Heterobasidion Root Rot in Norway Spruce

Modelling Incidence, Control Efficacy and Economic Consequences in Swedish Forestry

Magnus Thor
Faculty of Natural Resources and Agricultural Sciences
Department of Forest Mycology and Pathology
Uppsala

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Abstract

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In spite of its biological and economic impact on Swedish forestry, root rot caused by *Heterobasidion annosum* (Fr.) Bref. sensu lato has received no or little attention in forest planning. This thesis summarizes and discusses two experiments involving prophylactic treatment of stumps, and three investigations on the modelling and simulation of root rot in coniferous stands with special emphasis on Norway spruce (*Picea abies* [L.] Karst.).

In 14 previously unthinned stands of Norway spruce, the efficacy of mechanized stump treatments with disodium octaborate tetrahydrate (DOT), *Phlebiopsis gigantea* (Fr.) Jül. and urea was compared with no treatment of stumps cut in the summer and winter, and with manual treatment. Stump treatment reduced the stump area colonised by H. annosum s. l. by 88-99% as compared with untreated stumps cut in the summer. In terms of colonized stump area, there were neither differences between compounds, nor between mechanised and manual treatments.

Sensitivity of root rot antagonist *P. gigantea* spores to high temperature or pressure was tested in laboratory and field experiments using a mechanized application. The spores withstood 1,600-2,200 kPa for 24 h without losing viability. Spore germination of *P. gigantea* had an optimum at c. 30ºC. Mechanized application under normal summer conditions in Sweden did not obstruct spore germination of *P. gigantea*.

Functions for predicting the probability of decay in individual trees were developed using logistic regression from data in the Swedish national forest inventory 1983-2001. The functions use data readily available in most stand records, and are recommended for strategic, tactical and operational planning.

Models for simulation of disease development were developed based on known facts about the mode of infection and spread of *H. annosum* s. l. in Fennoscandian coniferous forests. The economic outcomes for a number of stands typical of Swedish forest management were modelled and predicted using the models for *H. annosum* s. l. dynamics and models for cross-cutting of trees. Stump treatment in thinning and previous final felling was profitable (interest rates 1, 3 and 5%) in pure stands of Norway spruce and in mixed conifer stands in southern Sweden.

Keywords: biological control, chemical control, disease management, forest management, operational planning, strategic planning, tactical planning.

Author's address: Magnus Thor, Skogforsk (The forestry research institute of Sweden), Uppsala Science Park, S-751 83 UPPSALA, Sweden.

To Emma, Simon and Malin

Contents

Appendix

Papers I-V

The present thesis is based on the following papers, which will be referred to by their Roman numerals:

I. Thor, M & Stenlid, J. *Heterobasidion annosum* infection of *Picea abies* following manual or mechanized stump treatment. *Scandinavian journal of forest research.* (Accepted.)

II. Thor, M., Bendz—Hellgren, M. & Stenlid, J. 1997. Sensitivity of root rot antagonist *Phlebiopsis gigantea* spores to high temperature or pressure. *Scandinavian journal of forest research, 12,* 356-361.

III. Thor, M., Ståhl, G. & Stenlid, J. Modelling root rot incidence in Sweden using tree, site and stand variables. *Scandinavian journal of forest research.* (Accepted.)

IV. Pukkala, T., Möykkynen, T., Thor, M., Rönnberg, J. & Stenlid, J. Modeling infection and spread of *Heterobasidion annosum* in even-aged Fennoscandian coniferous stands. *Canadian journal of forest research* (in press).

V. Thor, M., Arlinger, J.D. & Stenlid, J. *Heterobasidion annosum* root rot in *Picea abies* – modelling economic outcomes of stump treatment in Scandinavian coniferous forests. (Manuscript.)

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Introduction

The basidiomycete *Heterobasidion annosum* (Fr.) Bref. s. l.[1] is one of the most common fungal pathogens in the northern temperate regions. Although other fungal pathogens might be of higher importance locally, *H. annosum* s. l. occurs in most managed coniferous forests of the northern hemisphere, from Central America and Northern Africa to central Finland and northern Sweden (Woodward *et al*., 1998). Losses due to the degradation of decayed wood and reduced increment have been estimated at €790 million year^{-1} in Europe (Woodward *et al*., 1998). In Fennoscandia, the financial losses have been estimated at about €90 million year^{-1}, of which Sweden accounts for €54 million, or SEK475 million (Bendz-Hellgren *et al*., 1998). The figures do not include indirect impacts such as increased risk of death and windthrow, or increased risk of introducing infection in future generations. Calculations of economic losses tend to become out of date as the regulations and practices for timber and pulp wood assessment, as well as the prices for the assortments involved are altered. Nevertheless, the most recent Swedish estimates (Rosvall *et al*., 2004) indicate the same magnitude as above.

Heterobasidion annosum s. l. has been reported from more than 200 species of woody plants, including about 45 species of pine, 25 species of fir and 10 species of spruce (Sinclair, 1964; Wagn, 1987; Korhonen & Stenlid, 1998).

Although much research has been conducted in order to understand the biology and infection mechanisms of the pathogen and its relations to the host, surprisingly little has been implemented in forest management practice and forest planning in Swedish forestry. There is no information about decay frequencies in stand records, which should contribute to making forecasts of timber yields and to the timing of logging operations. Prophylactic treatment of stumps occurs in thinning operations in southern Sweden, but not much elsewhere or within final felling operations. Actually, little of the silvicultural control, biological/chemical control and wood supply management are based on strategic decisions where *H. annosum* s. l. is a component.

[1] s.l. = *sensu lato*, i.e. in a broad sense. Synonymous to *H. annosum sensu lato* is *H. annosum* coll., meaning the collective species concept.

The pathogen

History, occurrence and taxonomy

Heterobasidion annosum s. l. has been described with many scientific names: *Polyporus annosus* (Fr.) (Fries, 1821), *Trametes radiciperda* (Hartig) (Hartig, 1874), *Fomes annosus* (Fr.) Karsten (Karsten, 1879) and *Fomitopsis annosa* (Fr.) Bond. & Singer (Bondartsev & Singer, 1941). Brefeld (1888) suggested *Heterobasidion annosum* (Fr.) Bref.

Willkomm (1866-1867) was the first to report on microscopic studies of fungal decay of wood, as "rediscovered" by Hüttermann & Woodward (1998). Hartig (1874, 1878) connected the fruiting bodies of *H. annosum* to the disease. Rishbeth (1949, 1951a, 1957) demonstrated the role of stump infection in the fungus' infection biology.

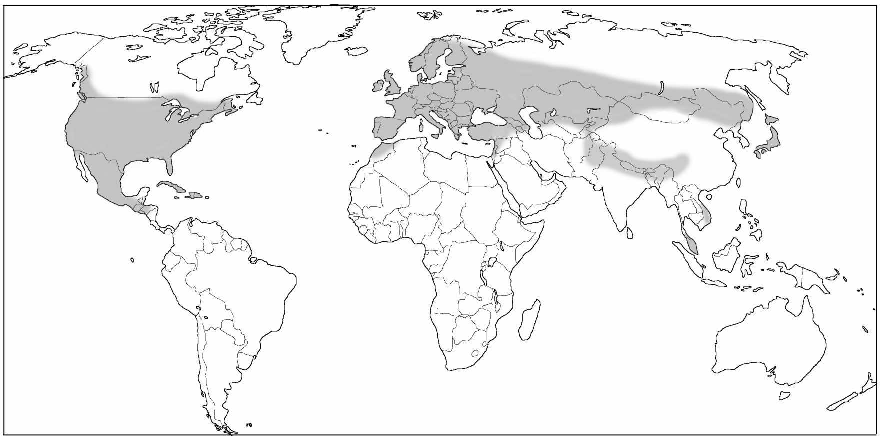

Fig. 1. Distribution of the *H. annosum* species complex in the world (map kindly provided by K. Korhonen, 2004).

The genus *Heterobasidion* is spread over large parts of the temperate zones of the world (Fig. 1). In Europe, *H. annosum* s. l. occurs in three inter-sterility (IS) groups[2] named after the main hosts, namely spruce (S) (*Picea* spp.), pine (P) (*Pinus* spp.) and fir (F) (*Abies* spp.) (Korhonen 1978; Capretti *et al.*, 1990) (Fig. 2). The low frequency of natural hybridization between IS groups occurring in the same regions indicates that these groups are true biological species (Korhonen & Stenlid, 1998). In Sweden and Finland, the S and P IS groups occur together in the southern parts of the countries, whereas only the S group is present in the north (Stenlid, 1987). In general, the S group is more common than the P group in both Sweden and Finland (Karlsson 1993; Korhonen & Piri 1994). However, the P group is considered more aggressive in Sweden since it also attacks, apart from

[2] Intersterility group of *H. annosum* s. l. Fungi belonging to different IS groups will not mate (e.g. Korhonen, 1978; Stenlid, 1985; Swedjemark & Stenlid, 1993).

Pinus spp., e.g. *Picea* spp., *Larix* spp., *Betula* spp. and *Alnus* spp. (Korhonen & Stenlid, 1998).

Niemelä & Korhonen (1998) named the S group *H. parviporum* Niemelä & Korhonen and the F group *H. abietinum* Niemelä & Korhonen. The P group is the original *H. annosum* (Fr.) Bref., or *H. annosum* s. str[3]. In the Fennoscandian context, only *H. parviporum* and *H. annosum* s. str. need to be considered.

Species of *Heterobasidion* have evolved together with their preferred hosts (Korhonen & Stenlid, 1998). For example, the main distribution area of *H. parviporum* follows the natural distribution of Norway spruce (*Picea abies* (L.) Karst.).

Fig. 2. Distribution of *H. annosum* s. str., *H. parviporum* and *H. abietinum* in Europe (map kindly provided by K. Korhonen, 2004).

Infection and spread

Heterobasidion annosum s. l. forms perennial sporocarps, or fruit bodies, on stumps, roots, logs, and dead or diseased trees (Rennerfelt, 1946; Greig, 1998; Redfern & Stenlid, 1998). In northern Europe, fruit bodies are often found on the roots of windthrown trees. In Fennoscandian conditions, vast amounts of spores are produced during the growing season (Yde-Andersen, 1962; Kallio, 1970; Brandtberg, Johansson & Seeger, 1996). Basidiospores of the fungus typically infect freshly exposed woody tissue – e.g. stumps of recently cut trees (Rishbeth 1951a, 1957; Redfern & Stenlid, 1998) or wounds (Isomäki & Kallio, 1974) – from which mycelia subsequently can grow and infect neighbouring trees via root contacts or grafts. The fungus grows at a rate of about 50 cm year^{-1} in stump roots,

[3] s. str. = *sensu stricto*, i.e. in the strict sense. In terms of *H. annosum*, s. str. refers to the P intersterility group.

although much higher growth rates have been reported (Bendz-Hellgren *et al.*, 1999; Swedjemark & Stenlid, 1993). Due to the tree's defence, the growth rate in living roots is lower than in stumps, about 10-30 cm year^{-1} (Bendz-Hellgren *et al.*, 1999). On soils with high pH, *H. annosum* can grow epiphytically on roots, avoid the tree's defence mechanisms, and hence achieve a much higher growth rate (Rishbeth, 1950). However, the fungus is not capable of growing freely in the soil (Rishbeth, 1949).

When a tree is infected, the disease can spread to adjacent root systems. In Scots pine (*Pinus sylvestris* [L.]), the mycelia grow in the cambium zone, causing root death, growth losses and mortality (Stenlid & Redfern, 1998). In Norway spruce, on the other hand, *H. annosum* s. l. causes decay, which lowers the timber value. Norway spruce can survive infection for extended periods of time, but severe decay results in growth losses as the sapwood function is inhibited (Bendz-Hellgren & Stenlid, 1995, 1997). The decay column in a stem of Norway spruce may reach up to 12 m (Stenlid & Wästerlund, 1986), but the average in old trees is around 4.5 m (Zycha, Dimitri & Kliefoth, 1970; Kallio & Tamminen, 1974; Tamminen, 1985). The growth of decay in the stem is more rapid in the first years, after which it generally slows down. The average growth rate over a period of 30 years of decay is estimated at c. 15 cm/year (Vasiliauskas, 2001; paper IV).

Factors influencing the infection and spread

The incidence of infection is reported to be higher under certain conditions. Soil fertility correlates well with root rot incidence (Korhonen & Stenlid, 1998). High Ca content and high pH in the soil is favourable to *H. annosum* s. l., mainly due to the lack of antagonistic fungi such as *Trichoderma* and *Penicillum* spp. (Schlenker, 1976; Korhonen & Stenlid, 1998). The same applies to first generation forest stands established on former agricultural land (Rennerfelt, 1946; Rishbeth, 1949, 1951b; Korhonen & Stenlid, 1998). The incidence of disease is also reported to be higher in mineral soils with a fluctuating water table (von Euler & Johansson, 1983).

On the other hand, the risks of infection and spread are lower in peat soil, probably due to low pH and the presence of antagonistic fungi (Rennerfelt, 1946; Redfern, Pratt & Whiteman, 1994). At high altitudes, the incidence of disease is lower than at sea level, probably due to climatic factors and a shorter growing season (Korhonen & Stenlid, 1998; paper III). The extension of decay is also affected by genotype to the same extent as other investigated traits, e.g. height growth (Swedjemark, Stenlid & Karlsson, 1997, 2001; Swedjemark & Karlsson, 2002, 2004).

Control

Silvicultural control

In natural forest eco-systems, *H. annosum* s. l. is less pathogenic and plays a more subordinate role than in managed forests (Shaw *et al.*, 1994). But in intensively managed forests, characterized by monocultures and, perhaps, establishment on former agricultural land, *H. annosum* s. l. will greatly influence the outcome for the forest manager (Korhonen *et al*., 1998). Consequently, forest management is the number one factor influencing disease, at least indirectly. Admixture of tree species normally decreases the incidence of disease by reducing the number of root contacts between susceptible trees (Rennerfelt, 1946; Huse, 1983; Piri, Korhonen & Sairanen, 1990; Lindén & Vollbrecht, 2002; paper III). Contrasting results have been reported by e.g. Werner (1971, 1973) and Huse (1983).

In areas with only *H. parviporum* present, e.g. in the northern part of Sweden or in western Finland, there is a possibility of replacing Norway spruce with e.g. Scots pine. However, the requirements on the site for a high volume production may differ between tree species. In addition, there are hardly any coniferous tree species, native or introduced, that are resistant to both *H. annosum* s. str. and *H. parviporum* (Korhonen *et al*., 1998). Often, the only practical solution is to continue to grow a susceptible species, and to accept a certain amount of disease. Although broadleaf tree species are not very susceptible to *H. annosum* s. l., birch planting did not fully prevent attack in the subsequent generation of pine in Finland and Lithuania (Piri, 2003; Lygis, Vasiliauskas & Stenlid, 2004).

Removal of stumps is practiced routinely after the clear-cutting of heavily infected stands on alkaline soils in England (Greig, 1984). Although stump removal has proved to be efficient in Sweden (Stenlid, 1987), the method is not practiced at all.

Natural regeneration of Norway spruce under shelter-trees promotes disease, since the infected old trees will transfer inoculum to the young seedlings and saplings (Piri & Korhonen, 2001).

The number of root contacts increases with the number of stems ha^{-1}, thus promoting a quicker spread of *H. annosum* (Venn & Solheim, 1994).

Logging favours the spread of disease, because a great number of infection routes are created in the form of stumps and wounds.

In Fennoscandian conditions, the season of the year during which logging is carried out influences the infection frequency. Logging in the winter (temperature< 0 ºC) minimizes the risk of spore infections in stumps, whereas stumps created during the growing season are highly susceptible to spore infection (Yde-Andersen, 1962; Brandtberg, Johansson & Seeger, 1996; paper I).

If it rains during logging, the spores will be washed away, and consequently, infect the fresh stumps to a lesser extent (Sinclair, 1964; Brandtberg, Johansson & Seeger, 1996).

Bendz-Hellgren & Stenlid (1998) investigated the relative susceptibility of different stump types. Thinning stumps were most susceptible to spore infection, probably due to a favourable micro-climate and because they were large enough to provide suitable nutrition and water conditions. Stumps created from a final felling were slightly less susceptible than stumps created from thinning, due to more extreme micro-climatic conditions. Stumps created in pre-commercial thinning were too small to provide a good substrate for *H. annosum* s. l., and dried out before the infection could spread to neighbouring root systems, which is supported by Vollbrecht, Gemmel & Pettersson (1995). The susceptibility of stumps created from a final felling to spore infections is sufficient enough to provide important inoculum for the next generation (Stenlid, 1987; Piri, 1996; Vollbrecht & Stenlid, 1999; Rönnberg & Jørgensen, 2000), and the fungus may survive in old stumps for several decades (Hodges, 1969; Greig & Pratt, 1976).

The disease dynamics imply that root rot incidence increases with stand age and tree diameter (e.g. Rennerfelt, 1946; paper III).

Stump treatment

When logging occurs during the spore-spreading period, stumps can be treated with a control agent to prevent spore infection (Rishbeth, 1957; Pratt, Johansson & Hüttermann, 1998; paper I). To be fully effective and acceptable, materials for stump treatment need to be efficacious in a wide range of conditions, cheap, readily available, non-toxic to the user or the environment, easy and safe to handle and approved for this use by regulatory authorities (Pratt, 1999; Pratt & Thor, 2001). Among many studied compounds, urea and disodium octaborate (DOT)[4], together with the biological control agent *Phlebiopsis gigantea* (Fr.) Jül., have proved both effective and possible to use (e.g. Rishbeth, 1963; Yde-Andersen, 1982; Korhonen *et al.,* 1994; Brandtberg, Johansson & Seeger, 1996; paper I; paper II). In many cases, the effect is as good as winter-logging, i.e. 95-100% control. However, there are also reports on poor efficacy of urea (Pratt, 1994) and *P. gigantea* (Berglund & Rönnberg, 2004). In Finland and Sweden, due to regulations and current certification schemes, *P. gigantea* is the only agent used in forestry practice (Thor, 2003). Being a biological substance, *P. gigantea* is sensitive to handling as regards e.g. temperature and pressure, which is of particular importance in a mechanized application. Across Europe, stumps are treated on more than 200,000 ha year^{-1}, with an average cost of 1.2 euro m^{-3} in thinning and 0.4 euro m^{-3} in final felling (Thor, 2003). In most countries, more than 95 % of the area is treated with mechanized methods, except in Britain (20% manual treatment) and Poland (100% manual treatment). In Sweden, where the degree of mechanization in stump treatment is close to 100%, c. 35,000 ha year^{-1} are treated, which is estimated to be half of the need in thinnings (Samuelsson & Örlander, 2001; Thor, 2003).

The control agent is applied to the stump surface at the same moment as the tree is severed from the stump. The harvester requires a tank containing the liquid, a pump, hoses and valves and a spraying device (Frohm & Thor, 1993). There are mainly two types of spraying devices (Fig. 3): the through-the-bar sprayer, i.e. the liquid control agent is sprayed through a row of holes on the underside of the bar; and the under-bar sprayer, i.e. a spray nozzle attached to the bar bracket, where the

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4 Disodium octaborate tetrahydrate (DOT) is a boron compound (trade name: Timbor), $Na_2B_8O_{13} \cdot 4\ H_2O$. It has been used to preserve wood in Australasia, south-east Asia and the USA. The compound is also called Polybor in the literature.

liquid is sprayed towards the underside of the bar. The drilled guide bars could provide a good coverage of stumps of all sizes, all of which would be possible to handle with the harvester head, although the spillage could be high on small stumps. The special guide bars are about 50% more expensive than conventional bars. By using an under-bar system, spillage is lower and the cost of special bars is avoided, but this system is not capable of treating stumps with a diameter greater than approximately 30 cm (Thor, unpublished; Axelsson, pers. comm.). Consequently, the under-bar system could be recommended in early thinning operations, and the through-the-bar system in later thinning and final felling. In practice, through-the-bar systems dominate in Sweden today (Axelsson, pers. comm.).

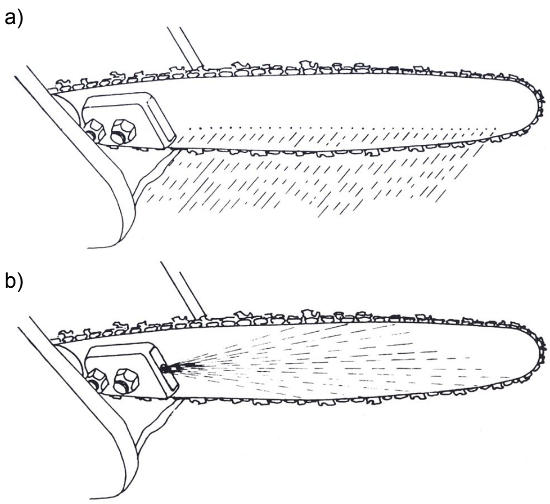

Fig. 3. Principles of mechanized stump treatment systems: a) through-the-bar system; b) spray nozzle directed into saw cut on underside of the guide bar (Pratt, Johansson & Hüttermann, 1998, p. 275).

Root-rot integrated management and planning

In order to direct the right control measure to the right time and place, knowledge about the root rot problems must be integrated into the planning of forestry operations (Thor *et al*., in press).

The short- and long-term effects can be evaluated with models (Pratt, Shaw & Vollbrecht, 1998). Models are also useful for researchers, as they help in understanding the mechanisms of spread and the impacts of *H. annosum* s l. Empirical models of *H. annosum* s. l. infection in Norway spruce have been produced for southern Sweden and Denmark (Vollbrecht & Agestam, 1995a; Vollbrecht & Jørgensen, 1995a). Mechanistic models have been developed for *H. annosum* s. str. in Sitka spruce (*Picea sitchensis* Bong Carr.) in the UK (Pratt, Redfern & Burnand, 1989) and for *H. annosum* s. l. in Norway spruce in Finland (Möykkynen *et al*., 1998; Möykkynen, Miina & Pukkala, 1999; Möykkynen & Miina, 2002). In Germany, Müller (2002) produced a model for predicting the risk of damage from wind, snow and root rot in stands of spruce. Other root diseases that have been modelled include *Phellinus weirii* (Murr.) Gilb. attack on Douglas fir (*Psedutsuga menziesii* (Mirb.) Franco) (Bloomberg, 1988). So far, however, the most comprehensive modelling effort is the western root disease (WRD) model describing the infection process of *H. annosum*, *Armillaria* spp. and *Phellinus weirii* on, for example, stands of *Abies* spp. and *Pinus ponderosa* Dougl. ex Laws. in western North America (McNamee *et al*., 1989; Stage *et al*., 1990; Frankel, 1998). The WRD model was designed to function in even-aged stands with one or several species of trees present. It was developed by US and Canadian forest pathologists over a period of more than ten years, and has inspired a European Concerted Action: Modelling of *Heterobasidion annosum* in European forests (MOHIEF) (Woodward *et al*., 2003), aimed at developing a model for *H. annosum* s. l. for European conditions considering variations in soil, forest conditions, climate and hosts. A Fennoscandian model within MOHIEF has been produced (paper IV). The WRD model focuses on tree mortality, whereas the model presented in paper IV also includes decay in the stems of Norway spruce.

In spite of its biological and economic impact, root rot has received no or little attention in systematic planning in Swedish forestry. There is a need to include knowledge about root rot and its control in the planning process.

Aims of the thesis

This thesis aims at

- evaluating the efficacy of mechanised stump treatment with three compounds (DOT, *P. gigantea* and urea), and comparing the outcomes with untreated stumps in summer and winter thinning, and with manual treatment
- testing the robustness of the biological control agent in a mechanical application, i.e. the compound's sensitivity to high temperatures or pressures
- predicting decay in a stand from data possible to collect from most stand records
- modelling of disease development based on known facts about the mode of infection and spread of *H. annosum* s. l. in order to simulate and compare the outcomes of various forest management and strategies to control root rot
- modelling and predicting the economic outcome for a number of stands typical of Swedish forest management using the models for *H. annosum* s. l. dynamics

Summary and discussion of results

The efficacy of stump treatment in practical thinning operations in Norway spruce (paper I)

Earlier experiments on stump treatment have focused on manual treatment. When applying the compound by harvesting machines, less perfect coverage of stumps is to be expected.

The main objective of this experiment was to study the colonization of *H. annosum* s. l. on Norway spruce stumps following mechanized thinning and stump treatment with 1) 35% aqueous urea solution, 2) aqueous suspension of *P. gigantea* oidiospores (10^7 l^{-1}) and 3) 5% aqueous solution of DOT. The treated stumps were to be compared with untreated stumps, from trees cut in the summer and in the winter, respectively, and stumps that were treated manually.

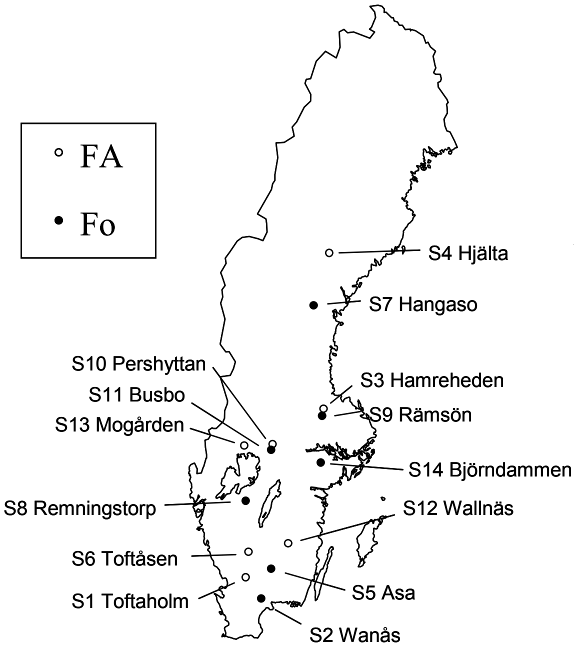

Fig. 4. Geographic location of the stands S1–S14 (paper I). FA=former arable land, Fo=forest land.

Material and sampling

Experimental plots were established in 14 previously unthinned stands of Norway spruce in Sweden (Fig. 4). The experiment was designed as a two-factor experiment with treatment and stand as the two factors. In each of the stands, the treatments were **i**) stump treatment with 35% aqueous solution of urea (urea), **ii**) stump treatment with oidial suspension of *P. gigantea* (Rotstop), **iii**) 5% aqueous solution of DOT (stands S5–S14 only) (DOT), **iv**) untreated stumps, thinning in the summer (summer), **v**) untreated stumps, thinning in the winter (winter), and **vi**) unthinned. The individual treatment plot was 38×54 m, and included three striproads opened up in the thinning. Outside the plots, 20–40 stumps were treated manually with each control agent to compare the effect of the best possible manual treatment with the effect of mechanized treatment. The summer thinnings were made within one or two adjacent days, and the winter thinnings were conducted on a single day. Medium-sized single-grip harvesters equipped with devices for mechanized stump treatment were used.

Six to seven weeks after thinning, 20 stump discs were randomly sampled from the mechanically treated stumps on each plot. From the manually treated stumps, 10 discs were randomly sampled from each treatment. The discs consisted of the top cm of the stump. Colonies of *H. annosum* s. l. were recognized by its conidial stage using a dissecting microscope.

Analyses and statistical methods

The frequency of *H. annosum* s. l. infested stumps, the stump area colonized by *H. annosum* s. l., the size of colonies and the number of colonies per stump were calculated. The quality of treatment in terms of stump coverage and its effect on the infected stump area were also evaluated.

To describe the probability of infection of a stump, p_{ij}, the following generalized linear model was used:

$\eta_{ij} = \mu + b_i + t_j + e_{ij}$,

where η_{ij} is a logit function:

$$\eta_{ij} = \log\left(\frac{p_{ij}}{1 - p_{ij}}\right)$$

μ is the overall mean, b_i is the effect of block (stand) i, t_i is the effect of treatment j, and e_{ij} is the random residual effect of stump ij. The procedure GENMOD in SAS (SAS Institute 1999-2001) was used. In this statistical analysis, each stand was regarded as a block. On the other hand, when calculating the stump area colonized by *H. annosum* s. l., and the number of colonies per infected stump, each plot constituted one observation unit. Here, we used a linear model (the procedure GLM in SAS) with a logarithmic transformation of the dependent variable:

$\ln y_{ij} = \mu + b_i + t_j + e_{ij}$

where y_{ij} is the stump area colonized by *H. annosum* (or the number of *H. annosum* colonies per infected stump) in stand i, treatment j.

Results and discussion

The infection rate varied considerably between stands (Fig. 5). In the stand with the heaviest infections (S11), *H. annosum* s. l. was able to colonize almost 30% of the total stump area on the control plots. Nevertheless, the stump treatment was very effective. On the other hand, in stands with more moderate infections of the control stumps, stump treatment did not always provide the desired protection level. The result of stump treatment was very poor in one stand where the equipment did not work satisfactorily.

The predicted probability of stump infection (p_{ij}) was 0.90 for SU plots. On the treated plots, p_{ij} was 0.02-0.42. Furthermore, p_{ij} was significantly higher for PG plots than for UR or WI plots. Manual treatments with *P. gigantea* or urea decreased p_{ij} significantly as compared to mechanical treatment. The colonies were significantly smaller on most of the treated and the winter-thinned stumps, about 1-2 cm^2 as compared to about 5 cm^2 on the SU plots. The number of colonies per infested stump was about the same regardless of treatment.

Stump treatment reduced the infected stump area by 88-99%, which raised the question as to which measure is the most appropriate to describe control efficacy: the number of colonized stumps or the colonized stump area. In theory, each infested stump is capable of spreading the disease to adjacent trees. However, small colonies are less likely than large colonies to persist and colonize the stump root systems, subsequently transferring disease. In the discussion it is argued that the colonized stump area was a more relevant measure of control efficacy in this experiment considering the short time elapsed between treatment and the sampling of discs.

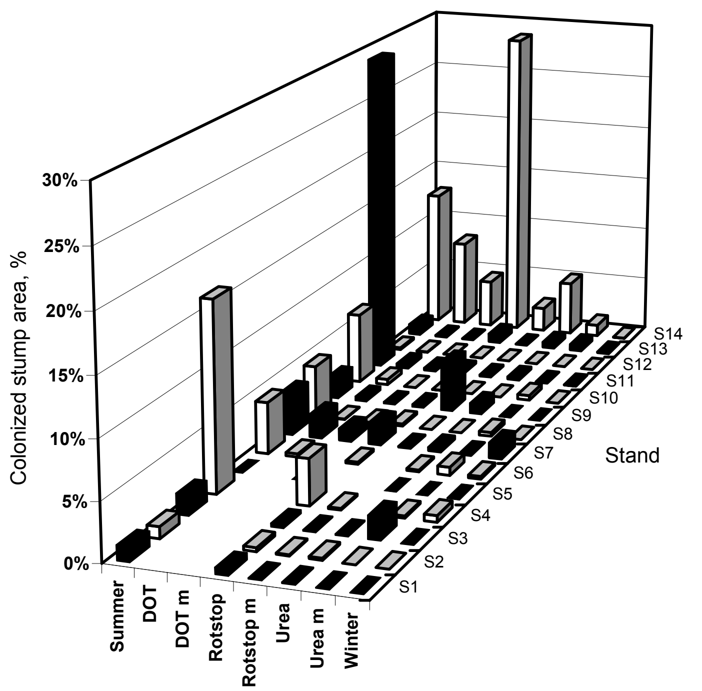

Fig 5. Proportion of the stump area colonized by *H. annosum* s. l. in the experiment (paper I). Summer=untreated stumps, summer, DOT=5% aqueous solution of DOT, Rotstop=*P. gigantea* (10^7 oidia l^{-1}), Urea=35% aqueous solution of urea, Winter=untreated stumps, winter. The letter ”m” after the treatment indicates manual treatment.

The conclusions from this study were 1) stump treatment with the three control agents studied reduced the colonised stump area 6-7 weeks after thinning by 88-99% as compared with untreated stumps from trees cut in the summer, 2) in terms of colonized stump area, the effects of the different treatments were neither different from each other nor from the effect of winter thinning, 3) mechanized stump treatment provided as good of protection as manual treatment against *H. annosum* s. l. infections, although the variation between stands was considerable. The variation was at least in one case due to poorly functioning equipment. The variation might also be due to endogenous factors in the stumps as well as e.g. differences in spore abundance and weather conditions. 4) Stump treatment reduced the probability of spore infection (p_{ij}) with 53-83% (mechanized treatment) and 79-98% (manual treatment) compared with untreated (summer) thinning. Furthermore, in terms of p_{ij}, there were differences in control efficacy between treatments: Urea was most effective whereas *P. gigantea* was least effective, and manual treatment performed better than mechanized treatment.

The robustness of *P. gigantea* ('Rotstop') used in mechanized stump treatment (paper II)

Being a biological control agent, *P. gigantea* requires caution when handled. According to the manufacturer, the spores should be stored at a temperature below 8ºC, and the upper temperature limit for the working suspension is 30ºC. In practical use, these restrictions might lead to problems. In a mechanized application, temperature as well as pressure is higher than in a manual treatment. The temperature stress is due to its warming-up during its passage through hoses, which are often mounted adjacent to warm hydraulic hoses on the machine. On machines with a poor design of spraying equipment, there is also a risk that insufficient insulation or an unsuitable positioning of the tank leads to warming by the machine's engine, by hydraulic components or by direct sunlight. The pressure applied is either short-term, during the moment the suspension is sprayed over the stump, or long-term, if a pressurized tank (600-800 kPa) is used. The experiment aimed at testing the survival of oidiospores of *P. gigantea* when exposed to high pressure or temperature.

Methods

A working suspension (10^7 l^{-1}) of *P. gigantea* oidiospores (Rotstop®) was kept in a pneumatic pressure chamber (P=1,600-2,200 kPa) for 24 h. Survival was monitored as colony-forming units on Hagem agar. Spore suspension was also put in heating cabinets with temperatures 30, 35, 40 and 60 ºC. A control suspension was kept at 20ºC. Samples were taken after 5 min, 1, 2, 4 and 8 h. In addition, one sample was taken from the control suspension after 72 h. Survival was measured as above.

On a Valmet 911/960 single-grip harvester in a clearfell operation, the temperature of the Rotstop® suspension was continuously measured at four positions: in the tank (25 l, mounted without protection from the sun), after passing through the hydraulic pump, where the hose entered the crane boom, and at the harvester head. Less comprehensive temperature measurements were also carried out on a Valmet 701 single-grip harvester in a thinning operation, where the temperature of the working suspension was measured in the tank (25 l, insulated from sunlight and engine heat) and at the harvester head. During both operations, ambient air temperature was 20-25ºC in the shade. From the Valmet 911, samples of spore suspension were taken from the can and from the harvester head at the beginning of work, after 3 h, and when the tank was almost empty (7 h). Survival was measured as above.

Results and discussion

The pressure treatment had no effect on *P. gigantea* survival, which implies that an application system applying no higher pressure to the working suspension will be harmless to the spores.

At 20ºC, there was no difference in the number of germinated spores up to 8 h from preparation (Fig. 6). Even after 72 h, the slight decrease observed was not significant. At 30ºC, the number of germinated spores increased over time up to 8 h. At 35ºC, the spore viability decreased with time: the number of germinated spores as well as the size of colonies decreased up to 8 h. The same pattern was observed for 40ºC, but the viability decreased faster. None of the oidia exposed to 40ºC for 4 h germinated. At 60ºC no spores germinated.

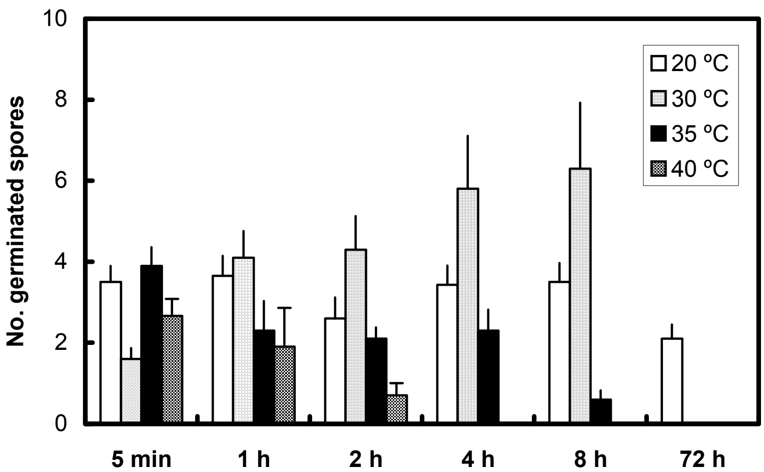

Fig. 6. Germination of *P. gigantea* oidia in the laboratory test (paper II). Average (n=10) number of germinated *P. gigantea* oidiospores from plates inoculated with 10 oidia, exposed to 20, 30, 35 and 40 ºC. Vertical bars represent standard error.

In the field study, the temperature recorded increased over time, and increased the closer to the harvester head the measurement was made. However, the temperature of the working suspension never exceeded 40ºC (Fig. 7).

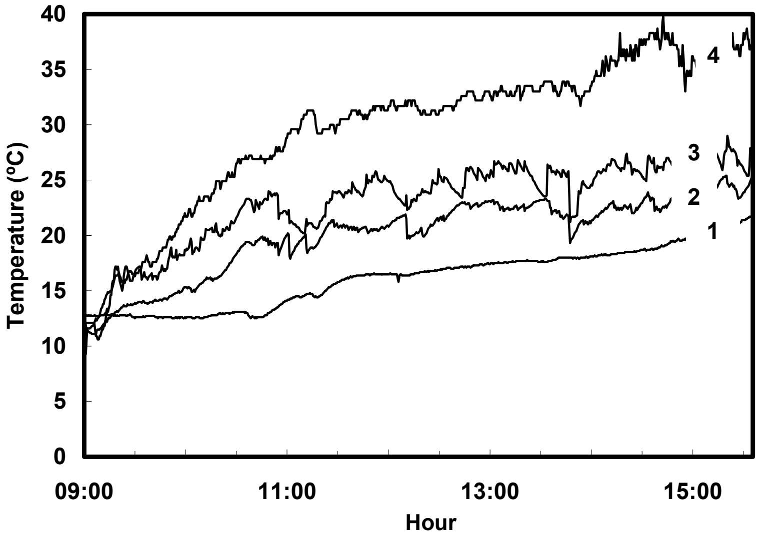

Fig. 7. Phlebiopsis gigantea spore suspension temperature (ºC) in the can (1), after passing through the hydraulic pump (2), where the hose enters the crane boom (3) and at the harvester head (4). Graph from the field study of the Valmet 911 (paper II), August 9, 1995, ambient air temperature around 20ºC.

The warming which occurred during its passage through the system was short-term, estimated at 5-10 min under normal working conditions. The germination of spores sampled from the harvester head did not differ from the samples taken in the can. Nor was any significant difference in germination found between samples early in the day as compared to 7 h later. On the contrary, an increase in germination was observed. This could be due to either a higher concentration in the can at the end, or to the possibility that the short-term warming of spores on the way from the can to the spraying device stimulated the germination. The latter explanation has some support from the laboratory results.

In conclusion, as long as the Rotstop® bags are handled according to the current instructions, there should not be any problems during practical stump treatment due to temperature or pressure stress on the spores.

Predicting decay in a stand (paper III)

In practice, decay detection from external signs is not possible (Vollbrecht & Agestam, 1995b). Still, the decay frequency in a stand is important economic information from a planning perspective. The aim of paper III was to produce models describing the probability of decay in individual trees of Norway spruce, based on variables that could be derived from most stand records.

Methods

Sample trees of Norway spruce from temporary sample plots in the Swedish national forest inventory (NFI) (1983-2001) were used. For the sample trees, many data were recorded including the presence of decay in bore cores sampled at 1.3 m height. The species of the decay-causing agent was not determined. In total, 45,587 Norway spruce trees in the regions 2-5 (Fig. 8) with an age of 20-149 years were included in the analysis.

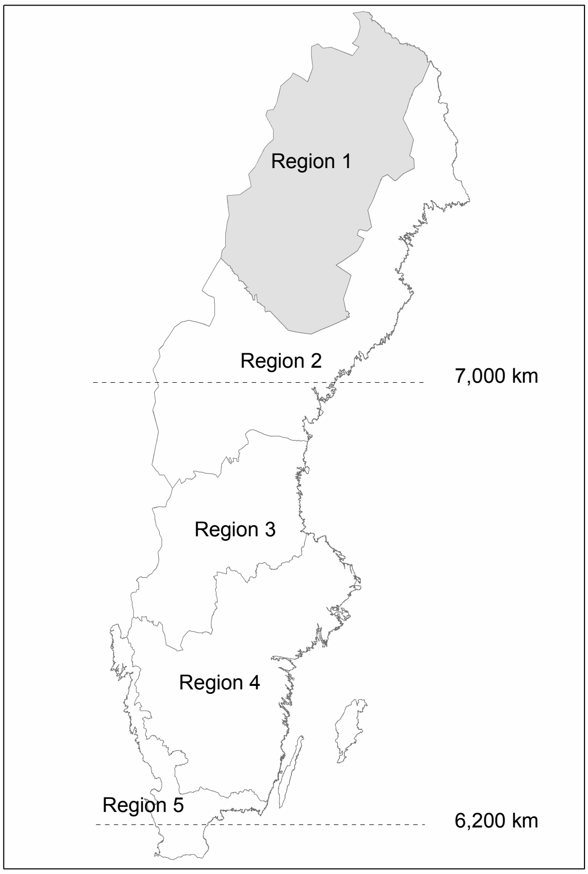

Fig. 8. Regions used in the Swedish National Forest Inventory (NFI) (Ranneby *et al*., 1987). Region 1 was excluded from the analysis. X-coordinate lines for 7,000 km and 6,200 km (RT90) are indicated.

Data were fitted to a logistic regression model (Tab. 1) in the procedure LOGISTIC in SAS software 8.02 (SAS Institute 1999-2001).

To validate and calibrate the model, another data set from NFI was used, comprising 7,893 stumps (diameter 5-40 cm) of Norway spruce. The function obtained from the logistic regression analysis was applied to the stumps (1-cm classes), hence showing the expected probability of decay at 1.3 m.

Results and discussion

The overall decay frequency in the sample trees was 7.0%. An increase from 6.4 to 7.9% was observed between the two halves of the time period.

Tab. 1. Summary of the parameter estimates in paper III: Intercept and parameters found to have significant correlation ($p<0.05$) with the probability of decay at breast height for individual trees. Function: $P(\text{decay})=e^{f(x)}/(1+e^{f(x)})$, where $f(x)=\alpha+\Sigma\beta_i \cdot x_i$, where α is an estimated intercept, β_i is an estimated parameter i, and x_i the corresponding independent variable. N denotes the number of sample trees included in the analysis

Component	Description	Parameter estimates (β) Country-wide N=45,587	South[a] N=38,029	North[a] N=7,543
Intercept (α)		-3.18388E1	-1.9303E1	-4.9300
Variables (x)				
EAST	East coordinate (km) (Sw. RT90) for the stand centre		6.5569E-4	-1.4949E-3
AGE	Stand total age (years)	-3.7414E-1	-3.6854E-2	7.4552E-3
Ln[AGE]		5.7919	2.6239	
AGE · ln[AGE]		5.7248E-2		
AGE · DBH			4.4097E-5	
SI	Site index (m) assessed on ground vegetation (Hägglund & Lundmark, 1977)	1.5533E-2		9.5968E-2
SI>15			-1.0206	
TSUM<800, or TSUM>=1100	Temperature sum (dd) for the threshold temp. 5ºC (Morén & Perttu, 1994)	3.3479E-1	2.2457E-1	
TSUM<900, or TSUM>=1000				4.2212E-1
ALT >100	Height above sea level (m)	-3.0993E-1	-2.4790E-1	
ALT/TSUM			-5.9550E-1	
DBH	Diameter at 1.3 m (mm)	-6.1511E-2	-8.6392E-3	4.8165E-3
ln[DBH)		3.3909	1.8944	
DBH · ln[DBH]		7.6693E-3		
MOIST	Soil moisture class (1=dry, 2=mesic, 3=mesic-moist, 4=moist, 5=wet)	-2.6827E-1	-3.1527E-1	
SOILTEX, ≠4	Soil texture class (1=stony till/stone, 2=gravelly till/ gravel, 3=sandy till/sand, 4=sandy-silty till/sand, 5=sandy-silty till/silt, 6-7=silty till/silt, 8=clayey till/clay	1.5098E-1	1.3148E-1	
SPRUCE	Proportion of Norway spruce in the stand (1/10)			6.3746E-2
ln[SPRUCE+0.1]		1.3704E-1	1.4648E-1	
Parameter (α) for conversion of P(decay) to stump height[b]		2.037 (R^2=0.85)	2.107 (R^2=0.85)	1.354 (R^2=0.85)

[a] The border line between northern and southern functions is 7,000 km (Northern coordinate, Swedish RT90).

[b] Function for conversion to stump height: P(decay stump height)= α · P(decay 1.3 m) + ε, where P(decay stump height) is the calibrated probability of decay at stump height, α is an estimated parameter, P(decay 1.3 m) is the predicted probability of decay at 1.3 m for 1-cm classes and ε is the random error.

The logistic regression showed significance for the variables in Tab. 1. An analysis of residuals indicated a possible need for two regional sets of functions;

one north of 7,000 km[5] (Swedish RT90 coordinate) and one south of 7,000 km. The reason is probably due to regional differences as to which decay fungus is most frequent. In the south, *H. annosum* s. l. is the most common pathogen, whereas in the north, e.g. *Phellinus chrysoloma* (Fr.) Donk and *Stereum sanguinolentum* (Alb. & Schw.: Fr.) Fr. might be more important.

Large trees were more frequently sampled than small trees. The probability of decay at 1.3 m in an individual tree, P(decay), was strongly correlated to diameter and age, and consequently, 7% is an overestimation of the "true" frequency considering the probability of sampling. On the other hand, the sample trees are more likely to represent the trees harvested in forest operations. When making predictions with the logistic functions, this is not a problem because the tree diameter is one of the independent variables.

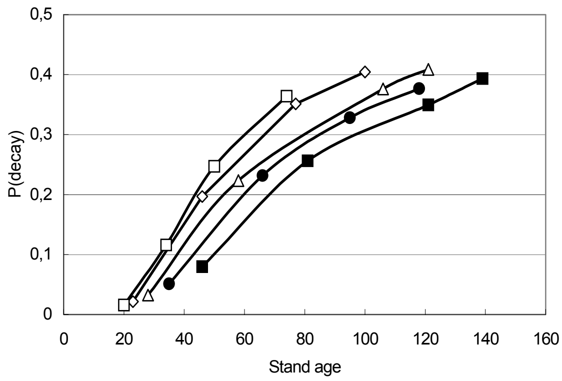

Fig. 9. Examples of estimates of P(decay) at stump height, using the functions in paper III (region 2-5). White squares: SI (site class index [Hägglund & Lundmark, 1977])=36, white diamonds: SI=32, white triangles: SI=28, black circles: SI=24, black squares: SI=20. Stand data derived from Eriksson (1976).

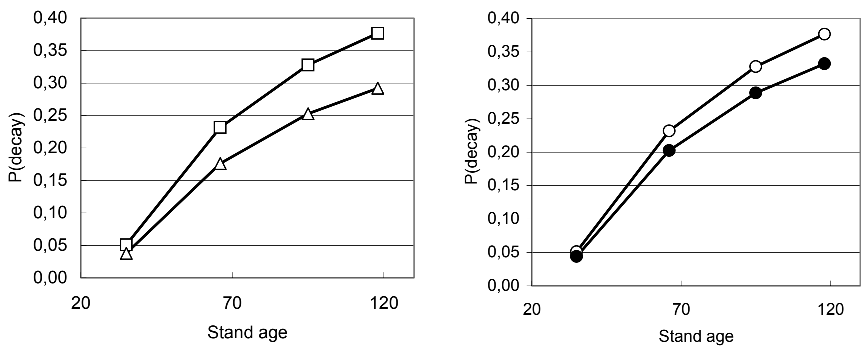

Fig. 10. Paper III: Estimated P(decay) at stump height depending on the proportion of Norway spruce in the stand (left) and the soil texture class (right). At 100% Norway spruce (white squares), P(decay) is higher than at 10% Norway spruce (white triangles). Norway spruce trees growing in sandy-silty till/sand (black circles) have lower P(decay) than trees in other soil texture classes (white circles).

[5] RT90 is the Swedish coordinate system including a false easting of 1,500 km. The x-coordinate 7,000 km corresponds to c. 63º 5' N.

The calibration to stump height doubled the decay frequency (R^2=0.85), because when drilling at 1.3 m, one misses decay that has not yet reached that height, as well as some of the laterally located decay columns. Figures 9 and 10 depict the calibrated P(decay) at stump height, depending on site index, the proportion of Norway spruce, and soil texture class.

In essence, the findings are supported by the literature. However, the correlations arrived at only show the degree of statistical relationship, and are not proven to be causal *per se*. Several of the independent variables, e.g. diameter and age, site index and temperature sum, interact. The conclusions of the study were: ***i***) the developed functions are supported by known facts about *H. annosum s. l.* infection biology; ***ii***) application of the functions in Swedish planning systems can be recommended; ***iii)*** the functions are also useful for calibrating and for estimating starting points in the modelling of disease development by means of mechanistic models; ***iv)*** the frequency of decay at stump height, as inspected after felling, is double that of the frequency at 1.3 m detected by an increment borer.

Modelling of disease development (paper IV)

The investigation was performed to produce a mechanistic model of *H. annosum* s. str. and *H. parviporum* in even-aged Fennoscandian conifer stands. The model includes the two economically most important Fennoscandian conifers, Norway spruce and Scots pine. The focus of the study was on the description of the model and its equations regarding the probability of infection, the rate of transfer and the rate of spread of the fungus. In addition, some examples of simulation were presented.

Brief model description

A stand was represented by a rectangular plot. Attributes, such as old stumps (infection centres) and trees of various species, were assigned to the plot. Growth and yield models were used together with mortality models to predict the height and basal area increment of trees in 5-year time steps. Input data included No. stems ha $^{-1}$, diameter distribution, basal area, height, site index and age in the initial stand.

Each of the seven sub-models describing the disease dynamics was designed to represent a fundamental stage of the infection process and biology of *Heterobasidion* spp. based on literature data (Fig. 11). (**I**): The probability of spore infection depended on temperature sum, the time of logging operation, stump treatment (Y/N), stump removal (Y/N), and the abundance of logging injuries on trees. (**II**): the process of stump colonisation was modelled by means of the probability of stump colonisation once spores germinate. (**III**): decay in stump root systems was supposed to first expand at a fast rate, then stay at stasis for a period of time, then subsequently decline until extinction (Fig. 12), all dependant on stump diameter. Root systems and decay were represented by circles. (**IV**): the transfer of disease between root systems was modelled by means of the probability of transfer given overlap between the infected part of a donor root system and a recipient root system. This probability depended on the soil type, e.g. the probability of transfer is much lower in peat soils than in soils of former agricultural land. Root systems of living trees were assumed to expand depending on tree diameter. (**V**): the spread rate of disease in roots of living trees was assigned. (**VI**): once the disease had reached a stem of a standing tree, decay was starting to advance upwards in the stem, and the disease in the root system was spreading outwards, enabling vegetative spread to adjacent root systems. (**VII**): models describing the disease effect on tree growth and survival were developed.

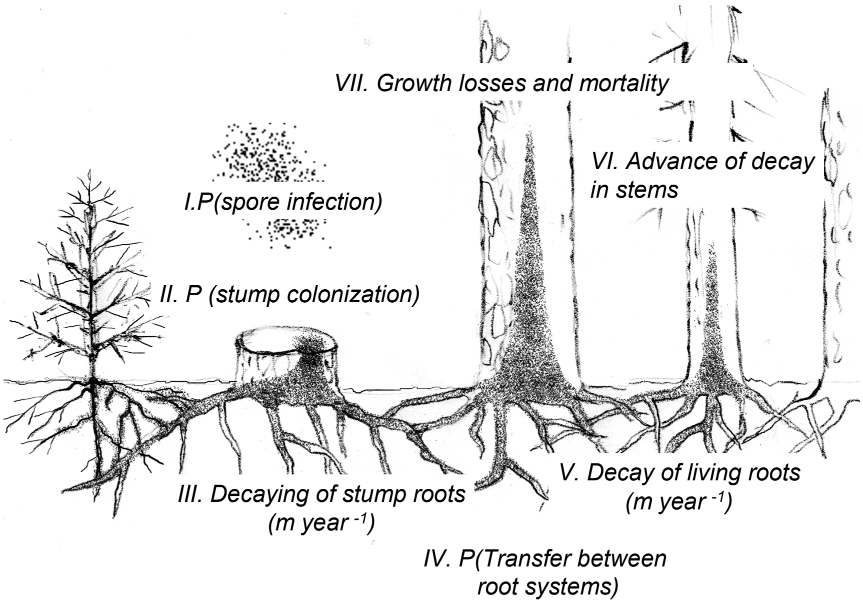

Fig. 11. The mechanistic model (paper IV) comprised seven sub-models, representing fundamental stages of the infection biology of *Heterobasidion* spp. (Illustration: Anna Marconi, Skogforsk.)

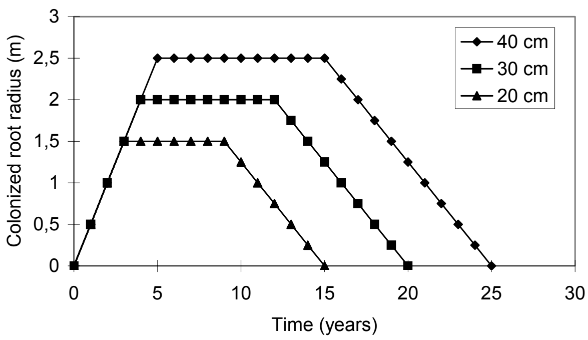

Fig. 12. Dynamics of stump root colonization in the MOHIEF model for three different tree diameters (paper IV).

Forest management programs for even-aged stands could then be simulated in a software program ('Rotstand') comprising the model. The user has to specify the thinning program (e.g. year of thinning, thinning intensity and control measures if any) and the rotation.

Simulation

To illustrate the model, a simulation was carried out with data representing a Swedish stand of Norway spruce, where logging occurred during the high-risk season for spore infection. Changes of parameters indicated that model predictions were sensitive to the spread rate (m $year^{-1}$) of disease in roots and presence of initial disease centres. Further research is called for in areas related to the development of coarse root systems of various tree species, and the probability and rate of transfer of disease from various sources of inoculum to healthy trees.

Modelling of the economic outcome of stump treatment (paper V)

The objective was to simulate and compare the economic outcomes of stump treatment for a number of stands typical of Swedish forestry and forest management, using models of growth and yield, disease development and cross-cutting of trees.

Methods

The tools for the simulations were the software programs ProdMod (Ekö, 1985), Rotstand (comprising the MOHIEF model in paper IV) and TimAn 2.0 (Arlinger *et al*., 2002; Bergstrand, Gustafsson & Laestadius, 1985). Four stand types typical of Swedish forestry were simulated: A) 100% Norway spruce on post-agricultural soil (first generation), i.e. no root rot present before first thinning. Site index (SI) was 32; B) 100% Norway spruce (SI=26) on forest soil, i.e. root rot was assumed to be present in old stumps; C) 50% Norway spruce and 50% Scots pine (SI=24) on forest soil. Only *H. parviporum* was assumed to be present, i.e. there was no possibility of inter-species spread of disease. D) Same as C, but with both *H. annosum* s. str. and *H. parviporum*, i.e. root rot could be present in old stumps and there was a possibility of inter-species spread of disease. The stump treatment programs were 1: no stump treatment at all; 2: stump treatment in thinnings only; 3: stump treatment in previous final felling only; 4: stump treatment in previous final felling and in all thinnings. In stands C and D, all stumps were treated irrespective of tree species.

The software Rotstand generated lists of harvested trees, including tree species, diameter at 1.3 m, and height of any decay column. The tree lists (an average of 5 repetitions of each combination of stand and treatment program) were imported to the TimAn 2.0 package, in which stem profiles were simulated and quality properties were assigned to the stems. Cross-cutting of stems was simulated to mimic the work of a harvester operating in Swedish conditions, using price list matrixes intended for use in southern Sweden for a number of assortments.

The costs for logging and stump treatment were calculated separately. The economy of stump treatment was expressed in terms of net future value (NFV) at the time of final felling of the present rotation, at interest rates of 1, 3 and 5%.

Results and discussion

Depending on stand type and treatment programme, the simulated decay frequency in the Norway spruce trees varied drastically (2-90%) at the time of final felling (Fig. 13). Stump treatment during all logging operations was the most profitable management option in stands A (first generation of Norway spruce), B (forest site, pure Norway spruce) and D (forest site, mixed conifer, both *H. annosum* s.str. and *H. parviporum*), but not in stand C (forest site, mixed conifer, *H. parviporum* only) (Fig. 14).

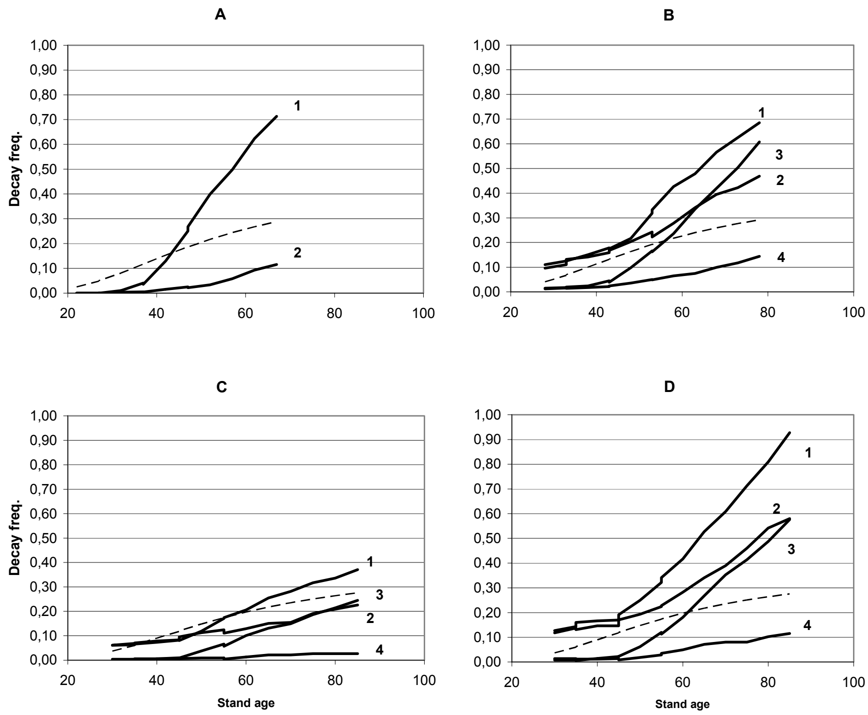

Fig. 13. Development of *Heterobasidion* spp. modelled in four stand types (paper V): A: 100% Norway spruce, SI=32, 1st generation; B: 100% Norway spruce, SI=26, forest land; C: 50% Norway spruce, 50% Scots pine, SI=24, *H. parviporum* only; D: same as C, but both *H. parviporum* and *H. annosum* s. str. present. Treatments: 1: no stump treatment at all; 2: stump treatment in thinnings only; 3: stump treatment in previous clearfell only; 4: stump treatment in previous clearfell and in all thinnings. The hatched line represents P(decay) at stump height (paper III).

In all stands at an interest rate of 3%, treatment 2 (treatment in thinnings only) gave a higher NFV than treatment 3 (treatment in final felling only). In stand C, treatments 3 and 4 (treatment in all operations) were never profitable, and there was no significant difference ($p<0.05$) between treatments 3 and 4. At an interest rate of 1 or 5%, treatment 3 gave a higher NFV than treatment 2 in stand D, although treatment 4 still resulted in the highest NFV. In stand B, there were no differences between treatments 2 and 3 at a 1 or 5% interest rate, whereas at a 3% interest rate, treatment 2 was significantly more profitable than treatment 3. In other respects, the obtained relations of NFV within stands were similar to 3% interest rate (Fig. 14). All differences between treatments within stands were statistically different ($p<0.05$), except B2-B3 (at a 1 and 5% interest rate), C1-C2 (1 and 3% interest rate), C1-C2-C3 (1 and 5% interest rate) and C3-C4 (1, 3 and 5% interest rate).

At a 3% interest rate, the difference between the highest (treatment 4) and the lowest (treatment 1) NFV within stands A, B and D was 23,000–28,000 SEK ha^{-1}. In stand C, the difference between the highest (treatment 1 and 2) and the lowest (treatment 3 and 4) NFV was c. 14,000 SEK ha^{-1}.

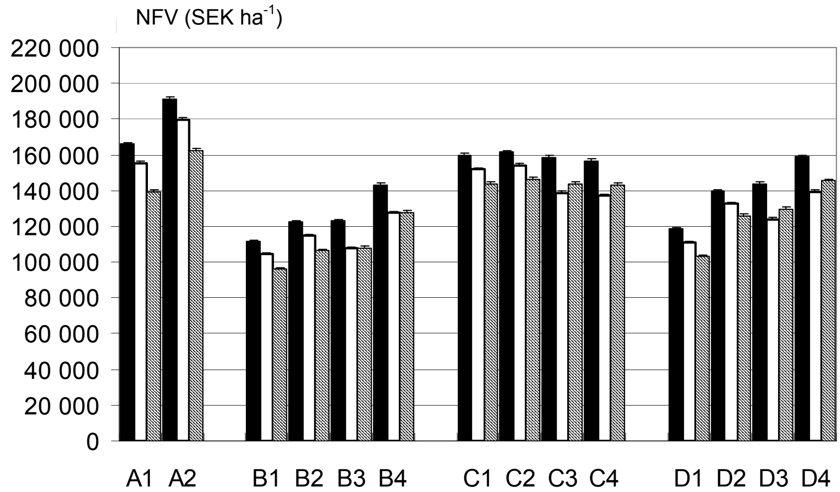

Fig. 14. Paper V: Net final value (NFV), SEK ha^{-1} for stands A-D at interest rates of 1% (black), 3% (white) and 5% (hatched). Treatments: 1: no stump treatment at all; 2: stump treatment in thinnings only; 3: stump treatment in previous clearfell only; 4: stump treatment in previous clearfell and in all thinnings. At a 3% interest rate, all differences within stand types are significantly different except C1-C2 and C3-C4. Bars represent standard error of the mean.

In conclusion, for forest conditions and price relations similar to what was simulated, the results suggest stump treatment to be carried out in all logging operations of Norway-spruce stands of at least site index 26, irrespective of the stand being established on forest soil or former agricultural soil. The same is implied for mixed stands in southern Sweden, containing at least 50% Norway spruce. In mixed stands (maximum 50% Norway spruce) north of c. lat. 60º N, or if *H. annosum* s. str. is not expected, stump treatment is not economically justified, at least not in final felling.

General discussion

Stump treatment

Spore infection of stumps and control efficacy

Spore infection of stumps can be expressed in several ways, e.g. by comparing the proportion of stumps become infected, or the number of individual spore infections per (total or sapwood) stump area, or the colonized proportion of stump area. The different measures may respond differently to variations in ambient spore loads. In terms of the proportion of infected stumps, one specific level of control efficacy could in practice result in totally different outcomes, depending on how many spore infections there are. For example, in conditions with high spore loads, an efficacy of 95% still will leave plenty of infected stumps, whereas in stands with low or moderate spore loads the control will be satisfactory (Fig. 15). High ambient spore loads in southern Sweden may be one explanation for the poor results seen in *P. gigantea* treatment as reported by Pettersson *et al*. (2003) and Berglund & Rönnberg (2004). On the other hand, in stand S11 (paper I), stump treatment with any of the three compounds (DOT, *P. gigantea* and urea) resulted in satisfactory control efficacy despite the fact that 30% of the total stump area was infected in the control stumps.

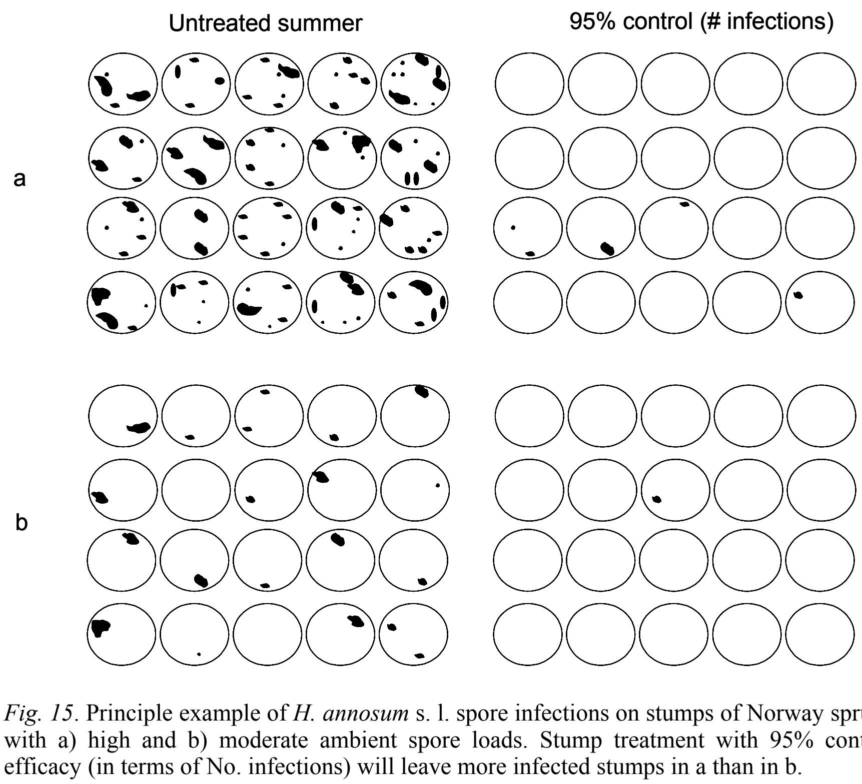

Fig. 15. Principle example of *H. annosum* s. l. spore infections on stumps of Norway spruce with a) high and b) moderate ambient spore loads. Stump treatment with 95% control efficacy (in terms of No. infections) will leave more infected stumps in a than in b.

In several studies (e.g. Korhonen *et al*., 1994; Pratt 1994; Brandtberg, Johansson & Seeger, 1996), the frequency of infected stumps is used as the measure to describe the effect of stump treatment. However, the time between infection and sampling of discs is critical for how many infected stumps can be expected. In a study of *H. annosum* infection of Sitka spruce, Morrison & Redfern (1994) found a significant positive correlation between the sapwood area colonized in year 2 and the total stump area colonized in year 8. The stump area colonized in years 2 and 8 and the percentage of stump and root volume colonized in year 8 were also significantly correlated. Moreover, they found that only stumps that had infections in the sapwood year 2 contained the fungus in year 8.

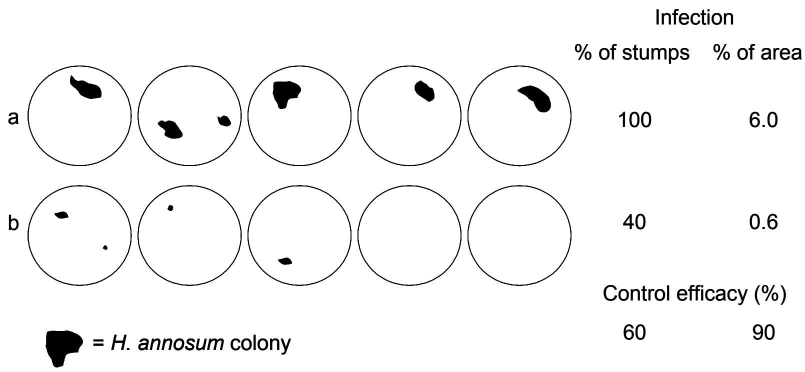

Fig. 16. Principle example of *Heterobasidion* spore infections on Norway spruce under conditions similar to the experiment in paper I. Depending on how infection and control efficacy are described, the values of control efficacy differ from each other (a=untreated stumps, b=treated stumps).

As a consequence of the relatively short time between inoculation and sampling in the study in paper I, paired with the sampling depth (1 cm down in the stump), the number or frequency of infected stumps is probably not the best way to describe the situation in this early stage. Furthermore, small colonies with low inoculum potential, that are likely to be replaced by other fungi (Dimitri, Zycha & Kliefoth, 1971; Holmer & Stenlid, 1993), would then be just as important as large colonies, which are more likely to grow and disperse to neighbouring trees. It was therefore necessary to take account of the colonized stump area for different treatments. Since the sapwood was most likely to be infected, the most appropriate measure might be to relate the spore infections to the area of the sapwood. An example of how colonies of *H. annosum* s. l. could appear on thinning stumps in an untreated (summer) stand and in a stump treated stand is depicted in Fig. 16, where two different measures of infection – % infected stumps and colonized stump area – result in entirely different figures of control efficacy: 40 and 90%, respectively. One measure is more quantitative and the other more qualitative. Using data from paper I, the two measures were correlated (Fig. 17). Consequently, both measures are relevant and should be stated in reports of experiments on stump treatment. The relevance of each measure is likely to vary between experiments depending on the experimental conditions, such as time elapsed between infection and sampling and at which level in the stump samples are taken (Pratt, pers. comm.; Berglund & Rönnberg, 2004). In paper I, the measure describing the infected stump area was considered most relevant.

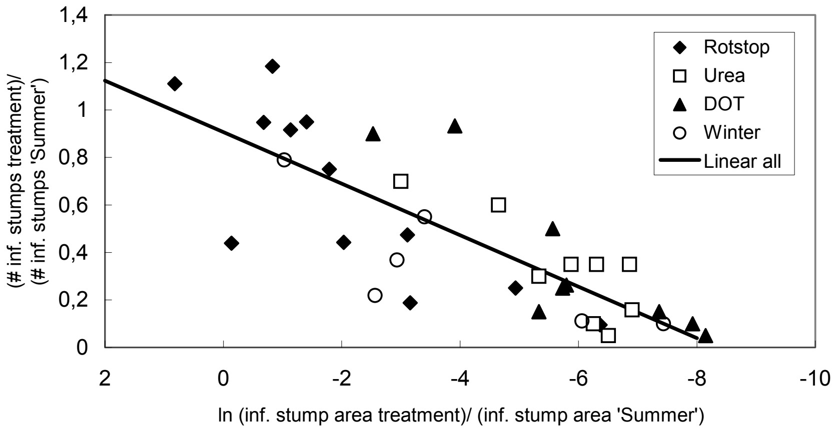

Fig. 17. Relationship between two different ways of expressing control efficacy, using relative infection rates for stump-treated and winter-thinned plots in paper I. The linear equation is $y = 0.1085x + 0.9069$, where y is the relative infection in terms of No. infected stumps and x is ln (relative infection) in terms of colonised stump area ($R^2 = 0.64$).

Control agents

Since Rishbeth (1949, 1951a, b, 1952, 1963) demonstrated the role of stump infections and explored possibilities for stump protection, many experiments using chemical compounds have been carried out. About 80 chemical compounds have been involved in chemical stump treatment (Pratt, Johansson & Hüttermann, 1998). Of these, borax, creosote, DOT, sodium nitrite and urea have been those most investigated. In biological treatment, apart from *P. gigantea*, *Trichoderma* spp. and *Resinicium bicolor* (Alb. & Schw. ex Fr.) Parm have received the most interest (Holdenrieder & Greig, 1998). Fifty years of research and practice of stump treatment reveals that so far, only *P. gigantea*, urea and possibly DOT reasonably meet the criteria of a good stump protectant.

Urea is cheap, readily available and can be stored without losing efficacy. There are many reports on good results using urea on Norway spruce (e.g. Yde-Andersen, 1982; Solheim, 1994; Brandtberg, Johansson & Seeger, 1996; paper I). Its failure to protect stumps of Sitka spruce (Pratt, 1994) is probably due to urea's mode of action resulting from urea hydrolysis by wood enzymes in living tissue (Johansson, Pratt & Asiegbu, 2000). In Scandinavian conditions, Norway spruce is often infected in the sapwood (living tissue); whereas in Sitka spruce in Britain, many infections often occur in the heartwood (dead tissue) (Redfern, 1993; Bendz-Hellgren & Stenlid, 1998). Urea has not been registered as a pesticide in Sweden, and consequently can not be used for stump protection in large-scale forestry. Urea in high concentrations, such as seen in spillage near the stump in mechanized application, may be toxic to plants (Thor, Nohrstedt & Weslien, 1997; Westlund & Nohrstedt, 2000).

DOT has the same advantages as urea regarding price and possibilities of handling and storage. It is efficient against *H. annosum* s. l. infection as long as the concentration is at least 5% (Pratt & Lloyd, 1996; Pratt, Johansson & Hüttermann, 1998, paper I). Boron in high concentration, as is the case in stump treatment, is toxic to plants and could harm ground vegetation near treated stumps (Thor, Nohrstedt & Weslien, 1997; Westlund & Nohrstedt, 2000). The primary mode of action from DOT is on the metabolism of basidiomycetes (Lloyd, 1997). DOT is not registered as a pesticide, and consequently can not be used in Swedish practical forestry.

Phlebiopsis gigantea is a wood decaying fungus with saprotrophic rather than pathogenic behaviour. It is a natural colonizer of e.g. pine and spruce stumps and wood (Käärik & Rennerfelt, 1957; Rishbeth, 1959; Kallio, 1973, 1976; Vasiliauskas *et al.*, 2002; Vasiliauskas *et al.*, 2004). It is used for stump treatment in three different formulations across Europe (Pratt, Niemi & Sierota, 2000), in Scandinavia (Rotstop®, Verdera Oy) it is based on a Finnish isolate with a high ability of colonizing spruce stumps (Korhonen *et al.*, 1994, Korhonen, 2003). From 2004, Rotstop contains a formulation of a Swedish strain (Berglund *et al.*, in press). The products used elsewhere in Europe are derived from isolates growing preferably on pine stumps.

Stump treatment decreases species richness both in *P. gigantea*-treated and urea-treated stumps of Norway spruce. However, stumps subjected to *P. gigantea* were colonized mainly by the same fungi as that occurring naturally in untreated stumps, whereas urea-treated stumps were colonized to a greater extent by Ascomycetes and Deuteromycetes rather than Basidiomycetes (including *H. annosum* s. l.) (Vasiliauskas *et al.*, 2004).

Equipment

Paper II demonstrates that *P. gigantea* in the Rotstop® formulation is well suited for mechanized stump treatment in thinning as well as in final felling. At present in practical forestry, a modified type of equipment is used as compared to when the experiment in paper II was conducted. The equipments using pressurized tanks are not in use anymore. Instead, what predominates is a pump that continuously mixes water and a higher concentration ($2.5\text{-}5 \cdot 10^7$ oidia l^{-1}) suspension of *P. gigantea* oidiospores into a working suspension. This improves hygiene and makes handling easier for the operator, who has to carry less water than previously. The pressure in these new systems is short-term (c. 5 short spikes on the way from the pump to the spraying device), but relatively high. In a through-the-bar system, the working pressure is 2,000-2,500 kPa, whereas in a spray-nozzle system, the working pressure might reach 4,000 kPa (Axelsson, pers. comm.). In the experiment, pressure was 2,200 kPa at the highest. Consequently, today’s through-the-bar systems are within the pressure limits tested in paper II, but spray-nozzle systems are not. Practical experience and results from paper I suggest, however, that survival of *P. gigantea* oidia is not affected by spray-nozzle systems. In Sweden, through-the-bar systems are most commonly used.

Root rot models and modelling

A model is just an abstraction of the real world, and as such it will never reach perfect fidelity. Therefore, models should be evaluated in the light of the context in which they have been developed. Input data determine what output is delivered. The user must be well aware of input data that are entered in the model. However, a good model of e.g. root disease will present the information available on the disease in a way that could be readily used to form management decisions, or to formulate new research problems (Shaw, Stage & McNamee, 1991; Pratt, Shaw & Vollbrecht, 1998). Usually, the models are most useful in comparative analyses (paper V). Caution should be taken when assessing absolute levels of decay or value losses.

If models are to be used in practical forest management, input data should be readily available, and output expressed in terms relevant to forest managers. In the model described in paper IV, data on spread rate in roots and stems could be entered directly from the literature. However, regarding e.g. the probability of spore infection and colonization, the situation is more complex. From paper I (and many other investigations) it is clear that the probability of spore infection in a specific stand is highly unpredictable, because of the large natural variation due to e.g. spore abundance, *H. annosum* species composition, weather conditions and stump properties. Simulations using the model in paper IV have shown sensitivity to the probability of spore infection. Consequently, when modelling scenarios using that model with the aims of detecting probable decay frequencies, there is reason to include several levels of spore infection probability.

Neither of the existing models can distinguish between the various measures of spore infection mentioned earlier. However, it is clearly possible to elaborate on the number of infected stumps, and on the probabilities of infection and transfer. A user familiar with the model could, by making estimates relying on best professional judgement, explore hypotheses or analyses of forest management under the risk of *H. annosum* s. l. attack.

Models of decay frequency

Many models intended for predicting the incidence of decay have been produced, but few are actually used in practice. In Germany, Müller (2002) developed a model for predicting the risk of damages including root rot. However, this model relies basically on a ratio between the diameter of decay and the tree diameter, and is not sensitive to variables critical for the development of *H. annosum*. Vollbrecht & Agestam (1995a) and Vollbrecht & Jørgensen (1995a, b) produced models predicting root rot incidence in southern Sweden and Denmark. They found significant correlation between root rot incidence and previous crops. Other parameters included were site index, stump treatment (yes/no) and data on previous thinnings such as accumulated thinned basal area and stems ha^{-1}

removed. The models were used to simulate the development of root rot for various scenarios. When stump treatment was applied at the previous thinning, the increase in root rot incidence was less than half that predicted when stumps were not treated. In a validation, the models developed from Danish plantations tended to over-estimate the observed decay frequency on sample plots in southern Sweden by 20% (Vollbrecht & Jørgensen, 1995a). These models are possible to use in research, or when making strategic decisions in southern Sweden and Denmark. However, they are less appropriate for use outside the region, and the data required are not easily collected from regular stand records. For the same reason, the model developed by Tamminen (1985) is less practical to handle on an operational scale. The model described in paper III was, however, developed to incorporate only data possible to derive from stand records in the greater part of Sweden. Thus, this model is developed to be used in strategic, tactical and operational planning systems in Swedish forestry. It is likely to give robust predictions of the decay frequency over a wide range of conditions, because it is based on individual trees. The underlying data represent forest management practices over a long time period. During this period winter-logging has been predominant, which should make the model under-estimate the probability decay resulting from today’s forest management, where a large proportion of the logging is carried out during the growing season without protection of the stumps. On the other hand, in the beginning of mechanization in forestry, the proportion of logging injuries was much higher than today (Fröding, 1992). Even though *H. annosum* s.l. is not the main colonizer of wounds (Isomäki & Kallio, 1974; Vasiliauskas, 2001) all kinds of decay are recorded in the NFI, which argue that the model in paper III could over-estimate the probability of decay in that respect.

Models in paper III are adopted to ascribe root rot incidence to stands where no such data are available. Should real incidence data be possible to collect, this is of course to be preferred.

Models of disease dynamics

In Europe, the model by Pratt, Redfern & Burnand (1989) requires the user to enter probabilities for, e.g. spore infection, the stump becoming infective and vegetative transfer of disease. The model has been used for simulating low risk and high risk scenarios for consecutive rotations of Sitka spruce in Britain (Redfern, Pratt & Whiteman, 1994; Pratt, Shaw & Vollbrecht, 1998).

So far, the model most frequently used by foresters is the WRD model (Frankel, 1998), which is relevant for California, Oregon, Washington and south-western Canada. It started with modelling of *P. weirii* and *A. ostoyae*, and later *H. annosum* s. l. was included. The infection can be illustrated by means of a forest vegetation simulator (Teck, Moeur & Eav, 1996), which places the model into a context in which foresters in the region are used to working.

The representation of root systems is similar in the WRD model and paper IV: circles that expand for living trees, and then decrease for dead trees or stumps. Once a tree is killed (or felled), the inoculum of *H. annosum* s. l. first expands, then stays at stasis for a number of years before it starts to decrease. More than the model in paper IV, the WRD model requires a lot of input parameters. This adds complexity to the modelling to a degree that makes it difficult for an inexperienced user to alter parameters. In the USA, the Forest Service has trained "power users" to carry out modelling together with forest managers (E. Goheen; C.G. Shaw, pers. comm.). The outputs from the WRD model are growth losses and mortality of trees. Additional information includes the area affected by disease centres, No. of centres, and changes in species composition and stand density. In contrast, the European models (Pratt, Redfern & Burnand, 1989; Möykkynen *et al*., 1998; paper IV) focus more on decay.

The overlapping root circles, used in paper IV and in the WRD model, cannot directly be translated into the frequency of physical root contacts. Recently, a stochastic model, "Root rot tracker" has been developed in Canada (Peet *et al.*, 1999). The model simulates the growth of individual roots and root contacts. In addition, the advance of disease is simulated in individual roots, resulting in more irregular patterns, and hence similar to what can be seen in real life. However, the user still has to feed the model appropriate data regarding root growth and the probability of root contact and transfer.

One key feature in any mechanistic model is the growth and yield model for trees. This is crucial to the outcome, and must be compatible with models for mortality and dynamics of root disease. Users of the MOHIEF model (paper IV) are strongly recommended to carefully compare and evaluate simulated stand data against empirical data or other models. Preferably, the first step of evaluation should not incorporate much root disease, since it will interact with other factors in the model. The models for basal area increment used in paper V (Elfving, unpublished) tend to overestimate the basal area in relation to the model used for comparison (Ekö, 1995) on poorer sites. In paper V this was handled by removing a few of the stems from the tree list where necessary, but in poorer site conditions than site index 24, the differences seem to increase further. The models for height increment (Elfving, unpublished) give appropriate tree heights at final felling, but require that the initial heights of trees on the simulated plot were set lower than what is realistic. In the simulations in paper V this was not a problem, since the heights of harvested trees were assigned in TimAn, reflecting Swedish averages for comparable tree sizes. Further work should include testing of the available growth and yield models within Rotstand (software comprising the MOHIEF model in paper IV) for a wide range of conditions. Other features of Rotstand that could be further addressed include the possibility of turning off *H. annosum* s. str. infection parameters more easily, and the possibility of running a specified number of repetitions in a less labour-intensive way to provide basic data for statistical analyses.

The MOHIEF model (paper IV) is sensitive to the spread rate of decay and the presence of initial disease centres. Empirically, the representation of root systems and inoculum in old stumps of a large diameter tend to provide too much transfer of decay between generations. In the simulations in paper V, a 20 cm stump diameter of old stumps was used, which did not reflect the true size of final felling stumps but resulted in decay frequencies in accordance with e.g. Rönnberg & Jørgensen (2000) and Rönnberg, Johansson & Pettersson (2003) for similar stand densities. How one should handle this problem needs to be addressed in a future interface of MOHIEF, intended for users in practical forestry.

In conclusion, the more complex the model, the higher demands on the user, who should be careful to maintain a healthy scepticism towards any model, especially the complex ones such as the WRD model or the MOHIEF model (paper IV).

Calibration and/or validation

Development of a model often requires that all data available are used for construction of the model. Consequently, data sets suitable for validation are rare. This was a problem in paper III. However, when the model was used in parallel with the model of *H. annosum* s. l. dynamics, the two models corroborated each other both as regards transfer of disease between subsequent generations and as regards the absolute levels of decay in Norway spruce over a rotation (Fig. 13 and paper V). The reason that P(decay), as predicted by the model in paper III, was closer to the scenarios where stump treatment was applied is that the decayed sample trees in the NFI largely represent forest management with logging during the winter.

Further validation work should include testing of the models in paper III and IV against data from Danish and Swedish experimental plots (Vollbrecht & Jørgensen, 1995a, b).

Planning and integration of models

The management of *Heterobasidion* root rot is just one part of forest management. Knowledge of root rot should hence be incorporated into all kinds of ordinary planning on strategic, tactical and operational levels (Thor *et al.*, in press). In practical forestry in Sweden today, however, little of root rot-adapted management can be observed. In both the national forest planning project "Heureka" (Lämås & Eriksson, 2002; paper III; paper IV) and within a research program on Norway spruce in southern Sweden (http://www-gran.slu.se/Program/granprogrammet.htm; 18-Nov-2004), root rot is integrated. National planning projects in other countries include Mela in Finland (Redsven *et al.*, 2002; Mattila & Nuutinen, 2004), where root diseases are considered, and the CLAMS project in coastal Oregon (Spies *et al.*, 2002; Bettinger *et al.*, in press), in which diseases on forest trees are not considered.

Root rot models should be integrated with the models regularly used for management and planning of harvests and logistics. In Heureka (Lämås & Eriksson, 2002), the units are individual trees and circular plots. From these units, forests and landscapes are modelled, and analyses can hence be performed. The simulation of *H. annosum* s. l. root rot is spatially sensitive, due to the dynamics in the root systems and the clustered appearance, which depends on the various sources of inoculum. Consequently, the dynamics of a root disease is more easily simulated on large, rectangular plots than on small circular plots. The model in paper III fits well with the general structure of e.g. Heureka, and is likely to be implemented relatively easily. However, further work is needed to apply the model in paper IV to small circular plots.

Supply of input data

There is a large potential of predicting and characterizing wood properties in a stand (Wilhelmsson, 2001), including decay that affects the value more than many other wood properties. To make valid predictions, input data are needed. At present, remote sensing, i.e. satellite pictures (e.g. Reese *et al*., 2003), aerial photographs and ground-based surveys are the available methods. The methods can also be combined, i.e. ground-based sampling can be used to improve the reliability of satellite data (Olofsson *et al*., in press). Sampling methods based on transect lines give the best result in ground-based surveys of root and butt rot (Bloomberg, Cumberbirch & Wallis, 1980), due to the root disease's clustered appearance. If the result of stump treatment is followed up by close monitoring of stumps, the possibility of assessing decay should be considered. Another possible method of inventory involves expanding the computer applications in a single-grip harvester. Today, the operator registers the assortment (e.g. decayed pulpwood) when processing the tree, and the computer can be programmed to count the number of decayed trees in relation to all trees cut, which could provide stand-wise figures of butt rot frequency. These data can be saved in a stand record data base for future planning or root rot modelling.

Management of *Heterobasidion* root rot in Swedish forestry

Heterobasidion root rot has caused economic damage to Swedish forestry for a long period (Lagerberg, 1923; Arvidsson, 1954; Rattsjö & Rennerfelt, 1955; Stenlid, 1990; Pratt, 1998; Rosvall *et al*., 2004; paper V). The pedagogical challenge in introducing the root rot issues is considerable. So far, the low-cost perspective has received more attention than long-term revenue. Knowledge about the role of stump infection and stump protection is 50 years old, but stump treatment was not initiated until the early 1990s in the south of Sweden. There is no doubt that the disease can be controlled (cf paper I and V). Nor is there doubt that if the disease is not controlled, the problem will get worse (cf paper III, IV and V). Today's knowledge is sufficient enough to make a difference if the forestry sector decides to make a move. However, there is a whole system consisting of policy makers, managers, researchers, engineers, trainers, forest owners, contractors and machine operators that need to collaborate (Pratt & Thor, 2001). In addition, for foresters to make the right decisions there is a need for integrated planning and decision support systems including root rot aspects. The development of information technology in forestry facilitates this (Forsberg & Rönnqvist, 2003; Peltola, 2003), although it is important to keep *H. annosum* s. l. in mind when working out specifications for these systems.

Further work is needed on several issues: The model of disease dynamics (paper IV) needs to be developed in two directions simultaneously. First, it needs to develop user interfaces that enable forest owners, managers and researchers to use the model, and second, the functions need to be adopted by general planning systems, such as Heureka applications and the systems used within various forest enterprises. The latter is valid also for the models in paper III.

Stump treatment, where and when?

Paper V clearly demonstrates the benefits of stump treatment, in thinning as well as in final felling. One might argue that there is no need for stump treatment in final felling if the old crop is severely decayed. Transfer of disease between consecutive generations of Norway spruce has been studied in southern Sweden and Denmark by Rönnberg & Jørgensen (2000) and Rönnberg, Johansson & Pettersson (2003), for example. In these investigations the decay frequency in the previous crop ranged between 7 and 100%, and the decay frequency of the new crop (age 11–39 years) was 0–38%, where *Heterobasidion* spp. accounted for 50–100% of the decay. No correlation between the incidences of butt rot in the two consecutive generations was found. There was no information about the spore infection of clear-cut stumps, but the results indicate an important role of spore infections regardless of present decay, which is also supported by Vollbrecht & Stenlid (1999) for the transfer of disease from Norway spruce to hybrid larch (*Larix* × *eurolepis* Henry). The simulations in paper IV and V corroborate other investigations on the transfer of disease between generations, taking into account the role of old decayed stumps as well as spore-infected clear-cut stumps. From these results and paper V, stump treatment in final felling can also be recommended in relatively decayed stands.

Half of the area of Norway spruce thinning that should be subjected to stump treatment is left untreated (Samuelsson & Örlander, 2001). Moreover, stump treatment in final felling rarely occurs in Sweden (Thor, 2003). Consequently, an increased activity of stump treatment is justified on economic grounds, in final felling as well as in thinning, in many Norway-spruce dominated stands (paper V). Non-market effects, e.g. long-term build-up of inoculum, support that argument (Pratt, Redfern & Burnand, 1989; Redfern, Pratt & Whiteman, 1994).

Concluding remarks

Inevitably, *H. annosum* s. l. is a part of managed coniferous forests in Sweden. There is no chance (or desire) of eradicating the fungus from the forest. The root rot problem will increase over time unless active control strategies are applied. However, there are a number of methods to control the disease in order to minimize the economic damages to forestry. In many sites with decay-affected Norway spruce, there are very few options that in practice outperform Norway spruce in the subsequent generation. The number of thinnings and the length of the rotation should be analyzed further to take *Heterobasidion* root rot into account to a larger extent than what is done at present. In addition, stump treatment programs (or, when possible, logging in the winter) should be applied.

Techniques and methods for stump treatment are available (paper I and II). For forest conditions and price relations similar to what was simulated in paper V, stump treatment should be applied in all logging operations of Norway-spruce stands of at least site index 26, irrespective of forest or post-agricultural soil. The same applies to mixed coniferous stands in southern Sweden with at least 50% Norway spruce. In mixed stands (maximum 50% Norway spruce) north of where *H. annosum* s. str. can be expected, stump treatment was not economically justified. Although the results from the simulations in paper V could change if the input variables are altered, it is obvious that there is room for more stump treatment than what is carried out at present in Swedish forestry.

After final felling of a stand, the net final value ha^{-1} for the forest owner can be of the magnitude 23,000-28,000 SEK higher (c. 16-26% of the total net revenue) if a stump treatment program has been applied from final felling of the previous crop.

Short rotations, few thinnings, winter-logging or stump treatment in logging operations in Norway-spruce dominated stands (and mixed coniferous stands in southern Sweden) all contribute to minimizing the impact of *H. annosum* s. l. root disease. However, there are other important parameters for the forest manager to consider as well, e.g. the market situation and wood supply issues. Bringing knowledge about root rot problems into forest planning by means of useful models (paper III and IV) enables the forest manager to make more well-informed and economically beneficial decisions.

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