

Review

Afforestation of Land Abandoned by Farmers Poses Threat to Forest Sustainability Due to *Heterobasidion* spp.

Tomasz Oszako ^{1,*} , Olga Kukina ² , Valentyna Dyshko ² , Warren Keith Moser ³ , Sławomir Ślusarski ¹ , Adam Okorski ⁴  and Piotr Borowik ¹ 

¹ Forest Protection Department, Forest Research Institute, Ul. Braci Leśnej 3, 05-090 Sękocin Stary, Poland

² Ukrainian Research Institute of Forestry and Forest Melioration Named after G. M. Vysotsky, 61024 Kharkiv, Ukraine

³ Rocky Mountain Research Station, Forest Service, U.S. Department of Agriculture, 2500 S. Pine Knoll Dr., Flagstaff, AZ 86001, USA

⁴ Department of Entomology, Phytopathology and Molecular Diagnostics, Faculty of Agriculture and Forestry, University of Warmia and Mazury in Olsztyn, Pl. Łódzki 5, 10-727 Olsztyn, Poland

* Correspondence: t.oszako@ibles.waw.pl

Abstract: *Heterobasidion annosum* (Fr.) Bref. sensu lato (s.l.) is a dangerous forest pathogen causing root and butt rot disease in most conifers of the northern hemisphere. This pathogen is most widespread in the forests of Europe and North America. The economic impact on forestry related to tree mortality, reduction in timber yield, and wood rot is calculated in millions of dollars and euros. The genus *Heterobasidion* (Basidiomycota; Russulales) has been relatively recently separated into three genetically distinct groups (*H. annosum*, *H. insulare* and *H. araucariae*) comprising a total of 12 species and one newly described hybrid taxon. These species are the best studied in terms of the ecology, the physiology of control methods, and the tree's resistance to the pathogen. The article gives an overview of the symptoms and the etiology of the disease and provides information on ways to recognize the disease and limit the economic damage.

Keywords: root and butt rot disease; *Pinus sylvestris*; *Picea abies*; conifer plantations; *H. parviporum*; *H. abietinum*; *H. irregulare*; selection; resistance; control measures



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1. Introduction

In Poland, as in many other European countries, the long-term use of land leads to its complete degradation—often to the point that agricultural production becomes unprofitable. These areas are abandoned by farmers, and they spontaneously become overgrown with pine and birch trees. When they are no longer suitable for growing agricultural crops, they are afforested.

The development of post-agricultural land through afforestation carries the risk that the first generation of trees will not live to be felled due to the threat of being affected by pathogenic fungi, the spores of which are widespread and cause primary infection when they attach to the stumps formed during the cultivation of the first thinning [1,2]. The most common species used for afforestation are Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* L.) However, these species are susceptible to many fungal diseases under such conditions. *H. annosum* is listed among the causal factors damaging roots, especially in pine and spruce stands growing on former agricultural land. This is due to the different physicochemical and biological properties of soils that have been used for agriculture for many years compared to soils in forestry [3].

Many researchers [4,5] often point out that there is a fundamental difference in nutrient management between agricultural and forestry soils, including nutrient retention and storage. Soils formerly used for agriculture have no organic layer in which humus is

formed, lack many elements such as magnesium, and are dominated by bacteria (no antagonistic or mycorrhizal fungi).

After World War II, about one million post-agricultural areas were afforested in Poland [6,7]. As a result, the first generation of coniferous stands becomes diseased, and numerous gaps appear at the age of about 40 years, forcing foresters to carry out clear-cutting and start forest regeneration all over again [2]. The damage occurs annually on an area of about 0.1 million ha. In pines, the damage affects the outer parts of the trunks (cambium), in spruces, it affects the middle part of the so-called heartwood. Currently, there are 9 million ha of forest, and forest cover is 30%, but there is an ambitious national afforestation plan to increase forest cover to 33% by 2050.

The most likely sites for afforestation are former agricultural areas where the root pathogen *H. annosum* has been able to thrive unhindered. Therefore, foresters need to detect diseases early in order to have enough time to develop an appropriate protection strategy.

Early warning (fungal detection) therefore helps foresters make appropriate decisions to counteract the progression of the disease. The situation is similar in other countries with a high proportion of state forests where coniferous stands have been planted on land formerly used for agriculture, e.g., Romania [8,9] or Bulgaria [10].

It is true that *H. annosum* also causes severe damage to spruce stands in private forests, as in France [11,12] or the northern hemisphere [13].

Among other things, this article explores the possibility of early detection of the pathogen, e.g., whether new tools such as an electronic “nose” that detects volatiles could be used. These chemicals can be produced by both the fungus and the plant, especially if they interact with the infection and infestation of the tissue. It is probably also possible to detect the smell of healthy or rotten wood. In addition, in the paper, the symptomatology and etiology of the pathogens causing root and stump rot were recalled as well as ways to control the disease in order to limit the economic damage.

In Figure 1, we present selected photos of fruiting bodies of *H. annosum* and pine trees affected by the pathogen.



Figure 1. (a) The fruiting bodies of the *H. annosum* on a Scots pine stump. (b) The fruiting bodies of the *H. annosum* in the zone of the root neck of Scots pine. (c) The trunk of an Scots pine affected by *H. annosum*. (d) Dead trees at the center of a mortality pocket of Scots pine in a plantation affected by *H. annosum*. (e) The crowns of Scots pine trees affected by *H. annosum*.

2. Methods

In order to prepare a comprehensive overview of the concept of root and stump rot caused by *H. annosum*, we reviewed several published studies on the subject. The Web of Science and Google Scholar databases were queried in February 2023 to collect the relevant literature. The Google Scholar database allowed searches of articles in Ukrainian and Russian, which were not available in the Web of Science database. To exclude irrelevant literature, the search was limited to topics in forestry and plant pathology.

Different keywords were used, starting with the more general ones, e.g., “*Heterobasidion*”, resulting in a search with 1236 entries from 1970 to 2023. Later, different keywords were used: “*Heterobasidion annosum*”, “root rot”, and “conifer”, resulting in a database with 75 entries suitable for this topic and forming the basis for further searches.

The present review is based on a selection of articles from these results as well as on some papers further cited in the selected articles.

As an example of the growing interest in research on *Heterobasidion*, we show in Figure 2 the number of scientific publications indexed in the Scopus database.

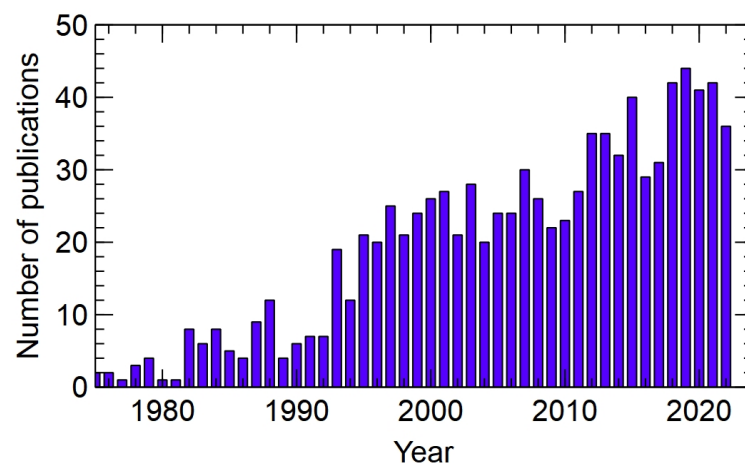


Figure 2. Number of publications by year in Scopus database queried for “*Heterobasidion*” search key. In total, there were 937 items from 1975 to 2022.

3. Variety of Complexes *Heterobasidion annosum*

The *H. annosum* complex is a species comprising in North America two species [14] *H. irregulare* Garbel and Otrosina and *H. occidentale* Otrosina and Garbel, and in Eurasia three species [15]: *H. abietinum* Niemelä and Korhonen, *H. annosum* (Fr.) Bref. and *H. parviporum* Niemelä and Korhonen.

In North America, *H. irregulare* generally attacks pines and junipers (*Juniperus* spp.), while the host range of *H. occidentale* includes *Abies*, *Picea*, *Tsuga*, *Pseudotsuga*, *Sequoia*, and *Sequoiadendron* [15–17].

The *H. annosum* complex in Europe includes three intersterility groups that show different host preferences [18–20]. In general, the S group (*H. parviporum* Niemelä and Korhonen) is restricted to spruce (*Picea abies* L.) [21] and the F group (*H. abietinum* Niemelä and Korhonen) is restricted to silver fir (*Abies alba* Mill.). The P group (*H. annosum* sensu stricto (see above)) has a lower host specialization and mainly attacks pine but also spruce [22]. To a lesser extent, it also causes root rot on some deciduous trees: *Quercus* sp., *Betula pendula*, *Fagus sylvatica*, and *Carpinus betulus* [23,24].

Studies [25] on the replacement of conifers by deciduous trees (*Betula* spp.) have shown that *H. annosum* is able to persist for decades in the root systems of diseased trees and easily infect birch trees transplanted to infested areas. Root rot infections in Norway spruce (*P. abies* L.) planted on *Heterobasidion*-infested sites occur about 10 years after planting, and the proportion of infected spruce increases steadily with tree age [26].

Zaluma et al. [27] investigated the origin and mode of spread of root disease in *P. contorta* stands in the forest and agricultural areas. Trees with *Heterobasidion* symptoms were identified as *H. parviporum* and *H. annosum*, and *P. contorta* proved to be highly susceptible to both pathogens of tree death. *H. annosum* from Scots pine (*P. sylvestris* L.) stumps from the previous rotation period was successfully transferred to *P. contorta*, which means that the pathogen survived in pine stumps for at least 26 years. The pathogens formed spreading territorial clones and their basidiospores colonized *P. contorta* (primary infections), with *H. parviporum* spreading more slowly than *H. annosum*. In contrast, clones from stumps with established secondary infections spread more rapidly than from stumps with primary infections, making it important to protect stumps from infection.

Groups S and P have a wide distribution, while group F has been found in southern Europe, mainly in the Apennines of Italy [28]. North American pathogen *H. irregulare* infests pine plantations in Italy and hybridizes readily with the pathogenic native species [16,29,30]. Invasion can spread at an estimated rate of 1.3 km/year through invasion corridors formed by individual trees but not necessarily through larger patches of forest [31].

Spruce in Europe is infested by both the S- and P-types of *H. annosum*, although the S-type dominates in spruce forests in southern Finland and central Scandinavia [18,32,33]. In northern Europe, the basidiomycete *H. annosum* consists of two intersterility groups, S and P. A third intersterility group, F, has been reported from southern Europe [19]. *H. annosum* isolates were collected from spruce, pine and mixed stands in Belarus, Lithuania, and Estonia on forest and former agricultural soils. Intersterility groups of the isolates were identified. Pine was infested only by the P group and spruce mainly by the S group. The frequency of the P group on spruce was higher on old forest soils and in mixed spruce and pine stands [18]. The F-type of *H. annosum* mainly attacks firs and occurs in natural plantations in the Carpathians and Pricarpathians, but throughout western Poland, *H. annosum* occurs epiphytically in pine plantations, which is also the case in the flat regions of western Ukraine [34].

All three intersterility groups, P, S, and F, were identified [35] in populations of *H. annosum* in Bulgaria. The P group was isolated from *P. sylvestris* and *P. nigra* and occasionally from stumps of *A. alba*. The F group caused severe damage to *A. alba*, but it was not even found as saprotrophs on mixed pines. The S group was only found on *P. abies*. In western Turkey, *Heterobasidion abietinum* (group F) is relatively virulent on *Abies* trees [36].

4. Damage to Conifer Plantations by *H. annosum*

H. annosum causes considerable wood losses in Scots pine, with the disease being particularly destructive in young stands [37,38]. This pathogen may also be responsible for high seedling mortality in pines [1]. However, the susceptibility to *H. annosum* s.s. decreases with age, and at older ages, damage by this pathogen rarely leads to tree death [39]. Losses caused by the disease were lower in mixed stands than in pure stands [33].

As a result of secondary infection via root grafting, tree death caused by *Heterobasidion* occurs in groups called root disease centers, which expand over time. Studies [40] carried out in southern Germany have shown that the frequency of infected trees increases with age (0% in age class 1 (1–10 years), 7.5% in class 2 (11–20 years), 33.3% in class 3 (21–30 years)). The most destructive outbreaks of *H. annosum* s.s. are observed [37] in young (up to 40 years old) pine plantations established at high initial densities on former agricultural soils. The proportion of trees affected by the root fungus in a plantation can be as high as 20%–60% and the yield of commercial timber can drop to 40% [41].

Research [42] on the forests of Ukraine (1994–2009) reported that the area of pine plantations where various pathological processes were becoming more and more obvious covered about 100,000 ha, and one-third of them were affected by root rot in 2009.

In eastern Lithuania, the resistance of Scots pine to *H. annosum* (Fr.) Bref. s.s. and its transfer to forest regeneration were studied. These plots represented *H. annosum* disease foci in *P. sylvestris* L. stands that had been completely felled and replanted with *Betula pendula* Roth 25 years before this study. The research of Lygis et al. [25] showed that *H.*

annosum can persist for decades in the root systems of diseased trees and easily infect birch replanted in infected areas.

With regard to the importance of this fungus as a pest, it should be mentioned that its extracts have been shown to have a potential anti-cancer effect. In this study, the apoptotic effect of *H. annosum* on colon cancer was confirmed in an in vivo model. The results obtained by Sadowska et al. [43] are novel and provide a basis for further studies on the anti-cancer effect of the extract of *H. annosum*, especially in relation to its interaction with anti-cancer chemotherapeutic agents.

5. Methods for the Determination of *Heterobasidion annosum* and Infected Trees in Mid-Root and Butt Rot Disease

Forest management promotes the spread of *Heterobasidion* spp. so that the increasing colonization of Norway spruce should be taken into account in the management of commercial forests. Spruce colonized by *Heterobasidion* spp. lead to the formation of fruiting bodies, which increase the risk of reinfection by basidiospores and subsequent spread of *Heterobasidion* root rot to living trees. The most numerous fruiting bodies of *Heterobasidion* are found on infected spruce trunks standing on moist or peaty soil. Numerous fruiting bodies are also observed on abandoned agricultural land and pastures [44].

Assessing the presence of *Heterobasidion* root rot in pine or spruce forests is often difficult. Basidiocarps (fruiting bodies) found on tree stumps or in the root system are the most reliable signs of the presence of root rot [1,45]. However, they are rare on living trees and may also be sparse on dead trees, thus limiting the effectiveness of superficial examinations. In the absence of basidiocarps, the reliable identification of annosum root rot on a single tree may require the cultivation of the fungus from samples of infected wood [46].

The presence of root rot in pine or spruce plantations is often determined by the external characteristics of trees, but this method is not always accurate. Root rot, caused by the fungus *H. annosum*, damages both the below- and aboveground parts of trees. Symptoms include a change in the color of the needles, thinning or transparency of the crown, reduced shoot growth, resin secretion, and slight swelling of the stump [23,47].

Mykhaylichenko et al. [48] discovered that differences in the length and mass of needles were found in trees from the foci of the disease and the inter-focal zone. A change in biometric indicators of needles in trees with different degrees of disease development (appearance of foci, their development, and extinction) was also established. However, these signs are not specific to a particular disease but can be caused by various biotic and abiotic environmental influences. Using these secondary signs as diagnostic indicators requires knowing the underlying cause in a particular case. An incorrect diagnosis could result in inappropriate or ineffective treatment.

Given that the presence of forest tree pathogens can lead to significant problems, their early detection during seed storage or in nurseries can be crucial for choosing an appropriate management strategy. In response, additional research methods are constantly being developed to detect the disease in the early stages when symptoms are not yet externally visible. For example, terrestrial laser scanning (TLS) can detect structural differences between healthy and diseased trees that are externally visible [47]. PICUS Sonic tomography is also used to detect stem rot [49].

A more specific technique currently being tested is the concept of an electronic “nose” consisting of a series of non-specific gas sensors equipped with machine algorithms for pattern recognition [50]. So far, it has been confirmed that the pathogen is not present in the soil at a distance of 0.5–1.5 m from infested tree trunks. This proves that secondary infection only occurs through contact between diseased and healthy roots and not through the development of hyphae in rotting woody debris in the soil. On the other hand, no difference could be detected between the smell of infested wood near fruiting bodies and wood above about 1.5 m. The smell of the resin as a peculiar background overlays other mycelium-specific smells, so that the latter are difficult to detect. Only when the fungus

decomposes the wood does the background odor of the resin disappear. No differences were found between spruce and pine decay caused by the activity of *H. annosum*.

Since it is challenging to detect root rot at an early stage using the above methods, sensitive molecular methods for identifying pathogenic organisms, especially various modifications of PCR, are widely used. Genetic-molecular methods are not only used to identify pathogens but also to determine the geographical distribution of the *H. annosum* complex based on taxonomic and phylogenetic characteristics [51].

Since the middle of the last century, the presence of a fungal pathogen has traditionally been determined by culturing plant samples and then visually identifying the fungi. The disadvantages of this approach are the time required to grow fungal cultures, the possibility that not all fungi can be cultured, and the difficulty in distinguishing fungi morphologically. More recently, PCR-based methods have been developed for the identification of all fungi present in a sample using universal primers [52,53]. With the development of next-generation sequencing (NGS), the genomes of *H. irregulare* and *H. annosum* have already been sequenced [54,55]. A computer program, Rotstand, has been developed to simulate the development of a forest stand together with root rot disease caused by s.l. on several tree species in Europe [56].

6. Bio-Ecological Characteristics of the Causal Agent of Root and Butt Rot and the Disease Process

Massive damage to pines and other conifers by root and butt rot is more common on agriculturally abandoned land and rehabilitated soils, but disease foci can also occur on forestland [15]. Sites with high water tables are not conducive to the spread of pathogens [23], and the risk of disease development on dry and poor soils is low.

To understand the reasons for the wide geographical and ecological spectrum of root disease, it is also necessary to take into consideration features such as peculiarities of the biology of the fungus and a variety of infection routes. For example, many specific enzymes enable *Heterobasidion* spp. to infect different wood species, destroying stable substances such as lignin, cellulose, terpenes, resins, phenolic compounds, and others [57].

This pathogen spreads both by conidiospores and basidiospores, but primary infection is mediated by basidiospores infecting fresh stump surfaces or wounds on the roots or stems [58,59]. *Heterobasidion* species produce basidiospores that infect freshly cut stumps and colonize, establish, and further infect healthy trees through root interactions [23,60]. The conidiospores of *H. annosum* can be released into the air by wind gusts associated with high humidity or fog, so conidia may play a role in aerial dispersal. However, this mode of dispersion is considered to be much less important compared to basidiospores [61].

H. annosum s.l. is not able to grow freely in the soil; therefore, the principal mode of spread belowground is via the mycelia. Direct root contact between trees or between stumps and trees is essential for the occurrence of secondary infections [62]. Although this secondary spread is common with *H. annosum* s.l., it spreads mainly via the primary infection of wounds and other openings in the bark, and vegetative spread is not as epidemiologically relevant as with other root disease fungi, such as *Armillaria* spp. [63,64].

In many coniferous forests, the rate of spread depends largely on the stand structure and composition, stand history, and soil properties including pH [65]. The rate of spread of *H. annosum* varies depending on the trees' vitality and the moisture content of the wood. The average growth rate was 25 cm/year in stump roots and 9 cm yr⁻¹ in tree roots, neither of which differed significantly between forest (spruce stands) and arable land, ref. [66] and 29 to 40 cm/year in spruce trunks [67]. Temperatures between +5 and +35 °C are optimal for fungus development [68].

The symptoms caused by *Heterobasidion* root rot, such as resin discharge and crown decay, are not particularly unique and cannot be distinguished from those caused by other root pathogens. The initial growth of the pathogen in the wood causes discoloration, which varies depending on the host tree species. The initial rot is usually pale yellow and develops

into a light brown rot, which in the advanced stage becomes a white pocket rot with black spots [23].

The spread of *Heterobasidion* root rot on peat soils is a new study by Gaitnieks et al. [69,70]. The authors investigated the effects of root colonization of Norway spruce by *H. annosum* on peat soils and showed that despite a reduction in the growth performance of the trees and an altered supply of photosynthetic products to the roots as a result of root rot infestation, there were no changes in the fungal communities inhabiting the roots of the infested trees.

7. Measures to Protect Plantations from *Heterobasidion* spp.

Current strategies to control *Heterobasidion* root rot include silvicultural, chemical, and biological methods. Since the rot occurs inside the tree, measures to control root rot at this stage are not possible; therefore, the focus must be on preventive measures to contain the spread of the disease and significantly minimize economic losses. Such measures aim to prevent *H. annosum* from depositing, germinating, and multiplying through basidiospores [23].

Silvicultural measures to protect conifers from root rot include sanitary cutting, which should be carried out in winter [71]. Stump removal and the careful removal of all roots is an effective control strategy against *Heterobasidion* root and butt rot [72,73]. However, it is an expensive and time-consuming control method that requires the use of machinery and is therefore not practical for most forest stands.

In addition to removing stumps and roots to control *Heterobasidion* [74], the digging of trenches to sever root connections is a technique used to control oak wilt (*Ceratocystis fagacearum* (Bretz) Hunt) in urban environments [75]. This procedure is called the “artificial gap method” and seems to be an effective prophylactic measure. However, it is also expensive and labor-intensive, and it is only recommended for high-value trees in residential neighborhoods.

It is significant to note that losses caused by the disease are lower in mixed stands than in pure stands [76]. Moreover, by choosing appropriate planting (preferably wide spacing) and mixtures (avoiding monocultures of susceptible species), thinning can be delayed, and a better yield can be achieved than in pure stands [37].

Chemical control methods include the application of fertilizers and the use of fungicides. The effect of nutrients on the incidence of *H. annosum* root rot was variable [77], with studies finding that the use of compound fertilizers (N, P, K) increased the resistance of pine to *H. annosum* [78,79]. To suppress infection in active disease foci, fungicidal preparations (Benomil) have been tested. Studies of Vasiliauskas et al. [80] have shown that the use of these agents has a positive effect at specific concentrations.

Protecting tree stumps from infection by airborne spores is one of the most important control strategies. Stumps remain susceptible to infection for varying lengths of time depending on the season, location, and host, with susceptibility rarely lasting longer than a month due to changes in nutrient chemistry on the tops of stumps and competition from other microorganisms [58].

A large number of chemicals have been tested as stump protectants over the last 50 to 60 years. The use of copper sulfate, ferrous sulfate, ground sulfur, and urea proved ineffective; preparations based on these elements suppressed the vital activity of beneficial microflora and reduced the resistance in pines [79].

Of the chemical agents, urea and borate are the most commonly used in practice and have the best effect [23,81]. The results of the investigations indicate that urea per se is not toxic to *H. annosum*, not even in the concentrations achieved by treatment with quantities intended for practical use. Hydrolysis of the urea produces ammonia, which raises the pH at the surface of the stump to a range toxic to *H. annosum*, so that the spores cannot germinate and the mycelium cannot survive [82,83]. An important side effect is that borate and urea solutions cause severe damage to common terrestrial vegetation species [82]. Processing also causes temporary changes in the chemical composition of the soil.

Organisms (fungi, bacteria) with antagonistic properties are often used as biological control agents (BCAs) to control *Heterobasidion* spp. The colonization of fresh tree stumps with root fungal antagonists is a preventive measure that has been used successfully in many countries around the world [84]. One of the best studied biological protective agents against root fungi is the fungus *Peniophora gigantea* (Fr.) [84–86]. Commercial preparations containing *P. gigantea* spores have been used throughout Europe.

The hyphae of *P. gigantea* oppose the hyphae of *Heterobasidion* spp. on contact. This phenomenon is called hyphal interference. When the hyphae of these fungi come into contact, the *Heterobasidion* hyphae are rapidly destroyed locally [87].

The effectiveness of inoculation of *P. gigantea* in pine stands is determined by the age of the plantation and the severity of the disease. Preventive measures implemented in young stands during the first thinning can significantly reduce the risk of spreading the disease throughout the plantations [2].

Studies [88] on commercial preparations (Rotstop®, PgIBL®) containing *P. gigantea* spores demonstrate the efficacy of their application in pine plantations against *Heterobasidion* conidiospore and basidiospore infection in spruce wood.

Latvian studies by Zaluma et al. [89] performed on former agricultural lands have shown that colonization rates of tree stumps by *Heterobasidion* spp. treated with the native strain of *P. gigantea* or with Rotstop® or urea were similar, especially when the stumps were not covered. However, covering the stumps with moss favored colonization by the Latvian strain of *P. gigantea* and Rotstop®, resulting in a significantly lower relative area colonized by *Heterobasidion* spp. Covering tree stumps seems to limit *Heterobasidion* colonization and may be a practical solution for forest owners if applied on a small scale. However, they should also consider applying Rotstop® without covering the stumps.

While the use of *P. gigantea* has been established in European forest practice, other wood-destroying fungi still require more detailed investigation for their antagonistic effect against *Heterobasidion* spp., such as *Trichaptum abietinum*, *Dichomitus squalens*, *Diplomitoporus flavescens*, *Hirshioporus abietinus*, fungi of *Trametes* spp. [90–93], *Bjerkandera adusta* (Polyporales, Coriolaceae) [94,95], *Fomitopsis pinicola* [96], *Resinicium bicolor* [96]. Ascomycetes such as *Trichoderma* spp. have antagonistic properties toward *H. annosum* [97,98].

Piri et al. [99] tested the effects of *P. gigantea* and urea in Scots pine and Norway spruce stands after silvicultural treatments (thinning, topping, clearcutting) on drained peatlands in Central Finland. The effectiveness of urea was higher (average 85.8 and 99.5, respectively), while the effectiveness of *P. gigantea* was very different for both tree species and ranged from full protection to negative control.

In addition to fungi, bacteria of the genus *Bacillus* have been found to be antagonistic to *Heterobasidion* spp. [100–102].

Raffa et al. [103] have proposed and implemented several approaches to risk assessment for the management of preventive measures aimed at preventing the spread of infectious pathogenic species.

The control methods outlined above vary in their effectiveness and longevity of effect, depending upon the vigor of the trees and the vigor of the pathogen. Therefore, the protection of forest plantations against diseases should not be considered as a temporary measure but rather as a complex of long-term measures aimed at increasing the sustainability of the forest.

8. Selection of Trees Resistant to *H. annosum*

Scots pine L., Norway spruce and other conifers are the economically most important tree species in Europe. However, they are very susceptible to the root rot fungus *H. annosum*. Climate change will favor the pathogen as the tree host is weakened by e.g., prolonged drought [104].

Breeding can improve forest health, and several genetic markers for root rot are proposed to improve resistance in these species [22,105–108]. In the study [105], the resistance (defined here as necrosis length) of spruce families and genotypes to two strains

of *H. parviporum* was compared under different water availability. The results showed that family and genotype within the family influenced necrosis length, which was related to the aggressiveness of the fungal strains. Under low water conditions, necrosis increased only in the horizontal direction in the phloem and sapwood. Growth (seedling height) was also not affected by abiotic stress (less water), indicating that the stress level (drought) was too low in this situation. The knowledge gained in this study could improve forest health under climate change by understanding the response of spruce to pathogenic attacks under additional stress at the family level. This knowledge could be used strategically in forest breeding to improve spruce resistance to root rot.

Similar results were obtained by Terhonen et al. [85], who conducted inoculation studies on three-year-old seedlings in a greenhouse. The seedlings were treated as high or low water level groups: The high water level group received double the amount of water of the low water level group. Necrosis observed after pathogen inoculation was measured and analyzed. Seedling growth was negatively affected in the lower water group. In addition, water availability increased the necrosis length of *H. parviporum* in phloem and sapwood (vertical length) in the low water group. *H. annosum* benefited only in horizontal length in the phloem. Disturbances related to water availability, especially at low water levels, could have a negative impact on the tree host and favor the infectivity of the pathogens in the host.

Despite 200 years of experience in studying the problem of the spread of the root fungus in coniferous forests, the mechanisms of resistance of pine to damage by the pathogen have not yet been completely explained [41].

In southern Sweden, deep stem inoculations with *H. annosum* were carried out on 34 clones (five to nine ramets) in a 17-year-old spruce field trial by Swedjemark et al. [109]. A hole (one-third of the boot diameter) was drilled and filled with *H. annosum* infected sawdust. Eight months later, the trees were felled and the trunks were cut into 5 cm thick slices, 2 m above the inoculum point. The slices were examined for the presence of the conidia stage of *H. annosum*, and the length of the lesion in the inner bark was measured. The infection success was 98.4%. The linear extension of the colonized xylem was large (140 cm on average), and in 32% of the trees, the extension of the fungus was longer than the collected stem (>2 m). Fungal expansion varied significantly between clones with heritability in the broader sense (H^2) being 0.18. A significant positive phenotypic and genotypic correlation was found between tree size and fungal growth. There was no significant genotypic correlation between fungal growth and the length of lesions in the inner bark.

Early diagnosis of the disease is complicated, because external signs appear rather late, the fungus is characterized by weak pathogenicity aboveground, and it mainly attacks the roots. The complex of infection control measures includes various methods to increase the ecological stability of the stands and measures to prevent the development of the disease. The selection of tree species plays an important role. By selecting stable forms, ecotypes, and elite trees in nature, managers can emphasize both high productivity and resistance to diseases, pests, and unfavorable climatic factors under local ecological conditions. These resistant trees can then produce seed material for future afforestation.

Little is known, however, about whether homokaryons of *H. parviporum* can infect trees under field conditions. In the study by Kerio et al. [110], 40-year-old clonal spruce stems and roots were inoculated with a homokaryotic isolate of *H. parviporum* under field conditions. After four months, the frequency of infection and the length of necrotic lesions were recorded. Among the spruce genotypes studied, a Russian clone had the smallest necrotic lesions, while a Finnish clone developed the largest necrotic lesions. Clones with higher growth rates were more susceptible to fungal infection and wound damage. On microscopic observation, *H. parviporum* grew on the cell walls of the lumen, colonized the tracheids adjacent to the rays, and induced lignification of the cell walls near the site of inoculation.

Resistant forms can be propagated both vegetatively and by seed, which makes it possible to enhance the most positive characteristics of the plants. Research [111] found that only 30%–40% of the selected trees confirm their elite traits in the seed progeny. Similar results [22,112] suggest that the strategy of mass selection of trees in affected areas to obtain seed material will not create future forests resistant to disease or other biotic disturbances.

In separate centers of drying plantations affected by the *H. annosum*, there are viable trees without external signs of damage next to the obviously infected trees. Such trees that maintain a satisfactory condition for a long time despite a high level of infection and do not show external signs of the disease are called “conditionally resistant” [41,113,114]. The proportion of trees falling into this “conditionally stable” category in the plantations is usually small. The increased resistance of such trees appears to be related to the morphological and anatomical structure of the roots and trunk [106], metabolic properties [22,107], and physiological properties [115].

Several researchers [39,116] established that the progeny of trees from old disease foci is characterized by genetically determined resistance to damage by *Heterobasidion* spp. A comparison of pine seedlings grown from the seeds of “conditionally resistant” trees with seedlings from elite seeds collected in the clonal seed orchards (CSOs) shows better (2 times higher) survival of the former [117]. The effectiveness of using seeds from trees with increased resistance to root fungal damage in silviculture is discussed in the work of many scientists [22,112].

However, selecting trees with increased resistance to damage by *Heterobasidion* spp. before the appearance of the first disease symptoms is complicated by the lack of simple and effective diagnostic methods. Such methods, ranging from visual assessment to modern molecular genetic methods [118,119], vary in their performance and usually trade simplicity and speed for accuracy. At the same time, a large number of researchers usually employ criteria that only indicate the actual spread of infection in the plantation or the degree of virulence of the pathogen [108,120]. Techniques using signs that indirectly indicate the potential resistance of trees to a particular disease are practically non-existent.

In Europe, researchers have focused on studying the genetic basis of resistance. In Ukraine, the diagnosis of pine resistance based on allozyme loci of genotype frequencies often found in pathogen-resistant trees was developed and patented [121]. The author found that increased heterozygosity for the entire set of loci is not a determining factor for the resistance of pines to root fungi. Instead, trees with increased resistance are characterized by lower genetic diversity than natural populations but have values of average heterozygosity that are close to them.

Studies of genotypic differences between families of pine half-sibs [22,122] suggest that the resistance of individual half-sibs is based on a combination of enhanced constitutive and induced mechanisms of phenolic protection. Despite the high informative value of biochemical traits, their use for diagnosis is hampered by the high variability of indicators and the difficulty of determination, and the results obtained are often contradictory.

The studies [123,124] of resin productivity, considered a genetically inherited trait, and its positive role in ensuring the resistance of pine to root fungi has been extensively reviewed. Researchers believe resin productivity can be used as a positive biochemical marker for diagnosing the resistance of Scots pine to damage by the root fungus. The indicator of inherited resin productivity determined by resin yield is greater in seed progeny than in clones (51% and 79%, respectively) [125,126]. In Ukraine, scientists developed and patented a method for diagnosing and selecting trees with increased resistance based on the ratio of the content of resinous substances in the fruiting tissue [127].

Methods based on the determination of bioelectric potentials (BEP), impedance of the cambial complex, and temperature parameters of tree trunks are also used to diagnose the physiological state of conifers in the natural environment. The parameters of bioelectric potentials (bioelectric potential, moisture of needles and shoots, speed of water flow, osmotic potential, impedance of the cambial complex of tissues, stem temperature) can be meaningful indicators for determining the degree of stability of trees in a plantation.

Using these traits even allows an early diagnosis of trees regarding their stability and productivity [128,129].

Anatomical and cytological studies have confirmed the advantages of “conditionally stable” trees over “diseased” trees [106,130]. Cytological studies showed the stability of mitotic activity in seedlings grown from the seeds of “conditionally stable” trees and confirmed their greater survival [111,131]. Studies show a positive role for latewood stability in the radial growth of trees. At an early age (up to 20 years), trees susceptible to the disease are characterized by a greater rate of growth in diameter and height in contrast to resistant trees [106].

Poplavskaya and Rebko [132] found that trees with increased resistance fructify better in the centers of desiccation, have a higher proportion of female reproductive organs, and are characterized by broadly shaped cones with a predominance of pyramidal and hooked apophyses. The studies did not confirm the relationship between cones and seeds' shape and pine's resistance to the root fungus [133]. Seedlings grown from black and brown seeds are better maintained and more adaptable [134]. Morphological methods for evaluating trees based on characteristics of the generative sphere proved to be insufficiently reliable, since phenotypic characteristics vary considerably due to self-regulatory processes and under the influence of environmental conditions. The use of a complex of genetic and morphological markers for conifer resistance to *Heterobasidion* spp. could allow a clearer identification of resistant genotypes and their degree of disease susceptibility [108,135].

Researchers in Ukraine [114,133] proposed using several traits that indicate increased resistance in addition to control traits and health status traits when assessing trees for resistance to root rot. Such signs include peculiarities in the development of the conductive system of the needles, the intensity of the accumulation of layers of latewood in the radial growth of the trees, and the release of resin after the micro wounding of the trunk. In Lithuania, researchers have proposed using a “stability index” to predict the overall stability of plantations [108]. This index derives from the ratio between living and infested trees in the plantation, taking into account the distance between the infested tree and the center of the cell.

9. Conclusions

- The selection of trees in disease centers is one of the most effective selection methods, as “conditionally resistant” trees are a product of natural selection. The initial growth of the pathogen in the wood causes discoloration that varies according to the host tree species. The initial rot is usually pale yellow and develops into a light brown rot, which in the advanced stage becomes a white pocket rot with black spots.
- An effective approach to increase the biological resistance of forests is to select trees resistant to *Heterobasidion* spp. based on a wide range of their natural variability in resistance to pathogen damage. The use of a complex of genetic and morphological markers for conifer resistance to *Heterobasidion* spp. could allow a clearer identification of resistant genotypes and their degree of disease susceptibility.
- Researchers recommend using high-quality and root rot-resistant planting material to reduce the spread of the root fungus in conifer plantations. However, given the cost and unreliability of more technical methods of assessing tree resistance to pathogens, scientists are better served by focusing on commonly accepted practices such as testing several generations of plants, selection, and controlled crossing to achieve their goals.
- Recently, PCR-based methods have been developed to identify all fungi present in a sample using universal primers. With the development of Next-Generation Sequencing (NGS), the genomes of *H. irregulare* and *H. annosum* have already been sequenced.

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