34].

A lower risk of disease transmission on peat soils compared to mineral soils would be expected based on a large body of literature [10]. A low infection risk was also confirmed on drained peat soils with only a single Norway spruce seedling (1%). Slightly higher infection rate (8% of Norway spruce seedlings within six years) on mineral soils [25]. The differences could be related to soil acidity as higher soil pH is favorable for infection [35]: soil pH in our study ranged from 3.0 to 3.7, but in Piri and Hamberg study, from 4.0 to 4.7 [25]. Lastly, the differences in seedling infection rate could also be related to seedling age, as the likelihood of contact with infected root fragments increases with age because of the greater size of the root systems: Piri and Hamberg [25] used two-year-old seedlings, while one-year-old seedlings were used in this study.

While the other causes of seedling mortality were not directly analyzed, field observations suggest that the high mortality in the first year after planting could be related to

environmental stress factors, especially drought, which agrees with other studies [28,36,37]. It should be noted that drought could have had an impact not only on seedling vitality but also on *H. parviporum* mycelium persistence.

The observed explicit relationship between root size and the survival of inoculate in drained peat soils indicates the need for fine-tuning of guidelines for managing Norway spruce on drained peat soils to minimize the risks associated with *H. parviporum*. In heavily infested sites, where stump removal could be suggested [8,9], removal of the roots (volume—from 250 cm³, 7.0 ± 2 cm in diameter) appears advantageous, thus omitting direct contact between sapling roots with larger size remnants of infected roots.

5. Conclusions

The persistence of viable *Heterobasidion parviporum* mycelium in root fragments of Norway spruce in the drained peat soils is similar to that in mineral soils; therefore, similar management measures appear applicable. Based on the relationship between root size and survival of inoculate, removal of root fragments greater than 250 cm³ in volume (more than 5 cm in diameter) during the soil preparation for new generation seedlings is advantageous for the health of the regenerating stand.

Supplementary Materials: The following supporting information can be downloaded at <https://www.mdpi.com/article/10.3390/f17010001/s1>.

Author Contributions: Conceptualization, T.G., L.S., D.K. and A.Z.; methodology, T.G., N.B., L.S. and D.K.; formal analysis, L.S., D.K. and M.S.; investigation, Z.S.; data curation, D.K., Z.S., L.S. and A.Z.; writing—original draft preparation, D.K., M.S., N.B., S.C. and Z.S.; writing—review and editing, A.Z., T.G., P.G., G.G.L. and J.J.; visualization, D.K. and M.S.; supervision, T.G., D.K. and P.G.; project administration, L.S., D.K. and J.J.; funding acquisition, J.J., D.K. and T.G. All authors have read and agreed to the published version of the manuscript.

Funding: This research was supported by JSC Latvian State Forests (project No. 5-5.9.1_007q_101_21_79 “Investigation of the impact of root rot and reducing risks caused by root rot”) and “Innovation in Forest Management and Value Chain for Latvia’s Growth: New Forest Services, Products and Technologies (Forest4LV)” (project No. VPP-ZM-VRIILA-2024/2-0002). The experimental planting was established within the JSC Latvian State Forests research “Forest regeneration, establishment, tending and thinning programme” (project No. 5-5.5_000p_101_16_22).

Data Availability Statement: Data are available upon personal request to the corresponding author.

Acknowledgments: Authors are grateful to Roberts Matisons, Dagnija Lazdiņa, Laima Ciseļonoka, Kristīne Kenigšvalde, Agriņa Kenigšvalde, Zane Saule, Annija Auniņa, Baiba Krivmane, Jānis Lekavičs, Mārtiņš Mednis and Liene Dārta Lukstiņa for their assistance in the laboratory, field work and data analysis. The authors have reviewed and edited the output and take full responsibility for the content of this publication.

Conflicts of Interest: The authors declare no conflicts of interest.

References

1. Garbelotto, M.; Gonthier, P. Biology, epidemiology and control of *Heterobasidion* species worldwide. *Annu. Rev. Phytopathol.* **2013**, *51*, 39–59. [CrossRef]
2. Kovalchuk, A.; Wen, Z.; Sun, H.; Asiegbu, F. *Heterobasidion annosum* s.l.: Biology, genomics, and pathogenicity factors. *For. Microbiol. For. Tree Health* **2022**, *2*, 345–359. [CrossRef]
3. Korhonen, K.; Capretti, P.; Karjalainen, R.; Stenlid, J. Distribution of *Heterobasidion* intersterility groups in Europe. In *Heterobasidion Annosum: Biology, Ecology, Impact and Control*; Woodward, S., Stenlid, J., Karjalainen, R., Huttermann, A., Eds.; CAB International: Wallingford, UK, 1998; pp. 93–104.
4. Vasiliauskas, R.; Juška, E.; Vasiliauskas, A.; Stenlid, J. Community of Aphyllophorales and root rot in stumps of *Picea abies* on clear-felled forest sites in Lithuania. *Scand. J. For. Res.* **2002**, *17*, 398–407. [CrossRef]

5. Arhipova, N.; Gaitnieks, T.; Donis, J.; Stenlid, J.; Vasaitis, R. Butt rot incidence, causal fungi and related yield loss in *Picea abies* stands of Latvia. *Can. J. For. Res.* **2011**, *41*, 2337–2345. [\[CrossRef\]](#)
6. Piri, T. The spreading of the S type of *Heterobasidion annosum* from Norway. *Eur. J. For. Pathol.* **1996**, *26*, 193–204. [\[CrossRef\]](#)
7. Greig, B.J.W.; Pratt, J.E. Some observations on the longevity of *Fomes annosus* in conifer stumps. *Eur. J. For.* **1976**, *6*, 250–253. [\[CrossRef\]](#)
8. Vasaitis, R.; Stenlid, J.; Thomsen, I.M.; Barklund, P.; Dahlberg, A. Stump removal to control root rot in forest stands. *Silva Fenn.* **2008**, *42*, 457–483. [\[CrossRef\]](#)
9. Burneiviča, N.; Zaļuma, A.; Kļaviņa, D.; Brūna, L.; Legzdina, L.; Gaitnieks, T. Initial and long-term fungal diversity and occurrence of *Heterobasidion* spp. in Norway spruce root fragments remaining in soil after stump extraction. *Scand. J. For. Res.* **2021**, *36*, 117–125. [\[CrossRef\]](#)
10. Redfern, D.B.; Pratt, J.E.; Hendry, S.J.; Low, J.D. Development of a policy and strategy for controlling infection by *Heterobasidion annosum* in British forests: A review of supporting research. *For. Int. J. For. Res.* **2010**, *83*, 207–218. [\[CrossRef\]](#)
11. Stenlid, J.; Redfern, D.B. Spread within the Tree and Stand. In *Heterobasidion Annosum: Biology, Ecology, Impact and Control*; Woodward, S., Stenlid, J., Karjalainen, R., Huttermann, A., Eds.; CAB International: Wallingford, UK, 1998; pp. 125–141.
12. Piri, T.; Vainio, E.J. Significance of *Heterobasidion* species among wood decay fungi in northern peatland forests. *For. Ecol. Manag.* **2024**, *568*, 122148. [\[CrossRef\]](#)
13. Redfern, D.B. Infection of *Picea sitchensis* and *Pinus contorta* stumps by basidiospores of *Heterobasidion annosum*. *Eur. J. For. Pathol.* **1982**, *12*, 11–25. [\[CrossRef\]](#)
14. Malinen, J.; Maltamo, M.; Verkasalo, E. Stem and Wood Properties of Norway Spruce on Drained Peatlands and Mineral Forest Lands in Southern Finland. *Balt. For.* **2005**, *11*, 2138.
15. Gaitnieks, T.; Silbauma, L.; Muižnieks, I.; Zaļuma, A.; Kļaviņa, D.; Burneiviča, N.; Grosberga, M.; Lazdiņš, A.; Piri, T. Spread of *Heterobasidion* genotypes in Norway spruce stands on drained peat soil in Latvia. *Can. J. For. Res.* **2022**, *52*, 499–510. [\[CrossRef\]](#)
16. Sun, H.; Terhonen, E.; Kovalchuk, A.; Tuovila, H.; Chen, H.; Oghenekaro, A.O.; Heinonsalo, J.; Kohler, A.; Kasanen, R.; Vasander, H.; et al. Dominant Tree Species and Soil Type Affect the Fungal Community Structure in a Boreal Peatland Forest. *Appl. Environ. Microbiol.* **2016**, *82*, 2632–2643. [\[CrossRef\]](#)
17. Szajdak, L.W.; Jezierski, A.; Wegner, K.; Meysner, T.; Szczepański, M. Influence of Drainage on Peat Organic Matter: Implications for Development, Stability, and Transformation. *Molecules* **2020**, *25*, 2587. [\[CrossRef\]](#) [\[PubMed\]](#)
18. Härkönen, L.H.; Lepistö, A.; Sarkkola, S.; Kortelainen, P.; Räike, A. Reviewing peatland forestry: Implications and mitigation measures for freshwater ecosystem browning. *For. Ecol. Manag.* **2023**, *531*, 120776. [\[CrossRef\]](#)
19. Piri, T. Silvicultural Control of *Heterobasidion* Root Rot in Norway Spruce Forests in Southern Finland. Regeneration and Vitality Fertilization of Infected Stands. Ph.D. Thesis, Helsingin yliopisto, Helsinki, Finland, 2003.
20. Piri, T.; Korhonen, K. Infection of advance regeneration of Norway spruce by *Heterobasidion parviporum*. *Can. J. For. Res.* **2001**, *31*, 937–942. [\[CrossRef\]](#)
21. Piri, T.; Korhonen, K. Spatial distribution and persistence of *Heterobasidion parviporum* genets on a Norway spruce site. *For. Pathol.* **2007**, *37*, 1–8. [\[CrossRef\]](#)
22. Piri, T.; Valkonen, S. Incidence and spread of *Heterobasidion* root rot in uneven-aged Norway spruce stands. *Can. J. For. Res.* **2013**, *43*, 872–877. [\[CrossRef\]](#)
23. Gaitnieks, T.; Bruna, L.; Zaluma, A.; Burnevica, N.; Klavina, D.; Legzdina, L.; Jansons, J.; Piri, T. Development of *Heterobasidion* spp. fruit bodies on decayed *Picea abies*. *For. Ecol. Manag.* **2021**, *482*, 118835. [\[CrossRef\]](#)
24. Stenlid, J. Controlling and predicting the spread of *Heterobasidion annosum* from infected stumps and trees of *Picea abies*. *Scand. J. For. Res.* **1987**, *2*, 187–198. [\[CrossRef\]](#)
25. Piri, T.; Hamberg, L. Persistence and infectivity of *Heterobasidion parviporum* in Norway spruce root residuals following stump harvesting. *For. Ecol. Manag.* **2015**, *353*, 49–58. [\[CrossRef\]](#)
26. Bušs, K. Forest ecosystem classification in Latvia. *Proc. Latv. Acad. Sci.* **1997**, *51*, 204–218.
27. Hantula, J.; Vainio, E. Specific primers for the differentiation of *Heterobasidion annosum* (s. str.) and *H. parviporum* infected stumps in northern Europe. *Silva Fenn.* **2003**, *37*, 181–187. [\[CrossRef\]](#)
28. Dumins, K.; Stals, T.; Lazdina, D. Forest regeneration quality assessment by asta system. In Proceedings of the International Scientific Conference “RURAL DEVELOPMENT 2017”, Kaunas, Lithuania, 23–24 November 2017; Aleksandras Stulginskis University: Kaunas, Lithuania, 2018; pp. 588–592. [\[CrossRef\]](#)
29. Dūmiņš, K.; Žigūre, S.; Celma, S.; Štāls, T.A.; Vendiņa, V.; Zuševica, A.; Lazdina, D. Impact of Soil Preparation Method and Stock Type on Root Architecture of Scots Pine, Norway Spruce, Silver Birch and Black Alder. *Forests* **2025**, *16*, 830. [\[CrossRef\]](#)
30. Stenlid, J. Population structure of *Heterobasidion annosum* as determined by somatic incompatibility, sexual incompatibility, and isoenzyme patterns. *Canad. J. Bot.* **1985**, *63*, 2268–2273. [\[CrossRef\]](#)
31. Bates, D.; Maechler, M.; Bolker, B.; Walker, S. Fitting Linear Mixed-Effects Models Using lme4. *J. Stat. Softw.* **2015**, *67*, 1–48. [\[CrossRef\]](#)

32. R Core Team. *R: A Language and Environment for Statistical Computing*; R Foundation for Statistical Computing: Austria, Vienna, 2025. Available online: <http://www.r-project.org/> (accessed on 20 June 2025).
33. Melin, Y.; Petersson, H.; Nordfjell, T. Decomposition of stump and root systems of Norway spruce in Sweden—A modelling approach. *For. Ecol. Manag.* **2009**, *257*, 1445–1451. [[CrossRef](#)]
34. Łakomy, P.; Kwaśna, H.; Dalke-Świdarska, M. The virulence of *Heterobasidion parviporum* population from Norway spruce stand in Suwałki Forest District. *Acta Sci. Pol. Silv.* **2011**, *10*, 27–36.
35. Hietala, A.M.; Nagy, N.E.; Burchardt, E.C.; Solheim, H. Interactions between soil pH, wood heavy metal content and fungal decay at Norway spruce stands. *Appl. Soil Ecol.* **2016**, *107*, 237–243. [[CrossRef](#)]
36. Helenius, P.; Luoranen, J.; Rikala, R.; Leinonen, K. Effect of drought on growth and mortality of actively growing Norway Spruce container seedlings planted in summer. *Scand. J. For. Res.* **2002**, *17*, 218–224. [[CrossRef](#)]
37. Luoranen, J.; Riikonen, J.; Saksa, T. Damage caused by an exceptionally warm and dry early summer on newly planted Norway spruce container seedlings in Nordic boreal forests. *For. Ecol. Manag.* **2023**, *528*, 120649. [[CrossRef](#)]

Disclaimer/Publisher’s Note: The statements, opinions and data contained in all publications are solely those of the individual author(s) and contributor(s) and not of MDPI and/or the editor(s). MDPI and/or the editor(s) disclaim responsibility for any injury to people or property resulting from any ideas, methods, instructions or products referred to in the content.