Impact of *Heterobasidion* spp. Root Rot in Conifer Trees and Assessment of Stump Treatment

With Emphasis on *Picea abies*, *Pinus sylvestris* and *Larix × eurolepis*

LiYing Wang
Faculty of Forest Sciences
Southern Swedish Forest Research Centre
Alnarp

Doctoral Thesis
Swedish University of Agricultural Sciences
Alnarp 2012

Acta Universitatis agriculturae Sueciae
2012: 97

Cover: Basidiocarps of *Heterobasidion* spp. on a Scots pine (*Pinus sylvestris*) stump (photo: LY. Wang)

ISSN 1652-6880
ISBN 978-91-576-7744-0

Print: SLU Service/Repro, Alnarp 2012

Impact of *Heterobasidion* spp. root rot in conifer trees and assessment of stump treatment. With emphasis on *Picea abies*, *Pinus sylvestris* and *Larix* × *eurolepis*

Abstract

In the thesis four studies were conducted to understand the impact of *Heterobasidion* spp. on *Picea abies*, *Pinus sylvestris*, and *Larix* × *eurolepis* in southern Sweden, and the efficacy of stump treatment against infection in order to economically assess control measures.

The ability of secondary spread of *H. parviporum* inoculated on Norway spruce stumps created at precommercial thinning (PCT) was investigated. Stumps with a minimum diameter of 2.5 cm were able to transfer infection to adjacent trees, indicating the spread of infections early in a rotation cannot be neglected.

Disease spread through PCT stumps was simulated and the economic benefits of stump treatment and winter thinning were compared. Decay frequency was affected by the intensity of PCT, and efficacy of control measures, but not by thinning age or the probability of stump infection. PCT with stump treatment was not profitable at a 3% discount rate regardless of the thinning age or the decay level at the previous rotation.

The intensity and distribution of root infection in 36-year-old Scots pine trees nine years after thinning and the relationship between belowground infection and stem growth loss was investigated. Twenty-four Scots pine trees were extracted from two plots and whole root systems and tree volumes were measured. Mean incidence of *Heterobasidion* spp. infection was 87.5%, but no trees showed any symptoms aboveground. The proportion of infected root volume ranged between 0% and 32%, and negatively affected annual volume increment of individual tree.

Both urea and *Phlebiopsis gigantea* were proved effective as stump treatment agents on hybrid larch stumps in two experiments by examining infection incidence and colony size on stump discs naturally infected by *Heterobasidion* basidiospores.

Heterobasidion spp. infection results in losses in productivity of Norway spruce, Scots pine and hybrid larch. The results of these studies suggest that stump treatment can be economically justified for commercial thinnings of Scots pine and hybrid larch, but not for precommercial thinning of Norway spruce currently.

Keywords: Heterobasidion annosum s.s., *H. parviporum*, precommercial thinning, root and butt rot, *Phlebiopsis gigantea*, urea, RotStand, growth loss, secondary spread.

Author's address: LiYing Wang, SLU, Southern Swedish Forest Research Centre, P.O. Box 49, 230 53 Alnarp, Sweden
E-mail: liying.wang@slu.se

Dedication

To Shi Jin

Ninety miles is only half of a hundred miles journey – the going is toughest towards the end of a journey.

Liu Xiang

行百里者半九十 --西汉·刘向 《战国策·秦策五》

Contents

List of Publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

I Gunulf, A., Wang, L.Y., Englund J.-E., Rönnberg, J. (2013). Secondary spread of *Heterobasidion parviporum* from small Norway spruce stumps to adjacent trees. *Forest Ecology and Management* 287, 1-8.

II Wang, L.Y., Gunulf, A., Pukkala, T., Rönnberg, J. Simulated *Heterobasidion* disease development in Norway spruce (*Picea abies*) stands following precommercial thinning and the economic assessment of control measures. Manuscript.

III Wang, L.Y., Zhang, J., Drobyshev, I., Cleary, M., Rönnberg, J. Severity and distribution of root infection by *Heterobasidion* spp. and its impact on growth of Scots pine trees in southern Sweden. Manuscript submitted to *Canadian Journal of Forest Research*.

IV Wang, L.Y., Pålsson, H., Ek, E., Rönnberg, J. (2012). The effect of *Phlebiopsis gigantea* and urea stump treatment against spore infection of *Heterobasidion* spp. on hybrid larch (*Larix* × *eurolepis*) in southern Sweden. *Forest Pathology* 42, 420-428.

Papers I and IV are reproduced with the permission of the publishers.

The contribution of LiYing Wang to the papers included in this thesis was as follows:

I I conducted 50% of the lab work. I wrote 20% of the manuscript and commented on the statistical analyses and the manuscript.

II I designed the experiment together with Anna Gunulf. I revised part of the code in the root disease model RotStand and did all the modelling work. The statistical analyses were done together with Anna Gunulf. I am the first and corresponding author of the manuscript.

III I developed the research idea and designed the experiment with Jonas Rönnberg and Jing Zhang. I did 50% of the field work. Jing Zhang conducted all the lab work. I did 90% of the statistical analyses and I am the first and corresponding author of the manuscript.

IV I designed the second part of the experiment. Henrik Pålsson and Erik Ek conducted the field work and lab work. I did all the statistical analyses and I am the first and corresponding author of the paper.

1 Introduction

Root and butt rot caused by *Heterobasidion* spp. causes severe economic and ecological impacts to forests in the northern temperate and boreal regions (Woodward *et al.*, 1998; Sinclair & Lyon, 2005). In Europe, losses are estimated at €790 million per annum mainly from degraded merchantable timber due to decay and reduced site productivity (Woodward *et al.*, 1998). This estimate however does not include indirect losses such as increased susceptibility to windthrow, the risk to the next rotation crop trees and the cost for preventive measures (Woodward *et al.*, 1998).

In Sweden, *Heterobasidion* root rot is the most important forest disease (Stenlid & Wästerlund, 1986; Bendz-Hellgren *et al.*, 1998), and the financial loss caused by *Heterobasidion* spp. is estimated to be approximately 475 million SEK (€54 million) annually (Bendz-Hellgren & Stenlid, 1995; Rosvall, 2004). Demand from industry for a sufficient and steady flow of woody products requires intensive management of forest resources, which has contributed to the increased incidence of *Heterobasidion* infection in forests (Korhonen *et al.*, 1998b).

Control methods, including biological, chemical and silvicultural measures, have been developed to reduce the impact of *Heterobasidion* spp. (Rishbeth, 1959; Korhonen *et al.*, 1993; Holdenrieder & Greig, 1998; Pratt *et al.*, 1998a). In practice, however, control methods are not applied in all susceptible stands (Thor, 2005) due to the lack of awareness of the risk of root rot by private forest owners (Blennow & Sallnäs, 2002) and the forest sector in Sweden. Furthermore, forest management and planning seldom consider the impact of *Heterobasidion* spp. when making productivity prognoses (Thor, 2005).

In Sweden, Norway spruce (*Picea abies* (L.) Karst.) and Scots pine (*Pinus sylvestris* L.) are the most economically important tree species (Skogsstyrelsen, 2012), while hybrid larch (*Larix* × *eurolepis* Henry) recently has rendered more interest due to its early rapid growth and resistance to wind-throw (Larsson-Stern, 2003). However, all of these tree species are susceptible to *Heterobasidion* spp. infection (Korhonen, 1978; Vollbrecht *et al.*, 1995b; Piri, 1996). Despite a lot of research on the biology and control of *Heterobasidion* spp. since Hartig (1874), there are still several gaps in knowledge. To better manage the forests, questions related to, e.g. the risk of precommercial thinning Norway spruce stumps to transfer disease, the effect of the disease on growth of Scots pine and hybrid larch as well as the necessity and profitability of stump treatment on Scots pine, hybrid larch and precommercially thinned Norway spruce needs further attention.

1.1 The pathogen

1.1.1 Taxonomy, hosts and distribution

The scientific names previously used for *Heterobasidion annosum* sensu lato (s.l.) were *Polyporus annosus* Fr., *Trametes radiciperda* R. Hartig, *Fomes annosus* (Fr.) Cooke, and *Fomitopsis annosa* (Fr.) (Karst.) Bond. & Sing. (Niemela & Korhonen, 1998). In Europe, three intersterility groups (ISGs) of *H. annosum* s.l. were delimited based on mating studies (Korhonen, 1978), and designated P, S and F for those isolates attacking pine (*Pinus* spp.), spruce (*Picea* spp.) and true fir (*Abies alba* Mill.), respectively. Later, separate taxonomic species were designated as *H. annosum* sensu stricto (s.s.) for the P ISG, *Heterobasidion parviporum* Niemelä & Korhonen for the S ISG, and *Heterobasidion abietinum* Niemelä & Korhonen for the F ISG (Capretti *et al.*, 1990; Niemela & Korhonen, 1998). The two North American *Heterobasidion* ISGs have recently been designated as *Heterobasidion irregulare* nom. nov. Garbelotto & Otrosina (P ISG) and *Heterobasidion occidentale* sp. nov. Otrosina & Garbelotto (S ISG) (Otrosina & Garbelotto, 2010). *Heterobasidion ecrustosum* Tokuda, T. Hatt. & Y.C. Dai (Tokuda *et al.*, 2009), formerly belonging to *H. insulare* complex, attacks *Pinus luchuensis* Mayr. in Taiwan (Yen *et al.*, 2002). Other species of *Heterobasidion* include *H. araucariae* Buchanan in Oceania, *H. melleum* (Bond. & Lyubarskii) M. Bondartseva and *H. perplexum* (Ryv.) Staplers in Eurasia, *H. pahangense* Corner in southeastern Asia, and *H. rutilantiforme* (Murrill) Staplers in central America; their pathogenicity though is generally not reported (Niemela & Korhonen, 1998).

Obviously the knowledge and awareness of local distribution and host specification of *Heterobasidion* spp. is crucial for both research and management. Species of *Heterobasidion* differ in host specialization and geographical distribution in Europe. *Heterobasidion annosum* s.s. mainly infects Scots pine, but also other species, including e.g. Norway spruce, larch spp. and silver birch (*Betula pendula* Roth.) (Korhonen, 1978; Vollbrecht *et al.*, 1995b; Werner & Łakomy, 2002b). *Heterobasidion annosum* s.s. is widely distributed across Europe extending as far north as 62°N in Finland (Korhonen *et al.*, 1998a). *Heterobasidion parviporum* mainly attacks Norway spruce, but also Scots pine seedlings, silver birch and Siberian larch (*Larix sibirica* Ledeb.) (Korhonen, 1978; Piri, 1996; Werner & Łakomy, 2002a). The distribution of *H. parviporum* coincides with the natural distribution of its primary host Norway spruce (Korhonen, 1978), and extends northward to 68°N in Finland. However it rarely causes damage north of 64°N latitude (Korhonen *et al.*, 1998a). *Heterobasidion abietinum* mainly infects *Abies* spp., and its distribution follows that of its host accordingly in Europe (Capretti *et al.*, 1990). In Scandinavia only *H. annosum* s.s. and *H. parviporum* are present (Bendz-Hellgren *et al.*, 1998) and the studies in this thesis refer to only these species.

1.1.2 Infection and spread

The mechanisms for disease spread are important since they affect disease impact and application of control measures. *Heterobasidion* spp. infect a tree by basidiospores dispersed from perennial basidiocarps, which normally form at the base of diseased trees or on infected stumps (Korhonen & Stenlid, 1998). The major infection courts are on freshly created stump surfaces and wounds of living trees (Rishbeth, 1951b; Isomäki & Kallio, 1974), but also very occasionally on stump roots through spores present in the soil (Jorgensen, 1961). Mycelia colonize the host substrate and subsequently spread to adjacent trees through root grafts and contacts (Rishbeth, 1951a; Paludan, 1966).

Primary infection is usually inhibited under extreme temperatures due to the less ambient basidiospores dispersed from basidiocarps (Redfern & Stenlid, 1998). For example, infection of *Heterobasidion* spp. seldom occurs in the cold winter in Scandinavia (Yde-Andersen, 1962; Kallio, 1970; Brandtberg *et al.*, 1996) nor during extremely hot summers such as in the southern United States of America (U.S.A.) (Driver & Ginns, 1969). Stump size also affects the incidence of primary infection by *Heterobasidion* spp., since higher infection frequencies are normally observed on larger stumps (Paludan, 1966; Solheim, 1994; Bendz-Hellgren & Stenlid, 1998; Morrison & Johnson, 1999). Small stumps, e.g. less than 10 cm in diameter, can also be infected by basidiospores of *Heterobasidion* spp. (Paludan, 1966; Solheim, 1994; Berglund *et al.*, 2007), but their ability to transfer inoculum to adjacent trees is not well understood.

Heterobasidion spp. usually cannot grow freely in the soil (Rishbeth, 1951a), due to competition from antagonistic microorganisms. However in soil with high pH, mycelia of *H. annosum* s.s. can grow ectotrophically on the bark of Scots pine roots before attacking the host (Rishbeth, 1951a). The growth rate of mycelia in stump roots of Scots pine was observed to be approximately 97 cm year^{-1} at 10°C (Rishbeth, 1951b). For Norway spruce, the spread rate from an infected stump to an adjacent tree was up to 90 cm year^{-1} (Swedjemark & Stenlid, 1993). It then can be assumed that in stands with trees planted at 1.5 m spacing, secondary infection of adjacent trees may occur within one or two years (Rishbeth, 1951b). Mycelia growth is generally much slower in roots of living trees than in stump roots (Bendz-Hellgren *et al.*, 1999; Pettersson *et al.*, 2003). Spread rates in roots of Norway spruce stumps were reported to be 25 cm and in roots of living trees 9 cm year^{-1} (Bendz-Hellgren *et al.*, 1999), though the variation can be high.

Inoculum of *Heterobasidion* spp. can remain viable for up to 60 years in conifer stumps (Greig & Pratt, 1976). The transfer of *Heterobasidion* spp. inoculum from old stumps of the previous rotation to susceptible tree species of the current rotation has been shown by Vollbrecht *et al.* (1995b), Piri (1996), Rönnberg *et al.* (1999) and Vollbrecht and Stenlid (1999). As a result, plantations of tree species susceptible to infection by *Heterobasidion* spp. on infested sites will likely have high disease incidence which can potentially impact stand productivity.

1.1.3 Impact on hosts

The resulting damage caused by *Heterobasidion* spp. infection varies among host species. The fungus often causes stem decay in Norway spruce and larch spp., but rarely in Scots pine. The decay column in mature hybrid larch and Norway spruce may reach up to 4.8 m and 12 m, respectively (Stenlid & Wästerlund, 1986; Stener & Ahlberg, 2002). Stem decay is a major problem for the forest sector since even incipient decay in the wood degrades the saw timber to pulpwood, and the pulpwood with advanced decay is regarded as waste. Thus, the economic outcomes of timber yield are reduced. Susceptibility to wind-throw is reported more frequently for infected Norway spruce than for other species. Mortality, on the other hand, is more frequently observed in diseased Scots pine stands (Burdekin, 1972; Gibbs *et al.*, 2002).

Growth reductions in diameter, height and volume of *Heterobasidion*-infected trees compared to healthy trees have been reported for a variety of coniferous species. Bendz-Hellgren and Stenlid (1997) found that diseased Norway spruce in southern Sweden lost up to 10% of the volume growth in 20 years. Bradford *et al.* (1978a) suggested loblolly pine (*Pinus taeda* L.) in eastern U.S.A. infected by *Heterobasidion* spp. lost up to 19% of diameter growth during a 5-year period. Froelich *et al.* (1977) found that basal area and height increment of diseased slash pine (*Pinus elliottii* var. *elliottii* Engelm.) were reduced by up to 32% and 40%, respectively. Growth loss caused by *Heterobasidion* spp. on Scots pine trees was detected by Burdekin (1972), but was not quantified.

Due to the presence of a decay column in the stem of Norway spruce and hybrid larch, methods such as obtaining increment bore cores at breast or stump height (Stenlid & Wästerlund, 1986) and observation of discoloration or decay on the stump surface (Vollbrecht *et al.*, 1995b; Stener & Ahlberg, 2002) can be used to detect *Heterobasidion* spp. However, such methods are not reliable in Scots pine trees. Aboveground symptoms such as thin and chlorotic crowns or the presence of basidiocarps at the stem base are also not reliable to estimate actual (i.e. belowground) disease incidence (Kurkela, 2002; Rönnberg *et al.*, 2006a). Consequently, the incidence of *Heterobasidion* spp. in Scots pine is usually underestimated and thus the related economic loss neglected.

1.1.4 Factors affecting disease incidence

The incidence of *Heterobasidion* attack is determined by a number of complex and interacting factors, such as the intensity of stump infection, host resistance and environmental factors that influence both the fungus and the host (Rishbeth, 1951a). In practice, it is difficult to distinguish the effects from various factors, and previous studies have instead tried to identify the common characteristics for high incidence sites. For example, high disease incidence in susceptible plantation species is usually associated with site conditions, such as high soil pH (Rishbeth, 1951a; Froelich *et al.*, 1966; Baker *et al.*, 1993), first rotation forest land (Rishbeth, 1951a), well-drained soil (Rishbeth, 1951a; Alexander *et al.*, 1975), coarse soil texture (Froelich *et al.*, 1966; Alexander *et al.*, 1975; Baker *et al.*, 1993) and low organic matter content (Rishbeth, 1951a; Froelich *et al.*, 1966; Alexander *et al.*, 1975; Baker *et al.*, 1993). Rishbeth (1951a) considered, and Froelich *et al.* (1966) agreed, that high disease incidence in alkaline soil was attributed to the more readily and rapid ectotrophic mycelial growth of *Heterobasidion* due to the lack of competitive microorganisms. However, Alexander *et al.* (1975) did not find a correlation between soil pH and disease incidence or severity for loblolly pine in eastern

U.S.A. First rotation forest land, especially those limed for cultivation, normally have higher soil pH (Rishbeth, 1951a), and thus a higher disease incidence. Bendz-Hellgren *et al.* (1999) tried to relate high disease incidence on former agricultural land with the more rapid spread rate of the fungus in Norway spruce roots, but found no differences between the spread rate of *Heterobasidion* spp. planted on former agricultural land and forest land. The prolonged periods of drought particularly on sites with well-drained sandy soil may cause water stress for the roots and thus increase host susceptibility to *Heterobasidion* spp. (Rishbeth, 1951a; Alexander *et al.*, 1975). On the other hand, high organic matter content can maintain adequate soil moisture during periods of drought, and thus reduce host susceptibility (Rishbeth, 1951a).

Based on common characteristics for high incidence sites, hazard rating systems have been developed in the U.S.A. (Morris & Frazier, 1966; Baker *et al.*, 1993) and Great Britain (Redfern *et al.*, 2010) to justify preventative control measures on susceptible sites, e.g. stump treatment. However the criteria used to distinguish high and low hazard sites has local limitations, and application of such a system to other ecosystems and geographical regions needs further adjustment. Although Thor *et al.* (2005) developed a method to predict disease incidence for Norway spruce based on the National Forest Inventory (NFI) data, in general, a hazard rating system at stand-level is lacking for Sweden.

1.2 Control methods

1.2.1 Biological treatment

Phlebiopsis gigantea (Fr.) Jül, which was formerly known under its synonym, *Peniophora gigantea* (Fr.) Massee, is a fast colonizing saprophytic fungus in boreal and temperate forests (Holdenrieder & Greig, 1998). Rishbeth (1951b) discovered that *P. gigantea* colonizing thinning stumps of Scots pine trees outcompeted *H. annosum* s.s. in the roots. Later studies were conducted to test and develop *P. gigantea* as a biological stump treatment agent (Rishbeth, 1963; Kallio & Hallaksela, 1979) for commercial use in forests. Korhonen *et al.* (1993) isolated a strain of *P. gigantea* from a Norway spruce stump and formulated it into a commercial product that later became available in Finland, Sweden and Norway. Currently *P. gigantea* is the most widely applied treatment agent against *Heterobasidion* spp. infection in Europe (Thor, 2001). In Sweden the treatment is conducted mechanically at the same time trees are harvested (Thor, 1996; Berglund, 2005).

The efficacy of stump treatment by *P. gigantea* against primary infection by *Heterobasidion* spp. has been tested on Scots pine (Rishbeth, 1963; Korhonen *et al.*, 1993) and Norway spruce (Korhonen *et al.*, 1993; Berglund & Rönnberg, 2004; Nicolotti & Gonthier, 2005; Thor & Stenlid, 2005; Rönnberg *et al.*, 2006b) in field trials, and proven effective. Its long-term efficacy against *Heterobasidion* spp. on Norway spruce stumps has also been shown by Oliva *et al.* (2011) and Rönnberg and Cleary (2012). On hybrid larch, *P. gigantea* was tested and shown to be effective in a lab experiment (Thomsen & Jacobsen, 2001), however trials are needed to confirm its efficacy in the field.

In Sweden, stump treatment is only conducted on commercial thinning stumps of Norway spruce (Thor, 2001). Norway spruce stumps created at final felling and precommercial thinning are generally not treated. Further, stumps of Scots pine and hybrid larch, though highly susceptible to infection by *Heterobasidion* spp., are not treated. The necessity of treatment on such stumps requires further investigation.

1.2.2 Chemical treatment

Urea and borate are the most commonly used chemical stump treatment agents in Europe and in North America, respectively (Pratt *et al.*, 1998a). Urea increases the pH on the stump surface to unfavourable levels for growth of the pathogen, thereby preventing basidiospore germination (Rishbeth, 1959; Johansson *et al.*, 2002). A high concentration of urea solution, e.g. 30%, is needed to guarantee the effect of the treatment (Nicolotti & Gonthier, 2005; Thor & Stenlid, 2005). The efficacy of urea as a stump treatment agent was shown on stumps of Scots pine (Rishbeth, 1959; Johansson *et al.*, 2002) and Norway spruce (Brandtberg *et al.*, 1996; Johansson *et al.*, 2002; Nicolotti & Gonthier, 2005; Oliva *et al.*, 2008), though its efficacy on stumps of hybrid larch is generally unknown.

In Europe, urea is used in Great Britain and Ireland though less frequently in Sweden (Thor, 2001) due to the desire of reducing the use of chemicals in forestry and the high cost of transportation of the ready-made urea solution.

1.2.3 Silvicultural control

Silvicultural control against *Heterobasidion* spp. aims to reduce stump infection and secondary spread of disease (i.e. stump-to-tree) using various silvicultural methods. In Scandinavia, thinning in the winter when temperatures are below 5°C reduces the risk of stump infection from basidiospores (Kallio, 1970; Solheim, 1994; Brandtberg *et al.*, 1996). Since thinning stumps and logging injuries can be entry points for *Heterobasidion* spp., reducing the number of thinnings can be an effective method to protect the stand from spore infection (Korhonen *et al.*, 1998b). Transfer of inoculum between different host species is less frequent than between the same species (Piri, 1990). Thus selection of non-susceptible host species (e.g. broadleaves) as crop trees on sites previously infested with *Heterobasidion* spp. or cultivation of mixed-species stands can result in lower disease incidence and help reduce losses. Planting the stand at the widest possible spacing can reduce the probability of root contacts and thus reduce disease transfer within the stand (Korhonen *et al.*, 1998b). Stump removal is an effective but expensive method for control disease spread (Greig & Low, 1975; Cleary *et al.*, 2012). In severely infested stands, trees suffering from stem decay, growth loss, or both, will have lower economic value and consequently a shortened rotation may be suggested to minimize further losses.

1.2.4 Economic appraisals

Economic aspects are important to justify the practical use of any effective control measure (Pratt *et al.*, 1998b). Stump treatment with *P. gigantea* is efficient in time, application and cost since the liquid agent is simultaneously applied during mechanical harvesting of the timber (Berglund, 2005; Thor *et al.*, 2006) and the cost includes the actual consumption of the agent (Thor, 1996). However, the quantity and value of the timber versus that lost to the disease is quite complex and difficult to forecast. Furthermore, indirect effects from stump treatment such as increased resistance to wind throw can be even more difficult to estimate. Economic justification of stump treatment can be done in two ways: 1) direct comparison between the losses associated with degraded timber over the long term, e.g. one or two rotations (Mäkelä *et al.*, 1994; Möykkynen *et al.*, 1998; Thor, 2005; Berglund *et al.*, 2007) and the cost of treatment; 2) calculate the critical amount of degraded timber equivalent to the cost of stump treatment (Harper, 1987; Pratt *et al.*, 1988). The application of stump treatment has been economically justified on *Pinus* spp. in Poland and in the U.S.A. (Hodges, 1974; Rykowski & Sierota, 1984), and on *Picea* spp. in the U.K., Finland and Sweden (Harper, 1987; Pratt *et al.*, 1988; Mäkelä *et al.*, 1994; Thor *et al.*, 2006; Redfern *et al.*, 2010). Benefits of stump treatment may be more prominent in stands with high infection frequency (Rykowski & Sierota, 1984; Möykkynen *et al.*, 1998; Pratt *et al.*, 1998b), however on previously infested sites stump treatment can be less profitable (Möykkynen *et al.*, 1998).

1.3 Modelling

1.3.1 Root disease models

Due to the difficulty in understanding disease development over the course of a rotation (i.e. 50-100 years), the long-term impact of infection by *Heterobasidion* spp. to timber yield becomes difficult to predict. Models, which are abstractions of the real world, can assist to understand the biology of disease and make forecasts based on real data and scientific assumptions. During the last 50 to 60 years, different root disease models have been developed to predict disease incidence and spread, timber yields and economic losses associated with the disease. The models can be categorized into two types: empirical models, which are based on real data; and simulation models, which are derived from the interpretation of fundamental concepts (Korzukhin *et al.*, 1996; Pratt *et al.*, 1998b).

Empirical models usually use a large amount of observation data to fit into regression equations in order to make prognoses for the future, extrapolate to large areas, or both. For example, Baker *et al.* (1993) and Redfern *et al.* (2010) estimated hazard of *Heterobasidion* spp. attack based on site conditions. Vollbrecht and Agestam (1995) and Vollbrecht and Jørgensen (1995) predicted butt rot frequency in Norway spruce stands in southern Sweden and Denmark under varied site conditions and management regimes. Thor *et al.* (2005) used national forest inventory data to predict the probability of decay of Norway spruce in Sweden.

Simulation models normally consist of a mechanism of key processes within a disease cycle, such as primary infection on stumps, disease spread and transfer in roots, and damage on trees; and thus require various initial variables or user inputs. Input variables for such processes are largely based on data obtained from experiments or from the literature. In the process model Root Rot Tracker, developed by Peet and Hunt (2005), individual root growth and disease development for *Armillaria ostoyae* and *Phellinus sulphurascens* Pliát (formerly *P. weirii* (Murr). Gilbn.) in British Columbia, Canada were stochastically simulated using parameters of known root physiological characteristics. Bloomberg (1988) developed the ROTSIM model to simulate the dynamics of *P. sulphurascens* in managed Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) stands. For this model, transfer of disease occurs as a probability when a healthy and a diseased root section are present in the same subdivided soil unit. The Western Root Disease model (WRD) (Stage *et al.*, 1990; Frankel, 1998) is a comprehensive model in western North America that simulates the infection process and disease development of *Heterobasidion* spp., *Armillaria* spp. and *P. sulphurascens* in managed forest stands and subsequently estimates the long-term impact of root disease on timber yield. In this model, disease spread between infected stumps and healthy trees occurs as a probability when two circular root plates overlap. In Europe, the first *Heterobasidion* root disease model was developed by Pratt *et al.* (1988) for Sitka spruce in the U.K. Disease spread was stochastically modeled in a disease cycle by assigning probabilities of occurrence of infection and transfer. Later, a joint endeavor by scientists under the project 'Modeling of *Heterobasidion annosum* in European forests' (MOHIEF) resulted in the RotStand model, which specifically simulates the infection and spread of *Heterobasidion* spp. and estimates the economic outcomes (Pukkala *et al.*, 2005). RotStand consists of two modules: stand dynamics and disease dynamics. The former simulates stand increment and cross cutting of trees using growth and yield models from corresponding countries, e.g. Sweden, Finland, Poland and the U.K. The latter simulates the infection and spread of *Heterobasidion* spp. in hosts such as Norway spruce and Scots pine with user-defined values for the probability of stump infection, the probability of disease transfer at root contacts and the rate of decay development within stumps and trees. RotStand was validated with empirical data from the U.K. (Moseley *et al.*, 2004) and Sweden (Oliva & Stenlid, 2011), and was considered a robust and accurate simulator of *Heterobasidion* spp. development in coniferous forests in Europe.

1.3.2 Model application

In Europe, researchers have used both empirical and simulation models for the purpose of predicting disease incidence of *Heterobasidion* spp. (Thor *et al.*, 2005; Berglund *et al.*, 2007), rating site risk level (Redfern *et al.*, 2010), calculating the economic benefit of stump treatment (Möykkynen *et al.*, 1998; Thor *et al.*, 2006) and optimizing forest management under different disease scenarios (Möykkynen *et al.*, 2000; Möykkynen & Miina, 2002; Möykkynen & Pukkala, 2009; Möykkynen & Pukkala, 2010). However, despite the reported losses caused by *Heterobasidion* spp. (Bendz-Hellgren *et al.*, 1998; Thor *et al.*, 2005), root rot is seldom considered in forest practice until obvious symptoms or degraded timber become evident. Existing decision support systems for forest management have not incorporated root disease as a component. Since the longevity of the inoculum residing in stumps can impact rotation production it is therefore necessary to integrate control methods against root rot also at the beginning of a rotation.

1.4 Research needs

Conclusively, the impact of *Heterobasidion* spp. infection on Norway spruce during precommercial thinning, and on Scots pine and hybrid larch during commercial thinnings has not been thoroughly examined, nor has the risk of *Heterobasidion* spp. to long-term site productivity been perceived by forest managers. Further, studies on the efficacy of stump treatment agents against spore infection by *Heterobasidion* spp. and the potential profitability of doing stump treatment is needed in order to formulate sound management decisions and adjust silvicultural practices to minimize losses.

2 Objectives

The overall aim of the thesis was to gain more knowledge about the impact of *Heterobasidion* spp. on Norway spruce, Scots pine and hybrid larch, and the efficacy of stump treatment against *Heterobasidion* spp. infection, in order to assess control measures.

The specific objectives of the thesis were to investigate:

- The role of small-sized stumps of Norway spruce in transferring *Heterobasidion parviporum* inoculum to adjacent crop trees (paper I), and the simulation of disease development using RotStand to assess the economic outcome of stump treatment at precommercial thinning (paper II).

- The incidence of *Heterobasidion* spp. in Scots pine stands in association with site conditions (a field survey and a soil sampling study).

- The growth reduction of Scots pine caused by *Heterobasidion* spp. infection and the justification for stump treatment (paper III).

- The efficacy of stump treatment with urea and *Phlebiopsis gigantea* on hybrid larch stumps (paper IV).

3 Methodology and major results

3.1 Experimental plots

The experimental sites used in the studies are shown in Fig. 1. All studies were conducted in southern Sweden. Sites S1-S14 were used for studying the ability of small-sized stumps of Norway spruce to transfer *Heterobasidion parviporum* inoculum (Paper I). Sites S1-S8 were located in central and southern boreal region while sites S9-S14 were located in the hemiboreal region. Sites P1-P13 were located in the hemiboreal region, and were used in the study to investigate site characteristics in association with high incidence of *Heterobasidion* spp. infection in Scots pine stands. Sites P14-P18 and L1-L10 were located in temperate region. On site P14, a study on the severity and distribution of root

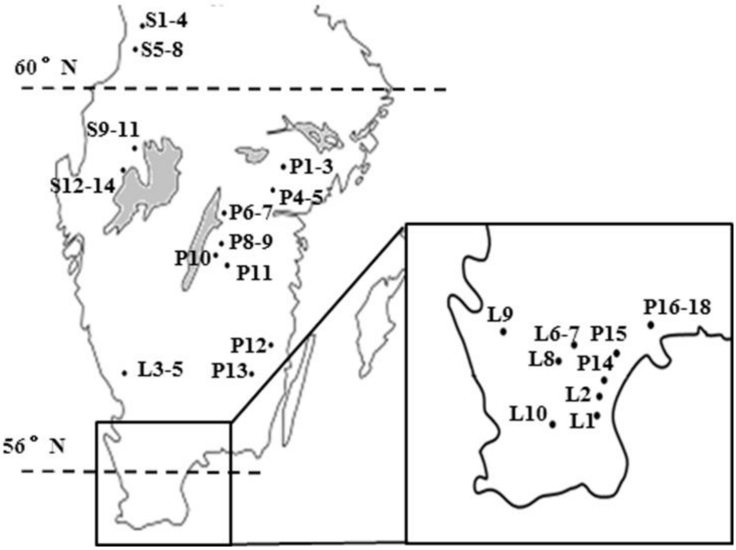

Figure 1. Location of experimental sites

infection by *Heterobasidion* spp. and its relationship with growth of Scots pine trees (Paper III) was conducted. On sites P15-P18, a stand-level survey was conducted to detect growth loss in diseased Scots pine. On sites L1-L10, the efficacy of stump treatment with urea and *P. gigantea* was tested on hybrid larch (Paper IV).

3.2 The role of small-sized stumps of Norway spruce in transferring inoculum (paper I)

The aims of this study were to 1) investigate the ability of small-sized Norway spruce stumps to transfer infection to neighbouring trees, and 2) determine the lower size and age limit for disease transmission.

3.2.1 Materials and methods

The experiment was conducted on fourteen Norway spruce-dominated sites (S1-S14 in Fig. 1). The site indices (dominant height at age 100 years) ranged between 20 and 36 m. On four sites each of the specific stump-height diameter classes, i.e. 5-8 cm and 8-11 cm was used as criteria to select trees for stump inoculation; on three sites each of the stump-height diameter classes 2-5 cm and 11-14 cm was used. Ten trees were then selected and cut with a chainsaw. The cut surface was sprayed with solution of conidiospores of a known strain of *Heterobasidion parviporum* (Rb175, kindly provided by Prof. J. Stenlid) at a concentration of 50 spores cm^{-2}. Sampling was conducted after five years by cutting a disc at stump height from each of the inoculated stumps and also from the four largest neighbouring Norway spruce trees within a 2 m radius. The distance between the inoculated stump and the neighbouring trees were measured. The diameter of each disc was measured and the age of the trees and stumps (tree age at stump creation) were obtained by counting the number of growth rings on discs. Infection of *Heterobasidion* spp. on stump discs was identified by investigating the presence of conidiophores under dissecting microscope after an incubation period of 7-11 days at room temperature (~20°C). All colonies of *Heterobasidion* spp. were marked and up to five isolations were made from each disc. The species of *Heterobasidion* was determined by the ability of the isolate to heterokaryotize homokaryotic mycelia of *H. annosum* s.s. and *H. parviporum* tester isolates (Korhonen, 1978) after 3 weeks. To investigate if the isolates were the same genet as Rb175 somatic compatibility tests with each isolate and RB175 were conducted and the interaction (Stenlid, 1985) was checked after 9-11 weeks.

The mixed model PROC GLIMMIX (SAS9.2, SAS Institute Inc., Cary, NC, USA) was used to investigate the relationship between the probability that a tree was infected by Rb175 and the variables “donor stump diameter”, “donor stump age”, “tree diameter”, “tree age” and “distance between donor and tree”.

3.2.2 Results

Stumps covering the whole range of sizes (min: 2.5 cm and max: 13.5 cm) and ages (min: 7 years and max: 43 years) could transfer infection of *H. parviporum* (Rb175) to neighbouring Norway spruce trees. Eighty-eight stumps (65%) transferred infection to at least one of the adjacent Norway spruce trees. Stumps that transferred infection (mean diameter: 8.81 cm) had significantly larger diameters than stumps that did not transfer (mean diameter: 6.87 cm) (p<0.001). Mean age did not differ between transferring and non-transferring stumps (p=0.531).

Of the 547 sampled trees, Rb175 was found in 180 trees. The smallest tree to become infected by Rb175 had a diameter of 1.6 cm and the youngest tree was 6-years-old at the time of stump inoculation. The probability that a tree was infected by Rb175 increased with increasing size of both donor stump and tree diameter (Table 1). The age of the donor stump also influenced the probability of infection; for a given stump size the probability of infection in the neighbouring tree decreased with increasing age of the stump (Table 1). The age of the tree and the distance between the donor stump and the tree did not influence the probability of infection. Since the age and the diameter of donor stumps were significantly correlated, $\text{Age}_{\text{stump}} = 7.995+1.733\ \text{Diameter}_{\text{Stump}}$ (R^2=0.33; p<0.001), the probability of infection by Rb175 in the experiment could be approximately described using only the diameter of the donor stump and the tree (Fig. 2).

Table 1. *Parameter estimate for the mixed model predicting the probability of a tree become infected by Rb175 (H. parviporum).*

Parameter	Estimate	P value
Intercept	-2.2838	<0.0001
Donor stump diameter	0.2331	0.0002
Tree diameter	0.1541	<0.0001
Donor stump age	-0.0745	0.0004

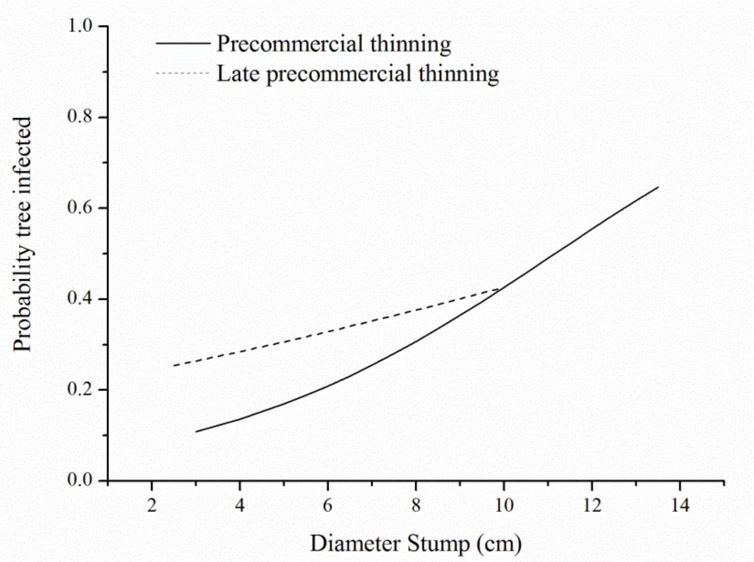

Figure 2. The estimated probability of a Norway spruce tree becoming infected by Rb175 (*H. parviporum*) from an adjacent Norway spruce stump depends on stump size. Solid line denotes a typical precommercial thinning, where trees were assumed to have the same diameter as the stumps; Dashed line denotes a late precommercial thinning, where trees were assumed to have a diameter of 10 cm.

3.3 Simulation of disease development to assess the economic outcome of stump treatment at precommercial thinning (paper II)

The aims of the study were to 1) adjust the stand growth module in RotStand to simulate the growth of young stands; 2) predict the development and impact of *Heterobasidion* spp. infection originating from precommercial thinning stumps in a Norway spruce stand over a rotation with different alternatives in the adjusted RotStand and 3) assess the economic outcomes of different control measures using the decision support system Heureka.

3.3.1 Adjusting growth simulation of young stands in RotStand

To properly simulate the development of young stands, a growth and yield model specified to young stands (Fahlvik & Nyström, 2006) was integrated into RotStand (Pukkala *et al.*, 2005) to simulate height and diameter increment of trees during stand establishment, i.e. between the age when tree height reached 1.3 m to when tree diameter at breast height (DBH) reached 15 cm.

After tree DBH reached 15 cm, the default growth and yield model by Söderberg (1986) in the original RotStand was used.

3.3.2 Simulation procedures in the adjusted RotStand

Infection, spread and decay development of *Heterobasidion* spp. were simulated using the adjusted RotStand. The default parameters for probabilities of infection and disease transfer and the rate of spread of decay were used (Pukkala *et al.*, 2005) (Table 2). All other changes are noted as follows. All infection was assumed to be caused by *H. parviporum*. The rate of disease spread in roots of a living tree was set to 0.2 m year^{-1} (Oliva & Stenlid, 2011). The probability of logging injury was set to 0 at all thinnings to show the sole impact of *H. parviporum* infection.

Table 2. *Parameter settings for Heterobasidion spp. dynamics in RotStand.*

Parameters	Values
Percentage incidence of *Heterobasidion parviporum* (%)	100
Rate of spread of decay in tree root (m year^{-1})	0.2
Probability of logging injury	0
Probability of stump infection by spores at commercial thinning	0.3
Efficacy of control measures	0.9
5-year probability of disease transfer from infected tree-to-tree	0.1
5-year probability of disease transfer from infected stump-to-tree	0.3
Rate of spread of decay in stump root (m year^{-1})	0.5
Probability of infected stump to transfer infection to adjacent trees or stumps	0.5

The simulation of a stand started at the age of 10 years with a basal area of 2 m^{2} ha^{-1} and an average height of 2 m. To compare the effect of *H. parviporum* infection through precommercial thinning stumps on timber production at rotation, a precommercial thinning was simulated with various parameters (Table 3). Further stand management was set according to the thinning guide for Norway spruce in southern Sweden (Skogsstyrelsen, 1984), i.e. three commercial thinnings conducted at a stand age of 30, 40 and 50 years with stump treatment, and a final felling at 75 years without stump treatment. The size of the simulated stands was 40 m × 40 m, and all stands were situated on forest land with a site index (dominant height at 100 years for Norway spruce) of 32 m.

The effects of factors such as stand age at precommercial thinning, precommercial thinning intensity, probability of stump infection and the efficacy of control measures on disease development were simulated. The effect from each factor was studied by altering the value of the focal factor while keeping the values of all other factors constant (Table 3). To compare decay frequency at final felling and total revenue of the whole rotation, alternatives with three different decay frequencies from the previous rotation and six different management options for precommercial thinning were also simulated as follows. The effect of decay from the previous rotation was simulated with decay incidences of 0%, 20% and 70%, representing a non-infested condition, an average condition in southern Sweden (Thor *et al.*, 2005) and a highly infected condition (Rönnberg & Jørgensen, 2000), respectively. The management options for precommercial thinnings included precommercial thinning at the age of 10 and 20 years during the summer, with and without stump treatment, or precommercial thinning during the winter without stump treatment. Each management option was simulated for each of the previous decay levels. Ten repetitions were run for each of the 36 alternatives in total.

Table 3. *Detailed settings of simulated alternatives for precommercial thinning (PCT) to investigate the effects of stand age, intensity and probability of spore infection at PCT and the efficacy of stump treatment.*

	Values of parameters				
Factors investigated	Stand age (yrs)	Intensity (stem ha^{-1} before and after PCT)	Prob. of infection	Treatment efficacy (%)	Treatment at PCT
Stand age at PCT	10, 20, 25	3000-2500	0.3	90	No
Intensity of PCT	20	2600-2500, 3000-2500, 3600-2500, 2100-2000, 2500-2000, 3000-2000	0.3	90	No
Prob. of infection	20	3000-2500	0.1, 0.2, 0.3	90	No
Efficacy of stump treatment	20	3000-2500	0.3	90, 95, 100	Yes, No

3.3.3 Economic calculations

The simulated alternatives for precommercial thinnings with different decay levels in the previous rotation were used for subsequent economic analysis. The decision support system Heureka (Lämås & Eriksson, 2003; Wikström *et al.*, 2011) was used to compare the economic outcomes based on various decay conditions at rotation simulated in the adjusted RotStand. The pricelist for timber yield was recalculated for each commercial thinning and final felling in each alternative based on the percentage of decayed stems simulated in the adjusted RotStand.

The time needed for manual stump treatment at precommercial thinning was similar to the time for an experienced brush saw operator to do a precommercial thinning, i.e. doubling the time for precommercial thinning, according to a small field trial on four Norway spruce plots in southern Sweden. The cost for manual stump treatment at precommercial thinning was estimated at a price similar to the cost for precommercial thinning, i.e. 2460 SEK ha^{-1} (Skogsstyrelsen, 2012). The cost for stump treatment was estimated at 12 SEK m^{-3} sub (solid under bark) for the first commercial thinning and 10 SEK m^{-3} sub for the second and third commercial thinnings (Thor, 2011). The net revenues were summed as the overall cash flow, and were also calculated using discount rates of 2%, 3% and 4% to the beginning of the rotation.

The difference in percentage of decayed stems and economic outcomes was compared among different alternatives using one-way ANOVA in Minitab16 (Minitab Inc., State College, PA, USA) and pairwise comparison was done using Turkey's method. In the case of non-normality, the Kruskall-Wallis test was used with further pairwise comparison using Mann-Whitney's test.

3.3.4 Results

The probability of infection transfer before the first commercial thinning (30 years) increased with increasing precommercial thinning age. However, there was no significant difference in the percentage of decayed stems at final felling depending on the precommercial thinning age (p=0.136). A higher probability of spore infection of 0.3 did not result in a significantly higher decay frequency compared to probability of spore infection of 0.1 and 0.2 (p=0.072). A higher percentage of removal at precommercial thinning resulted in a higher decay frequency at final felling (p<0.001, Table 4). Irrespective of treatment at precommercial thinning, control efficacy influenced the decay frequency at final felling; higher control efficacy resulted in a lower decay frequency (p<0.001, Table 5). Stump treatment during precommercial thinning reduced the percentage of decayed stems with 100% and 95% control efficacy (p<0.001 and p=0.019, respectively). At an efficacy of 90%, the decay incidence did not differ between the treated precommercial thinning stumps and the non-treated (p=0.051).

When no decay and 20% decay occurred at the previous final felling, winter thinning at the age of 20 resulted in significantly lower frequency of decayed stems at the end of a rotation compared to summer thinning without treatment (p=0.018 and p=0.048, respectively, Fig. 3). However the difference was not significant when precommercial thinning was conducted at the age of 10 or when the stand was previously heavily (70%) infested with *Heterobasidion* spp.

Table 4. *Average percentage (and number) of decayed stems per hectare at final felling for different alternatives of precommercial thinning (PCT) intensities. Treatments that do not share a letter are significantly different at the level of 5%.*

Thinning intensity	Stem ha^{-1} before and after PCT	Percent removed (%)	Percentage (number) of decayed stems
Light	2600-2500	3.8	6.8 (46) b
Light	2100-2000	4.8	6.9 (42) b
Medium	3000-2500	16.7	22.3 (148) a
Medium	2500-2000	20.0	14.6 (88) ab
Heavy	3600-2500	30.6	23.9 (160) a
Heavy	3000-2000	33.3	23.0 (136) a

Table 5. *Average percentage (and number) of decayed stems per hectare at final felling for different alternatives of control efficacy of stump treatment during the summer for stumps treated or not treated during precommercial thinning (PCT). Commercial thinnings are all treated with the same control efficacy as the corresponding precommercial thinning. Treatments that do not share a letter in a column are significantly different at the level of 5%.*

Efficacy of treatment at commercial thinning and PCT (%)	Percentage (number) of decayed stems	
	Stumps not treated at PCT	Stumps treated at PCT
100	4.8 (33) a	0 (0) a
95	15.5 (106) b	8.8 (60) b
90	22.2 (117) b	12.7 (55) b

From an economic standpoint, using a 3% discount rate, precommercial thinning during the summer with stump treatment resulted in lower net present values compared to summer and winter thinnings without treatment, irrespective of stand age at precommercial thinning and the decay level at the previous rotation (Fig. 3). With a discount rate of 2% or 4%, the economic outcomes of different management options did not differ from that with a discount rate of 3%. However, when the economy was calculated using cash flow, i.e. with a discount rate of 0%, on stands without previous decay the three alternatives of precommercial thinnings resulted in similar outcomes. On previously infested stands, stump treatment during summer precommercial thinning was less profitable than conducting a summer or winter thinning without stump treatment.

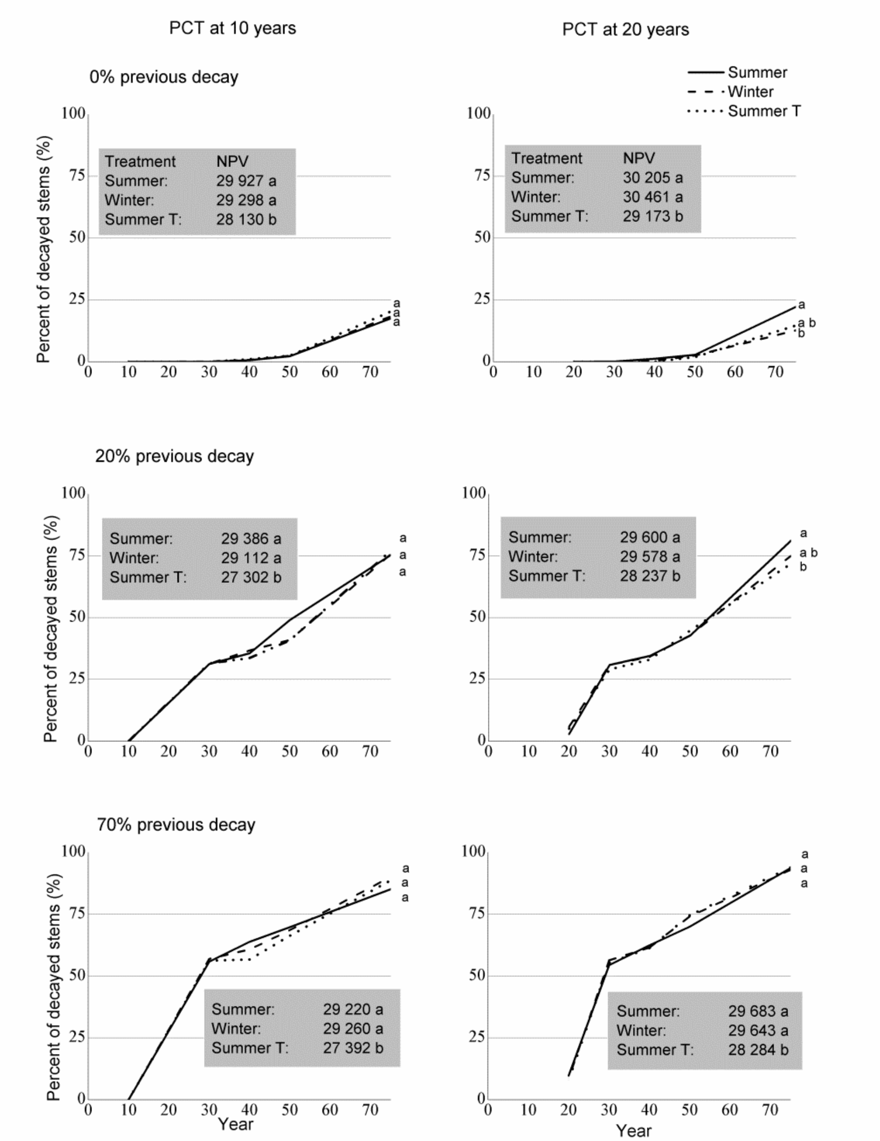

Figure 3. Decay frequency depending on the age, season, and treatment of precommercial thinning (PCT) for sites with different levels of decayed stems at the previous rotation. Solid line denotes PCT during the summer; dashed line denotes PCT during the winter; and dotted line denotes PCT during the summer with stump treatment. Total net present values (SEK ha^{-1}) for thinnings and final felling with a 3% interest rate discounted to the beginning of the rotation are shown in the grey boxes. Different letters denote significant differences at the level of 5%.

3.4 Soil assessment in association with high incidence of *Heterobasidion* spp. in Scots pine stands

The objectives of the study were to 1) investigate soil properties in association with high incidence of infection by *Heterobasidion* spp. on Scots pine stands, and 2) determine the criteria for rating site-level hazard for infection by *Heterobasidion* spp.

3.4.1 Materials and methods

Soil samples were collected from 13 pure Scots pine stands (stand age ranged between 27 and 56 years) in southern Sweden (sites P1-P13 in Fig. 1) in 2009. At each site, ten soil pits systematically located were dug and soil samples were collected from the humus layer and a mixed sample of mineral soil from 10, 20 and 30 cm depths. Additional samples were taken at 50 cm depth from three soil pits on each site. The soil pH was measured at the laboratory using an electrode immersed in soil-water suspensions. Mineral soil samples were dried at 30 °C for 24 hours. Organic matter content of the mineral soil was measured as the weight loss after ignition (at 650 °C for one hour). Soil texture, measured as the distribution of sand, silt and clay, was performed by sedimentation and wet sieving of the 50-cm depth samples. Other site variables such as ground vegetation, exposure and steepness of slope were also recorded. Site index, previous land use and the incidence of *Heterobasidion* spp. were obtained from an earlier study (Rönnberg *et al.*, 2006a). Sites in Rönnberg *et al.* (2006a) that were classified as high incidence sites had at least three of the four trees sampled in two plots together infected by *Heterobasidion* spp. The remaining sites were considered to have low disease incidence. Soil pH at 50-cm depth and in the mineral soil mixture was square root transformed to ensure normality. The difference between soil characteristics of high and low incidence sites was compared using a t-test in Minitab16.

3.4.2 Results

Ten out of 13 Scots pine sites were classified as high incidence sites and three as low incidence sites (Table 6). Of the ten high incidence sites, eight were located on former agriculture land, one on former pasture land and one on forest land. Low incidence sites were former pasture and forest lands. On high incidence sites, the soil pH was generally higher and organic matter content was significantly lower (p<0.012) than on low incidence sites (Table 6). Clay content was significantly lower on high incidence sites (p=0.006), while sand and silt content showed no difference between the high or low incidence sites.

There was no correlation between disease incidence and other site variables i.e. ground vegetation, exposure, steepness of slope or site index.

Table 6. *Soil pH (at humus layer, at 50-cm depth and with a mixture of mineral soil from 10, 20 and 30-cm depths), organic matter content (at 50-cm depth and with a mixture of mineral soil from 10, 20 and 30-cm depths) and the soil texture (at 50-cm depth) of high and low incidence sites. Ranges of the values are shown in brackets.*

Incidence level	No. of sites	Mean pH at humus layer	Mean pH of mineral soil mixture	Mean pH at 50 cm	Organic matter content at 50 cm (%)	Organic matter content of mineral soil mixture (%)	Sand content (%)	Silt content (%)	Clay content (%)
High	10	5.4 (4.8-6.0)	5.7 (5.3-6.7)	5.9 (5.4-6.8)	1.3 (0.7-2.4)	1.6 (1.0-2.8)	86 (64-98)	13 (2-33)	1 (0-3)
Low	3	4.7 (4.5-5.1)	5.2 (5.1-5.3)	5.3 (5.0-5.7)	3.0 (2.1-4.7)	3.6 (2.7-4.7)	77 (68-87)	19 (11-27)	4 (2-5)
p =		0.031	0.060	0.002	0.012	0.001	0.263	0.384	0.006

3.5 Stand-level surveys to detect growth loss in Scots pine

In this study the objective was to detect whether trees with obvious signs of *Heterobasidion* spp. differ in growth compared to the average growth of the stand in order to estimate the effect of the disease on stand productivity.

3.5.1 Methodology and results

Field surveys were conducted in four mid-rotation monoculture Scots pine plantations, in southeastern Sweden (sites P15-P18 in Fig. 1) in 2011. Infection of *Heterobasidion* spp. was prevalent on all sites as indicated by the presence of disease centers, i.e. aggregation of dead trees and basidiocarps on thinning stumps. In each stand, line-transects were run at 15-meter intervals and any tree within a 5-meter radius that appeared symptomatic, i.e. with chlorotic needles, defoliation and asymmetric crowns (Kurkela, 2002), was investigated for the presence of basidiocarps by removing the surface vegetation and soil around the base. Stumps were also examined and when basidiocarps were found, the neighboring trees were investigated even if outside the transect boundaries.

Across all sites, 240 symptomatic trees were investigated for the presence of basidiocarps at the stem base. Of those, only seven trees at site P15 (12%) and one tree at site P16 (2%) had basidiocarps. The average incidence of trees showing basidiocarps of *Heterobasidion* spp. as a proportion of the total number of symptomatic trees was 3%. Due to the low presence of basidiocarps, any attempt to compare growth of diseased trees with the average growth of stands was deemed impossible. Thus, more reliable methods were needed to assess the impact of *Heterobasidion* spp. on growth of Scots pine (see Section 3.6).

3.6 Severity and distribution of root infection by *Heterobasidion* spp. and its impact on growth of Scots pine trees (paper III)

The study aimed at 1) determining the relationship between aboveground symptoms in Scots pine trees and belowground incidence caused by *Heterobasidion* spp. by examining the whole root system; 2) detecting any correlation between the growth characteristics of trees and the severity of root infection; 3) determining the influence of infection by *Heterobasidion* spp. on volume growth.

3.6.1 Materials and methods

Two circular plots each with a radius of 8 m were established in a 36-year-old first rotation Scots pine plantation in south-eastern Sweden (site P14 in Fig. 1). The site was formerly pasture land with sandy, alkaline soil (pH = 6.2 and sand content = 88%), and with a site index of 30 m. Each of the two plots was centered around a stump with and without basidiocarps, and were considered as diseased or healthy, respectively. Tree diameter, height, needle retention and crown area were measured. A total of 24 trees with root systems intact were extracted from the two plots using a single-grip harvester. The soil and roots smaller than 0.5 cm in diameter were removed from the root systems. Stem discs were cut at 0m, 0.5 m, 1 m, 1.3 m (breast height), 2 m and then at every 2 m interval until the stem diameter was less than 5 cm. Annual volume increment was retrospectively calculated from the stem discs using the computer software WinDendro (2005, Régent Instruments Inc., Canada) and WinStem (2005, Régent Instruments Inc., Canada).

Roots were transported back to the lab and the length and diameter of primary, secondary and tertiary roots were measured. A 5-cm root disc was sampled at every 25-cm length interval to check the presence of *Heterobasidion* spp. using a dissecting microscope after an incubation period of 7-10 days at room temperature (~20°C). If the sampled root section was infected by

Heterobasidion spp., the entire 25-cm root length was also regarded as infected. The proportion of infected root volume of each tree was calculated as the volume of infected root segments in proportion to the total root volume. Infected trees were categorized into lightly and highly infected groups using infection classes above and below the median proportion of infected root volume. Relative volume growth (RVG) of each year was calculated as the current annual volume growth in proportion to the total tree volume at the beginning of that year. To account for different competition status in the plots, relative DBH, i.e. the ratio between tree size and the average size of all trees in each plot (Pukkala, 1989), was computed.

The difference in growth characteristics of the trees, i.e. DBH, height, tree volume, crown area, needle retention, total root volume and the proportion of infected root volume, between the two plots was investigated using a t-test in Minitab 16. The relationship between each growth characteristic and the proportion of infected root volume was tested using Pearson's correlation. All statistical analysis was performed with a significance level of 5%.

A mixed-effect regression model in SAS 9.3 was fit to estimate annual volume increment of a tree, using the tree growth characteristics and root infection conditions as independent variables. The variables included in the model were: tree volume in 2002 (V2002), relative DBH in 2011 (RelDbh) and percentage of infected root volume (Damage). All variables were scaled for analysis. Time was considered as a continuous variable. Since there was an increase in volume increment in 2009 due to the thinning, that year was chosen as the center of the year variable. The change in growth pattern over years was expressed using a quadratic function. The model was fit to an initial dataset including measurement of annual volume increment from the year 2002 to 2011. The measurement from the earliest year in the dataset was extracted until the percentage of infected root volume (Damage) was included in the model, indicating the point at which damage in the root system started to negatively impact volume growth. The model of annual volume increment is given as:

$$y_{ijk} = \beta_0 + \beta_1 V2002_{ij} + \beta_2 RelDbh_{ij} + \beta_3 Damage_{ij} + \beta_4 year_{ijk} + \beta_5 {year_{ijk}}^2 + a_{0j} + a_{1j} plot_j + b_{0i} + b_{1i} tree_i + \varepsilon_{ijk}$$

where y_{ijk} is the annual volume increment (dm^3) of tree *i* in plot *j* at year *k*. β_0 is the intercept. β_1 is the fixed effect of tree volume in 2002, β_2 is the fixed effect of relative DBH in 2011 and β_3 is the fixed effect of percentage of infected root volume for tree i in plot j measured in 2011. β_4 and β_5 are the linear and quadratic parameters of the year centered around 2009 for tree i in plot j at year k, respectively. a_{0j} is the random intercept for plot j, and a_{1j} is the random effect of plot j. b_{0i} is the random intercept for tree i, and b_{1i} is the random effect of tree i. ε_{ijk} is the residual error.

3.6.2 Results

Twelve trees were sampled in each of the healthy and diseased plots. Mean disease incidence across both sites was 87.5% (75% in the healthy plot and 100% in the diseased plot). The two plots did not differ in growth characteristic of trees or disease severity. The average proportion of infected root volume was 9.7% (min: 0% and max: 32.2%). A total of 1899 root sections with a diameter larger than 1 cm were examined for the presence of *Heterobasidion* spp., and 7% (n=135) were infected. Discoloration and resin staining was sometimes observed on infected root sections. A higher percentage of infection occurred on root sections located closer to the root collar (Fig. 4).

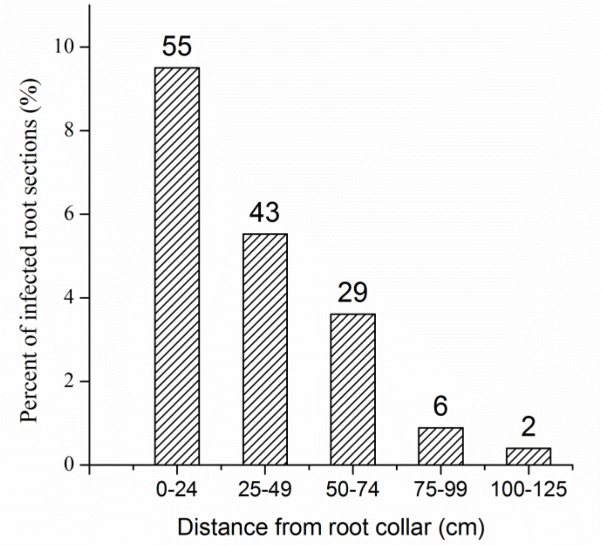

Figure 4. Percentage of root sections infected by *Heterobasidion* spp. at different distances distal to the root collar as a proportion of the number of root sections present at the corresponding locations. The numbers above bars are the number of infected root sections.

The proportion of infected root volume was negatively correlated with RVG in 2011 (R=-0.541, *p*=0.006) for all sampled trees. For all trees, the most recent 5-year RVG (2007-2011) was lower than the previous 5-year period (2002-2006), and the reduction was positively correlated with the proportion of infected root volume (R=0.526, *p*=0.008). There was no correlation between the proportion of infected root volume and the growth characteristics, such as DBH, height, total tree volume, total root volume, crown area or needle retention. Trees with needle retention higher than the median had though a lower proportion of infected root volume (*p*=0.018). Infected trees had significantly larger DBH and total tree volume compared to healthy trees (*p*=0.033 and *p*=0.013, respectively). The lightly infected trees (i.e. trees with less than 10% of infected root volume) had significantly larger DBH than highly infected trees (*p*=0.042).

The model was fit to a dataset that included the measurement of volume increment from 2005 to 2011. Annual volume increment decreased with increasing infection in the roots (Table 7). For example, with 10 % root volume infected, 1.427 dm^3 of volume increment was reduced compared to if it had no infection. Assuming the amount of infection increases linearly from 0 % (at 2005) to the average and maximum proportion of infected root system at 2011, the annual volume increment in 2011 of an intermediate tree (relative DBH=1) with 10 % root infection was reduced by 12.6 % , and by 22.6 % for a large tree (relative DBH=1.33) with 32 % infection (Fig. 5).

Table 7. *Parameter estimates for the mixed model predicting the annual volume increment of Scots pine trees in the two plots.*

Parameters	Estimates	P value
RelDBH	0.3405	<0.0001
V2002	-0.5251	0.0123
Damage	-0.1427	0.0195
Centeryear	-0.08052	0.0003
Centeryear square	-0.04155	<0.0001
Intercept	-12.7546	

Tree tapering, indicated by the height-to-diameter ratio was lower for diseased trees than healthy trees, and a divergence between the two curves was apparent after 2005 (Fig. 6a). Lightly infected trees appeared to follow the same trend as healthy trees, while highly infected trees showed a decline in height-to-diameter ratio after 2005, suggesting a more tapered stem form. The diameter increment of infected trees for the last three years declined sharply compared to healthy trees (Fig. 6b). Though height increment showed a slight decline on all trees (both infected and healthy) over the years, the decline was markedly greater after 2005 for highly infected trees (Fig. 6c).

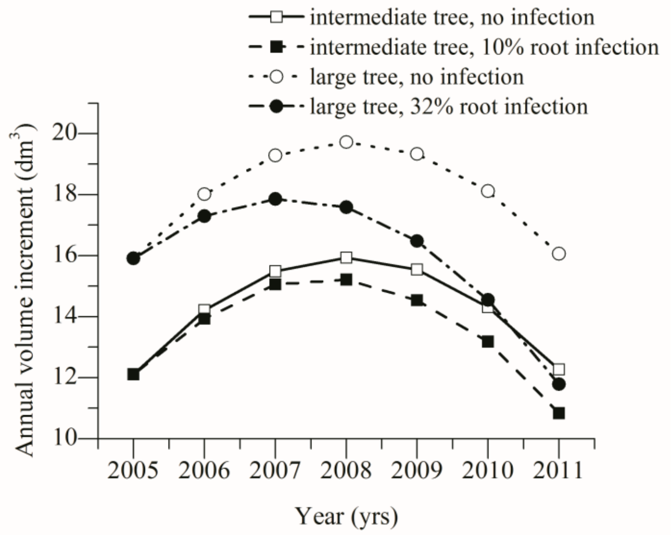

Figure 5. Estimated annual volume increment for an intermediate tree (relative DBH=1) and a large tree (relative DBH=1.33) with no infection, compared to 10 % and 32 % of root volume infected in 2011, respectively. The amount of root volume infected was assumed to increase linearly from 0% in 2005 (3 years after the first thinning in 2002 which was considered the first entry point of *Heterobasidion* spp. in the stand).

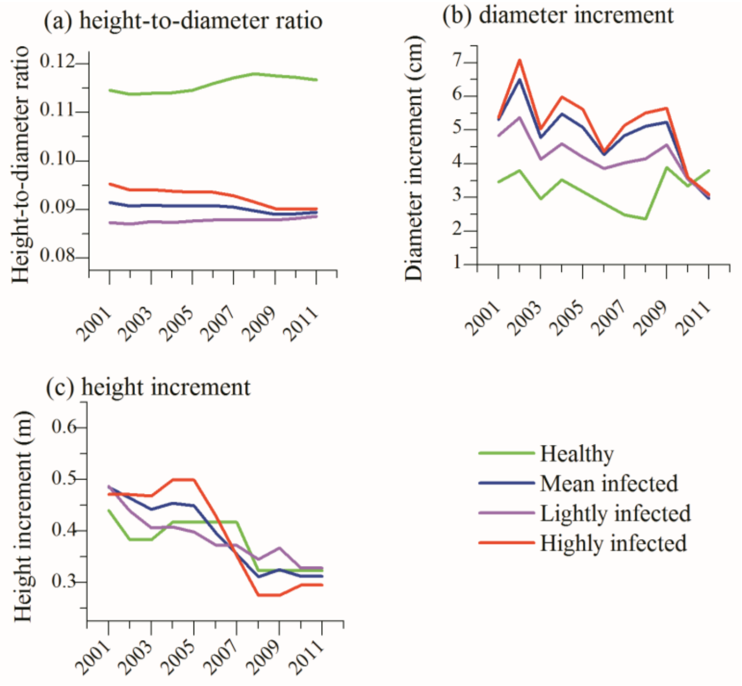

Figure 6. Annual a) height-to-diameter ratio, b) diameter increment and c) height increment of healthy, infected, lightly and heavily infected trees between 2001 and 2011.

3.7 Efficacy of stump treatment with urea and *P. gigantea* on hybrid larch stumps *in situ* (paper IV)

The objective of this study was to compare and quantify the efficacy of *P. gigantea* and urea in preventing the establishment of *Heterobasidion* spp. on hybrid larch stumps *in situ,* in order to determine the optimal treatment agent for use.

3.7.1 Materials and methods

The study consisted of two experiments and involved ten monoculture hybrid larch stands. In the first experiment, 75 healthy-looking hybrid larch trees were randomly felled with a chainsaw at five sites (sites L1-L5 in Fig. 1). Twenty five stumps were treated with a 40% urea solution, 25 were treated with a suspension of *P. gigantea*, and the remaining 25 were left untreated (i.e. control). In the second experiment, 40 trees were randomly cut on each of the five sites (sites L6 to L10 in Fig. 1). Half the stumps were treated with a suspension of *P. gigantea* and the other half were exposed to natural infection. On each site, ten sets of woody spore traps, each set consisting of a fresh stem disc of Norway spruce, Scots pine and hybrid larch, were placed close to the control stumps and exposed for 2 to 3 hours to detect the presence of *Heterobasidion* spp. basidiospores. Sampling of stump discs was conducted after three months in the first experiment and after two months in the second experiment. A disc from each of the stumps was sampled to detect any infection coming from the roots. On stump discs and spore traps, the incidence of *Heterobasidion* spp. was checked under a dissecting microscope after an incubation period of 7 to 10 days at room temperature (~20°C), and colony area was measured. Up to two and five isolates were isolated from stump discs and spores traps, respectively. The species of *Heterobasidion* was determined by the ability of the isolate to heterokaryotize homokaryotic mycelia of *H. annosum* s.s. and *H. parviporum* testers after 3 weeks.

The incidence of infected stumps, the control efficacy, relative infected area and total infected area were used to assess the efficacy of both stump treatment agents. The difference in control efficacy, relative and total infected area among treatments was tested using general linear model in Minitab16. The difference in incidence of infected stumps was tested using the binary logistic regression model. Pearson’s correlation was made between infections on hybrid larch control stump discs and each of the species spore traps that were placed close to the corresponding control stumps. Fisher’s exact test was used at a significance level of 5% to compare the proportion of *Heterobasidion* species between two treatments and to compare the spatial distribution of colonies on discs for different treatments and for different *Heterobasidion* species.

3.7.2 Results

The incidence of *Heterobasidion* spp. on stumps treated with urea was lower ($p<0.001$) compared to *P. gigantea*-treated stumps and the control (Table 8). *Phlebiopsis gigantea* was effective at reducing incidence of infection ($p=0.007$), relative infected area ($p=0.031$) and total infected area ($p=0.020$) in the second experiment but not in the first (Table 8). Sites L2 and L5 (29% and 74%) had a higher frequency of infected control stumps than the other three sites (ranged between 4% and 8%) in experiment I.

Table 8. *Incidence, relative and total infection area of Heterobasidion infection and control efficacy on stumps treated with Phlebiopsis gigantea (P.g.), urea, and on the control (C) discs in experiment I and experiment II. Different letters denote differences at a significant level of 5%.*

	Incidence (%)			Control efficacy [a] (%)		Relative inf. area (%)			Tot. inf. area (cm^2)		
Sites	Urea	P. g.	C	urea	P. g.	urea	P. g.	C	urea	P. g.	C
L1	4	0	8	63.9	100	0.5	0	0.6	0.5	0	1.3
L2	4	74	74	99.5	66.7	0.3	1.7	4.7	0.5	31.3	87.0
L3	8	4	8	-5.2	68.3	0.9	0.6	0.9	1.8	0.5	1.5
L4	0	0	4	100	100	0	0	1.3	0	0	2.0
L5	4	13	29	95.3	25.5	0.5	1.0	0.6	0.5	8.5	11.3
Mean	4.0**a**	18.2**b**	24.6**b**	70.7	72.1	0.6**a**	1.6**a**	3.0**a**	1.0**a**	16.7**a**	39.6**a**
L6		6	28		83.6		0.3	0.4		0.5	3.0
L7		6	27		89.9		0.4	0.7		0.5	4.5
L8		12	47		91.6		0.8	1.6		1.0	12.0
L9		17	32		72.2		0.5	0.6		1.5	5.5
L10		11	28		82.7		0.6	1.2		1.5	8.5
Mean		10.1**a**	32.2**b**		84.0		0.4**a**	1.0**b**		1.0**a**	6.7**b**

[a] control efficacy was calculated as the reduced relative infected area by treatment compared to the control (Berglund & Rönnberg, 2004)

Infections on stumps and spore traps were caused by both *H. parviporum* (39% and 60% in experiment I and II, respectively) and *H. annosum* s.s. (61% and 40% in experiment I and II, respectively). In the first experiment, the amount of *H. annosum* infection in proportion to *Heterobasidion* spp. was significantly lower on stumps treated with *P. gigantea* compared to the control ($p=0.027$), however the proportion of *H. parviporum* on the treated stumps was not higher than the control (Table 9).

Table 9. *Number and proportion (%) of Heterobasidion annosum s.s. and H. parviporum colonies on stumps treated with Phlebiopsis gigantea (P.g.), urea and on the control stumps in experiment I and II. Note that statistics for the different experiments are separated. Different letters denote differences of the proportion of a specific fungal species on stumps with different treatments, i.e. in each row, at a significant level of 5%.*

	Experiment I				Experiment II		
	P. g.	urea	control	total	P. g.	control	total
H. annosum	2 (22) **b**	5 (83) **a**	10 (77) **a**	17 (61)	3 (25) **a**	17 (45) **a**	20 (40)
H. parviporum	7 (78) **a**	1 (17) **a**	3 (23) **a**	11 (39)	9 (75) **a**	21 (55) **a**	30 (60)

There was a significant difference among all treatments in the spatial distribution of infections on discs, i.e. in the heartwood, heartwood-sapwood boundary and sapwood. Infection in the heartwood was only found on stumps treated with urea or *P. gigantea*, not on the control stumps, and only caused by *H. annosum* s.s.

Scots pine spore traps had significantly higher (*p*=0.002) infection frequency than Norway spruce and hybrid larch (Table 10). *Heterobasidion annosum* s.s. colonized a larger area on Scots pine spore traps than on Norway spruce and hybrid larch spore traps (*p*=0.039 and *p*=0.043, respectively), however this host specialization was not observed for *H. parviporum* (Table 10). Of all the species tested only hybrid larch showed a significant correlation in relative infected area between spore traps and control stumps (*p*=0.006), suggesting that spore traps made from the same species as control stumps can serve as a reliable indicator for the abundance of *Heterobasidion* spp. basidiospores that may germinate on the stumps.

Table 10. *Infection by H. annosum s. s. (H.a.) and H. parviporum (H.p.) on the different species of spore traps. Different letters denote differences among species of spore traps, i.e. in each column, at a significant level of 5%.*

Trap species	Infection Freq. (%)	Relative inf. area (%)	Total inf. area (cm^2)			Ave. colony size (cm^2)		
			H. a.	*H. p.*	total	*H. a.*	*H. p.*	total
Scots pine	98 **a**	25.5 **a**	54.1 **a**	36.1 **a**	93.2 **a**	3.2 **a**	2.5 **a**	2.8 **a**
Norway spruce	79 **b**	2.4 **b**	11.8 **b**	11.9 **a**	24.2 **b**	1.6 **b**	0.9 **a**	1.4 **b**
hybrid larch	63 **b**	5.5 **b**	12.9 **b**	14.4 **a**	27.3 **b**	1.2 **b**	1.3 **a**	1.3 **b**

4 General discussion

The studies in this thesis were focused on the effect of *Heterobasidion* spp. infection on the host species, e.g. Norway spruce, Scots pine and hybrid larch, as well as the efficacy and economic benefit of stump treatment in order to give recommendations for forest management against root rot. There are a number of interesting issues to consider, e.g. disease spread and subsequent decay development through precommercially thinned Norway spruce stumps and stem growth reduction in Scots pine caused by root infection of *Heterobasidion* spp.

4.1 Some new findings of disease impact on host species

4.1.1 Secondary infection and decay in Norway spruce stems

Paper I showed the ability of very small Norway spruce stumps to transfer infection of *H. parviporum*, suggesting that the risk of introducing infection at precommercial thinning cannot be ignored. This conclusion is also supported by the simulation in Paper II, which showed that when precommercial thinning was conducted during the summer without stump treatment on average 4.8% of the trees may be decayed at the end of a rotation even when all commercial thinning stumps were properly treated (efficacy of treatment with *P. gigantea* was 100%). These results conflict with the traditional assumption that stumps created at precommercial thinning are of little importance for disease spread (Vollbrecht *et al.*, 1995a). The probability that a Norway spruce stump becomes infected increases with the diameter of the stump (Paludan, 1966). Thus it can be assumed that the probability of stump infection at a precommercial thinning is lower than at a commercial thinning, though this probability may vary under different conditions due to the varied availability of ambient spores at the time of experiments (Redfern & Stenlid, 1998). For example, Berglund *et al.* (2007) reported up to 40% of small sized Norway spruce stumps were infected by *Heterobasidion spp.* after precommercial thinning, while Bendz-Hellgren and Stenlid (1998) reported a low incidence of only 1%. In the simulation (Paper II), even with a lower probability of spore infection (at 0.1 and 0.2), the decay frequency at final felling was not significantly reduced compared to a higher probability of spore infection at 0.3. As a result, regardless of probability of spore infection on stumps, infection by *H. parviporum* through precommercial thinning stumps can negatively influence timber yield at rotation, i.e. the importance and spread of a few infections early in a rotation cannot be neglected.

The probability of disease transfer between an infected stump and tree depended on the size of both stump and tree (Paper I). Results from this study and Morrison and Johnson (1999) suggest that larger trees with more extensive root systems are more likely to contact inoculum than smaller trees. In Paper II, the frequency of disease transfer also increased with increasing stand age at precommercial thinning. According to the estimation derived from the model in Paper I, when the stumps and trees have the same diameter, cutting an older Norway spruce stand with a mean diameter of 10 cm will have twice as high a probability of disease transfer compared to a younger stand with a mean diameter of 6 cm, and four times as high a probability of disease transfer compared to a younger stand with a mean diameter of 3 cm (Fig. 2). Given the same size of the trees removed in a late precommercial thinning, where the remaining trees have a larger diameter than the trees removed, the probability of trees becoming infected is even higher (Fig. 2). Hence, to reduce the spread of *Heterobasidion* spp. infection in Norway spruce, conducting precommercial thinning when tree diameters are small is recommended.

However, both the amount of infection that is able to spread to adjacent trees as well as the timing of infection will influence the long-term impact of the disease at final felling. Precommercial thinning at an early age, e.g. 10 years could potentially lead to more severe decay considering that infections that manage to get established early in a rotation have longer time to grow before the final felling (Greig & Pratt, 1976; Kåre & Solheim, 1993). On the other hand, at an early precommercial thinning, when the stump diameter is usually small, the probability of disease transferring to an adjacent tree is lower than in a later precommercial thinning (Fig. 2). Both the time for disease to develop and the probability of disease transfer are associated with stand age at precommercial thinning, and they have counteracting effects on disease frequency at final felling. As a result, in Paper II, stand age at precommercial thinning did not affect long-term disease impact.

An increasing precommercial thinning intensity can though result in a higher decay frequency at final felling (Paper II). Heavier precommercial thinning exposes a larger area of fresh stump surfaces and suggests a higher probability of *H. parviporum* colonizing stumps leading to an increase in decay incidence. In Paper II, the heaviest thinning intensity simulated was 33.3%. In practice, the percentage removed can be even higher considering the stand being more dense at the time of thinning due to the naturally regenerated Norway spruce. In these cases the probability of stump infection and subsequent spread of disease could potentially be even higher than was simulated in Paper II. Cutting the naturally regenerated birch (*Betula* spp.) is a also common practice for precommercial thinning in Norway spruce dominated stands in Sweden (Fahlvik, 2005). Since stump infection on birch is negligible (Bendz-Hellgren, 1997), the possibility of infection on birch stumps was not considered. It is plausible that removing the naturally regenerated birch in a spruce-dominated stand could result in a lower decay frequency.

Traditionally, a higher number of Norway spruce seedlings are planted to compensate for the damage to seedlings during the regeneration phase. However, improvements in techniques for protecting seedlings have recently been implemented in practice, reducing both the need and cost for planting at higher density (Nilsson *et al.*, 2010), and also the percentage removed during precommercial thinning on stands without natural regeneration. This practice is beneficial also from a root disease management perspective, since the probability of infection decreases with lower intensity of precommercial thinning. Thus, one management option to reduce the risk of *Heterobasidion* spp. infection through precommercial thinning is to plant the target number of Norway spruce seedlings after precommercial thinning.

4.1.2 Stem growth loss caused by *Heterobasidion* spp.

When trees are infected, both the quality of the wood and also growth of trees are negatively affected. This was suggested for Scots pine (Burdekin, 1972), but not quantitatively measured, as what has been done for Norway spruce (Bendz-Hellgren & Stenlid, 1997). The results from Paper III showing reduced stem volume growth in Scots pine trees infected by *Heterobasidion* spp. are in agreement with that reported for other pine species including loblolly pine (Bradford *et al.*, 1978a; Bradford *et al.*, 1978b) and slash pine (Froelich *et al.*, 1977). There are two possible mechanisms that could result in the stem growth loss following infection: loss of root function and induction of defense mechanisms leading to decreased allocation of assimilates to stem growth. Fungal growth in roots causes occlusion of tracheids (Joseph *et al.*, 1998) and impaired water and nutrient uptake which usually leads to shedding of needles in conifers and subsequently reduces carbon assimilation through photosynthesis (Kozlowski & Pallardy, 1997).

The amount of volume growth of Scots pine was correlated with infection severity in the roots (Paper III). However, Bradford *et al.* (1978b) examined whole root systems but did not find such a relationship in loblolly pine infected by *Heterobasidion* spp. at the plot level, though he only considered the percentage of root length infected. Larger roots are more frequently infected by *Heterobasidion* spp. than smaller roots (Paper III**,** Garbelotto et al., 1997), and they are usually more involved in the transportation of water and nutrients compared to smaller roots (Kozlowski & Pallardy, 1997). As a result, dysfunction caused by *Heterobasidion* spp. of the larger roots may have a greater impact on aboveground tree growth. In addition, since the growth of trees infected by *Heterobasidion* spp. can be reduced abruptly before death (Cherubini *et al.*, 2002), it is plausible to assume that highly diseased trees, such as those with greater than 30% of the root volume infected, are likely to succumb to mortality. However, lightly infected trees may survive for decades and remain asymptomatic but with reduced productivity overall. Such losses can be significant over a rotation, and thus would need further attention. The reduced volume increment in Scots pine caused by *Heterobasidion* spp. in 2011 can be tentatively estimated. Assuming a 36-year-old Scots pine plantation with trees of the similar size and infection levels, i.e. 87.5 % of the trees infected having 10% of root volume infected, the annual growth reduction under similar conditions as in 2011 could amount to 0.87 m^3 ha^{-1}, corresponding to approximately 9.9% of the average annual volume increment per hectare in a similar Scots pine stand, i.e. with site index of 30 m (Skogsstyrelsen, 1984).

In practical forestry, the question regarding disease development on different stand types from the one in paper III (e.g. former forest land with acid soil) still remains unanswered. However, it does not seem far-fetched to expect growth losses of living Scots pine trees also in such stands. It is well known that stumps of Scots pine become infected by both *H. annosum* s.s. and *H. parviporum* (Rönnberg *et al.*, 2006a). These stump infections clearly will have the ability to spread to neighboring trees or seedlings. The infected trees may appear asymptomatic, but the disease may very likely present in the roots in high levels impacting stem growth.

Volume increment reduction, as a combination of reductions in both diameter and height increment occurred on Scots pine trees infected by *Heterobasidion* spp. (Paper III), similar to Norway spruce (Bendz-Hellgren & Stenlid, 1997; Oliva *et al.*, 2010), loblolly pine (Bradford *et al.*, 1978a) and slash pine (Froelich *et al.*, 1977). For diseased Scots pine and Norway spruce, height increment is further reduced compared to the diameter, resulting in a stronger tapering of the stem. Bloomberg and Wallis (1979) observed similar results on Douglas-fir infected by *Phellinus sulphurascens* suggesting a lower competitive ability of diseased trees compared to healthy trees and less desirable stem form, reduced wood utilization, and lower timber product value (Malinen *et al.*, 2007).

4.1.3 Susceptibility to *Heterobasidion* spp.

The susceptibility to spore infection of *H. annosum* s.s. varies for different host species (Greig, 1962). Spore traps in the form of excised stem discs, from Scots pine were more susceptible to infection by *H. annosum* s.s. than discs of Norway spruce and hybrid larch (Paper IV). Greig (1962) found that in mixed plantations, Scots pine stumps had a higher incidence of infection by *H. annosum* s.s. than other host species, including Norway spruce and European larch (*Larix decidua* Mill.). Werner and Łakomy (2002b) also found *H. annosum* s.s. to be more virulent on Scots pine seedlings than on Norway spruce and true fir seedlings. These results suggest that under the same environmental conditions, Scots pine stumps are more susceptible to *H. annosum* s.s. infection than hybrid larch and Norway spruce stumps, but susceptibility is similar between the latter two species. Since Norway spruce stumps are generally treated during commercial thinning in practice, it is also recommended to consider preventive measures against primary infection on Scots pine and hybrid larch stumps.

Hybrid larch stumps are susceptible to basidiospore infection of *Heterobasidion* spp., as indicated by the high frequency of infection on the control stumps (74%) in Paper IV. Primary infection was caused by both *H. annosum* s.s. and *H. parviporum*. No secondary infection by *H. parviporum* in hybrid larch stands has previously been reported (Rönnberg & Vollbrecht, 1999; Vollbrecht & Stenlid, 1999; Rönnberg *et al.*, 2007), though Piri (1996) showed that *H. parviporum* was able to spread between Siberian larch and Norway spruce. There may be a risk that preexisting inoculum of *H.*

parviporum in hybrid larch stumps can infect neighboring Norway spruce trees, but this still remains to be confirmed.

4.2 Controlling disease with stump treatment

4.2.1 Efficacy of *Phlebiopsis gigantea* and urea

Treatment with *P. gigantea* on hybrid larch stumps was generally effective in reducing primary infection by *Heterobasidion* spp. (Paper IV), as has been previously shown for Norway spruce and Scots pine stumps. However, on sites L2 and L5 in experiment I (Paper IV), *P. gigantea* was not effective. The occasional unsatisfactory effect of *P. gigantea* has also been reported previously on Norway spruce (Berglund & Rönnberg, 2004; Thor & Stenlid, 2005; Rönnberg *et al.*, 2006b), and may be attributed to environmental factors, such as high *Heterobasidion* spore deposition rates during stump treatment (Berglund, 2005; Thor, 2005). As a competing saprophytic fungus, the ability for *P. gigantea* to colonize stumps depends on the concentration of both *P. gigantea* and *Heterobasidion* spp. on the stumps and also environmental conditions (Meredith, 1960). Though the variation in infection frequency in experiment I was unknown, it is worth noticing that on sites L2 and L5 either the incidence of infection or the relative infected area was reduced by *P. gigantea* (Table 7). The efficacy of *P. gigantea* on sites L2 and L5 may nevertheless be justified, since using only the incidence of infection or the reduced relative infected area as a measure to assess the efficacy of stump treatment can be misleading (Redfern, 1982; Berglund & Rönnberg, 2004; Thor *et al.*, 2006). However, there is still a risk that *P. gigantea* treatment on hybrid larch stumps may not be effective enough when spore infection pressure is high.

When comparing *P. gigantea* and urea, the latter was very effective on sites L2 and L5, indicating its ability to reduce *Heterobasidion* spp. infection even with high spore loads. Although the control efficacy of urea varied among sites in experiment I, stump treated with urea at all sites showed a comparatively low infection incidence and low relative infected area. Treatment with urea generally results in a low infection frequency when applied at a high concentration, e.g. 40% urea solution on hybrid larch stumps (paper IV), 20% and 30% on Norway spruce (Nicolotti & Gonthier, 2005), and 35% on Norway spruce (Thor & Stenlid, 2005). The success of urea as a treatment agent against *Heterobasidion* spp. infection also relies on the high proportion of urease-sufficient sapwood (Johansson et al. 2002), which generally occurs more frequently on younger trees. Hybrid larch stumps created at the first commercial thinning, such as those described in Paper IV (between 12-20-years old), usually comprise a substantial amount of sapwood, which may have contributed to the satisfactory control effect obtained from urea treatment. Due to the lack of heartwood formation at this age (Longuetaud *et al.*, 2006), urea may be efficient on Norway spruce stumps created at precommercial thinning. However, since the proportion of heartwood in hybrid larch (Larsson-Stern, 2003) and Norway spruce (Seilin, 1996) increases with tree diameter, the efficacy of urea on stumps at later thinnings might be lower (Johansson et al. 2002).

The results of Paper IV indicated that *P. gigantea* is more effective at competing with *H. annosum* s.s. than *H. parviporum* on hybrid larch stumps. Korhonen (2001) reported similar results on Norway spruce logs. It is probable that *P. gigantea* can out-compete *H. annosum* s.s. better than *H. parviporum*, though this assumption warrants further investigation. Since infection by *H. annosum* s.s. is observed more frequently on hybrid larch trees (Rönnberg & Vollbrecht, 1999; Rönnberg *et al.*, 2007), and it can be reduced further by *P. gigantea* compared to *H. parviporum*, it can be speculated that *P. gigantea* may actually have a higher control efficacy for hybrid larch stands. On the other hand, it seems that when *P. gigantea* is used for stump treatment, more inoculum by *H. parviporum* than *H. annosum* s.s. may remain. Consequently a greater hazard would be passed on to the next rotation when highly susceptible host species, e.g. Norway spruce (Oliva *et al.*, 2011), are planted. A future aspect may be to select and breed strains of *P. gigantea* with better capacity to compete also against *H. parviporum* when applying the treatment on Norway spruce stumps.

Treatment seems to increase the infection ratio for heartwood versus sapwood in hybrid larch and Norway spruce stems, i.e. treatment results in a relatively higher proportion of heartwood infections, as shown in Bendz-Hellgren and Stenlid (1998), Oliva *et al.* (2011) and Paper IV. This is probably due to the unfavourably dry conditions in the heartwood for *Heterobasidion* spp. in untreated stumps. In Paper IV, the amount of infection in the heartwood was higher also in absolute numbers than in sapwood. Since heartwood proportion increases as a tree matures, stump treatment may not be as efficient in older stands compared to younger stands. However, this is speculative, and none of the studies referred to were designed to look at the effect of stump treatment on the proportion of infection in heartwood versus sapwood, nor the subsequent long term influence on disease development in the stand.

4.2.2 Economic appraisal of mechanized stump treatment

Besides treatment efficacy, the choice of stump treatment agent relies on a number of other factors, such as economic justification and environmental concerns. Urea is cheap and has a long shelf life (Thor, 2005). However, the cost for transportation of the ready-made urea solution can be higher than *P. gigantea* (Thor, 1996). The tax for using urea as a pesticide in Sweden is also higher *P. gigantea*. Urea can perform very well on Norway spruce (Brandtberg *et al.*, 1996; Johansson *et al.*, 2002; Nicolotti & Gonthier, 2005; Oliva *et al.*, 2008), Scots pine (Rishbeth, 1959; Johansson *et al.*, 2002) and also hybrid larch stumps (Paper IV). Thus, from a biological point of view, urea can be a good choice as a stump treatment agent, but the use in Sweden may be difficult to justify economically.

On the other hand, the use of *P. gigantea* as stump treatment on Norway spruce in Sweden is prevalent (Thor, 2001; Berglund, 2005) and has been economically justified for commercial thinnings and final felling (Thor & Stenlid, 2005). The cost for mechanized stump treatment is usually expressed in terms of cost per volume of harvested timber. This cost may vary according to the amount of timber harvested, the size of harvester used in the thinning operation and the consumption of treatment agents (Thor, 2011). The cost for stump treatment is lower at later thinnings and at final felling when trees are bigger compared to earlier thinnings (Mäkelä *et al.*, 1994; Thor, 1996). In Sweden, estimated cost for stump treatment on Norway spruce, Scots pine and hybrid larch stumps over a rotation was 2498, 1568 and 2493 SEK ha^{-1}, respectively (Table 11). The calculation was based on traditional silvicultural practices in southern Sweden for those species (Skogsstyrelsen, 1984; Ekö *et al.*, 2004) and the cost for mechanized stump treatment was obtained from Thor (2011) for Norway spruce.

The benefit of stump treatment depends on the probability of infection, which is affected by the intensity of the thinning, the abundance of ambient basidiospores and the ability of established infections to spread within the stand. On sites with high probability of infection, such as the Scots pine site in paper III, stump treatment can be easily justified. However on sites with a low probability of infection, stump treatment cannot always be justified. Furthermore, stump treatment in previously infested stands are less profitable than first rotation forests (Möykkynen *et al.*, 1998).

Table 11. *Cost for mechanized stump treatment with Phlebiopsis gigantea over a whole rotation under typical management scenarios for Norway spruce, Scots pine and hybrid larch discounted back to the first thinning using a discount rate of 3% (cost 3%) and 0% (Cost 0%). Cost for stump treatment at first commercial thinning, later commercial thinnings and final felling is 12, 10 and 4 SEK m^{-3}sub, respectively (Thor, 2011)*

Tree species	*Management scenario*	*Cost 3% (SEK)*	*Cost 0% (SEK)*
Norway spruce	Three commercial thinnings at 30, 40 and 50 years, and final felling at 80 years	2563	5224
Scots pine	Three commercial thinnings at 30, 40 and 55 years, and final felling at 80 years	1568	3092
Hybrid larch	Five commercial thinnings at 15, 20, 25, 30 and 35 years, and final felling at 40 years	2493	3690

4.2.3 Economic appraisal for manual stump treatment

Stump treatment is almost always mechanically conducted in Sweden (Thor, 2001), under some conditions though, e.g. during precommercial thinning, manual treatment is needed. Although the efficacy of stump treatment on precommercial thinning stumps has not been tested directly, it was assumed the same as on commercial thinning stumps in Paper II. When all commercial thinning stumps were treated at a high efficacy (at least 95%), not treating the precommercial thinning stumps can result in a higher decay frequency at final felling compared to treating the stumps. Consequently, if the stand is to be protected against *Heterobasidion* spp. infection in future commercial thinnings, it seems prudent to treat the precommercial thinning stumps as well, so as to not jeopardize the effect from stump treatment during commercial thinnings. However, due to the high cost of manual stump treatment (Paper II), profitability at precommercial thinning, especially for previously infested stands, is low. Perhaps future improvements with the brush saw can be explored with, for example, combining precommercial thinning and stump treatment as is done with mechanized stump treatment on harvesters. This would increase the efficiency of stump treatment during precommercial thinning and benefit the forest industry. If the cost for manual stump treatment during precommercial thinning can be reduced to 500 SEK ha^{-1}, the profitability of conducting stump treatment during a summer precommercial thinning will be similar compared to precommercial thinning during the winter, when calculated using a discount rate of 3%. On the other hand, precommercial thinning of Norway spruce stands during the winter when the weather conditions make this possible, can be a good alternative.

Discounting the net revenues at the commercial thinnings and final felling to the beginning of the rotation decreases the difference in economic outcomes as a result of various silvicultural practices. This effect becomes more pronounced when the rotation age is long as is typical in Sweden, e.g. 80 years for Norway spruce in southern Sweden. One silvicultural practice can for instance result in higher stand productivity than another from a biological point of view, but may not necessarily have a higher net present value when calculated using a discount rate of e.g. 3%. One example of this was shown in Paper II, where precommercial thinning with stump treatment conducted at a stand age of 20 resulted in a lower decay frequency and a similar total net revenue at final felling compared to not treating the stumps, but the treatment was not profitable at any of the discount rates of 2%, 3% or 4%.

Stump treatment or winter thinning is recommended at precommercial thinning on previously non-infested sites, e.g. first rotation forests on previously arable land, even though it may not result in a higher economic outcome compared to no treatment. If commercial thinning stumps are treated but precommercial thinning stumps are not, infection established early in a rotation may still increase over the rotation through secondary spread at root contacts and its inoculum carried over in stumps to the next rotation. Thus the profitability from stump treatment at commercial thinnings is likely to be less than expected, due to the influence from infection through precommercial thinning stumps. Even with around 5% of the stumps infected at the beginning of the rotation, more than half of the stems at final felling can be decayed (Paper II, Thor et al. 2005b). Thus long-term site productivity should be maintained especially on previously non-infested sites.

4.3 Other measures to assist disease control

4.3.1 Assessing disease incidence

Assessing disease incidence is important for planning and applying correct silvicultural measures, e.g. conducting stump treatment. Examining fresh stump surfaces for discoloration and decay can be used to detect *Heterobasidion* spp. in Norway spruce and hybrid larch (Vollbrecht *et al.*, 1995b; Stener & Ahlberg, 2002; Thor *et al.*, 2005), but not for Scots pine since trees seldom show decay in the stem (Bendz-Hellgren *et al.*, 1998). Although aboveground symptoms and signs are commonly used to assess forest health conditions in Sweden (Wulff, 2011), it seems that for Scots pine stands they would not serve as adequate indicators for determining the actual incidence of

Heterobasidion spp. For example, in Paper III, the apparently disease-free plot had 75% of trees infected belowground. In Rönnberg *et al.* (2006a), 67% of the healthy-looking trees had infection belowground. The stand level surveys conducted in this thesis showed very low incidence of basidiocarps on live trees. Furthermore, crown condition and needle retention may not be practical indicators of *Heterobasidion* incidence since the variation can be attributable to factors other than disease, e.g. climate (Reich *et al.*, 1996).

Mortality rates have been used to assess disease incidence in Scots pine stands in the U.K. (Burdekin, 1972; Gibbs *et al.*, 2002). However, when an aggregation of dead trees appears, the disease is usually at a later stage of development and asymptomatic trees beyond the border of a disease center are likely infected belowground. Preventative measures can no longer be applied to reduce the established damage. Identifying high hazard sites, i.e. those with a high probability of becoming infected, and protecting those sites with preventative stump treatment, will minimize the damage and long-term impact on site productivity.

4.3.2 Identifying high hazard sites

Characteristics of high incidence sites have been used as criteria for classifying sites with high and low hazard (Morris & Frazier, 1966; Alexander, 1989; Baker *et al.*, 1993; Redfern *et al.*, 2010). Based on this principle, hazard rating systems have been developed in the U.K. (Redfern *et al.*, 2010) and the eastern U.S.A. (Morris & Frazier, 1966) to assist forest managers and policy makers to prevent or control disease epidemiology. However, high disease incidence may not only be attributable to site conditions but also to the frequency of thinnings, season of thinning, whether stumps are treated and the proximity to previously infested sites (Rishbeth, 1951a; Korhonen *et al.*, 1998b). A large number of sites need to be sampled to identify the criteria for hazard rating. As a result, the criteria derived from the small number of high incidence sites (section 3.4) may not be representative on a large scale. By the same token, a supposed high hazard site may not always have a high incidence of disease. In risk analysis of high hazard sites and in order to assess the expected level of losses caused by disease and justify preventative treatment or management options, the probability of stump infection must be taken into consideration.

In spite of the small sample size in the soil sampling study (Section 3.4), the results are in agreement with previous research (Froelich *et al.*, 1966; Morris & Frazier, 1966; Alexander *et al.*, 1975; Redfern *et al.*, 2010) indicating that high hazard sites are associated with high soil pH, low organic matter content, sandy soil texture and anthropogenic-influenced land use, i.e. previous arable or pasture land. Although soil pH and organic matter contents were indicators for hazard rating, it was not practical to set a numeric boundary between high and low hazard since the range of the values were almost overlapping (between 5.1 and 5.3 for low hazard sites and between 5.3 and 6.7 for high hazard sites). Previous land use can be a practical criterion for distinguishing high and low hazard sites, as all previous agricultural lands in the soil sampling experiment had high infection incidence. A high incidence of disease was also observed on two former pasture lands in Paper III and the soil sampling study. Stem growth reduction can be pronounced on previous agricultural or pasture land following commercial thinning; for example, up to 10% of annual volume growth in Scots pine nine years post-thinning (Paper III), and up to 23% in a five-year period in Norway spruce 17 years post-thinning (Bendz-Hellgren & Stenlid, 1997).

First rotation forests usually have higher soil pH compared to stands with a number of successive of rotations. The high soil pH may restrict antagonistic microorganism against *Heterobasidion* spp., and thereby increase the probability of infection. First rotation forests also lack the substantial build-up of inoculum as seen in stands with a number of successive rotations. Considering the longevity of and difficulty to eradicate *Heterobasidion* spp. inoculum in conifer stumps (Greig & Pratt, 1976) and the impact on the current and subsequent rotations, protecting first rotation forest stands at thinnings is beneficial both in the short and long term.

4.3.3 Modeling for disease control and management

For the purpose of justifying stump treatment at thinnings, it is recommended to use simulation models, such as RotStand to compare the outcome of timber yield with or without treatment. Even though simulation of disease development and projections of yield loss using computer models inevitably involves uncertainty, considering the parameters used in the simulation process were based on published data and scientific assumptions, the results from simulation can have practical use.

However, models should always be used with some cautions. One example is the somewhat contradictory results from Paper I and Paper II. In Paper I, it was estimated that precommercial thinning stumps may be of importance for the disease development in the stand. It was however not explicitly studied to what extent this will happen in practice. The simulation in Paper II on the other hand indicated that the precommercial thinning stumps do affect disease development, but perhaps not as much as could have been expected. When using RotStand for modeling, one must be cautious of its limitations for modeling young stands, e.g. the root plates for young trees are based on few observations (Laitakari, 1927). It is hence possible that RotStand actually underestimates the importance of young small stumps in the spread of the disease. Future research on root morphology of young trees can probably improve the accuracy of prediction by RotStand.

To enable a more practical use, the results from RotStand can be integrated into a forest management system. For example, it is recommended to combine RotStand and Heureka to estimate the disease impact and the economic outcomes from various management scenarios. Alternatively, the disease impact can be included as a module in forest management systems, e.g. Heureka, in order to control the disease, maintain forest productivity and reduce losses.

5 Practical implications

- Small-sized Norway spruce stumps created at precommercial thinning are able to spread infection by *Heterobasidion* spp. to adjacent trees. Precommercial thinning is recommended to be conducted early in a rotation, e.g. tree height below 6 meters, to reduce the impact by *Heterobasidion* spp.

- Stump treatment at precommercial thinning is not economically beneficial, due to the high cost of manual stump treatment. Future improvement can focus on combining stump treatment and precommercial thinning to reduce the cost. Alternatively, precommercial thinning during the winter can be beneficial to control *Heterobasidion* spp. in Norway spruce stands.

- Aboveground signs and symptoms of *Heterobasidion* spp. are not reliable indicators for disease presence in Scots pine stands. Incidence and severity of *Heterobasidion* infection in Scots pine trees can be greatly underestimated.

- Scots pine productivity can be greatly reduced by *Heterobasidion* spp. Stem growth reduction becomes apparent seven years after the first thinning and the loss is expected to increase over time with subsequent thinnings. Stump treatment should be considered as a profitable preventive measure to control the disease.

- Due to the high hazard of *Heterobasidion* spp. infection on Scots pine trees planted as first rotation forest land on former agricultural or pasture land, and the lack of build-up of inoculum in the stand, control measures should be applied on such stand to prevent future losses.

- Stump treatment with urea or *P. gigantea* should be applied on hybrid larch stumps to avoid losses caused by *Heterobasidion* spp., though the choice of stump treatment agent may differ in different regions based on economic assessment.

References

Alexander, S.A. (1989). Annosus Root Disease Hazard Rating, Detection and Management Strategies in the Southeastern United States. In: Otrosina, W.J., *et al.* (Eds.) *Proceedings of the symposium on research and management of annosus root disease (Heterobasidion annosum) in western North America*, Monterey, CA., US, April 18-21 1989. pp. 111-116: Pacific Southwest Forest and Range Experiment Station, Forest Service, U.S. Department of Agriculture.

Alexander, S.A., Skelly, J.M. & Morris, C.L. (1975). Edaphic Factors Associated with the Incidence and Severity of Disease Caused by Fomes annosus in Loblolly Pine Plantations in Virginia. *Phytopathology* 65(5), 585-591.

Baker, F.A., Verbyla, D.L., Hodges, C.S. & Ross, E.W. (1993). Classification and regression tree analysis for assessing hazard of pine mortality caused by *Heterobasdion annosum*. *Plant Disease* 77(2), 136-139.

Bendz-Hellgren, M. (1997). *Heterobasidion annosum Root and Butt Rot of Norway Spruce, Picea abies : colonization by the fungus and its impact on tree growth.* Diss. Uppsala:Swedish University of Agricultural Sciences.

Bendz-Hellgren, M., Brandtberg, P.O., Johansson, M., Swedjemark, G. & Stenlid, J. (1999). Growth rate of *Heterobasidion annosum* in *Picea abies* established on forest land and arable land. *Scandinavian Journal of Forest Research* 14(5), 402-407.

Bendz-Hellgren, M., Lipponen, K., Solheim, H. & Thomsen, I.M. (1998). The Nordic Countries. In: Woodward, S., *et al.* (Eds.) *Heterobasidion annosum: Biology, Ecology, Impact and Control*. pp. 333-345. Cambridge, UK: CAB International. ISBN 0-85199-275-7.

Bendz-Hellgren, M. & Stenlid, J. (1995). Long-term reduction in the diameter growth of butt rot affected Norway spruce, *Picea abies*. *Forest Ecology and Management* 74(1–3), 239-243.

Bendz-Hellgren, M. & Stenlid, J. (1997). Decreased volume growth of *Picea abies* in response to *Heterobasidion annosum* infection. *Canadian Journal of Forest Research* 27(10), 1519-1524.

Bendz-Hellgren, M. & Stenlid, J. (1998). Effects of clear-cutting, thinning, and wood moisture content on the susceptibility of Norway spruce stumps to

Heterobasidion annosum. *Canadian Journal of Forest Research* 28(5), 759-765.

Berglund, M. (2005). *Infection and growth of Heterobasdion spp. in Picea abies: Control by Phlebiopsis gigantea stump treatment.* Diss. Alnarp, Sweden:Swedish University of Agricultural Sciences.

Berglund, M., Carlsson, T. & Rönnberg, J. (2007). Infection of *Heterobasidion* spp. in late pre-commercial thinnings of *Picea abies* in southern Sweden. In: Garbelotto, M., *et al.* (Eds.) *Proceedings of the 12th International Conference on Root and Butt Rots of Forest Trees* Berkeley, California - Medford, Oregon 2007. pp. 221-225: The University of California, Berkeley, USA. ISBN 9780615230764.

Berglund, M. & Rönnberg, J. (2004). Effectiveness of treatment of Norway spruce stumps with *Phlebiopsis gigantea* at different rates of coverage for the control of *Heterobasidion*. *Forest Pathology* 34(4), 233-243.

Blennow, K. & Sallnäs, O. (2002). Risk perception among non-industrial private forest owners. *Scandinavian Journal of Forest Research* 17(5), 472-479.

Bloomberg, W.J. (1988). Modeling control strategies for laminated root rot in managed Douglas-fir stands: Model development. *Phytopathology* 78, 403-409.

Bloomberg, W.J. & Wallis, G.W. (1979). Comparison of indicator variables for estimating growth reduction associated with *Phellinus weirii* root rot in Douglas-fir plantations. *Canadian Journal of Forest Research* 9(1), 76-81.

Bradford, B., Alexander, S.A. & Skelly, J.M. (1978a). Determination of growth loss of Pinus taeda L. caused by Heterobasidion annosus (Fr.) Bref. *European Journal of Forest Pathology* 8(3), 129-134.

Bradford, B., Skelly, J.M. & Alexander, S.A. (1978b). Incidence and severity of annosus root rot in Loblolly pine plantation in Virginia. *European Journal of Forest Pathology* 8(3), 135-145.

Brandtberg, P.O., Johansson, M. & Seeger, P. (1996). Effects of season and urea treatment on infection of stumps of *Picea abies* by *Heterobasidion annosum* in stands on former arable land. *Scandinavian Journal of Forest Research* 11(3), 261-268.

Burdekin, D.A. (1972). A Study of Losses in Scots Pine caused by *Fomes annosus*. *Forestry* 45, 189-196.

Capretti, P., Korhonen, K., Mugnai, L. & Romagnoli, C. (1990). An intersterility group of *Heterobasidion annosum* specialized to *Abies alba*. *European Journal of Forest Pathology* 20(4), 231-240.

Cherubini, P., Fontana, G., Rigling, D., Dobbertin, M., Brang, P. & Innes, J.L. (2002). Tree-life history prior to death: two fungal root pathogens affect tree-ring growth differently. *Journal of Ecology* 90(5), 839-850.

Cleary, M.R., Arhipova, N., Morrison, D.J., Thomsen, I.M., Sturrock, R., Vasaitis, R., Gaitnieks, T. & Stenlid., J. (2012). Stump removal to control root disease in Canada and Scandinavia: A synthesis of results from long-term trials. *Forest Ecology and Management.* In press.

Driver, C.H. & Ginns, J.H.J. (1969). Ecololgy of slash pine stumps: Fungal colonization and infection by *Fomes Annosus*. *Forest Science* 15, 2-10.

Ekö, P.M., Larsson-Stern, M. & Albrektson, A. (2004). Growth and yield of hybrid larch (*Larix x eurolepis* A. Henry) in southern Sweden. *Scandinavian Journal of Forest Research* 19(4), 320-328.

Fahlvik, N. (2005). *Aspects of Precommercial Thinning in Heterogeneous Forests in Southern Sweden.* Diss. Alnarp, Sweden:Swedish University of Agricultural Sciences.

Fahlvik, N. & Nyström, K. (2006). Models for predicting individual tree height increment and tree diameter in young stands in southern Sweden. *Scandinavian Journal of Forest Research* 21(S7), 16-28.

Frankel, S.J. (1998). *User's guide to the Western Root Disease Model, Version 3.0*. Pacific Southwest Research Station: USDA, Forest Service. (General Techinical Report; PSW-GTR-165).

Froelich, R.C., Cowling, E.B., Collicott, L.V. & Dell, T.R. (1977). Fomes Annosus Reduces Height and Diameter Growth of Planted Slash Pine. *Forest Science* 23(3), 299-306.

Froelich, R.C., Dell, T.R. & Walkinshaw, C.H. (1966). Soil Factors Associated with Fomes annosus in the Gulf States. *Forest Science* 12(3), 356-361.

Gibbs, J.N., Greig, B.J.W. & Pratt, J.E. (2002). Fomes root rot in Thetford Forest, East Anglia: past, present and future. *Forestry* 75(2), 191-202.

Greig, B.J.W. (1962). Fomes annosus (Fr.) Cke. and other Root-rotting Fungi in Conifers on ex-Hardwood Sites. *Forestry* 35, 164-182.

Greig, B.J.W. & Low, J.D. (1975). An experiment to control *Fomes annosus* in second rotation pine crops. *Forestry* 48(2), 147-163.

Greig, B.J.W. & Pratt, J.E. (1976). Some observations on the longevity of Fomes annosus in conifer stumps. *European Journal of Forest Pathology* 6(4), 250-253.

Harper, W. (1987). Economic evaluation of damage by *Heterobasidion annosum* and the benefits of stump treatment *Peniophora gigantea*. In: Knutell, H. (Ed.) *Proceedings of Development of Thinning Systems to Reduce Stand Damages, the meeting of IUFRO project group P4.02 and subject group S1.05-05.*, Garpenberg (Sweden)1987. pp. 84-102. ISBN 91-576-3104-2.

Hartig, R. (1874). *Wichitige krankheiten der Waldbäume: Beiträge zur Mycologie und Phytopatologie fur Botaniker und Forstmänner.* Berlin: Julius Springer.

Hodges, C.S.J. (1974). Cost of Treating Stumps to Prevent Infection by *Fomes Annosus*. *Journal of Forestry* 72(7), 402-404.

Holdenrieder, O. & Greig, B.J.W. (1998). Biological methods of control. In: Woodward, S., *et al.* (Eds.) *Heterobasidion annosum: Biology, Ecology, Impact and Control*. pp. 235-258. Cambridge, UK: CAB International. ISBN 0-85199-275-7.

Isomäki, A. & Kallio, T. (1974). Consequences of injury caused by timber harvesting machines on the growth and decay of spruce (*Picea abies* (L.) Karst.). *Acta Forestalia Fennica* 136, 1-25.

Johansson, S.M., Pratt, J.E. & Asiegbu, F.O. (2002). Treatment of Norway spruce and Scots pine stumps with urea against the root and butt rot fungus *Heterobasidion annosum* - possible modes of action. *Forest Ecology and Management* 157, 87-100.

Jorgensen, E. (1961). On the spread of *Fomes annosus* (Fr.) Cke. *Canadian Journal of Botany* 39(6), 1437-1445

Joseph, G., Kelsey, R.G. & Thies, W.G. (1998). Hydraulic conductivity in roots of ponderosa pine infected with black-stain (*Leptographium wageneri*) or annosus (*Heterobasidion annosum*) root disease. *Tree Physiology* 18(5), 333-339.

Kallio, T. (1970). Aerial distribution of the root-rot fungus *Fomes annosus* (Fr.) Cooke in Finland. *Acta Forestalia Fennica* 107, 1-55.

Kallio, T. & Hallaksela, A.M. (1979). Biological control of *Heterobasidion annosum* (Fr.) Bref. (*Fomes annosus*) in Finland. *European Journal of Forest Pathology* 9(5), 298-308.

Kåre, V. & Solheim, H. (1993). Root and butt rot in first generation of Norway spruce affected by spacing and thinning. In: Johansson, M.*, et al.* (Eds.) *Proceedings of the Eighth International Conference on Root and Butt Rots*, Wik, Sweden and Haikko, Finland. 1993. pp. 642-645: INFO/REPRO, Uppsala.

Korhonen, K. (1978). Intersterility groups of *Heterobasidion annosum*. *Communicationes Instituti Forestalis Fenniae* 94(6), 1-25.

Korhonen, K. (2001). Simulated stump treatment experiments for monitoring the efficacy of *Phlebiopsis gigantea* against *Heterobasidion*. In: Laflamme, G.*, et al.* (Eds.) *Proceedings of Root and Butt Rots of Forest Trees: 10th International Conference on Root and Butt Rots*, Québec City, Canada, 16–22 September 2001. pp. 206-210. ISBN 0-662-33332-2.

Korhonen, K., Capretti, P., Karjalainen, R. & Stenlid, J. (1998a). Distribution of *Heterobasidion annosum* Intersterility groups in Europe. In: Woodward, S.*, et al.* (Eds.) *Heterobasidion annosum: Biology, Ecology, Impact and Control*. pp. 93-104. Cambridge, UK: CAB International. ISBN 0-85199-275-7.

Korhonen, K., Delatour, C. & Greig, B.J.W. (1998b). Silvicultural Control. In: Woodward, S.*, et al.* (Eds.) *Heterobasidion annosum: Biology, Ecology, Impact and Control*. pp. 283-313. Cambridge, UK: CAB International. ISBN 0-85199-275-7.

Korhonen, K., Lipponen, K., Bendz, M., Johansson, M., Ryen, I., Venn, K., Seiskari, P. & Niemi, M. (1993). Control of *Heterobasidion annosum* by stump treatment with ’rotstop’, a new commercial formulation of *Phlebiopsis gigantea*. In: Johansson, M.*, et al.* (Eds.) *Proceedings of the Eighth International Conference on Root and Butt Rots*, Wik, Sweden and Haikko, Finland.1993. pp. 675-683: Info/Repro, Uppsala.

Korhonen, K. & Stenlid, J. (1998). Biology of *Heterobasidion annosum*. In: Woodward, S.*, et al.* (Eds.) *Heterobasidion annosum: Biology, Ecology, Impact and Control*. pp. 43-70. Cambridge, UK: CAB International. ISBN 0-85199-275-7.

Korzukhin, M.D., TerMikaelian, M.T. & Wagner, R.G. (1996). Process versus empirical models: Which approach for forest ecosystem management? *Canadian Journal of Forest Research* 26(5), 879-887.

Kozlowski, T.T. & Pallardy, S.G. (1997). Chapter 11. Absorption of Water and Ascent of Sap. In: *Physiology of Woody Plants*. Second. ed. pp. 237-268. California, USA: Academic Press, Inc. ISBN 0-12-424162-X.

Kurkela, T. (2002). Crown condition as an indicator of the incidence of root rot caused by *Heterobasidion annosum* in Scots pine stands. *Silva Fennica* 36(2), 451-457.

Laitakari, E. (1927). The root system of pine (*Pinus sylvestris*). A morphological investigation. *Acta For. Fenn.* 33, 1-380.

Lämås, T. & Eriksson, L.O. (2003). Analysis and planning systems for multiresource, sustainable forestry: the Heureka research programme at SLU. *Canadian Journal of Forest Research* 33(3), 500-508.

Larsson-Stern, M. (2003). *Aspects of hybrid larch (Larix x eurolepis Henry) as a potential tree species in southern Swedish forestry.* Diss. Alnarp:Swedish University of Agricultural Sciences.

Longuetaud, F., Mothe, F., Leban, J.-M. & Mäkelä, A. (2006). *Picea abies* sapwood width: Variations within and between trees. *Scandinavian Journal of Forest Research* 21(1), 41-53.

Mäkelä, M., Ari, T., Korhonen, K. & Lipponen, K. (1994). Kantokäsitterly koneellisessa hakkuussa. (Stump treatment in mechanized timber harvesting). *Metsäteollisuus* 3, 1-8.

Malinen, J., Kilpeläinen, H., Piira, T., Redsven, V., Wall, T. & Nuutinen, T. (2007). Comparing model-based approaches with bucking simulation-based approach in the prediction of timber assortment recovery. *Forestry* 80(3), 309-321.

Meredith, D.S. (1960). Further Observation on Fungi Inhabiting Pine stumps. *Annals of Botany* 24(93), 63-78.

Morris, C.L. & Frazier, D.H. (1966). Development of a hazard rating for Fomes annosus in Virginia. *Plant disease reporter* 50(7), 510-511.

Morrison, D.J. & Johnson, A.L.S. (1999). Incidence of *Heterobasidion annosum* in precommercial thinning stumps in coastal British Columbia. *European Journal of Forest Pathology* 29, 1-16.

Moseley, D., Pratt, J.E., Pukkala, T., Thorpe, K., Tracey, D. & Woodward, S. (2004). Modelling *H. annosum*: validating MOHIEF with real-time data from a species-susceptibility trial in Britain. In: Manka, M., *et al.* (Eds.) *Proceedings of the 11th International Conference on Root and Butt Rots of Forest Trees*, Poznan and Bialowieza, Poland, August 16-22 2004. pp. 485-493.

Möykkynen, T. & Miina, J. (2002). Optimizing the management of a butt-rotted Picea abies stand infected by Heterobasidion annosum from the previous rotation. *Scandinavian Journal of Forest Research* 17(1), 47-52.

Möykkynen, T., Miina, J. & Pukkala, T. (2000). Optimizing the management of a *Picea abies* stand under risk of butt rot. *Forest Pathology* 30(2), 65-76.

Möykkynen, T., Miina, J., Pukkala, T. & von Weissenberg, K. (1998). Modelling the spread of butt rot in a *Picea abies* stand in Finland to evaluate the profitability of stump protection against *Heterobasidion annosum*. *Forest Ecology and Management* 106, 247-257.

Möykkynen, T. & Pukkala, T. (2009). Optimizing the management of a Norway spruce stand on a site infected by *Heterobasidion* coll. *Scandinavian Journal of Forest Research* 24(2), 149-159.

Möykkynen, T. & Pukkala, T. (2010). Optimizing the management of Norway spruce and Scots pine mixtures on a site infected by Heterobasidion coll. *Scandinavian Journal of Forest Research* 25(2), 127-137.

Nicolotti, G. & Gonthier, P. (2005). Stump treatment against *Heterobasidion* with *Phlebiopsis gigantea* and some chemicals in *Picea abies* stands in the western Alps. *Forest Pathology* 35(5), 365-374.

Niemela, T. & Korhonen, K. (1998). Taxonomy of the genus Heterobasidion. In: Woodward, S., *et al.* (Eds.) *Heterobasidion annosum: Biology, Ecology, Impact and Control*. pp. 27-34. Cambridge, UK: CAB International. ISBN 0-85199-275-7.

Nilsson, U., Luoranen, J., Kolström, T., Örlander, G. & Puttonen, P. (2010). Reforestation with planting in northern Europe. *Scandinavian Journal of Forest Research* 25(4), 283-294.

Oliva, J., Bendz-Hellgren, M. & Stenlid, J. (2011). Spread of *Heterobasidion annosum s.s.* and *Heterobasidion parviporum* in *Picea abies* 15 years after stump inoculation. *Fems Microbiology Ecology* 75(3), 414-429.

Oliva, J., Samils, N., Johansson, U., Bendz-Hellgren, M. & Stenlid, J. (2008). Urea treatment reduced *Heterobasidion annosum* s.l. root rot in *Picea abies* after 15 years. *Forest Ecology and Management* 255(7), 2876-2882.

Oliva, J. & Stenlid, J. (2011). Validation of the Rotstand model for simulating *Heterobasidion annosum* root rot in *Picea abies* stands. *Forest Ecology and Management* 261(11), 1841-1851.

Oliva, J., Thor, M. & Stenlid, J. (2010). Reaction zone and periodic increment decrease in *Picea abies* trees infected by *Heterobasidion annosum* s.l. *Forest Ecology and Management* 260(5), 692-698.

Otrosina, W.J. & Garbelotto, M. (2010). *Heterobasidion occidentale* sp. nov. and *Heterobasidion irregulare* nom. nov.: A disposition of North American *Heterobasidion* biological species. *Fungal Biology* 114(1), 16-25.

Paludan, F. (1966). Infection by Fomes annosus and its spread in young Norway Spruce. *Forstlige Forsoksvaesen i Danmark* 30(1), 19-47.

Peet, F.G. & Hunt, R.S. (2005). A New Simulator for the Spread of Forest Root Diseases by Individual Root Contacts. *Forest Science* 51(5), 425-437.

Pettersson, M., Rönnberg, J., Vollbrecht, G. & Gemmel, P. (2003). Effect of thinning and Phlebiopsis gigantea stump treatment on the growth of Heterobasidion parviporum inoculated in Picea abies. *Scandinavian Journal of Forest Research* 18(4), 362-367.

Piri, T. (1990). Occurrence of Heterobasidion annosum in pure and mixed spruce stands in southern Finland. *Scandinavian Journal of Forest Research* 5(1-4), 113-125.

Piri, T. (1996). The spreading of the S type of *Heterobasidion annosum* from Norway spruce stumps to the subsequent tree stand. *European Journal of Forest Pathology* 26, 193-204.

Pratt, J.E., Johansson, M. & Hüttermann, A. (1998a). Chemical control of *Heterobasidion annosum*. In: Woodward, S., *et al.* (Eds.) *Heterobasidion* *annosum: Biology, Ecology, Impact and Control*. pp. 259-282. Cambridge, UK: CAB International. ISBN 0-85199-275-7.

Pratt, J.E., Redfern, D. & Burnand, A.C. (1988). Modelling the spread of *Heterobasidion annosum* in sitka spruce planatation in Britain. In: Morrison, D.J. (Ed.) *Proceedings of the Seventh International Conference on Root and Butt Rots of Forest Trees*, Victoria, BC, Canada., August 9-16 1988. pp. 308-319.

Pratt, J.E., Shaw, C.G., III & Vollbrecht, G. (1998b). Modelling disease development in forest stands. In: Woodward, S., *et al.* (Eds.) *Heterobasidion annosum: Biology, ecology, impact and control*. pp. 213-233. Cambridge, UK: CAB International. ISBN 0-85199-275-7.

Pukkala, T. (1989). Predicting diameter growth in even-aged Scots pine stands with a spatial and non-spatial model. *Silva Fennica* 23(2), 101-116.

Pukkala, T., Möykkynen, T., Thor, M., Rönnberg, J. & Stenlid, J. (2005). Modeling infection and spread of *Heterobasidion annosum* in even-aged Fennoscandian conifer stands. *Canadian Journal of Forest Research* 35(1), 74-84.

Redfern, D.B. (1982). Infection of Picea sitchensis and Pinus contorta stumps by basidiospores of Heterobasidion annosum. *European Journal of Forest Pathology* 12(1), 11-25.

Redfern, D.B., Pratt, J.E., Hendry, S.J. & Low, J.D. (2010). Development of a policy and strategy for controlling infection by *Heterobasidion annosum* in British forests: a review of supporting research. *Forestry* 83(2), 207-218.

Redfern, D.B. & Stenlid, J. (1998). Spore dispersal and infection. In: Woodward, S., *et al.* (Eds.) *Heterobasidion annosum: Biology, Ecology, Impact and Control*. pp. 105-124. Cambridge, UK: CAB International. ISBN 0-85199-275-7.

Reich, P.B., Oleksyn, J., Modrzynski, J. & Tjoelker, M.G. (1996). Evidence that longer needle retention of spruce and pine populations at high elevations and high latitudes is largely a phenotypic response. *Tree Physiology* 16(7), 643-647.

Rishbeth, J. (1951a). Observation on the biology of *Fomes annosus*, with particular reference to East Anglian pine plantations. III Natural and experimental infection of pines, and some factors affecting severity of the disease. *Annals of Botany* 15(58), 221-247.

Rishbeth, J. (1951b). Observation on the biology of *Fomes annosus*, with particular reference to East Anglian pine plantations. II Spore production, stump infection and saprophytic activity in stumps. *Annals of Botany* 15(57), 1-21.

Rishbeth, J. (1959). Stump protection against *Fomes annosus*. II. Treatment with substances other than creosote. *Annals of Applied Biology* 47, 529-541.

Rishbeth, J. (1963). Stump protection against *Fomes annosus*. III. inoculation with *Peniophora gigantea*. *Annals of Applied Biology* 52, 63-77.

Rönnberg, J. & Cleary, M.R. (2012). Presence of *Heterobasidion* infections in Norway spruce stumps 6 years after treatment with *Phlebiopsis gigantea*. *Forest Pathology* 42(2), 144-149.

Rönnberg, J. & Jørgensen, B.B. (2000). Incidence of Root and Butt Rot in Consecutive Rotations of Picea abies. *Scandinavian Journal of Forest Research* 15(2), 210-217.

Rönnberg, J., Mårtensson, S. & Berglund, M. (2007). Incidence of *Heterobasidion* root and butt rot in first rotation *Larix* stands and justification for stump treatment. In: Garbelotto, M., *et al.* (Eds.) *Proceedings of the 12th International Conference on Root and Butt Rots of Forest Trees* Berkeley, California - Medford, Oregon 2007. pp. 86-89: The University of California, Berkeley, USA. ISBN 9780615230764.

Rönnberg, J., Petrylaitė, E., Nilsson, G. & Pratt, J. (2006a). Two studies to assess the risk to *Pinus sylvestris* from *Heterobasidion* spp. in southern Sweden. *Scandinavian Journal of Forest Research* 21(5), 405-413.

Rönnberg, J., Sidorov, E. & Petrylaite, E. (2006b). Efficacy of different concentrations of Rotstop® and Rotstop® S and imperfect coverage of Rotstop® S against *Heterobasidion* spp. spore infections on Norway spruce stumps. *Forest Pathology* 36(6), 422-433.

Rönnberg, J. & Vollbrecht, G. (1999). Early infection by *Heterobasidion annosum* in *Larix* x *eurolepis* seedlings planted on infested sites. *European Journal of Forest Pathology* 29(1), 81-86.

Rönnberg, J., Vollbrecht, G. & Thomsen, I.M. (1999). Incidence of butt rot in a tree species experiment in northern Denmark. *Scandinavian Journal of Forest Research* 14(3), 234-239.

Rosvall, O. (2004). *Ökad produktion i familjeskogsbruket: analys av tillväxthöjande och skadeförebyggande åtgärder*. Uppsala: Skogforsk.

Rykowski, K. & Sierota, Z. (1984). The economic aspects of the occurence of Fomes annosus in Scots pine stands on former agricultural land: UK Forestry Commission translation. *Sylwan* 128(1), 11-21.

Seilin, A. (1996). Sapwood amount in Picea abies (L.) Karst. determined by tree age and radial growth rate. *Holzforschung* 50, 291-296.

Sinclair, W.A. & Lyon, H.H. (2005). Disease caused by Basidiomycota. In: *Diseases of trees and shrubs*. Second. ed. pp. 326-342. New York, US: Cornell University Press. ISBN 0-8014-4371-7.

Skogsstyrelsen (1984). *Gallringsmallar - Södra Sverige*. Jönköping, Sweden: Skogsstyrelsen.

Skogsstyrelsen (2012). *Swedish statistical yearbook of forestry*. Jönnköping, Sweden: Swedish Forest Agency. (Official statistics of Sweden; 0017). ISSN 0491-7847.

Söderberg, U. (1986). *Funktioner för skogliga produktionsprognoser.Tillväxt och formhöjd för enskilda träd av inhemska trädslag i Sverige. [Functions for forecasting of timber yields: increment and form height for individual trees of native species in Sweden.]*. (Avdelningen för skogsuppskattning och skogsindelning; Rapport 14).

Solheim, H. (1994). *Seasonal infection of Heterobasidion annosum on stumps of Norway spruce and surface coating with urea*. (Research Paper of Skogforsk; 3).

Stage, A.R., Shaw, C.G., III, Marsden, M.A., Byler, J.W., Renner, D.I., Eav, B.B., McNamee, P.J., Sutherland, G.D. & Webb, T.M. (1990). *User's manual* *for Western Root Disease model*. Intermountain Research Station, Ogden, Utah: USDA, Forest Service. (General Techinical Report; GTR-INT-267).

Stener, L.G. & Ahlberg, G. (2002). *Study of root and butt rot frequency in hybrid larch stands in southern Sweden*. Uppsala, Sweden: SkogForsk. (SkogForsk Arbetsrapport; Nr 521). ISSN 1404-305X.

Stenlid, J. (1985). Population structure of *Heterobasidion annosum* as determined by somatic incompatibility, sexual incompatibility, and isoenzyme patterns. *Canadian Journal of Botany* 63(12), 2268-2273.

Stenlid, J. & Wästerlund, I. (1986). Estimating the frequency of stem rot in *Picea abies* using an increment borer. *Scandinavian Journal of Forest Research* 1(3), 303-308.

Swedjemark, G. & Stenlid, J. (1993). Population dynamics of the root-rot fungus *Heterobasidion annsoum* following thinning of *Picea abies*. *Oikos* 66(2), 247-254.

Thomsen, I.M. & Jacobsen, J.B. (2001). Testing of RotStop on Sitka spruce, Douglas-fir and larch. In: Laflamme, G., *et al.* (Eds.) *Proceedings of Root and Butt Rots of Forest Trees: 10th International Conference on Root and Butt Rots*, Quebec City, Canada, September 16-22 2001. pp. 216-220. ISBN 0-662-33332-2.

Thor, M. (1996). *Stump treatment against root and butt rot cause by root fomes (Heterobasidion annosum) - a study of the literature*. Oskarshamn. (Research Paper of Skogforsk; Nr 2). ISSN 1103-4580.

Thor, M. (2001). Operational stump treatment against *Heterobasidion annosum* in European forestry – current situation. In: Laflamme, G., *et al.* (Eds.) *Proceedings of Root and Butt Rots of Forest Trees: 10th International Conference on Root and Butt Rots*, Québec City, Canada, September 16-22 2001. pp. 170-175. ISBN 0-662-33332-2.

Thor, M. (2005). *Heterobasidion root rot in Norway spruce: Modelling incidence, control efficacy and economic consequences in Swedish forestry* Diss. Uppsala, Sweden:Swedish University of Agricultural Sciences.

Thor, M. (2011). *Stubbehandling mot rotröta -- beräkning av ekonomiskt utfall på Sveaskog* Uppsala: Skogforsk. (Resultat från SkogForsk; Nr. 19).

Thor, M., Arlinger, J.D. & Stenlid, J. (2006). *Heterobasidion annosum* root rot in *Picea abies*: Modelling economic outcomes of stump treatment in Scandinavian coniferous forests. *Scandinavian Journal of Forest Research* 21(5), 414-423.

Thor, M., Ståhl, G. & Stenlid, J. (2005). Modelling root rot incidence in Sweden using tree, site and stand variables. *Scandinavian Journal of Forest Research* 20(2), 165-176.

Thor, M. & Stenlid, J. (2005). *Heterobasidion annosum* infection of *Picea abies* following manual or mechanized stump treatment. *Scandinavian Journal of Forest Research* 20(2), 154-164.

Tokuda, S., Hattori, T., Dai, Y.C., Ota, Y. & Buchanan, P.K. (2009). Three species of *Heterobasidion* (Basidiomycota, Hericiales), *H. parviporum, H. orientale* sp nov and *H. ecrustosum* sp nov from East Asia. *Mycoscience* 50(3), 190-202.

Vollbrecht, G. & Agestam, E. (1995). Modeling incidence of root-rot in *Picea abies* plantations in southern Sweden. *Scandinavian Journal of Forest Research* 10(1), 74-81.

Vollbrecht, G., Gemmel, P. & Pettersson, N. (1995a). The effect of precommercial thinning on the incidence of *Heterobasidion annosum* in planted picea abies. *Scandinavian Journal of Forest Research* 10(1-4), 37-41.

Vollbrecht, G., Johansson, U., Eriksson, H. & Stenlid, J. (1995b). Butt rot incidence, yield and growth pattern in a tree species experiment in southwestern Sweden. *Forest Ecology and Management* 76, 87-93.

Vollbrecht, G. & Jørgensen, B.B. (1995). Modelling the incidence of butt rot in plantations of *Picea abies* in Denmark. *Canadian Journal of Forest Research* 25(12), 1887-1896.

Vollbrecht, G. & Stenlid, J. (1999). Transfer of the P-type of *Heterobasidion annosum* from old-growth stumps of *Picea abies* to *Picea abies* and *Larix* x *eurolepis*. *European Journal of Forest Pathology* 29(2), 153-159.

Werner, A. & Łakomy, P. (2002a). Intraspecific variation in *Heterobasidion annosum* for mortality rate on *Pinus sylvestris* and *Picea abies* seedlings grown in pure culture. *Mycologia* 94(5), 856-861.

Werner, A. & Łakomy, P. (2002b). Host specialization of IS-group isolates of *Heterobasidion annosum* to Scots pine, Norway spruce and common fir in field inoculation experiments. *Dendrobiology* 47, 59-68

Wikström, P., Edenius, L., Elfving, B., Eriksson, L.O., Lämås, T., Sonesson, J., Öhman, K., Wallerman, J., Waller, C. & Klintebäck, F. (2011). The Heureka forestry decision support system: An overview. *Mathematical and Computational Forestry & Natural-Resource Sciences* 3(2), 87-94.

Woodward, S., Stenlid, J., Karjalainen, R. & Hüttermann, A. (1998). *Heterobasidion annosum: Biology, Ecology, Impact and Control*. Cambridge, UK: CAB International. ISBN 0-85199-275-7.

Wulff, S. (2011). *Monitoring forest damage: methods and development in Sweden.* Diss. Umeå, Sweden:Swedish University of Agricultural Sciences.

Yde-Andersen, A. (1962). Seasonal incidence of stump infection in Norway spruce by air-borne *Fomes annosus* spores. *Forest Science* 8(2), 98-103.

Yen, P.C., Chang, T.T. & Kuo, S.R. (2002). Root and butt rot of *Pinus luchuensis* caused by *Heterobasidion insulare* and its nutrient physiology. *Taiwan Journal of Forest Science* 17(1), 31-39.

Acknowledgements

Coming to study in Sweden is the greatest opportunity for me and it has substantially changed my life and my way of thinking. I wouldn’t have accomplished the thesis without the kind help and great inspirations from the people I have met during the past four and half years.

First of all, I give my sincerest gratitude to my principal supervisor Dr. Jonas Rönnberg. Thank you for being so patient and encouraging through all the years. It is so amazing that you always make things possible. I have learnt the most from you. You have been more than an excellent supervisor but also a very good friend.

Thank you Dr. Michelle Cleary! Although you have been my assistant supervisor for not more than one year, your hardworking and rigorous attitude deeply impressed me and you have given the most intensive help in the science and the language revision of the manuscripts. Thank you so much for pushing me!

I am very lucky to have a remarkable group of assistant supervisors. Jim Pratt, thank you for taking me to Thetford forest and made what was written in the book came into reality. Thank you for all the guidance and discussions. Dr. Mattias Berglund, thank you for always supporting me, caring about my progress and inspiring my thoughts from both scientific and practical perspectives. Prof. Jan Stenlid, thank you for all the encouragement and valuable suggestions!

Thank you Anna Gunulf, I enjoy discussing with you on all kinds of topics and it has been wonderful time to work together with you! Jing Zhang, I am really impressed by your diligence and persistence, and it has been really nice to

work with you on the pine project. Thank you, Erik Ek and Henrik Pålsson, for the wonderful master thesis work.

Field work and lab work were assisted by Torkel Welander, Anna Gunulf, Rebecka McCarthy, Maria Bikedal, Jing Zhang, Wioleta Zakrzewska and Emma Gunulf. Thank you so much for the great job you have done. Thank you Kent Hansson for helping me in developing tools for field and lab work.

Great acknowledgement is given to Mike Cruickshank for hosting the study visit in British Columbia, Canada, and for reviewing one of the manuscripts; to Duncan Morrison for also hosting the study visit in BC, Canada; to Fred Peet for reviewing one of the manuscripts. Dr. Iben Thomsen is greatly acknowledged for the review and comments on the thesis. Thanks to Mats Olsson from department of Biochemistry and Environmental Assessment for the guidance in soil sampling and analysis; Ulf Johansson at Tönnersjöheden research park for the four-month practical work and support for trial of manual stump treatment at precommercial thinning; Acknowledgement to Jim Lyon, at Thetford forest, UK, for a preliminary trial of uprooting pines on his land and helpful assistance. Jan-Eric Englund for all the statistical support, without you I cannot finish my statistical analyses.

Thank you all at Southern Swedish Forest Research Center, P-M, Erik, Ola, Urban, Johanna, Igor, Lars, Johan B, Mattias, Henrik, Rolf, Adam, Eugene, P-O, Magnus, Violeta, Margareta, Desiree and my fellow PhD students, Renats, Kathrin, Giulia, Mateusz, Samuel, Rebecka, Clementine, Naran, Ida and many I may have forgotten to mention, but you truly have made the work and life here more joyful.

Financial support was kindly provided by Verdera Oy, InterAgro Skog AB, AmphoChem AB, JL-tuotteet Oy, Södra Skog AB, Sydved AB Stiftelsen Rattsjö, Brattåsstiftelsen, and Future Forests. The lab was equipped by support from Stiftelsen Nils och Dorthi Troëdssons Forskningsfond.

感谢我的父母对我一如既往的爱和鼓励，感谢你们一直支持和尊重我的选择。最后，也是最深沉的感谢给我的丈夫，时金。感谢你为我，为我们的家庭作出的奉献。没有你的支持，我真的不可能完成这一切。谢谢你给了我每天微笑的理由和工作的动力。我爱你！