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Modelling the mechanisms behind the key epidemiological processes of the conifer pathogen *Heterobasidion annosum*

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ABSTRACT

The *Heterobasidion annosum* species complex is a widely distributed group of fungal conifer pathogens causing root and butt rots. We studied the key processes of *Heterobasidion* epidemiology by compiling models that rely on biological processes. Models were included in the mechanistic model with stochastic elements, Hmodel, simulating the fungal dynamics in even-aged Norway spruce stands. The results from the modelling and stand-level simulations indicated that primary infections are affected by the stump size and spore deposition. In addition, we found that *Heterobasidion* dynamics at the scale of the stand are driven by several infections in large stumps, rather than by numerous infections in small stumps. We assessed the need for quantitative results in *Heterobasidion* biology, especially in the spread mechanisms, to support the development of complex mechanistic models.

1. Introduction

Heterobasidion annosum species complex is one of the most destructive groups of fungal conifer pathogens in the Northern Hemisphere. *Heterobasidion* species infect several tree species, causing root and butt rot. They rely on two infection strategies: long-distance dispersal via basidiospores and short-distance vegetative spread via mycelia (Garbelotto and Gonthier, 2013).

Long-distance dispersal by basidiospores is used to infect new, healthy stands. The basidiospores need fresh wood tissue, such as freshly cut stump surfaces or logging wounds, to germinate and grow (Rishbeth, 1951). Homokaryotic basidiospores germinate and start to grow as primary mycelia. These homokaryotic mycelia with different mating alleles usually pair and form heterokaryotic secondary mycelia (Rayner et al., 1987), which most often are found to be the cause of the disease (Korhonen and Piri, 1994). However, reports exist of homokaryotic mycelia being able to infect living trees as well (Garbelotto et al., 1997; Vainio et al., 2015).

Clear temporal variation exists in the spore production (Kallio, 1970; Brandtberg et al., 1996; Gonthier et al., 2005), and the daily temperatures seem to affect the sporulation most significantly in the Nordic countries. Prolonged drought and high temperatures may also interrupt the spore production, especially in the Mediterranean climate (Garbelotto et al., 2010). The spatial variation is considered to be related to the amount of basidiocarps in the vicinity (Garbelotto and Gonthier, 2013), as the majority of the basidiospores fall within a few hundred meters of their origin (Kallio, 1970). Annual mean temperatures or temperature sums do not seem to correlate with the spatial variation of spore deposition in Fennoscandia (Kasanen et al., 2011; Witzell et al., 2011). Because the heartwood area of stumps is crucial for the colonization process (Oliva et al., 2013), stump surfaces at the end of the rotation would create more opportunities for fungal spore infection than small stumps with a small area of heartwood at the beginning of the rotation. Heartwood formation in Norway spruce is a function of diameter and age (Sellin, 1994; Wilhelmsson et al., 2002). However,

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Gunulf et al. (2013) found that even small sapling stumps of Norway spruce with stump diameters from 2 to 14 cm were infected and several reports indicate that sapwood is more readily colonized than heartwood by *Heterobasidion* species (Swedjemark and Stenlid, 1993; Johansson and Brandtberg, 1994; Nicolotti et al., 1999).

The second mechanism for spread is short-distance dispersal within a stand through mycelial growth via root-to-root contacts and connections, both within and between tree generations. *Heterobasidion* can spread from the infected stumps to young seedlings in the first years of the rotation (Piri, 1996). Unlike many other root-decay-causing fungi, *Heterobasidion* species cannot spread in the soil (Hodges, 1969). The mycelial growth rate is considered temperature related, although with high within-population variation (Müller et al., 2014, 2015). The pathogen benefits from many forest-management measures and has, therefore, especially become established in intensively managed conifer stands (Korhonen et al., 1998).

The progress of decay in the root system affects tree growth (Bendz-Hellgren and Stenlid, 1995, 1997), anchorage (Oliva et al., 2008) and mortality (Swedjemark and Stenlid, 1993), but no quantitative results are available on the mechanical weakening of roots as a function of advancing decay. Trees can survive even after losing some of their main roots but die when the loss of the main roots substantially decreases the transport of water and nutrients.

The Hmodel (Honkaniemi et al., 2014) is a complex mechanistic model, developed to simulate *Heterobasidion* dynamics in even-aged Norway spruce (*Picea abies*) stands. The Hmodel is implemented in the MOTTI stand-growth simulator (Hynynen et al., 2005; Salminen et al., 2005), which is responsible for simulating the host dynamics. Honkaniemi et al. (2014) showed that the Hmodel is sensitive to three parameters: the probability of the spores colonizing a fresh stump (P_{col}), the growth rate of the fungus in the roots of a living tree (rH_{tr}) and the probability of the fungus spreading from the stump to the tree ($P_{transferST}$). Submodels including these parameters can be considered the key processes of *Heterobasidion* dynamics in Hmodel.

In this article, we have added several new features to the Hmodel (Honkaniemi et al., 2014). First, we modified the spore infection and stump colonization process which, in the earlier version of Hmodel, included one of the sensitive parameters, P_{col}. Second, we described the linkage between the temperature sum and the mycelial growth rate. Third, we added mortality of trees due to advanced decay in the root system, and fourth, we included a more detailed description of the young stand before the stand dominant height of 8 m. Parameter abbreviations and their explanations, values and sources used in this paper are presented in Table 1. The Hmodel that included these new modifications was further used to simulate different Norway spruce stands to see the effects of these four processes on the model output and to study the model sensitivity.

2. Materials and methods

2.1. New submodels for the key processes

2.1.1. Disease probability ($P_{disease}$): pairing of primary mycelia and survival in stumps

The stump-specific disease probability ($P_{disease}$) of primary infection was based on the density of the germinated homokaryotic spore colonies on the wood surface (D_{spore}), i.e., the number of colonies landing and germinating m^{-2} hr^{-1} and the areas of heartwood (A_{hea}) and sapwood (A_{sap}) on the stump surface. The main assumption of the process was that the pairing and formation of heterokaryotic mycelium is needed for the effective growth and competition ability of the fungus (Platt et al., 1965; Redfern et al., 2001). The infection and colonization process consists of four parts: (i) the distribution of the spores between the basidiocarps of the population; (ii) spatial distribution of the spores on the stump surface; (iii) pairing and formation of heterokaryotic mycelia; and (iv) survival of heterokaryotic mycelia in the stump.

Spores were assumed to originate from different basidiocarps. Spore deposition in the first 24 h after exposure of the wood was considered to be sufficient (Bendz-Hellgren, 1997). Spore colonies were randomly distributed on the stump surface area. Distances to all other homokaryotic spores were calculated for each spore in a randomized order. If the spore was within the maximum pairing distance ($dist_{pairmax}$) from another spore and these two spores originated from the same basidiocarp, pairing occurred with a probability of 0.5. If the spores were from different basidiocarps, the pairing occurred with probability of 1.0, assuming that each basidiocarp produces spores with unique mating alleles. Paired spores were not able to pair again; that is, they were excluded from computation with the remaining spores.

For this study, we parameterized the submodel as follows:

- To mimic short-distance spore dispersal we assumed the distribution of D_{spore} among the five most closest and abundant basidiocarps to be 50%, 30%, 13%, 4.5% and 1.5%. The remaining 2% of D_{spore} were attributed to long-distance dispersal from several basidiocarps. A distribution was achieved by fitting a negative binomial distribution to the five most abundant basidiocarps. Distribution parameters were $\mu = 0.78$ and $\delta = 2.66$.
- The maximum distance between two spores able to pair ($dist_{pairmax}$) was set to 1.0 cm after evaluation against data from Möykkynen and Kontiokari (2001) (Fig. 1). The study of these researchers was replicated by simulating different spore densities on 9 cm diameter wood discs and imitating the sampling method. The sensitivity of $dist_{pairmax}$ was studied by simulating the study with values ranging from 0.25 to 10 cm.
- Colonization probabilities of a single heterokaryotic colony in the heartwood ($P_{survhea}$) and sapwood ($P_{survsap}$) of the stump in this study were 0.03% and 0.005%, respectively. Oliva et al. (2013) reported that the probability of *Heterobasidion* spores colonising a stump was 12.5% in sapwood and 75% in heartwood. However, Oliva et al. (2013) did not measure the spore density of the suspension used, and thus, we were not able to derive the probabilities directly. We did 1000 iterative simulations with various spore densities (0–10,000 m^{-2}) and compared the output against field data from the literature (Dimitri et al., 1971; Schönhar, 1971). The results of the simulations were compared visually against field data, and the best fit was achieved by assuming the spore suspension in the study of Oliva et al. (2013) to be approximately 2500 spores m^{-2}. Sensitivity analysis was carried out for colonization probability parameters in three scenarios: 1) heartwood preference ($P_{survhea} = 0.03\%$ and $P_{survsap} = 0.005\%$), 2) sapwood preference ($P_{survhea} = 0.005\%$ and $P_{survsap} = 0.03\%$), and 3) no preference ($P_{survhea} = 0.03\%$ and $P_{survsap} = 0.03\%$) for spore survival. The $P_{disease}$ values for the sensitivity analysis were simulated for different spore densities ($D_{spore} = 0$ to 3000 m^{-2} h^{-1}), stump diameter ($d_s = 0$–60 cm) and heartwood diameter ($d_{heart} = 0$–100% of d_s).
- The number of iterations needed was studied by running the model with various amounts of iterative simulations (0–10,000). The Monte Carlo error for the number of heterokaryotic colonies was considered sufficiently small (<0.1%) with 1000 iterations.

The spore-pairing simulations were summarized with simple