Establishment of *Heterobasidion annosum s.l.* Infections in Young Norway Spruce Dominated Stands

Implications for Silviculture

Anna Gunulf
Faculty of Forest Sciences
Department of Southern Swedish Forest Research Centre
Alnarp

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Abstract

One of the worst pathogens on Norway spruce, *Heterobasidion annosum s.l.*, can establish in previously healthy trees by spores landing on freshly made stumps from where mycelia can grow via root grafts and contacts to the adjacent tree. The risk of spore infection as well as disease transfer has been considered to be negligible in young stands due to the small target size of stumps and their small root systems. Consequently, small stumps created during precommercial thinning and late precommercial thinning are usually not treated with protective agents against spore infections as is commonly done during commercial thinnings. The objective of this thesis was to increase the knowledge regarding establishment of *H. annosum s.l.* infections in young Norway spruce dominated stands, in order to provide a renewed knowledge-base for forest management decisions.

The results from field studies showed that although the risk of spore infections increased with increasing stump size more than half of small Norway spruce stumps created during precommercial thinning and late precommercial thinning were infected with *H. annosum s.l.* (Paper I, II). Of the two *Heterobasidion* species present in Sweden *H. parviporum* had a competitive advantage over *H. annosum s.s.* during colonization of Norway spruce wood (III). Norway spruce stumps as small as 2.5 cm in diameter could transfer infection to trees and the risk of transfer increased with increasing stump size (IV). Stump treatment with the biocontrol agent *Phlebiopsis gigantea* decreased the amount of spore infections on small stumps (I). The reduction was within the lower range reported from commercial thinning stumps. Simulations of decay development after late precommercial thinning indicated that a substantial amount of the decay at final felling could be attributed to late precommercial thinning. Further, the simulations indicated that stump treatment could reduce the decay at final felling if removal intensities were high. However, the economic outcome of stump treatment varied (II).

In conclusion, there is a risk of new *H. annosum s.l.* infections establishing during silvicultural operations in young Norway spruce dominated stands. Precautionary measures to reduce the risk such as early precommercial thinnings or, where applicable, winter fellings or stump treatment could be considered.

Keywords: root and butt rot, *Heterobasidion annosum s.l.*, Norway spruce, birch, precommercial thinning, late precommercial thinning, stump treatment

Author's address: Anna Gunulf, SLU, Department of Southern Swedish Forest Research Centre, P.O. Box 49, 230 53 Alnarp, Sweden
E-mail: Anna.Gunulf@ slu.se

Dedication

To my grandmother, Rona Andersson, who taught me how to read and who didn't get the opportunity to achieve her own academic goals.

The farmers and the fishermen represent the nobility of modern society; they share their crumbs with the rest of us, who run about with papers and screwdrivers attempting to build a better world without a blueprint.

Thor Heyerdahl

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., McCarthy, R., Rönnberg, J. (2012). Control efficacy of stump treatment and influence of stump height on natural spore infection by *Heterobasidion* spp. of precommercial thinning stumps of Norway spruce and birch. *Silva fennica* 46, 655-665.

II Gunulf, A., Berglund, M., Carlsson, T., Rönnberg, J. Late precommercial thinning of Norway spruce in southern Sweden and the risk of *Heterobasidion* spp. root rot. Manuscript.

III Gunulf, A., Rönnberg, J., Berglund, M. (2012). Comparison of colonization capacity by asexual spores of *Heterobasidion* species in Norway spruce wood. *Forest pathology* 42, 338-244.

IV 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.

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The contribution of Anna Gunulf (AG) to the papers included in this thesis was as follows:

I AG developed the research idea and designed the experiment with Jonas Rönnberg and Rebecka McCarthy. She did 90 % of the statistical analyses and as first author 60 % of the writing. Overall input during the complete study for AG: ca 50 %

II AG did all of the modelling and statistical analyses and wrote 85 % of the manuscript. Overall input during the complete study for AG: ca 55 %.

III AG did all of the statistical analyses and as first author wrote 90 % of the manuscript. Overall input during the complete study for AG: ca 55 %.

IV AG planned and conducted the second part of the fieldwork. She did 50 % of the lab work and statistical analyses. As first author she wrote 75 % of the manuscript. Overall input during the complete study for AG: ca 60 %.

1 Introduction

1.1 The pathogen

1.1.1 Impact

Root and butt rot caused by the fungal species complex *Heterobasidion annosum* (Fr.) Bref. *sensu lato* (*s.l.*) cause severe economic losses for the forest industry in the northern hemisphere (Woodward *et al*., 1998). The losses are a result of reduced timber value due to decay as well as growth loss and an increased risk of windthrow for diseased trees (Woodward *et al*., 1998). *Hesterobasidion annosum s.l.* is considered to be the most important forest pathogen affecting Norway spruce (*Picea abies* (L.) Karst.) (Bendz-Hellgren *et al*., 1998) and the majority of decay found in Norway spruce in the Nordic countries is associated with it (Hallaksela, 1984; Stenlid & Wästerlund, 1986; Huse *et al*., 1994). In Sweden, 6.7 % of mature Norway spruce trees are decayed at breast height (Forestry statistics, 2004), corresponding to a decay frequency of 11-22 % at stump height (Stenlid & Wästerlund, 1986). The impact varies among stands and can be considerably higher than the average; e.g. decay frequencies over 70 % have been reported from some Norway spruce stands (Stenlid & Wästerlund, 1986; Rönnberg *et al*., 2007). Thus for the individual forest owner the impact from decay can be significant, a decay frequency of 70 % at final felling could result in 19 % of the harvested volume being affected by decay (Rönnberg *et al*., 2013).

1.1.2 Infection route

Understanding the infection route of *H. annosum s.l.* is important to recognize how to reduce the long-term impact. The infection route can be considered in two stages: primary and secondary infection. Primary infection entails establishment of infection by spores on newly cut stump surfaces or wounds (Rishbeth, 1951a; Isomäki & Kallio, 1974). Two types of spores are known to exist *in vivo*; basidiospores (sexual spores) and conidiospores (asexual spores)

(Redfern & Stenlid, 1998). Airborne basidiospores are released from basidiocarps as long as basidiocarps are not frozen or suffering from severe drought (Rishbeth, 1951a) and are believed to be more important for the spread of the fungus compared to asexual conidiospores (Redfern & Stenlid, 1998). Secondary infection entails vegetative spread by mycelia from a colonized substrate to a new substrate, e.g. from stumps to trees (Rishbeth, 1951b) through root grafts or contacts (Rishbeth, 1950).

1.1.3 Hosts and species

While the species in the *H. annosum s.l.* complex follow the same general infection route their distribution and hosts differ. Two species of the complex are known to exist in Sweden, *Heterobasidion parviporum* Niemelä & Korhonen and *Heterobasidion annosum* (Fr.) Bref. *sensu stricto* (*s.s.*) (Korhonen *et al*., 1998a; Niemelä & Korhonen, 1998). When both species are discussed together in this thesis they are referred to as *Heterobasidion* spp. While *H. parviporum*´s distribution to the north approximately follows the distribution of Norway spruce *H. annosum s.s*. has not been found in the northernmost parts of Scandinavia (Korhonen *et al*., 1998a). *Heterobasidion parviporum* mainly infects Norway spruce and occasionally saplings of Scots pine (*Pinus sylvestris* L.) while *H. annosum s.s*. has a broader range of hosts, among which include Norway spruce, Scots pine, juniper (*Juniperus communis* L.) and several broadleaved tree species such as birches (*Betula* spp. L.) (Korhonen, 1978). Although both species have the ability to infect Norway spruce, *H. parviporum* is more common in Norway spruce stands in northern and eastern Europe (Korhonen *et al*., 1998a). The processes behind this pattern are unknown though it has been hypothesized that selection during primary and secondary infection could influence *Heterobasidion* spp. establishment (Hanso *et al*., 1994). Oliva *et al*. (2011) found that *H. parviporum* spread more frequently from stumps to trees of Norway spruce, as compared to *H. annosum s.s.* It is unknown if the capacity for primary infection of Norway spruce stumps differs between *H. parviporum* and *H. annosum s.s.* Increased knowledge regarding which *Heterobasidion* species to expect depending on host substrate, e.g. stumps or trees, could improve forest management decisions since choice of tree species to be used in admixtures or in the subsequent rotation could influence the impact of the disease (Korhonen *et al*., 1998b).

1.1.4 Control by stump treatment

Planting mixed forests is one control method to reduce the impact from *H. annosum s.l*. (Korhonen *et al*., 1998b), but other options are also available. One such option, which aims to prevent the establishment of new infections in a stand, is to treat the stumps with chemical or biological control agents directly after felling (Holdenrieder & Greig, 1998; Pratt *et al.*, 1998). Among the chemical agents urea is used in Europe while borax is preferred in North America (Pratt *et al*., 1998). In Sweden, the most common treatment agent used is the fungus *Phlebiopsis gigantea* (Fr.) Jül. (Thor, 2003). The mode of action of *P. gigantea* as treatment agent is not known in detail but it is probable that establishment of *H. annosum s.l.* in stumps is obstructed by resource competition (Asiegbu *et al*., 2005).

In Sweden, it is common to treat Norway spruce stumps created during commercial thinnings (Thor, 2003). The control efficacy of treatment with *P. gigantea*, defined by Berglund and Rönnberg (2004) as the reduction of infected area on stumps by treatment application, on Norway spruce commercial thinning stumps was reported to range between 50-100 % (Korhonen *et al*., 1994; Thor & Stenlid, 1998; Berglund & Rönnberg, 2004; Berglund *et al*., 2005; Nicolotti & Gonthier, 2005; Rönnberg *et al*., 2006). A recent study on the long-term effect of treatment on Norway spruce commercial thinning stumps revealed that stump treatment decreased the number of genets being established in the stands (Oliva *et al*., 2010). A reduction of rot frequency in the remaining trees on former agricultural land was also found while the effect on rot frequency on old forest land was more unclear (Oliva *et al*., 2010). Simulations of decay development following stump treatment during commercial thinnings indicated a substantial reduction of decay at final felling as well as an economical gain from treatment (Thor *et al*., 2006). On precommercial thinning stumps however, neither the control efficacy nor the long-term effect of stump treatment with *P. gigantea* have been investigated.

1.2 Young stands

1.2.1 Silvicultural operations in young Norway spruce stands

Norway spruce is an important tree species in Sweden accounting for 42 % of the standing volume on productive forest land (Forestry statistics, 2012). A considerable proportion of the stands in Sweden are young; approximately 20 % of the forest land outside of reserves are occupied by young forest (Forestry statistics, 2002). Since downy birch (*Betula pubescens* Ehrh.) and silver birch (*Betula pendula* Roth.) frequently regenerates abundantly on forest regeneration areas in Sweden (Fries, 1985) both Norway spruce and birch can be found in young Norway spruce dominated stands. Potential entry points for

Heterobasidion spp., i.e. stumps, are created in young stands during precommercial thinning and late precommercial thinning. When both operations are discussed together in this thesis the term "silvicultural operations in young stands" is used. Precommercial thinning is a common practice in Sweden (Skogsstyrelsen, 2001) and is performed on approximately 336000 ha per year (Swedish statistical yearbook, 2012). The aim is to promote the desired trees by removing trees with unwanted characters or positions and is usually performed when the stand reach two to six meters in height (Pettersson *et al*., 2012). During precommercial thinning in Norway spruce dominated stands, stumps of both Norway spruce and birch can be created (Pettersson *et al*., 2012). Late precommercial thinning is performed in dense stands just prior to the first commercial thinning since a high density of stems per hectare can reduce the efficiency of the first commercial thinning (Kärhä, 2006). The extent of late precommercial thinning conducted in Sweden and what species and sizes of stumps created during the operation have not been recorded.

1.2.2 *H. annosum s.l.* infection and small stumps

Many studies on disease dynamics have been conducted in thinning stands. It is possible though that the risk of both primary and secondary infection in younger stands, e.g. during precommercial thinning, differ from infection in the older commercial thinning stands (Vollbrecht *et al*., 1995). Therefore, conclusions drawn from studies on commercial thinning stumps might not be directly applicable to young stands. The risk of primary infection on small and young stumps has been suggested to be lower due to the smaller target area for spore infections as well as possible differences in wood properties (Vollbrecht *et al*., 1995). Indeed, a positive relationship between stump size and infection frequency has been reported for Norway spruce (Paludan, 1966; Solheim, 1994; Bendz-Hellgren & Stenlid, 1998) and Scots pine (Rishbeth, 1951a). For the North American species of *H. annosum s.l.* a similar relationship has been shown for Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), amabilis fir (*Abies amabilis* (Dougl.) Forbes), Sitka spruce (*Picea sitchensis* (Bong.) Carr.) and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) (Morrison & Johnson, 1999). Although this positive relationship between stump size and primary infection is well described the extent of primary infection on small stumps created during silvicultural operations in young Norway spruce dominated stands is poorly explored. The risk of secondary infection has also been suggested to be affected by stump size, small stumps may decompose faster relative to large stumps and therefore only provide inoculum for a short time (Stenlid & Redfern, 1998) and the number of root contacts between stump and adjacent trees could be lower (Vollbrecht *et al*., 1995). Stump size has been shown to be positively correlated with the probability of secondary infection from commercial thinning stumps of Norway spruce to adjacent trees for *H. parviporum*, while no correlation could be found for *H. annosum s.s.* (Oliva *et al*., 2011). So far, the relationship between stump size and secondary infection in precommercial thinning stumps has not been studied and it is unknown whether the small stumps have the ability to transfer infection at all.

1.2.3 *H. annosum s.l.* infection and recipient trees

The wood properties of the recipient tree could also influence secondary infection. In trees with non-resinous heartwood, e.g. Norway spruce, *H. annosum s.l.* root rot is considered to be a disease of older stages of tree development since it prefers heartwood (Korhonen & Stenlid, 1998). Thus, it could be expected that even if a small, young stump became infected an adjacent young tree could perhaps not receive the infection. However, although infection frequency increased with size and age of trees, Piri (2003) detected infection in trees planted just seven years prior to sampling and Piri and Korhonen (2001) found *Heterobasidion* spp. infection in an 11-year-old advanced regenerated Norway spruce. There is also a report of infections in 11-14-year-old plantations (Rönnberg & Jørgensen, 2000). The majority of these infections in young trees most likely originated from larger infected stumps, or in the case of advanced regeneration also from trees, belonging to the previous generation. Thus, it seems possible for young trees to become infected and they are consequently at risk if the surrounding stumps and trees can transfer infection.

1.2.4 Impact from early silvicultural operations on decay development

If stumps created during precommercial- and late precommercial thinning in Norway spruce dominated stands act as entry points for *Heterobasidion* spp. infection the disease will have a long time to develop and the damage at final felling could therefore be substantial (Venn & Solheim, 1994; Vollbrecht & Agestam, 1995). On the other hand, the lower probability of primary and possibly also secondary infection due to the small size of stumps could reduce disease development. Vollbrecht *et al*. (1995) did not find a single tree decayed from Norway spruce precommercial thinning stumps and concluded that precommercial thinning of Norway spruce is of minor importance for decay in the residual stand. However, Vollbrecht *et al*. (1995) did not monitor spore abundance during and after stump creation and thus the seemingly low impact on disease from precommercial thinning could also be a consequence of low spore loads. The impact of silvicultural operations in young Norway spruce stands on the risk of root and butt rot due to *Heterobasidion* spp. is therefore still uncertain.

1.3 Knowledge gaps

The knowledge gaps identified above reduce the possibility to make sound forest management decisions to decrease the impact of *Heterobasidion* spp. root and butt rot, and underline the need to better comprehend the establishment of *Heterobasidion* spp. infections in young Norway spruce dominated stands. Processes at both primary and secondary stages of infection need to be elucidated. The extent of primary infection on stumps created during precommercial thinning and late precommercial thinning is currently unknown. It is important to investigate whether small stumps, if they do get infected, have the ability to transfer infection to adjacent trees. Since efficacy of stump treatment by *P. gigantea* has only been evaluated on thinning stumps there is also a need to test it also for precommercial thinning stumps before recommendation about stump treatment in young stands can be made. Knowledge regarding which species of *Heterobasidion* that can be expected to establish in young Norway spruce stands have implications for the further management of the stand with regards to admixtures of other tree species.

2 Objectives of thesis

The main objective of this thesis was to provide new scientific information about the establishment of *Heterobasidion* spp. infections in young Norway spruce dominated stands to facilitate appropriate forest management decisions. Specific questions addressed were:

- To what extent are the stumps created during precommercial thinning and late precommercial thinning in young Norway spruce dominated stands subjected to primary infection? (I, II)

- Does the colonization capacity of *H. parviporum* and *H. annosum s.s*. differ during primary infection of Norway spruce stumps? (III)

- Can treatment with *Phlebiopsis gigantea* on Norway spruce stumps created during silvicultural operations in young stands significantly reduce primary infection and decay frequency at final felling? (I, II)

- Does stump size influence secondary infection and do infected precommercial thinning and late precommercial thinning stumps of Norway spruce have the ability to transfer the disease to adjacent trees? (IV)

3 Methodology and major results

3.1 Primary infection on precommercial thinning stumps and effect of stump treatment (Paper I)

The aims of the study were to investigate the extent of primary infection of *Heterobasidion* spp. on precommercial thinning stumps of Norway spruce and birch and to see if infection was influenced by the height of the stumps. Furthermore, the effect of stump treatment with *P. gigantea* on precommercial thinning stumps of Norway spruce was examined.

3.1.1 Materials and methods

The experiment was established in five Norway spruce dominated precommercial thinning sites in southern Sweden during June 2010. Stand age varied between 8 and 15 years with site indices (dominant height at age 100 years in Norway spruce) between 26 and 32 m. The previous land use was forest on all sites. Six different stump types were created by felling trees with a chainsaw: low cut spruce (15 cm above ground), low cut spruce treated with *P. gigantea* (see below), high cut spruce (100 cm above ground), high cut spruce treated with *P. gigantea*, low cut birch and high cut birch. The diameters of the stumps created ranged between 2.4 and 14.5 cm at 15 cm height. In each stand, 30 stumps belonging to each stump type were created. *P. gigantea* (Rotstop®S) was applied as stump treatment with a density of approximately 100-1000 oidiospores/cm^2 directly after felling the trees. To minimize the probability of preexisting infection in stumps, only stumps without discoloration were included. The stumps were left exposed to natural spore infection by *Heterobasidion* spp. for two months at which time they were sampled by cutting a 5 cm thick disc with a sterilized handsaw after discarding the top 1 cm of the stump. Discs were incubated at room temperature (≈20°C) for 7-10 days. Both sides of discs were visually inspected for *Heterobasidion* spp. using a dissecting microscope and *Heterobasidion* spp. was recognized by the presence of conidiophores. All colonies of *Heterobasidion* spp. were marked, the number of discrete colonies counted and the total area occupied on each side of the disc measured by covering the disc surface with a transparent grid. Infected area and number of colonies were calculated for each infected disc as the average of the two sides. Relative infected area was determined by dividing infected area by the total disc area. Differences in infection parameters among stump types were analyzed as factorial and block designs with GLM and Friedman's test in Minitab 16 (Minitab Inc., State college, PA, USA). The relationship between stump size and the probability of infection was investigated with PROC GLIMMIX in SAS 9.2 (SAS Institute Inc., Cary, NC, USA) with binomial distribution and logit as link. The model included the random factor "Site", i.e. the dependence of stumps in the same site was taken into account.

3.1.2 Results

More than half of the untreated Norway spruce precommercial thinning stumps were infected (Table 1) and the probability of infection increased with increasing stump diameter ($p = 0.002$). Norway spruce stumps treated with *P. gigantea* had lower infection frequency as well as smaller mean infected area and relative infected area on infected stumps compared to untreated stumps, yet still almost one third of the treated Norway spruce stumps were infected (Table 1). The efficacy of stump treatment on Norway spruce stumps, i.e. the reduction of relative infected area due to treatment (Berglund & Rönnberg, 2004), was 61-65 %. Birch stumps had significantly lower infection frequency compared to untreated Norway spruce stumps and smaller infected area compared to both untreated and treated Norway spruce (Table 1). Stump height of Norway spruce and birch did not significantly influence infection frequency nor any of the other infection parameters.

Table 1. *Heterobasidion spp. infection on birch, untreated Norway spruce and treated Norway spruce precommercial thinning stumps. Means within columns that do not share a letter are significantly different with 95 % confidence.*

		Infection frequency (%)		Relative infected area of infected stumps (%)		Infected area of infected stumps (cm^2)		No. of colonies on infected stumps	
Stump type	N	Mean	p-value	Mean	p-value	Mean	p-value	Mean	p-value
Birch	5	14.8b		1.9c		0.37c		0.98a	
Treated spruce	5	31.3b	0.022	4.3b	0.007	1.18b	0.007	1.66a	0.074
Untreated spruce	5	55.0a		11.3a		3.46a		2.52a	

3.2 Primary infection on late precommercial thinning stumps and influence of stump treatment on decay frequency at final felling (Paper II)

Late precommercial thinning in Norway spruce dominated stands was studied in southern Sweden. The aims were to assess the risk of *Heterobasidion* spp. spore infection on the stumps created and to simulate the influence of those infections, with or without stump treatment, on disease development in the stands.

3.2.1 Materials and Methods

To investigate the frequency, size and species of stumps created during late precommercial thinning, eight Norway spruce dominated stands that had recently undergone late precommercial thinning were inventoried in 2006. Stand age varied between 28 and 39 years with site indices (dominant height at age 100 years in Norway spruce) between 28 and 36 m. Ten sample plots with eight meters radius were evenly distributed in each stand. Within each plot all Norway spruce stumps remaining after the late precommercial thinning with diameters greater than 5 cm were measured with a caliper and assigned to one of four diameter classes; 5.0-6.9 cm, 7.0-8.9 cm, 9.0-10.9 cm and ≥11.0 cm. Stumps from other tree species with diameters greater than 5 cm were counted. The number of stumps depending on diameter class was analyzed with PROC GLIMMIX in SAS 9.2 with negative binomial distribution and log as link. The model included diameter class and the random factor stand. Pairwise comparisons were done between different diameter classes with adjustment according to Tukey.

To investigate infection on Norway spruce stumps remaining after late precommercial thinning, stumps in four Norway spruce dominated stands that had undergone the operation during the previous two years were sampled in 2005. Two stands were established on former agricultural land and two on former forest land. Stand age varied between 27 and 30 years with site indices between 26 and 28 m. To ensure similar conditions for stumps of different sizes each stand was subdivided into four equal-sized parts. From each part up to eight randomly selected Norway spruce stumps without discoloration were sampled from each diameter class; 5.0-6.9 cm, 7.0-8.9 cm, 9.0-10.9 cm and ≥11.0 cm. Sampling was done by cutting a disc from the stump using a chainsaw, to facilitate detection of *Heterobasidion* spp. the sampling depth, which ranged between 1 and 8 cm, was adjusted to time passed since late precommercial thinning. Discs were incubated for 7-10 days in room temperature (≈20˚C) before being examined for conidiophores of

Heterobasidion spp. with a microscope. The proportion infected stumps depending on diameter class was analyzed with PROC GLIMMIX in SAS 9.2 with binomial distribution and logit as link. The model included diameter class and the random factors stand and "part of stand" within stand. Pairwise comparisons were done between different diameter classes with adjustment according to Tukey.

Disease development following late precommercial thinning was simulated in the mechanistic model Rotstand 7.1 (Pukkala *et al*., 2005). Two strata of Norway spruce trees were plotted in the simulated stands (site index 30 m); one for larger trees with a density of 2200 trees/ha with mean diameter at breast height of 12 cm and one for smaller trees with mean diameter of 6 cm that were to be removed during the late precommercial thinning. Based on the stump inventory three different removal intensities were tested; 5 %, 10 % and 20 %. To investigate disease development without late precommercial thinning, one stand solely consisting of the larger strata was also plotted. Late precommercial thinning, both with and without stump treatment, was conducted at age 31 and afterwards the 2200 trees/ha from the larger strata remained in the stand irrespective of late precommercial thinning intensity. The remaining trees were subjected to three management options. The first management option followed a thinning guide for southern Sweden (Gallringsmallar: södra Sverige, 2002); four commercial thinnings and final felling at a stand age of 85 years. The second option entailed three commercial thinnings and final felling at 65 years. The third option was based on the earliest allowable age for final felling in the Swedish forestry Act; 55 years (Skogsvårdslagstiftningen…, 2012), and the final felling was preceeded by two commercial thinnings. All commercial thinnings were conducted during the summer and the stumps were treated. The final felling of the previous rotation was assumed to have been done during the winter with 100 % reduction of spore infection. When decay in the previous rotation was simulated this was done in accordance with Thor *et al*. (2006). The default settings for *Heterobasidion* spp. dynamics (Pukkala *et al*., 2005) were used for all parameters of *Heterobasidion* spp. dynamics except for the inoculum expansion rate which was set to 0.2 m/year (Oliva & Stenlid 2011) and the probability for logging injury during late precommercial thinning which was set to 0. In accordance with the result of the investigation of stump infection (Table 2) the probability of spore infection was set to 0.4 for the late precommercial thinning stumps while 0.6 was used for the commercial thinning stumps. Efficacy of stump treatment was set to 90 % (Korhonen *et al*. 1994; Thor & Stenlid 2005). Each late precommercial thinning option, i.e.

with or without stump treatment or without late precommercial thinning, within each management scenario was repeated five times and the decay frequency at final felling recorded. Within each management scenario the mean proportion of trees with decay depending on late precommercial thinning option were compared. The statistical analyses were done with PROC GLM in SAS 9.2, with further pairwise comparisons between different late precommercial thinning situations with adjustment according to Tukey. An economic assessment of stump treatment with *P. gigantea* was performed and compared to the result of the simulations. The cost of treatment was assumed to be comprised of substrate (7 SEK/g, 1g/m^2 consumed, stump diameter 7 cm) and labor (340 SEK/h, preparation 10 min/ha, application 8 s/stump) costs. The total cost for each late precommercial thinning intensity was discounted with 3 % interest rate to the time of final felling for each management option. From the discounted total cost, the volume at final felling needed to finance the treatment was calculated by assuming that the price of decayed wood was decreased by 200 SEK/m^3sub (solid under bark). The proportion of the volume at final felling was calculated by dividing the volume needed to finance the treatment with the simulated total volume at final felling and the proportion of the volume was converted to the proportion of decayed trees by dividing the volume by 3.7 (Rönnberg *et al*. 2013) and then compared to the result of the simulations.

3.2.2 Results

On average 63 % of the trees removed during late precommercial thinning were Norway spruce while 36 % were broadleaves the rest of the trees were Scots pine. Thinning intensity of Norway spruce trees ranged between 7 % and 22 % of the total number of stems prior to late precommercial thinning. Norway spruce stump abundance varied among diameter classes ($p < 0.001$). Stumps belonging to the two smaller diameter classes were more common than stumps belonging to larger diameter classes (Table 2). Of the 340 sampled late precommercial thinning Norway spruce stumps, 182 were infected by *Heterobasidion* spp. The proportion of infected stumps differed among diameter classes ($p = 0.001$). Almost two fifths of the stumps in the smallest diameter class, i.e. 5-6.9 cm, were infected which was significantly fewer compared to diameter classes 7-8.9 and 9-10.9 cm (Table 2).

The trend in all but one scenario was that not treating the stumps at late precommercial thinning resulted in most decay at final felling followed by treating the stumps, not performing the late precommercial thinning resulted in the least amount of decay (Table 3, Table 4). The differences were more pronounced with increasing thinning intensity, all scenarios with 20 % removal resulted in significant differences among late precommercial thinning options while only two out of the six scenarios with 5 % removal resulted in significant differences (Table 3, Table 4). Treating the stumps during late precommercial thinning reduced the decay frequency by on average 0.9 to 17.9 percent points for the different management scenarios. Using the option of avoiding late precommercial thinning as the baseline, on average 18 % of the decay at final felling could be attributed to untreated stumps from late precommercial thinning if 5 % of the trees were removed during the operation and the previous rotation was healthy. The corresponding numbers for 10 % and 20 % removal were decay levels of 20 % and 37 %, respectively. If the previous rotation was decayed, a smaller proportion of the decay at final felling could be attributed to late precommercial thinning; on average 9 % if 5 % of the trees were removed, 12 % if 10 % were removed and 24 % if 20 % were removed. According to the economic assessment the decay frequency had to be reduced by 2.2-9.3 percent points at final felling to finance stump treatment during late precommercial thinning (Table 3, Table 4). In five of the nine management scenarios of previously healthy stands the average reduction in decay frequency by application of stump treatment was higher than or equal to the required reduction to finance the treatment (Table 3). This was only true for one management scenario when previous decay was simulated (Table 4).

Table 2. *Average number of Norway spruce late precommercial thinning stumps and average proportion of stumps infected by Heterobasidion spp. in different diameter classes. Means within columns that do not share a letter are significantly different with 95 % confidence.*

		Proportion infected stumps	
Diameter class	Mean stumps/ha (SE)	N sampled	Mean (SE) (%)
5-6.9 cm	161 (22.7) a	128	37.6 (5.7) a
7-8.9 cm	130 (18.7) a	128	59.8 (5.8) b
9-10.9 cm	43 (7.4) b	68	68.1 (6.9) b
≥ 11 cm	7 (2.2) c	16	67.7 (12.8) ab

Table 3. *Simulated proportion decayed trees at final felling of different management scenarios from simulations without previous decay depending on the situation at late precommercial thinning (pct). The estimated required reduction of decay incidence at final felling to finance the cost of stump treatment during late precommercial thinning is also shown. Means within each management scenario that do not share a letter are significantly different with 95 % confidence according to Tukey's test.*

Management scenario			Proportion decayed trees at final felling (%)				Mean difference of decay incidence between treated and untreated (pp[a]) (95 % CI[b])	Required reduction of decay incidence to finance treatment (pp[a])
Late pct intensity	Further management	Late pct options	Min	Max	Mean			
5 %	Option 1	Untreated stumps	36.3	43.9	40.5 a			
		Treated stumps	31.4	38.3	34.1 a	p=0.042	6.4 (-0.5:13.4)	2.5
		No late pct	25.1	40.1	33.9 a			
5 %	Option 2	Untreated stumps	20.7	25.2	22.4 a			
		Treated stumps	18.5	21.1	20.0 ab	p=0.055	2.4 (-1.1:6.0)	2.4
		No late pct	15.5	23.2	18.8 b			
5 %	Option 3	Untreated stumps	13.1	15.3	14.6 a			
		Treated stumps	10.6	14.6	12.5 b	p=0.001	2.1 (0.4:3.9)	2.2
		No late pct	10.8	12.1	11.4 b			
10 %	Option 1	Untreated stumps	41.0	47.8	43.9 a			
		Treated stumps	31.4	38.6	34.4 b	p=0.003	9.5 (2.9:16.1)	4.3
		No late pct	25.1	40.1	33.9 b			
10 %	Option 2	Untreated stumps	21.1	24.7	22.6 a			
		Treated stumps	16.4	22.4	19.6 a	p=0.053	2.9 (-0.9:6.7)	4.0
		No late pct	15.5	23.2	18.8 a			
10 %	Option 3	Untreated stumps	11.8	16.5	14.5 a			
		Treated stumps	11.9	15.2	13.2 ab	p=0.021	1.2 (-1.3:3.8)	3.7
		No late pct	10.8	12.1	11.4 b			
20 %	Option 1	Untreated stumps	52.9	59.2	56.1 a			
		Treated stumps	33.7	40.5	38.2 b	p<0.001	17.9 (11.5:24.3)	8.5
		No late pct	25.1	40.1	33.9 b			
20 %	Option 2	Untreated stumps	27.8	32.2	30.0 a			
		Treated stumps	20.1	23.4	21.7 b	p<0.001	8.3 (4.8:11.8)	8.0
		No late pct	15.5	23.2	18.8 b			
20%	Option 3	Untreated stumps	16.2	18.3	17.4 a			
		Treated stumps	11.7	17.0	13.5 b	p<0.001	3.9 (1.6:6.2)	7.2
		No late pct	10.8	12.1	11.4 b			

[a)] pp, percent points
[b)] CI, confidence interval

Table 4. *Simulated proportion decayed trees at final felling of different management scenarios from simulations with previous decay depending on the situation at late precommercial thinning (pct). The estimated required reduction of decay incidence at final felling to finance the cost of stump treatment during late precommercial thinning is also shown. Means within each management scenario that do not share a letter are significantly different with 95 % confidence according to Tukey's test.*

Management scenario			Proportion decayed trees at final felling (%)				Mean difference of decay incidence between treated and untreated (pp[a]) (95 % CI[b])	Required reduction of decay incidence to finance treatment (pp[a])
Late pct intensity	Further management	Late pct options	Min	Max	Mean			
		Untreated stumps	56.5	59.9	58.5 a			
5 %	Option 1	Treated stumps	53.1	59.2	55.8 a	p=0.102	2.7 (-3.3:8.7)	2.8
		No late pct	47.1	59.0	53.2 a			
		Untreated stumps	32.2	36.3	34.1 a			
5 %	Option 2	Treated stumps	29.2	35.6	32.2 a	p=0.133	1.9 (-2.2:6.0)	2.5
		No late pct	27.3	33.7	30.7 a			
		Untreated stumps	20.6	25.3	22.9 a			
5 %	Option 3	Treated stumps	18.5	22.9	20.7 a	p=0.133	2.2 (-0.7:5.1)	2.3
		No late pct	19.3	22.6	20.9 a			
		Untreated stumps	55.1	66.7	61.7 a			
10 %	Option 1	Treated stumps	52.4	62.6	57.4 ab	p=0.045	4.3 (-3.7:12.3)	4.7
		No late pct	47.1	59.0	53.2 b			
		Untreated stumps	31.8	37.4	34.6 a			
10 %	Option 2	Treated stumps	29.8	38.1	33.6 a	p=0.090	0.9 (-3.5:5.3)	4.3
		No late pct	27.3	33.7	30.7 a			
		Untreated stumps	21.6	26.1	23.7 a			
10 %	Option 3	Treated stumps	21.8	23.7	22.4 ab	p=0.030	1.3 (-1.1:3.7)	3.9
		No late pct	19.3	22.6	20.9 b			
		Untreated stumps	68.2	71.8	69.6 a			
20 %	Option 1	Treated stumps	54.2	63.6	58.6 b	p<0.001	11.1 (4.7:17.4)	9.3
		No late pct	47.1	59.0	53.2 b			
		Untreated stumps	36.9	43.3	40.4 a			
20 %	Option 2	Treated stumps	32.3	37.5	34.8 b	p<0.001	5.7 (1.5:9.9)	8.5
		No late pct	27.3	33.7	30.7 b			
		Untreated stumps	24.4	30.1	27.4 a			
20 %	Option 3	Treated stumps	21.5	22.7	22.0 b	p<0.001	5.4 (2.9:7.8)	7.7
		No late pct	19.3	22.6	20.9 b			

a) pp, percent points
b) CI, confidence interval

3.3 *H. annosum s.s.* and *H. parviporum* colonization capacities during primary infection (Paper III)

The aim of the study was to examine the interspecific competition between *H. annosum s.s.* and *H. parviporum* and their colonization rate on fresh Norway spruce wood following infection by conidiospores.

3.3.1 Materials and Methods

Five uninfected Norway spruce trees with diameters ranging between 13 and 22 cm at stump height were felled and cut into six one meter sections. Each section was subdivided into three billets for a total of 18 billets per tree. Diameters at the top of the billets ranged between 11 cm and 20 cm. The three billets within each section were randomly distributed among three inoculation treatments and placed in climate chambers. The temperature in the chambers was kept at 18º C (relative humidity 70 %) during the day and at 14º C (relative humidity 80 %) during the night. The first inoculation treatment contained conidiospores from five *H. annosum s.s.* isolates, the second from five *H. parviporum* isolates and the third contained a mixture of spores from all of the *H. annosum s.s.* and *H. parviporum* isolates (all isolates were kindly provided by K. Korhonen). The spore suspensions were applied to the top of the billets with a density of approximately 25 spores/cm^2, with equal contribution from each isolate.

Three weeks after inoculation the billets were subdivided into 3-cm thick discs using a sterilized hand saw or tiger saw. After an incubation period of one week at about 20°C, the lower side of each disc (i.e. 3 cm, 6 cm, 9 cm, etc.) was scanned for *Heterobasidion* spp. colonies using a dissecting microscope. The top disc of each billet was checked first, followed by the second, and the third and so on. When no colonies of *Heterobasidion* spp. could be found on a disc, the discs further down the billets were not checked. All colonies of *Heterobasidion* spp. were marked and the total area occupied by the colonies was measured. The diameter of each disc was measured. For the billets inoculated with the mixture of *H. annosum s.s.* and *H. parviporum*, several isolations (Swedjemark & Stenlid, 1993) were made both from the top disc and the lowest disc of each billet where *Heterobasidion* spp. was detected. From billets inoculated with either *H. annosum s.s.* or *H. parviporum*, only one isolation was made from the top disc. Mating tests, where two homokaryotic tester strains of each species were paired with the unknown isolate, were used to assign isolates to *H. annosum s.s.* or *H. parviporum* (Korhonen, 1978). Species assignment was done based on the external appearance of the interaction zone between the isolate and the tester strains as well as the presence of clamped hyphae in the tester strain after pairing (Korhonen, 1978).

The disc furthest down in each billet where *Heterobasidion* spp. infection was detected was used as measurement of infection depth. To get a number describing the horizontal spread the infected area per disc was added for each billet. Both infection depth and the infected area were analyzed in GLM with a split plot model using Minitab 16 with further pairwise comparisons with Tukey's test. To test whether the two species competed a χ^2-test in Minitab 16 was used.

3.3.2 Results

Both infection depth and infected area differed depending on the inoculation treatment of the billets ($p = 0.008$ and $p < 0.001$ respectively). On average infection was detected at a depth of 7.5 cm in the billets inoculated with *H. parviporum* which was significantly ($p < 0.05$) higher compared to the infection depth of 5.2 cm in the billets inoculated with H. *annosum s.s.* The infected area followed the same pattern; 33.0 cm^2 for the billets inoculated with *H. parviporum* compared to 5.5 cm^2 ($p < 0.05$) for the billets inoculated with *H. annosum s.s.* Neither the infection depth nor the infected area was significantly influenced by the billets' vertical position in the tree ($p = 0.487$ and $p = 0.272$, respectively). The inoculation treatments showed similar growth patterns irrespective of the billets vertical position; no interaction between the billets vertical position and inoculation treatment could be found for the infection depth ($p = 0.356$) nor for the infected area ($p = 0.518$). On the billets inoculated with the mixture 196 of the isolated colonies from the top disc could be assigned to either *H. annosum s.s.* or *H. parviporum* by the mating test, and of those 195 were *H. parviporum*. This differed significantly ($p < 0.001$) from the expected value (121) if no competition took place, or if the ability to compete was equal between the two species. The 54 isolations derived from discs further down in the billets inoculated with the mixture of *H. annosum s.s.* and *H. parviporum* were all *H. parviporum*.

3.4 Secondary infection and the influence of stump size (Paper IV)

The aim was to study secondary infection by *H. parviporum* from small Norway spruce stumps. The ability of small-sized Norway spruce stumps to transfer infection to neighboring trees and the influence of size and age of stumps on disease transmission was investigated.

3.4.1 Materials and methods

The experiment was established on fourteen Norway spruce dominated sites located in western Sweden during 2003. At each site donor stumps were created by felling ten randomly selected Norway spruce trees within a specific diameter class with a chainsaw. Diameter was measured at stump height (about 10 cm above ground) with a calliper and ranged between 2 and 14 cm. After felling the tree, the stump was inoculated with a spore suspension of a single heterokaryotic strain of *H. parviporum*, Rb175, (kindly provided by J. Stenlid) by spraying the suspension onto the cut surface using a spray bottle.

Five years after establishment the donor stumps as well as the four largest Norway spruce trees within a two meter radius from each donor stump were sampled by cutting a disc 10-20 cm above ground with a chainsaw. The distance between donor stump and the tree was measured. After incubation for 7-11 days at room temperature (≈ 20°C), one side of each disc was scanned for *Heterobasidion* spp. using a dissecting microscope. *Heterobasidion* spp. was recognized by the presence of conidiophores. All colonies of *Heterobasidion* spp. were marked and conidia were picked with a sterile needle and transferred onto a Petri dish containing Hagem agar, up to five isolations were made from each disc. The diameters of the discs from the trees were measured perpendicularly with a ruler. The age at stump height of trees and stumps were measured by counting the number of growth rings on the discs. To determine if isolates were Rb175 they were paired against a stored sample of Rb175 in a somatic compatibility tests, a compatible reaction was recognized by a continuous mycelial mat (Stenlid, 1985). For species identification the isolates were put against two homokaryotic strains of *H. parviporum* and *H. annosum s.s.* in mating tests (Korhonen, 1978). Species assignment was done based on the external appearance of the interaction zone between the isolate and the tester strains as well as the presence of clamped hyphae in the tester strain after pairing (Korhonen, 1978).

As size and age of trees as well as distance between tree and donor stump were measured five years after stump inoculation these variables were adjusted, based on the number and width of year rings so that they described the situation in the forest at the time of stump inoculation. All statistical analyses were made in SAS 9.2. Age and size differences between stumps that transferred infection and stumps that did not transfer infection were investigated with a t-test. The relationship between the probability that a tree was infected by Rb175, as well as by *H. annosum s.s.* or *H. parviporum* other than Rb175, and the variables “Donor diameter”, “Donor age”, “Tree diameter”, “Tree age” and “Distance between donor and tree” was investigated using PROC GLIMMIX with binomial distribution and logit as link. The model included the random factor “Donor”, i.e. the dependence of the four trees associated with the same donor stump was taken into account. The analysis was conducted with backward elimination using the p-value 0.1 as the limit for elimination. The relationship between diameter and age of the donor stumps was analyzed with linear regression in PROC REG.

3.4.2 Results

Sixty-five percent of the stumps had transferred Rb175 infection to at least one of the adjacent trees. The smallest stump that transferred infection had a diameter of 2.5 cm and the youngest was 7 years old at the time of stump inoculation. Stumps that transferred infection were, on average, larger than stumps that did not transfer ($p < 0.001$). Mean age, i.e. number of year rings, did not differ significantly between transferring and non transferring stumps ($p = 0.531$).

The probability that a tree was infected by Rb175 increased with increasing size of both donor stump (parameter estimate 0.23; $p < 0.001$) and tree (parameter estimate 0.15; $p < 0.001$). The age of the donor stump also influenced the probability, for a given stump size the probability of infection in the nearby tree decreased with increasing age of the stump (parameter estimate -0.07; $p < 0.001$). The age of the tree and the distance between donor stump and tree did not significantly influence the probability of infection. Using the estimated regression line between the age and the diameter of donor stumps, $Age_{Stump}=7.995+1.733Diameter_{Stump}$ ($p < 0.001$, $R^2 = 0.33$), the probability of infection could be approximately described using only diameters of donor stump and tree (Figure 1).

In 44 % of the trees wild infections, i.e. isolates of *Heterobasidion* spp. other than Rb175, were detected. Not counting Rb175, *H. parviporum* was found in 35 % of the trees and *H. annosum s.s.* was found in 16 %. The probability of finding *H. parviporum* other than Rb175 in the trees was influenced by donor diameter (parameter estimate 0.17; $p = 0.003$), tree diameter (parameter estimate 0.27; $p < 0.001$) and tree age (parameter estimate -0.07; $p < 0.001$) while the probability of finding *H. annosum s.s.* in the trees was only significantly influenced by the diameter of the tree (parameter estimate 0.09; $p = 0.005$).

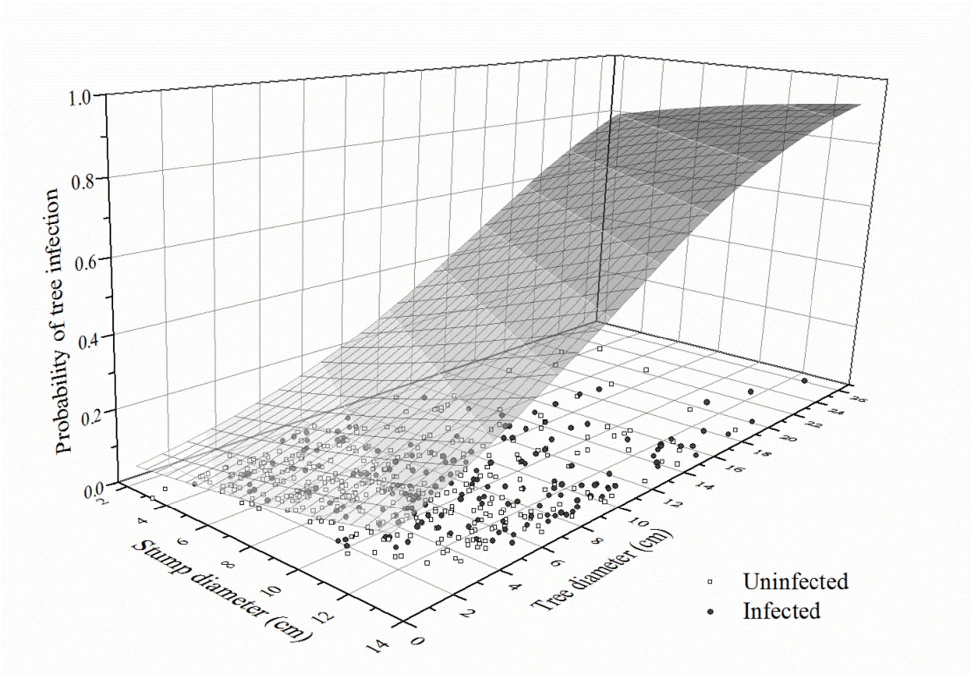

Figure 1. Estimated probability of finding Rb175 (*H. parviporum*) infection in a tree in the experiment depending on the size of the tree and the transferring stump. The probability is predicted by the relationship $p_{infected} = (1+e^{-(-2.28+0.23DiameterStump+0.15DiameterTree-0.07AgeStump)})^{-1}$. The age of the stump is expressed by the linear relationship AgeStump=7.995+1.733DiameterStump. Filled circles and open squares represent sampled trees. (Figure reproduced from Gunulf, A., Wang, LY., 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.)

4 General discussion

4.1 Stumps created in young Norway spruce dominated stands and the risk of primary infection

4.1.1 Influence of Norway spruce stump size

In accordance with previous studies (Rishbeth, 1951a; Paludan, 1966; Solheim, 1994; Bendz-Hellgren & Stenlid, 1998; Morrison & Johnson, 1999) a positive relationship between stump size and *Heterobasidion* spp. infection frequency was found in papers I and II. Thus, the risk of primary infection during precommercial thinning and late precommercial thinning is probably lower compared to commercial thinnings due to the smaller size of the stumps created during the early forestry operations. However a substantial amount of the untreated Norway spruce stumps created in the young stands were still infected; 55 % of the precommercial thinning stumps (I) and 54 % of the late precommercial thinning stumps (II). Thus, although less than during commercial thinnings, there is a substantial risk of primary infection on Norway spruce stumps during silvicultural operations in young Norway spruce dominated stands.

4.1.2 Birch stumps

In addition to Norway spruce, birch stumps are also commonly created during silvicultural operations in young Norway spruce dominated stands (Pettersson *et al*., 2012). Although *Heterobasidion* spp. infection has been found in birch (Korhonen, 1978), conifers are generally considered more susceptible than deciduous trees (Korhonen & Stenlid, 1998). It was therefore surprising to find as much as 15 % of the precommercial thinning birch stumps infected by *Heterobasidion* spp. (I). Whether these infections pose a risk to the remaining trees is not clear. The area covered by *Heterobasidion* spp. infection in the birch stumps were on average considerably smaller than the infected area found in the adjacent Norway spruce stumps. Although the impact of infection size at stump height on infection probability in the adjacent trees is basically unknown, Morrison and Redfern (1994) found a positive correlation between stump area colonized two years after felling and root volume colonized six years later on Sitka spruce suggesting a greater impact from larger infections. Furthermore, the risk of birch stumps transmitting the disease to adjacent Norway spruce trees may be lower than the corresponding risk for Norway spruce stumps since the probability of interspecific root grafts is lower than that of intraspecific ones (Epstein, 1978). Due to differences regarding the vertical distribution of roots in the soil between birch and Norway spruce (Kalliokoski *et al*., 2008) the probability of interspecific root contacts and thus of disease transmittance may be further reduced. However, severe infection by *Heterobasidion* spp. in birch stands planted after diseased Scots pine has been reported (Lygis *et al*., 2004), thus it is possible for the fungus to grow in and heavily impact birch at least during certain circumstances. Furthermore since many birch stumps can be created during silvicultural operations in young Norway spruce dominated stands and a substantial proportion of them can be infected it could be valuable to monitor the development of the infections found in birch stumps before they are disregarded.

4.1.3 Height of stumps

Trees that are removed during precommercial thinnings are commonly cut with a brushsaw although also a new type of saw which cuts the stems higher up is available on the market (Pettersson *et al*., 2012). The tapering of trees led a to smaller stump area being exposed to basidiospores for trees that were cut higher up the stem (I). However this difference did not have a significant effect on primary infection on either Norway spruce stumps or birch stumps. Thus equal amount of primary infection can be expected irrespective of whether a normal brushsaw or the new type of saw are used during precommercial thinning in Norway spruce dominated stands. Nevertheless, there could still be an effect of stump height on the amount of *Heterobasidion* spp. infection entering the stand. Since infection of *Heterobasidion* spp. can die out from small stumps already within five years from stump creation (IV) the longer distance, and thus time, the fungus have to grow in a high cut stump before reaching the adjacent tree could reduce the risk of secondary infection. On the other hand, the larger volume of woody material associated with high cut stumps could serve as a large inoculum source which could increase the risk to the remaining stand compared to if low cut stumps were created. More detailed studies are needed to further elucidate the influence of stump height on the different parameters of secondary spread.

4.2 Secondary infection from small Norway spruce stumps

Surprisingly, Norway spruce stumps of all sizes and ages investigated in paper IV could transfer infection of *H. parviporum* to adjacent trees. As discussed above, the small Norway spruce stumps created during precommercial thinning and late precommercial thinning can suffer substantially from primary infection. Consequently, there is a risk of new infections entering young Norway spruce dominated stands during silvicultural operations if Norway spruce is being removed.

Not only primary infection was influenced by stump size, but also secondary infection of *H. parviporum* between Norway spruce stumps and trees are affected by the size of the stump (IV). The probability of transfer increased with increasing size of stump which is in accordance with the results of Oliva *et al*. (2011) who studied this aspect in commercial thinning stumps. Also the size of the recipient tree will influence the probability of secondary infection which increased with increasing size of trees (IV). A similar relationship was found by Piri and Korhonen (2001) who sampled young trees on previously infected sites. Thus, increasing size of both stump and tree positively affect the likelihood of disease transfer from stump to tree. Increasing odds of root contacts, and thus for disease transfer, with increasing size could be an explanation for this pattern since stem diameter is positively correlated with coarse root biomass (Drexhage & Gruber, 1999) and with root extension (Hakkila, 1972).

Since both the size of the infected stump and the surrounding trees influenced the probability of disease in the tree the risk will vary depending on the diameter distribution in the forest. Using the relationship between infection probability and size of tree and stump (Figure 1) it is possible to tentatively compare different scenarios. For example, during a typical precommercial thinning, when the trees removed will have approximately the same size as the trees remaining, the estimated relative risk from an infected stump would be twice as big if the trees were 10 cm compared to if they were 6 cm (Figure 2). Hence, it would be preferable, from a root rot control perspective, to conduct precommercial thinnings early in Norway spruce dominated stands if Norway spruce needs to be removed. The larger residual trees during a late precommercial thinning could have a substantial effect on the probability of transfer. If the residual trees have diameters of 12 cm at stump height during a late precommercial thinning the relative risk of infection from a 5-6 cm stump is twice as high than during a conventional precommercial thinning when the stand is still even-sized. However, if the trees removed during the late precommercial thinning are older than in the normal precommercial thinning the risk is reduced (Figure 2). If late precommercial thinnings could be avoided by planting fewer Norway spruce seedlings per unit area or by removing Norway spruce trees in an early precommercial thinning, the risk of introducing root rot in the stand could be reduced.

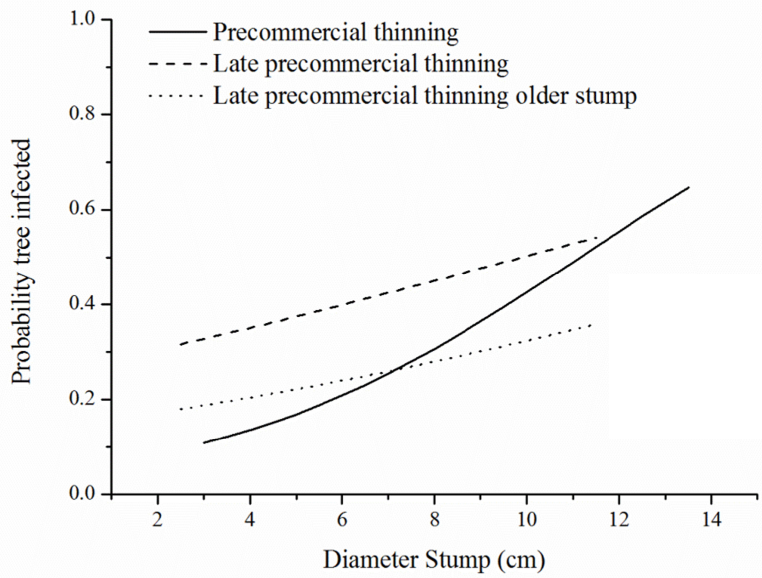

Figure 2. Probability of tree infection by Rb175 (*H. parviporum*) for different scenarios of silvicultural operations derived from the relationship between probability and the characteristics of tree and stump described in Figure 1. In the scenario of precommercial thinning (solid line), stumps and trees are assumed to have equal size and at the late precommercial thinning scenario (dashed line) trees are assumed to have a diameter of 12 cm at stump height. The scenario of late precommercial thinning with older stump (dotted line) is the same as late precommercial thinning but the age of the stump is increased with 10 years. (Figure reproduced from Gunulf, A., Wang, LY., 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.)

It is important to realize that as a consequence of the artificial infection with high spore loads of one individual of *H. parviporum* (IV) the result does not reveal the actual risk of infection after a precommercial thinning or a late precommercial thinning. Instead the result indicates the relative risk depending on the size and age of stump and size of the tree for Norway spruce stands in general within the array of investigated site indices, former land useage and stump and tree size distributions. The actual risk could vary depending on local spore pressure (Redfern *et al*., 1997) and the virulence of the *Heterobasidion* genets present (Swedjemark *et al*., 1999). Higher rot incidence can be expected in trees adjacent to stumps inoculated with high densities of *Heterobasidion* spp. spores, as was done in paper IV, compared to trees close to naturally infected stumps (Oliva *et al*., 2008). In addition, the performance during secondary infection of the genet used as inocula on the stumps in paper IV was consistent with 11 other *H. parviporum* genets (Oliva *et al*., 2011). Thus, in many cases the actual risk of infection during silvicultural operations in young Norway spruce dominated stands is probably lower than the results of paper IV indicate.

4.3 Establishment of *H. parviporum* vs. *H. annosum s.s.* in young Norway spruce dominated stands

4.3.1 Primary infection

Both *H. parviporum* and *H. annosum s.s.* have the ability to colonize Norway spruce stumps by primary infection (III; Swedjemark & Stenlid, 1993; Korhonen & Piri, 1994). Since spore deposits decline with increasing distance from basidiocarps (Kallio, 1970) the chance of colonization will increase for the *Heterobasidion* species established and sporulating in the close vicinity of a newly cut stump. However, if spores from both species are present a greater probability for establishment by *H. parviporum* in Norway spruce stumps could be expected since *H. parviporum* can outgrow and outcompete *H. annosum s.s.* during early colonization of Norway spruce wood (III). This suggests that Norway spruce stumps can act as a selective media favoring *H. parviporum* over *H. annosum s.s.*, a possibility previously discussed by Hanso *et al*. (1994) and Korhonen and Piri (1994) based on field studies of natural infection. The difference in competitive ability may in part explain the dominance of *H. parviporum* over *H. annosum s.s.* in Norway spruce stands reported from previous studies (Hanso *et al*., 1994; Korhonen & Piri, 1994; Wellendorf & Thomsen, 2008). In areas outside the natural distribution of Norway spruce where *H. annosum s.s.* has been found to be common in Norway spruce trees, e.g. southern Sweden and Denmark (Stenlid, 1987; Thomsen, 1994), a shift towards dominance by *H. parviporum* in Norway spruce stands could thus be expected over time.

In the results presented in paper III, *H. parviporum* almost completely excluded *H. annosum s.s.* when spores of both species were applied in equal amounts on the same substrate. However, in natural conditions the competitive advantage of *H. parviporum* over *H. annosum s.s.* does not need to be absolute since colonies of both *H. parviporum* and *H. annosum s.s.* have been found in the same Norway spruce stump (Gonthier *et al*., 2003; Swedjemark & Stenlid, 1993). The species may also show different competitive ability in relation to each other depending on the conditions. Competition between different genets of *Heterobasidion* spp. becomes increasingly important with increasing spore loads (Redfern *et al*., 1997). Possibly, high spore densities, for example in areas close to basidiocarps (Kallio, 1970) or during the summer in Scandinavia (Yde-Andersen, 1962; Solheim, 1994; Brandtberg *et al*., 1996), could favour colonization of Norway spruce stumps by *H. parviporum* over *H. annosum s.s.* while lower spore densities, for instance in spring and autumn in the alps (Gonthier *et al*., 2005) would allow also *H. annosum s.s.* to establish.

Some of the billets used as substrate in paper III were larger than stumps typically created during silvicultural operations in young stands. Thus the performance of *H. parviporum* and *H. annosum s.s.* at primary infection of the smallest Norway spruce stumps created during precommercial thinning might differ from the result in paper III. It would therefore be of interest to study the colonization ability of *Heterobasidion* spp. also on smaller stumps.

Also birch stumps can be substantially infected by *Heterobasidion* spp. during precommercial thinnings (I). Assuming a corresponding process of stump selectivity for birch as found for Norway spruce (III) it is, due to host preferences (Korhonen, 1978), reasonable to assume that the majority of those infections were *H. annosum s.s*. The colonies of *Heterobasidion* spp. found in paper I were however not tested, thus it is possible that both species can establish in birch stumps as has been found in Scots pine stumps (Rönnberg *et al*., 2006). Thus, primary infection on stumps created in young Norway spruce stands could be expected by both *H. parviporum* and *H. annosum s.s.* in areas where both species occur. If the spore pressure is high after stump creation the probability of colonization by *H. parviporum* could be higher on at least the larger Norway spruce stumps, while *H. annosum s.s.* can be expected to colonize birch stumps as well as Norway spruce stumps if the spore pressure is low.

4.3.2 Secondary infection

On commercial thinning stumps, Oliva *et al*. (2011) found a higher frequency of secondary infection from Norway spruce stumps infected by *H. parviporum* compared to those infected by *H. annosum s.s.* The probability of secondary infection increased with increasing stump size for *H. parviporum* while no such relationship between stump size and secondary infection could be detected for *H. annosum s.s.* (Oliva *et al*., 2011). Intriguingly, the natural infections, i.e. *Heterobasidion* spp. genets other than that inoculated, found in the trees in paper IV showed a similar pattern when assuming that they originated from the stumps; the size of the stump did not influence secondary infection of *H. annosum s.s.* Thus, a possibility, suitable for future investigations, is that *H. annosum s.s.*, if established in a Norway spruce stump, could gain entrance to the remaining Norway spruce trees more easily during early silvicultural operations compared to later when stumps are larger and the competition from *H. parviporum* is more pronounced.

In conclusion, although *H. parviporum* seems to outperform *H. annosum s.s.* during both primary infection of Norway spruce stumps and secondary infection between Norway spruce stump and tree, both species can be expected to establish in young Norway spruce dominated stands. If reduction of disease impact by growing resistant tree species, as admixtures or in the subsequent rotation, is desired, trees that are resistant to both species of *Heterobasidion* should therefore be chosen in areas where both species are present.

4.4 Stump treatment in young Norway spruce dominated stands

4.4.1 Reduction of primary infection

Due to the risk of primary and secondary infection during silvicultural operations in young Norway spruce dominated stands precautionary measures against spore infection could be warranted. Stump treatment with *P. gigantea* is one measure that is commonly used during commercial thinnings of Norway spruce (Thor, 2003) and the results from paper I indicate that it could reduce primary infection significantly also on precommercial thinning stumps (Table 1). However, almost one-third of the treated Norway spruce stumps were still infected by *Heterobasidion* spp. two months after the treatment. The control efficacy, i.e. the reduction of relative infected area by treatment, was 61-65 % on the precommercial thinning stumps treated with *P. gigantea*, i.e. Rotstop®S. Previous studies dealing with commercial thinning stumps of Norway spruce have reported control efficacies ranging between 50-100 % for Rotstop® (the original strain presently used in Finland) (Korhonen *et al*., 1994; Thor & Stenlid, 1998; Berglund & Rönnberg, 2004; Berglund *et al*., 2005; Nicolotti & Gonthier, 2005; Rönnberg *et al*., 2006) and 63-94 % for Rotstop®S (the strain presently used in Sweden) (Berglund *et al*., 2005; Rönnberg *et al*., 2006). Thus, although the control efficacy found in paper I could be considered low, it is well within the range reported by studies on commercial thinning stumps. Therefore, it seems conceivable that stump treatment with *P. gigantea* renders similar results whether applied on the small precommercial and late precommercial thinning stumps or the larger commercial thinning stumps.

It should be noted that the previous land use of forest on the experimental sites in paper I may have contributed to the apparent low control efficacy as well as the high infection frequency of treated stumps. In other words, it is possible that residual stumps from the previous rotation may have infected some of the precommercial thinning stumps thru secondary infection (Piri, 2003). However, it is not likely that the majority of the detected infections in paper I were present before cutting the trees as infection frequency in general is positively correlated with tree age (Piri & Korhonen, 2001). Infection frequencies in Norway spruce trees of similar ages as in paper I have been reported to range between 2 and 13 % despite heavy infection in the previous rotation (Rönnberg & Jørgensen 2000; Piri, 2003) while the infection frequency in paper I was considerably higher; 31.3 %.

Further studies on the impact of stump size on the effect of stump treatment would be interesting since it is unknown whether the low efficacy found in paper I was a result of natural variation, previous land use or perhaps the small sizes of stumps. It is possible that environmental differences on precommercial thinning stumps compared to that of commercial thinning stumps, e.g. moisture content (Bendz-Hellgren & Stenlid, 1998), inhibits colonization by *P. gigantea* and its overall treatment effect to some degree. Vasiliauskas *et al*. (2002) found fewer sporocarps of *P. gigantea* on smaller stumps of Norway spruce compared to larger stumps, possibly indicating a suitable habitat for the fungus. If the protecting effect of *P. gigantea* is negatively influenced by the small size or young age of precommercial thinning stumps, treatment with urea could be a better option on these stumps. Treatment with urea inhibits *Heterobasidion* spp. growth by raising pH levels at stump surface above 7 (Johansson *et al*., 2002). The increased pH on newly created stumps is a result of the hydrolysis of urea into ammonia caused by enzymes produced by the stump which is more pronounced in young wood (Johansson *et al*., 2002). Thus, although it remains to be tested, urea could be very effective against *Heterobasidion* spp. infection during precommercial thinnings and late precommercial thinnings.

4.4.2 Long term effects

The simulations in paper II indicate that stump treatment during late precommercial thinning could substantially reduce the impact of decay in both previously healthy and decayed stands if the removal intensity is high. In previously healthy stands, 37 % of the decay at final felling could be attributed to late precommercial thinning if 20 % of the trees were removed in the operation. The assessment of the economic outcome of stump treatment indicates that it could be profitable when the previous rotation is healthy and when the rotation length is long. However when the previous rotation is decayed or the final felling is done at the earliest allowable age, the average decay reduction at final felling from stump treatment may not be enough to finance the cost. Although the economic outcome from stump treatment during late precommercial thinning varied the effect of stump treatment on reduction of the number of *Heterobasidion* spp. genets establishing (Oliva *et al*. 2010) and thus possibly on the long term health of the stand should also be considered during decisions concerning protective measures.

It should, however, be noted that the assessment of the economic benefit of stump treatment is calculated conservatively since the decreased volume growth (Bendz-Hellgren & Stenlid, 1997) as well as the increased risk of wind throw (Oliva *et al*., 2008) due to infection is not included. In other words the economic gain from stump treatment is higher than indicated only by the decay reduction. It is also important to note that the assessment of the economic outcome is based on assumptions that reflect the conditions today. The profitability could, for example, increase with improved treatment application technique. If the time consumed for treatment application could be reduced by half by mounting a nozzle on the brush saw the treatment could be justified by the decay reduction in 14 of the 18 management scenarios (II). Due to the variable result of the economic assessment of stump treatment, measures to reduce the risk of root rot during late precommercial thinning should, with the present technique available, generally focus on performing the operation during the winter (Yde-Andersen, 1962; Solheim, 1994; Brandtberg *et al*., 1996) if late precommercial thinnings cannot be avoided. Stump treatment may though be considered in previously healthy stands.

The use of models to predict the future inevitably leads to approximations and uncertainties. Although Rotstand has been validated against empirical data with satisfactory result there are processes of stand and disease development that are not covered by the validation (Oliva & Stenlid, 2011). One such process is the disease transfer among small sized trees and stumps. Disease transfer is dependent on the function of root expansion in Rotstand which is based on the diameter of the tree or stump. The function for root expansion is critical for secondary spread of *Heterobasidion* spp. since it regulates root contacts as well as mycelial colonization of the roots (Pukkala *et al*., 2005). The function in use is based on measurements on 44 Norway spruce trees from one stand in southern Finland with a mean age of 108 years (Hakkila, 1972) and may thus not accurately predict the root expansion of young trees in southern Sweden. It predicts a coarse root expansion radius of approximately 0.5 meters for trees with a diameter of 8 cm at stump height. Empirical data shows that roots of Norway spruce trees of similar sizes can expand well over 3 m (Kalliokoski *et al*., 2008). Although the concept of coarse root expansion radius, which in Rotstand forms a circular root plate that when in contact with other root plates can transfer disease, is not the same as the actual root expansion measured by Kalliokoski *et al*. (2008) it is possible that Rotstand underestimates the probability of disease transfer from the small stumps created during late precommercial thinning. Thus, the impact from late precommercial thinning on decay occurrence at final felling might, in reality, be greater than that indicated by the simulations in paper II. Consequently, the need for protective measures against spore infections and the profitability of stump treatment could also be greater than indicated by the simulations.

The long term effect of stump treatment during conventional precommercial thinnings might be less pronounced than during late precommercial thinnings. The technique available for treatment and the size of stumps treated should be fairly similar as during late precommercial thinning. Still, it is likely that the effect and profitability of treatment during normal precommercial thinning is less pronounced due to the smaller size of surrounding trees, which could lead to lower relative risk of secondary infection (IV). Indeed, in simulations of decay development, Wang (2012) found no significant effect of stump treatment on decay frequency at final felling if precommercial thinning was conducted at a stand age of 10 years. Thus, with the present technique and knowledge available, also precommercial thinnings might, from a root rot control perspective, be best conducted during the winter if Norway spruce needs to be removed.

5 Practical implications

- Small Norway spruce stumps created during silvicultural operations in young stands can suffer substantially from spore infection by *Heterobasidion* spp. Infected Norway spruce stumps as small as 2.5 cm in diameter have the ability to transfer the disease to adjacent trees. The risk of *Heterobasidion* spp. infection establishing in the stand as a consequence of precommercial thinning and late precommercial thinning should therefore be considered as a factor when planning silvicultural operations.

- Since the probability of spore infections and disease transfer increases with increasing stump size it would be preferable, from a root rot perspective, to conduct precommercial thinnings as early as possible in Norway spruce dominated stands if Norway spruce needs to be removed.

- Due to the positive relationship between disease transfer and tree size the risk of introducing *Heterobasidion* spp. infection is larger during late precommercial thinnings compared to conventional precommercial thinnings even if stumps of the same sizes are created. Thus the risk of infection during late precommercial thinnings could be avoided by conducting heavier conventional precommercial thinnings or by planting fewer Norway spruce trees.

- If present in the area, both *H. parviporum* and *H. annosum s.s.* can be expected to establish in young Norway spruce dominated stands. If reduction of disease impact is sought by planting resistant tree species as admixtures or in the subsequent rotation, tree species with high resistant against both *Heterobasidion* species should be chosen, e.g. *Abies* spp. or deciduous tree species.

- Similar intensities of spore infections can be expected on small Norway spruce and birch stumps irrespective of whether the stumps are cut near the ground or one meter up. Thus, similar infection pressure can be anticipated irrespective of whether a normal brushsaw or the new saw that cuts at waist height is used.

- Stump treatment during late precommercial thinning could reduce the future decay in Norway spruce dominated stands if removal intensities of Norway spruce are high. The economic outcome of stump treatment, with the current application technique available, is however not convincing in every situation. Thus, there is a need to develop faster application techniques than hand held spray bottles. Measures to reduce the risk of root rot should, from an economic standpoint, focus on performing late precommercial thinning during the winter, i.e. when the risk of primary infection is low, if decay is already present in the stand or if the planned rotation length is short. If the previous rotation was healthy and the rotation length is planned to be longer stump treatment could be economically justified.

6 Future research needs

- There is a need for more studies quantifying the risk of *Heterobasidion* spp. infection during silvicultural operations in young Norway spruce dominated stands. Due to the time requirements of empirical studies simulations have an important role here. In Rotstand, the program commonly used to simulate decay development, the function describing root expansion needs revision to ensure accurate predictions of the potential impact from small stumps on decay development.

- The impact of stump size on the effect of stump treatment with *P. gigantea* and urea calls for further investigations to maximize and ensure satisfactory treatment against spore infections during silvicultural operations in young stands.

- Birch stumps created during silvicultural operations in Norway spruce dominated stands can suffer from primary infection by *Heterobasidion* spp. It is important to clarify whether these infections can spread to the remaining stand.

- Two kinds of saws are currently in use during precommercial thinnings, resulting in stumps that are cut either close to the ground or at waist height. The height of precommercial thinning stumps had no impact on primary infection but the development of the infections over time depending on stump height still needs to be studied.

- *H. parviporum* has a greater colonization capacity on Norway spruce stumps compared to *H. annosum s.s.* Also the ability to transfer from stumps to trees is larger for *H. parviporum*. However a small stump size does not seem to have as inhibitory an effect on *H. annosum s.s.* as it does on *H. parviporum*. It would therefore be of interest to compare the success of *H. parviporum* and *H. annosum s.s.* during primary and secondary infection on and from small Norway spruce stumps to map *H. annosum s.s*. potential entry points into Norway spruce dominated stands.

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