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Review

EFFECT OF SOIL PROPERTIES ON THE SPREAD OF HETEROBASIDION ROOT ROT

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The literature review focuses on the effect of forest soil properties on infection of coniferous trees and stumps by Heterobasidion *spores and further growth of mycelium from tree to tree. Spread of the fungus is greater in alkaline soil. Forest plantations on former agricultural lands have an increased risk of infection, due to lack of antagonistic soil microorganisms. In Latvia, severe infection of spruce stands by Heterobasidion root rot has been observed on peat soils.*

Key words: Annosus root rot, mycelium growth, primary infection, secondary infection.

INTRODUCTION

The disease Heterobasidion root rot is caused by a number of fungal species belonging to the genus *Heterobasidion*. Two species — *H. annosum* (Fr.) Bref. and *H. parviporum* Niemelä & Korhonen — occur in Scandinavia, Finland and the Baltic countries (Korhonen *et al*., 1992; Piri, 2003). Both species can attack Norway spruce and Scots pine, but root and butt rot of spruce is caused mainly by *H. parviporum* and root rot of pine by *H. annosum* (Korhonen and Piri, 2003; Arhipova *et al*., 2011a).

Heterobasidion root rot causes serious economic losses in conifer forests (Woodward *et al*., 1998; Korhonen and Holdenrieder, 2005; Garbelotto and Gonthier, 2013). In spruce stands of Latvia, on average 23% of mature trees are infected, and economical losses caused by *Heterobasidion* to forestry be up to 4800 euro per hectare (Gaitnieks *et al*., 2008). *Heterobasidion* can live in infected trees or stumps for decades, being a long-term infection source for new tree generation (Piri, 1996; Möykkynen and Pukkala, 2010). Spread of *Heterobasidion* takes place via spores that germinate on fresh stump surfaces and injured trees (primary infection), and by mycelial growth along roots from tree to tree (secondary infection) (Redfern and Stenlid, 1998; Stenlid and Redfern, 1998). Secondary infection is possible only if roots of two trees are in close contact with each other, because growth of *Heterobasidion* outside roots in soil is very restricted and depends on soil properties. Hence it is important to know the soil characteristics in managed forests in order to restrict the spread of *Heterobasidion* in a tree stand, to choose the optimal forest management strategy for forests infected by *Heterobasidion*, and to decrease the infection risk in the new tree generation.

GROWTH OF *HETEROBASIDION* MYCELIUM IN SOIL

Several investigations have shown that growth of *Heterobasidion* in soil is very limited, if it occurs at all (Stenlid and Redfern, 1998; Garbelotto and Gonthier, 2013; Gonthier and Thor, 2013). A. Vasiliauskas (1989) points out that soil properties do not have direct influence on the spread of *Heterobasidion* because it takes place in roots. Successful transfer of *Heterobasidion* from an infected spruce to a healthy one takes place if the contacting roots are at least 2–3 centimetres in diameter, according to published data, reviewed by Korhonen and Stenlid (1998). Nevertheless, several authors (J. Stenlid, Z. Sierota, R. Vasaitis, personal communication) point out that mycelium of *Heterobasidion* can infect roots of nearby growing spruce if root diameter in the contact zone is as small as five millimetres. Pine roots with even smaller diameter (down to 0.3 cm) can be infected (Rishbeth, 1951b).

Under suitable conditions fruitbodies of *Heterobasidion* can develop in the litter layer (Negrutskii, 1986; Rishbeth, 1951a). Our observations confirm this: in Latvia, close to an infected pine sapling (age ca. 10 years), *Heterobasidion* fruitbodies were found on the soil surface approximately 20 cm from the sapling, without direct contact to wood or roots below it (unpublished data). In Poland, fruitbodies were recently found on grass roots in an infected pine stand, thus demonstrating that *Heterobasidion* mycelia can develop also in soil (Sierota *et al.*, 2016).

IMPACT OF SOIL ABIOTIC FACTORS ON THE SPREAD OF HETEROBASIDION ROOT ROT

Pratt and Greig (1988) emphasise the role of edaphic factors on the development of Heterobasidion root rot. Favourable soil properties for the spread of *Heterobasidion* in a tree stand are increased pH, high sand content, and low amount of organic matter (Korhonen and Stenlid, 1998). More specifically, lower amounts of N, Fe and Mn are characteristic for soils in spruce stands infected by *Heterobasidion* (Alcubilla *et al.*, 1971). A particularly high risk of root rot infection is in first rotation conifer plantations established on previous agricultural lands (Bernadzki, 1997; Korhonen and Stenlid, 1998). Vollbrecht and Agestam (1995) present a great amount of data (survey of approx. 20 000 stumps) showing that spruce stands on soils previously used for pasture or agriculture are particularly susceptible to root rot. Nutrient imbalance and compressed soil structure are characteristic properties of previous agricultural lands; there is a shallow root distribution zone and, consequently, more root contacts (Bendz-Hellgren *et al.*, 1999 and cited literature; Piri, 2003 and cited literature). Despite the fact that *Heterobasidion* mycelium can grow in a fairly wide pH range (Korhonen and Stenlid, 1998), increased pH promotes spread of the fungus (Rishbeth, 1951a; Rishbeth, 1951b; Siepmann, 1976; Greig, 1984; Redfern *et al.*, 1994; Korhonen and Stenlid, 1998; Gibbs *et al.*, 2002). However, in our study on spruce root mycorrhization in mixed spruce and pine stands, high infection by *Heterobasidion* was observed also in stands with soil pH as low as 2.6 (Gaitnieks *et al.*, 2016).

Data about the impact of soil organic matter content on the spread of Heterobasidion root rot are contradictory. Rishbeth (1950) concluded that *Heterobasidion* mycelium does not grow in humus. He also found that in pine plantations the amount of organic matter in soil influences the severity of disease. When organic matter content in soil was 1–10%, the percentage of infected trees was on average 15%, but when soil contained more than 20% organic matter, only 3% of trees were infected (Rishbeth, 1951b). On the other hand, Rennerfelt (1946) in Sweden observed growth of *Heterobasidion* mycelium in humus extracts. Evers (1973) observed no relationship between soil humus content and incidence of Heterobasidion root rot in Norway spruce stands. Several studies have shown that peat soils restrict the spread of *Heterobasidion* in tree stands; hence the infection risk of trees growing on such soils is low (Korhonen and Stenlid, 1998).

Nevertheless, evaluation of Heterobasidion root rot incidence in six spruce stands on peat soils in Latvia showed that on average 16.3% of trees were infected. In one 45-year-old stand, the percentage of infected spruce stems reached up to 40% and, in addition, many spruce trees were infected by *Armillaria* spp. (unpublished data). On permanently wet soils *Heterobasidion* does not occur. However, periodic rise of groundwater-may damage roots and expose them to infection by root rot (Korhonen and Stenlid, 1998).

ROLE OF SOIL BIOTIC FACTORS

The review article by Hodges (1969) indicates that mycelium of *Heterobasidion* can grow only a few centimetres in unsterilised humus, and its further development is limited by presence of antagonistic soil microorganisms. Also Negrutskii (1986) reported that growth of *Heterobasidion* mycelium in sterilised soil is approximately five times faster than in unsterilized soil. Vasiliauskas (1989) found that microorganisms antagonistic for *Heterobasidion,* which are frequently present in forest soils, are absent in agricultural land. Similar results were obtained in Latvia by N. Arhipova (Arhipova *et al.*, 2008) and T. Gaitnieks (Gaitnieks *et al.*, 2008) when they analysed soil microflora in spruce stands. Polish researchers observed that the lack of antagonistic microorganisms in soil of agricultural lands promotes the growth of *H. annosum* (Mańka and Łakomy, 1995). Several studies put emphasis on the role of *Trichoderma* species in restricting the development of *Heterobasidion* in agricultural land (Sierota and Kwasna, 1988; Capretti and Mugnai, 1989). A Latvian study demonstrates that many fungi isolated from the rhizosphere of spruce growing on forest soil are antagonists of *Heterobasidion*: 69% of isolated fungal strains showed antagonism against *H. parviporum* and 62% against *H. annosum*. Corresponding figures obtained from agricultural soil were 31% and 13%. Strains of *Trichoderma, Mortierella, Penicillium, Verticillium, Arthrobotrys, Dicoccum, Mycogone* and *Streptomyces* showed strong antagonism against *Heterobasidion* species (Gaitnieks *et al.*, 2009). Likewise, microorganisms antagonistic to *H. annosum* are well represented in root rhizosphere of grey alder *Alnus incana* (Johansson and Marklund, 1980). Obtained data from more than 450 trees of *A. glutinosa* and more than 400 trees and 220 stumps of *A. incana* in Latvia indicate resistance of these *Alnus* species against *Heterobasidion* (Arhipova *et al.*, 2011b; Arhipova *et al.*, 2012). Moreover, admixture of *A. incana* in spruce stands infected by *Heterobasidion* promotes vitality of mycorrhizal fungi (higher frequency of live mycorrhiza) and increases their species diversity (Gaitnieks *et al.*, 2000a).

Mycorrhizal fungi have to be competitive with soil microorganisms (Bücking, 1979), and they may have some role in protecting conifer roots against *Heterobasidion*. Edaphic factors determine the abundance of mycorrhizal fungi in forest stands including former agricultural lands (Lange, 1993). Studies carried out in Latvia show differences in typological structure of *P. abies* ectomycorrhizas between agricultural and forest soils. In forest soil mycorrhizal fungi *Cortinarius* sp. and *Cenococcum geophilum* were found more frequently. Moreover, in forest lands morphological parameters such as fine root length and volume of roots were significantly higher in comparison with agricultural soil (Gaitnieks *et al*., 2008). In mineral soil, differences were found in mycorrhizal colonization between healthy and diseased spruce (infected by *Heterobasidion*), but on peat soil no significant differences between healthy and diseased spruce were found in mycorrhizal colonization and composition of fungal communities (Gaitnieks *et al*., 2000b; Gaitnieks *et al*., 2016).

INTERACTION OF SOIL PROPERTIES AND INDIRECT IMPACT OF SOIL ON *HETEROBASIDION* INFECTION

Rishbeth (1951b) relates *Heterobasidion* infection risk with multiple factors and notes that it is hard to separate factors that influence fungal activity from those related to tree resistance. Soil microorganisms affect the development of *Heterobasidion* on the root surface, whereas soil pH affects the community of soil microorganisms. For instance, *Trichoderma viride*, a fungus antagonistic to *Heterobasidion*, is more common in acid forest soils than in alkaline and post-agricultural soils (Korhonen and Stenlid, 1998), where the absence of this antagonist allows *Heterobasidion* to grow fast along pine root surfaces, and makes spread of the fungus in a tree stand faster (Rishbeth, 1950; Rishbeth, 1951a). Several authors relate the low level of *Heterobasidion* infection on peat soils with low pH and presence of antagonistic microorganisms (Korhonen and Stenlid, 1998 and cited literature).

Spores of *Heterobasidion* are present in soil, where they can maintain their vitality at least for a year, and infect injured tree roots (Korhonen and Stenlid, 1998). Sand content, soil aeration and other soil properties are essential factors in the root infection process because of their impact on soil water movement and the washing of spores into deeper soil horizons. Rishbeth (1951a) found spores of *Heterobasidion* in soil even at depth of 50 to 90 cm. R. Siepmann (1974; 1976) in Germany isolated *Heterobasidion* both from litter and humus layers (0–3 cm depth), and demonstrated spruce root infection by *Heterobasidion* directly from the soil. S. F. Negrutskii (1986) showed that healthy pine roots became infected after being covered with a humus layer that was taken from a pine stand infected by *Heterobasidion*. Probably, spores of *Heterobasidion* present in soil caused the infection in the above mentioned cases.

Moreover, soil has indirect impact on spread of *Heterobasidion* because of its crucial effect on tree growth, health conditions and persistence against unfavourable environmental conditions (Negrutskii, 1986). All these factors have an impact also on tree resistance against pathogenic fungi. Productivity of a forest stand depends on efficient use of the main input elements of the forest ecosystem — light, water, carbon dioxide, oxygen and mineral nutrients. The impact of soil properties on tree growth is particularly high if other factors are optimal. In forest science, the effect of soil properties on tree growth is often indicated by the *Site Index*, which is related to tree growth increment in a particular period. Several models that describe root rot development in forest stands include the *Site Index* together with other relevant factors (Vollbrecht and Agestam, 1995; Lindén and Vollbrecht, 2002; Pukkala *et al*., 2005; Thor *et al*., 2005; Rönnberg *et al*., 2007).

Indirect soil impact to Heterobasidion root rot is related also to the ability of trees to produce resin (Gibbs, 1968). Resin inhibits growth of fungal mycelia, and hence increases the resistance of trees (Pechmann *et al*., 1973). Already in 1951, Rishbeth (1951b) pointed out the importance of adequate resin production in restricting the growth of *Heterobasidion* in a tree. Gibbs (1968) analysed resistance of pine against *Heterobasidion* and found that the resistance is correlated with the ability of a tree to mobilise resin, and this is influenced by site factors. Importance of physical properties of soil in resin production by roots of Corsican pine was shown also by Prior (1975).

Indirectly, soil properties affect the moisture content of stump wood (Redfern, 1993) and hence infection of stumps by *Heterobasidion* spores and further development of fruitbodies on stumps. Infection frequency of trees and stumps by *Heterobasidion* spores is related to the number of nearby fruitbodies in a forest stand and to their activity (Rishbeth, 1951b; Rishbeth, 1959; Greig, 1962; Yde-Andersen, 1962; Redfern *et al*., 1994; Redfern and Stenlid, 1998). Soil moisture and understory vegetation influence the growth of fruitbodies on stumps and logs. In studies conducted in Latvia, a larger amount of *Heterobasidion* fruitbodies were found on spruce logs in the nutrient rich *Oxalidosa* forest type, which is characterized by a well-developed understory vegetation (Stivriņa *et al*., 2010).

Expansive spread of root rot on previous agricultural lands is related not only to lack of antagonistic microorganisms but also to fast growth of trees due to high nutrient supply from soil (R. Vasaitis, personal communication). *Heterobasidion* grows faster in fast growing spruce trees with wide tree rings (Isomäki and Kallio, 1970).

Wood structure has also an effect on fruitbody formation. In Poland, abundant fruitbody formation was observed in root rot infected pine stands on previous agricultural land (Łakomy and Werner, 2003). Likewise, Dimitri *et al*. (1971) noted that *Heterobasidion* fruitbodies are particularly frequent on rotted spruce on calcium-rich soils. Previous agricultural lands usually are calcium-rich areas, and our studies show increased occurrence of fruitbodies on spruce wood in previous agricultural lands (unpublished data). In another study we evaluated the occurrence of *Heterobasidion* fruitbodies on spruce wood, and concluded that fruitbody formation is less intense on drained mineral soils than on drained organic soils (Stivriņa *et al*., 2010). Although trees on water-saturated areas are relatively seldom infected by *Heterobasidion*, still in such areas very intense fruitbody development was observed on windthrown trees and logs (p.e. *Myrtilloso-sphagnosa*).

CONCLUSIONS AND FURTHER PROSPECTS

Overall, the examples presented above show that the impact of soil properties on Heterobasidion root rot is quite complex. The spreading of this disease both by spores and mycelial growth is greatly affected by soil properties.

High pH and mineral nutrient content in soil are properties that favour the spread of Heterobasidion root rot in a tree stand. The spread is particularly fast in pine plantations established on agricultural lands. In such soils, *Trichoderma* species and other antagonistic organisms against *Heterobasidion* occur less frequently compared to forest soil. Increased humus content in soil decreases tree root infection by *Heterobasidion*; nevertheless, extensive spread of *Heterobasidion* has been observed in several spruce stands on peat soils in Latvia. Soil properties like aeration, mechanical composition, nutrient content etc. can have a direct impact on the growth of *Heterobasidion* in the root system of forest trees. In addition, soil indirectly influences spread of *Heterobasidion* by providing more or less favourable conditions for fruitbody development and spore production, and by affecting the flow of water carrying spores of *Heterobasidion* in soil. Finally, the impact of soil on the vitality of trees should also be noted because it determines the resistance of trees against pathogens.

In further studies, growth of *Heterobasidion* in spruce roots (including roots of small dimension stumps) on mineral and organic soils should be evaluated. An effective way to reduce root rot in severely infected areas is stump removal (Vasaitis *et al*., 2008; Cleary *et al*., 2013). However, this procedure changes biotic and abiotic properties of soil. Therefore, the possible risks of stump removal should be carefully assessed, concerning changes in flora, fauna and fungal community.

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AUGSNES IETEKME UZ *HETEROBASIDION* SAKŅU TRUPES IZPLATĪBU

Sniegts literatūras apskats par šādu tēmu: augsnes īpašības ietekmē gan sakņu piepes primāro izplatību ar sporām, gan sekundāro — ar micēliju sakņu kontaktu vietās. Paaugstināts pH un palielināts barības vielu saturs augsnē veicina *Heterobasidion* izplatību audzē. Īpaši intensīvi sakņu piepes micēlijs attīstās augsnē priežu stādījumos lauksaimniecības zemēs. Šādās platībās *Trichoderma* spp. un citi pret sakņu piepi antagonistiskie mikroorganismi ir konstatējami daudz retāk, salīdzinot ar meža zemēm. Palielināts humusa saturs augsnē samazina koku sakņu inficēšanās risku ar *Heterobasidion* micēliju. Tomēr Latvijā intensīva *Heterobasidion* izplatība ir konstatēta atsevišķās egļu audzēs ar kūdras augsnēm. Augsnes aerācija, mehāniskais sastāvs, barības vielu saturs būtiski ietekmē *Heterobasidion* sekundāro infekciju. Turklāt, augsne arī netieši ietekmē *Heterobasidion* izplatību, nodrošinot vairāk vai mazāk piemērotus apstākļus augļķermeņu attīstībai un sporu produkcijai, kā arī ietekmējot sporu ieskalošanos augsnē. Savukārt kokaugu vitalitāte, ko lielā mērā nosaka augsnes īpašības, ietekmē rezistenci pret patogēniem, tajā skaitā *Heterobasidion*.