Silvicultural control of Heterobasidion root rot in Norway spruce forests in southern Finland

Regeneration and vitality fertilization of infected stands

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Academic dissertation in Forest Pathology

To be presented, with the permission of the Faculty of Agriculture and Forestry of the University of Helsinki, for public criticism in Auditorium XIII of the University Main Building, Unioninkatu 34, on October 17th, 2003, at 12 o'clock noon.

Wir leben mitten in ihr (Natur) und sind ihr fremde. Sie spricht unaufhörlich mit uns und verrät uns ihr Geheimnis nicht. Wir wirken ständig auf sie und haben doch keine Gewalt über sie.

J. W. v. Goethe, 1783

To Valtteri and Elena

List of original articles

This thesis is based on the following articles, which are referred to in the text by the Roman numerals **I-IV**. All the articles are reprinted with kind permission of the publishers.

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

II   Piri, T. and Korhonen, K. 2001. Infection of advance regeneration of Norway spruce by *Heterobasidion parviporum*. Canadian Journal of Forest Research 31: 937-942.

III   Piri, T. 2003. Early development of root rot in young Norway spruce planted on sites infected by *Heterobasidion* in southern Finland. Canadian Journal of Forest Research 33: 604-611.

IV   Piri, T. 1998. Effects of vitality fertilization on the growth of *Heterobasidion annosum* in Norway spruce roots. European Journal of Forest Pathology 28: 391-397.

Paper **II** was planned jointly by Tuula Piri and Kari Korhonen. Kari Korhonen also participated in the preparation of the manuscript.

Contents

Abstract

Heterobasidion root rot is a significant management problem on Norway spruce (*Picea abies*) in southern Finland. Once the fungus has entered a stand, control of the disease has proved to be difficult. Consequently, any forest management practice that reduces losses caused by *Heterobasidion* is of great value.

This thesis concerns the effects of tree species selection and regeneration method on the transfer of Heterobasidion root rot from diseased spruce stands to the next tree rotation. In addition, the effect of vitality fertilization on the growth rate of *Heterobasidion* in roots of mature Norway spruce was also investigated. The studies were carried out on old spruce sites in southern Finland, where *Heterobasidion parviporum* is the dominant *Heterobasidion* species and by far the most important agent causing decay on Norway spruce.

Investigations on old stumps of the previous rotation showed that final cutting stumps remain as effective infection sources for several decades. Viable mycelium and active basidiocarps of *Heterobasidion* were found even in the oldest spruce stumps investigated, cut 46 years ago. The spread of *Heterobasidion* from old spruce stumps via root contacts to the surrounding regeneration was quantified. The fungus was isolated from stumps and regeneration and the fungal genotypes (genets) were identified by means of somatic incompatibility tests. Trees in the new tree generation were, regardless of species, principally infected by a genet that was also isolated from old stumps, indicating that the fungus had spread vegetatively through root contacts from the previous to the next tree generation. When planted after a spruce rotation infected by *H. parviporum*, silver birch (*Betula pendula*) and Scots pine (*Pinus sylvestris*) effectively prevented spread of the disease. The average number of regeneration trees infected per decayed spruce stump of the previous rotation was 0.04 trees in birch regenerations and 0.05 trees in Scots pine regenerations. Birch was more frequently infected by *H. parviporum* only in cases where the provenance was not adapted to the site. In the subsequent stands of lodgepole pine (*Pinus contorta* var. *latifolia*) an average of 0.5 trees per stump were infected, suggesting that lodgepole pine is more susceptible to *H. parviporum* than native Scots pine. The corresponding value in stands planted with Siberian larch (*Larix sibirica*) was 0.3 trees. Although the decay frequency will probably remain lower in the subsequent lodgepole pine and Siberian larch stands compared to the previous spruce stand, the possible consequences should be considered before these tree species are planted as monocultures on sites heavily infected by *H. parviporum.*

The tree species most heavily attacked by *H. parviporum* was Norway spruce. The average frequency of infected trees was clearly higher in the current than in the previous spruce stand only on sites regenerated with spruce. On infested sites, the regeneration derived from advance-growth spruce that had developed naturally under spruce overstorey proved to be more frequently infected by *Heterobasidion* than planted spruce regeneration of the same size. The number of regeneration spruces infected per decayed stump or tree of the previous rotation was 4.5 in advance-growth stands and 1.2 in planted stands. Not only the infection frequency but also the mode and progress of infection were related to the regeneration method. Planted spruce was mainly infected by a genet originating

from old stumps (71 % of all infected trees), whereas in advance regeneration only about half of the trees (53 %) were found to be infected by such a genet. The origin of infections not attributable to old stumps could not be identified with certainty. It seems conceivable, however, that suppressed advance-growth spruce is more susceptible to primary spore infection than planted spruce. On the other hand, the decay had advanced faster in the wood of rapidly growing, planted spruce than in the wood of slow-growing, advance-growth spruce.

In young, unthinned spruce stands the vegetative spread of *Heterobasidion* between regeneration trees was uncommon and, consequently, the occurrence of naturally established, broad-leaved trees in a stand did not have any significant influence on the disease frequency in Norway spruce. However, in planted stands, where the transplants were mainly infected vegetatively from old stumps, a mixed plantation favouring broad-leaved trees or Scots pine around decayed spruce stumps may considerably restrict the transfer of Heterobasidion root rot into the subsequent tree generation. In planted spruce stands, a 2.5-meter-wide area without spruce around colonized stumps decreased the number of infected trees by 50 %, and a 4-meter-wide area by 80 %.

The effect of vitality fertilization on the growth rate of *H. parviporum* in spruce roots was also investigated. The treatments were: 1) unfertilized control, 2) compound fertilizer containing P, K, Ca, Mg, S, Cu, Zn and B, 3) compound fertilizer plus nitrogen, 4) compound fertilizer plus nitrogen and limestone, and 5) stand-specific fertilizer containing N, P, K and Cu. *H. parviporum* was inoculated into the roots of spruce. The roots were sampled after 12 months and the growth of the fungus in the roots was determined. The mean linear growth in different treatments was: 1) 18.2 cm, 2) 25.6 cm, 3) 21.3 cm, 4) 26.0 cm, and 5) 29.8 cm. Because of the considerable variation in fungus growth on individual trees, as well as in different roots of the same tree, there were no statistically significant differences in mean fungal growth between the treatments. Nevertheless, the result indicates that the use of vitality fertilizers in diseased Norway spruce stands may, at least in the short term, slightly accelerate rather than slow down the development of Heterobasidion root rot.

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Eino, who since our student years in Göttingen has shared with me all the projects of my life – also this one.

Vantaa, September, 2003

1 Introduction

1.1 The *Heterobasidion annosum* complex

Until the late seventies, *Heterobasidion annosum* Bref. (*Polyporus annosus* Fr., *Fomes annosus* (Fr.) Cooke), was regarded as a single taxonomic unit. In 1978, Korhonen identified, on the basis of mating experiments, two host-specialized intersterility groups within *H. annosum* in Finland and designated them as the "S" and the "P" group. The S spruce) group was mainly isolated from butt-rotted Norway spruce (*Picea abies* (L.) Karsten), but occasionally also from Scots pine (*Pinus sylvestris* L.) saplings. The P group was isolated from Scots pine and a range of other native conifers and broad-leaved trees (Korhonen 1978a). Later on, a third European intersterility group of *Heterobasidion* called the "F" group was identified in Italy (Capretti et al. 1990). The F (fir) group is confined to southern and central Europe and its principal host is silver fir (*Abies alba* Mill.) and other *Abies* species of southern Europe (Capretti et al. 1990, Capretti et al. 1994, Tsopelas and Korhonen 1996). Recently, the European intersterility groups were described as taxonomic species: the P group as *H. annosum sensu stricto*, the S group as *H. parviporum* Niemelä & Korhonen and the F group as *H. abietinum* Niemelä & Korhonen (Niemelä and Korhonen 1998).

Both the S and P groups are present in North America (Chase 1985, Harrington et al. 1989, Chase and Ulrich 1990). As in Europe, the North American P group has most often been isolated from *Pinus* hosts. Compared to the European S group, the North American S group has a wider host range, including trees in genera such as *Picea*, *Abies*, *Thuja*, *Pseudotsuga*, *Tsuga*, *Sequoiadendron*, *Pinus* and *Juniperus* (Chase 1985, Korhonen et al. 1998).

Only little is known about the variation of the *H. annosum* complex in Asia. So far, *H. parviporum* has been reported to occur in southern Siberia, northeastern China, Japan and eastern Himalayas (Dai and Korhonen 1999, Korhonen et al. 2001). The most eastern record of *H. annosum s. str*. is from the Altai area, southern Siberia (Korhonen et al. 2003). Although the puzzle of the *H. annosum* complex has not yet been solved, the ability to identify intersterile groups of *H. annosum* has increased our understanding of the behaviour of this widely distributed pathogen, and helped to develop disease-control strategies based on the different host preferences among the groups.

1.2 Heterobasidion root rot: initiation and development in Norway spruce forests

1.2.1 Primary infection by spores

Heterobasidion is capable of spreading over long distances by means of airborne spores. Basidiospores are produced in basidiocarps that often occur in the cavities of old stumps, on logs containing advanced decay, and on the roots of windthrown trees. At the time when spore production is at its highest, the number of *Heterobasidion* spores deposited

in an infection centre in a mature Norway spruce stand in southern Finland can be as high as 42 000–151 000 spores/cm^2 per hour (Kallio 1970, Möykkynen et al. 1997). A small proportion of the released spores can be spread by air currents over distances from 50 to 500 km, but most of them are deposited within a distance of a few meters from the basidiocarp (Kallio 1970, Stenlid 1994a). Consequently, the basidiocarps are locally important inoculum sources in spruce stands. In Sweden, Rennerfelt (1946) and Stenlid (1987) have observed that *Heterobasidion* produces fewer basidiocarps in the northern part than in the southern part of its distribution area, which may be reflected in the increasing disease incidence on moving southwards.

In addition to basidiospores, *Heterobasidion* also produces asexual spores, conidia (Brefelt 1889). The conidial stage has been found on infected timber lying on the ground and on the cut surfaces of spruce stumps covered with logging residues (Rishbeth 1957, Peace 1962, Kallio 1971). Conidiophores have also been found in insect galleries (Bakshi 1950, 1952, Hunt et al. 1976), and some insects such as weevils (*Hylobius abietis*) have been shown to distribute the conidia of *Heterobasidion* (Nuorteva and Laine 1968, 1972, Kadlec et al. 1992). Although conidial inoculation of the roots, seedlings and stump surfaces has been used successfully in several studies (e.g. Kuhlman and Henrix 1964, Kuhlman 1969, 1970, Hyppel 1970, Schönhar 1978, 1979, Asiegbu et al. 1993, Bendz-Hellgren and Stenlid 1998), the role of the conidia in the natural infection process is not well understood. Möykkynen (1997) showed that conidia might be liberated into the air by wind gusts associated with high humidity or mist. Under Finnish conditions, however, basidiospores constitute the major part of spore inoculum (Kallio 1970, 1971, Möykkynen 1997).

After landing on the ground, a proportion of the spores are washed into the soil, where they can survive for several months (Molin 1957, Kuhlman 1969, Schönhar 1980). Inoculation experiments carried out by Dimitri (1969a) showed that basidiospores are able to infect wounded spruce roots in the soil. There is also some evidence that roots of suppressed trees are susceptible to spore infection (Rishbeth 1951b, Schönhar 1995). In managed forests, however, the spore infections occurring through wounds in the roots are considered to be of minor importance as compared with infections occurring through fresh stump surfaces or deep wounds above ground level (Redfern and Stenlid 1998). As a result of round-the-year fellings, fresh stump surfaces are available for spore deposition also in those seasons of the year (from May to October) when the spore distribution is profuse in southern Finland (Kallio 1970). Immense numbers of basidiospores with a wide range of genetic variation produced in perennial basidiocarps offer a good starting point for stump infection. On the other hand, even a low rate of spore discharge by *Heterobasidion* may lead to extensive stump infection if the spores of competing fungi are few or absent (Rishbeth 1951a).

1.2.2 Secondary spread by mycelium

Germination of individual basidiospores produces primary, homokaryotic mycelia. Conidiospores, in contrast, can be either heterokaryotic or homokaryotic. Apparently, most of the homokaryotic mycelia of *Heterobasidion* become heterokaryotized relatively rapidly as a result of a compatible mating (Rayner et al. 1987). Low infection rates may,

however, make heterokaryotization less probable and a high proportion of the colonies in one-year-old stumps can be homokaryotic (Stenlid 1994b, Korhonen and Piri 1994, Möykkynen and Kontiokari 2001). Although homokaryons of *Heterobasidion* have been shown to cause disease in North America (Platt et al. 1965, Garbelotto et al. 1997b), homokaryons in Finland very seldom, if ever, cause disease in living trees (Korhonen and Piri 1994). The secondary spread of *Heterobasidion* normally takes place through growth of the heterokaryotic mycelium.

Heterobasidion is incapable of growing freely in the soil (Hodges 1969). On alkaline soils, *Heterobasidion* can grow ectotrophically on the bark of pine roots (Rishbeth 1950). On soils with a low pH, the mycelium of *Heterobasidion* lives and spreads only in wood tissue (Yde-Andersen and Malla 1977). As indicated by Hartig as early as 1882, *Heterobasidion* spreads from infected stumps or trees to adjacent healthy trees through root contacts and grafts. *Heterobasidion* spreads faster in the roots of dead trees or in stump roots than in the roots of living trees because the former lack active defence systems (Schönhar 1978, Bendz-Hellgren et al. 1999). Studies carried out in the Nordic countries have shown that the fungus advances at a rate of about 9–12 cm per year in inoculated living spruce roots (Stenlid and Johansson 1987, Bendz-Hellgren et al. 1999), and about 25 cm in stump roots (Bendz-Hellgren et al. 1999). In stem wood of Norway spruce, *Heterobasidion* tends to grow slightly faster than in living root wood, i.e. on an average 30–40 cm per year (Huse and Venn 1994, Hallaksela 1993, Bendz-Hellgren et al. 1999). In Finland, the maximum annual growth rate measured in spruce stem wood is one meter (Hallaksela 1993). Differences in fungal growth rate between individual trees are large and, at least in artificially inoculated trees, the growth rate tends to slow down with time, being at its highest in the first year after successful infection (Richter 1974, Hallaksela 1993).

Secondary spreading from old-growth stumps, thinning stumps or scarred trees to adjacent healthy trees is affected by host-related factors such as individual resistance, physiological condition and age of the tree (Ekman and von Weissenberg 1981, Lindberg and Johansson 1992, Dimitri 1994, Swedjemark and Stenlid 1997), pathogen-related factors such as size of the inoculum (Holmer and Stenlid 1993), virulence and age of the fungal individual (Swedjemark and Stenlid 1997, Huse and Venn 1994), soil properties directly or indirectly affecting the frequency of root contacts (Kuhlman 1973, Redfern 1984, 1998), and competition and antagonism from other microorganisms (Rennerfelt 1949, Greig 1962).

Heterobasidion is able to spread vegetatively not only into the same tree species growing in the same rotation, but also into other susceptible tree species of the same or subsequent tree generation (Greig 1962, Yde-Andersen 1978, Stenlid 1987, Piri et al. 1990, Capretti and Goggioli 1992, Vasiliauskas and Stenlid 1998, Rönnberg and Vollbrecht 1999, Vollbrecht and Stenlid 1999).

1.2.3 The somatic incompatibility reaction in studying the population structure of *Heterobasidion*

Somatic (= vegetative) incompatibility systems restrict the free exchange of nuclei and cytoplasm between genetically dissimilar mycelia and hence maintain the individuality

of secondary mycelia (Rayner et al. 1984, Rayner 1991). Within a *Heterobasidion* species, somatic incompatibility appears as a zone of sparse growth between paired heterokaryotic isolates of different genetic composition, whereas genetically identical isolates grow together to form a continuous mycelial mat (Stenlid 1985). The genetic mechanism of somatic incompatibility in *Heterobasidion* has not been clearly elucidated, but at least three or four loci are involved, one of them multiallelic, and it seems that the mechanism is controlled by nuclear genes that are not linked with sexual compatibility loci (Hansen et al. 1993a).

Although the somatic incompatibility system of higher fungi is still poorly understood, it has proved to be a useful tool to distinguish individuals of natural fungal populations (e.g. Stenlid 1985, Piri et al. 1990, Hansen et al.1993a). One disadvantage of this very simple method is that it does not always recognize small genetic differences between very closely related heterokaryons, like sib-related heterokaryons, for instance (Hansen et al. 1993b). The probability of any two unrelated *Heterobasidion* isolates being somatically compatible is extremely low (Hansen et al. 1993a).

Recognition of individual *Heterobasidion* mycelia (genets) in natural populations provides valuable information on the establishment of spore infections and mycelial spread of the fungus in forest stands. A high number of small genets indicates that the stand has been exposed to primary spore infection, most probably as a result of thinning operations, whereas genets of large size (high number of trees infected by the same genet) suggests that most of the trees have been infected through mycelial growth via root contacts. This information has obvious potential when assessing the effectiveness of different control measures against Heterobasidion root rot. The vegetative spread of the fungus can be controlled by reducing the number of root contacts between susceptible host trees (mixed stands or low stand density). A high number of spore infections emphasizes the importance of stump treatment as a control measure against *Hetero-basidion* infection.

1.3 Impacts of Heterobasidion root and butt rot in Norway spruce forests in southern Finland

"The devil took, what the miser hoarded" owner of a rotten spruce stand in Mäntsälä, 1997

1.3.1 Incidence of Heterobasidion root rot and direct losses caused by it

In southern Finland, Norway spruce is economically the most important host of *Heterobasidion*. Almost 90 % of the total decay volume in Norway spruce stands in southern Finland is due to butt rot caused by *Heterobasidion* (Tamminen 1985). The known northern border of the distribution area of *Heterobasidion* is at approximately latitude 68° N. The fungus becomes more common towards the south, and the most serious damage caused by *Heterobasidion* on Norway spruce occurs along the coastal regions of southern Finland (Tamminen 1985, Mäkelä et al. 1998). *Heterobasidion* is a problem particularly in old, pure spruce stands on fertile, non-paludified, old spruce

sites, which are close to sea level. Based on the material collected from 146 clear cutting areas in southern Finland, the relative butt-rot frequency, expressed as the proportion of butt-rot spruces out of the total stem volume of the spruces, averaged 18.5 %. In the southernmost part of the country, where *Heterobasidion* is the most common, the decay frequency averaged 35.4 % (Tamminen 1985). Butt rot causes, on an average, a 6 to 9 %, max. 37 % reduction in saw timber yield in final cuttings (Tuimala 1979, Tamminen 1985, Kaarna-Vuorinen 2000). In single stands, the reduction in the sales revenues due to butt rot can be over 30 % (Tamminen 1985, Kaarna-Vuorinen 2000).

1.3.2 Indirect losses

In addition to the reduction of timber yield and quality, Heterobasidion root rot reduces the growth of spruce (Arvidson 1954, Henriksen and Jørgensen 1953, Kallio and Tamminen 1974, Tamminen 1985, Bendz-Hellgren and Stenlid 1995, 1997) and deteriorates the stem form by causing thickening of the lower part of the trunk (Henriksen and Jørgensen 1953, Arvidson 1954, Kallio and Tamminen 1974, Tamminen 1985). The role of Heterobasidion root rot as a major cause of a growth reduction in Norway spruce stands is often overlooked. In Sweden, decayed trees produce ca. 10 % less volume growth compared with healthy trees over a 5-year period (Bendz-Hellgren 1997). In individual stands and in the longer term, the growth losses can be considerably higher (Henriksen and Jørgensen 1953, Bendz-Hellgren and Stenlid 1997). Moreover, butt rot renders trees susceptible to wind damage (Bazzigher and Schmid 1969, Schmid-Haas 1994, Vollbrecht et al. 1994) and to attacks by the bark beetle *Dendroctonus micans* (Kangas 1952, Petersen 1952, Francke-Grosmann 1954). The result is reduced forest productivity and increased expenses in logging small numbers of damaged trees, scattered throughout the forest.

The use of various control methods to reduce disease in the current and future rotations requires investments. The abandonment of logging in summertime because of the high infection risk or, alternatively, the use of control methods to prevent infection of stump surfaces in summer cuttings, means extra costs. Most of the silvicultural control methods, such as reduced rotation length, prescribed burning, stump removal and change of tree species, involve costs. At the present time it is difficult to predict the benefits of the control measures due to the lack of long-term experience. Thus, no detailed calculations of the total costs caused by *Heterobasidion* in Finnish forests have been made. Based on a rough estimate, the annual economic losses due to root and butt rot in Finland are reported to be around 35 million € (Bendz-Hellgren et al. 1998).

1.4 Factors favouring *Heterobasidion* in managed forests

"H. annosum is a fungus that follows man's footsteps into the forest" Korhonen et al. 1998.

1.4.1 Logging operations

Several recent reports support the early statement of Meinecke (1914) that increased human activities in the forest has contributed to an increased incidence of Heterobasidion

root rot (e.g. Venn and Solheim 1994, Shaw et al. 1994, Otrosina and Garbelotto 1998, Filip and Sullivan 1998). Unquestionably, the greatest losses are associated with the stumps left after cutting operations. The pioneering work by Rishbeth (1949, 1951a) showed that air-borne spores of *Heterobasidion* colonize freshly exposed stump surfaces, and therefore operations such as thinning enable the fungus to become established in pine plantations where it was formerly absent. Since then, the importance of freshly cut stumps as the primary sources of infection has been recognized on Norway spruce (Molin 1957, Yde-Andersen 1962, Kallio 1965, 1970, 1971, Paludan 1966) and several other tree species (e.g. Kuhlman and Hendrix 1964, Cobb and Barber 1968, Driver and Wood 1968, Wallis and Reynolds 1970, Morrison et al. 1986). Weather conditions and the number of airborne inoculum at the time of harvesting are the most important factors determining the incidence of stump infection (Rishbeth 1957, Yde-Andersen 1962, Solheim 1994, Brandtberg et al. 1996). In southern Finland, spores of *Heterobasidion* are in the air from April to November, most frequently from later May to the end of October (Kallio 1970). During that period the infection percentage of freshly cut spruce stumps varies from about 5 to 26 % (Kallio and Hallaksela 1979, Hallaksela and Nevalainen 1981, Lipponen 1991). Although not all stump infections result in stump colonization, even a small percentage of colonized stumps markedly increases the amount of inoculum on the site and enables the infection of stands where the fungus is initially absent (Morrison and Johnson 1978, Hallaksela and Nevalainen 1981).

In addition to stump surfaces, also other fresh wood surfaces, such as logging wounds in the aerial parts of trees and stumps, expose a Norway spruce stand to primary infection by air-borne spores. Especially the employment of heavy thinning machines in young forest stands often leaves scars on the trunks and roots of the remaining trees, which are subsequently prone to infection by decay fungi including *Heterobasidion* (Nilsson and Hyppel 1968, Isomäki and Kallio 1974, Aufsess 1978). The number of successful *Heterobasidion* infections of standing trees increases with increasing size and depth of the lesion (Dimitri 1969a). Generally, root injuries near the stem base often cause decay, while decay in root injuries distant from the stem is less frequent and the extent of the decay is more limited (Nilsson and Hyppel 1968, Isomäki and Kallio 1974). The most important wound decay fungus on Norway spruce is *Stereum sanguinolentum* (Alb. & Schw.) ex Fr. (von Aufsess 1978, Roll-Hansen and Roll-Hansen 1981, Vasiliauskas et al.1996). Unlike *Heterobasidion*, it does not spread via root contacts into the adjacent trees (Vasiliauskas 1994). In southern Finland, *Heterobasidion* was isolated from 7 % of root injuries and 14 % of trunk injuries on Norway spruce damaged by timber harvesting machines. In other material also collected from southern Finland, the proportion of wounds infected by *Heterobasidion* was as low as 2 % (Hallaksela 1984). According to Norwegian studies, *Heterobasidion* is the most frequent wound parasite in summer injuries, whereas *S. sanguinolentum* more frequently invades injuries inflicted at other times of the year (Roll-Hansen and Roll-Hansen 1980, Solheim and Selås 1986, Solheim 2003). In summer thinnings in which the stumps are treated but the proportion of damaged standing trees is high, logging wounds may thus be an important avenue of *Heterobasidion* infection under favourable weather conditions.

1.4.2 Improvement of forest productivity

Forest management that is oriented towards speeding up the growth rate of trees has been shown, at least partially, to increase the incidence of Heterobasidion root rot. *Heterobasidion* tends to attack fast-growing spruce (Arvidson 1954), and the decay proceeds faster in fast-growing than in slow-growing trees (Isomäki and Kallio 1974, Laiho 1983, Dimitri and Schumann 1989, Dimitri 1994). Measures designed to improve tree growth such as fertilization, thinning and drainage have, in some studies, been found to be associated with increased decay incidence (Rennerfelt 1946, Basham 1973, Dimitri and Schumann 1989, Alcubilla et al. 1990). Other studies have shown, however, that while forest fertilization improves tree growth, it does not necessarily decrease the resistance of trees to decay (Seibt 1964, Cowling et al. 1969, Yde-Andersen 1977a, Laiho 1978).

Several studies have shown that liming, especially in the long term, may increase the risk of infection by *Heterobasidion* and also accelerate the growth rate of fungus already present in Norway spruce stands (e.g. Matthesen 1982, Dimitri and Schumann 1989, Stenlid and Bendz-Hellgren 1996). Although the primary goal of older liming trials and practices was to improve tree growth (Ilvessalo 1923), it has subsequently been found that liming has a long-term negative effect on the growth of spruce (e.g. Derome et al. 1986). Thus, the increased butt rot incidence in limed stands does not seem to be connected to the improved tree growth. Instead, liming raises the soil pH, which may have a contributory influence on disease development (Rishbeth 1951b, Evers 1973). Some of the negative effects of liming on conifers, such as the death of fine roots and mycorrhizal root tips (Lehto 1994), may increase the risk of infection by *Hetero-basidion*. Regardless of its negative effects, liming has proved to be an effective way to counteract soil acidification in forests suffering from decline in Central Europe (Huettl and Zoettl 1993).

The high growing capacity of Norway spruce has been mentioned as one reason for high butt rot frequencies in spruce stands in Denmark and southern Sweden where spruce, introduced outside its natural range, has better growth than the original deciduous forests (Rennerfelt 1946). Even when planted within its natural range, the ecophysiological maladaption of spruce to specific sites may increase the susceptibility of artificially regenerated stands to root disease (Rennerfelt 1946, McDonald 1990). Spruce seedlings subjected to moderate drought stress showed an increased infection frequency by *Heterobasidion* through the bark, and an accelerated growth rate of the fungus (Lindberg and Johansson 1992).

Until recently it was a common practice in Finland to manage forests for single species stands. The tree species composition was controlled already at the seedling stage by cleaning to make the stand even-aged, homogeneous and rapid growing. Both the cultivation of monocultures (Rishbeth 1973) and use of high planting density in pure regenerations (Venn and Solheim 1994) increase the number of root contacts available for the disease to spread.

Because Norway spruce is a fast-growing species and produces timber preferred by industry, consecutive spruce rotations are becoming more common even on infested sites. Several earlier studies have demonstrated that the incidence of Heterobasidion

root rot tends to increase in successive spruce rotations (Jørgensen et al. 1939, Holmsgaard et al. 1961, Schönhar 1973, Yde-Andersen 1978). The determining factor in these situations is the infection potential of the infected stumps of the previous stand. Where spore infections of healthy stumps after final felling are frequent, regenerations established even after a healthy spruce rotation can be severely infected, and the relationship in disease incidence between successive spruce generations may be unclear (Rönnberg and Jørgensen 2000, Rönnberg et al. 2003).

1.4.3 Afforestation of Norway spruce on agricultural land

A high incidence of Heterobasidion root rot is characteristic of new conifer plantations established on sites with no previous forest history (Rohmeder 1937, Rennerfelt 1946, Rishbeth 1949, 1957, Holmsgaard et al. 1968, Werner 1971, Graber 1996). The disease incidence on former agricultural land seems to be connected to certain soil properties favouring the pathogen; such as high soil pH (Rishbeth 1951b, Maraite and Mayer 1966, Werner 1971) and sparsity of soil microflora antagonistic or competitive to *Heterobasidion* (Rishbeth 1949, 1951b, Mańka and Łakomy 1995, Sierota and Kwaśna 1998). Factors unfavourable to the host tree include an unbalanced nutrient status (Rennerfelt 1946), soil compaction (Ankudinov 1950) associated with shallow root systems and frequent intertree contacts (Kuhlman 1973, Reynolds and Bloomberg 1982) and an absence of ectomycorrhizal fungi (Lange 1993). Ultimately, it is difficult to distinguish between the effect of factors influencing activity of the fungus and that of factors affecting host resistance.

As in the first spruce rotation generally, infection of thinning stumps is a major determinant in the establishment of *Heterobasidion* in a spruce plantation on former arable land (Rishbeth 1950, Schönhar 1971, Werner 1971, Pratt and Greig 1988, Swedjemark and Stenlid 1993, Hanso et al. 1994, Venn and Solheim 1994, Bendz-Hellgren et al.1999). However, it is also possible that root lesions resulting from unfavourable physical soil properties are infection routes for *Heterobasidion* (Dimitri 1969b). It has been shown that the level of resistance of living bark to *Heterobasidion* infection is strongly dependent on site conditions and may be less in very productive stands on fertile arable soils (Redfern 1984, Lindberg and Johansson 1991). Inoculation experiments carried out in Sweden showed that the growth rate of *Heterobasidion* in root wood of spruce planted on arable land is no faster than that in the roots of spruce growing on old forest land (Bendz-Hellgren et al. 1999). The authors suggest that the shallower root system with frequent root contacts and grafts, as well as less competition from soil fungi, may increase disease transfer between trees and thus the overall frequency of Heterobasidion root rot on arable land (Bendz-Hellgren 1997, Bendz-Hellgren et al. 1999).

1.4.4 Air pollution

Increasing levels of pollutant emissions have been shown to predispose a number of tree species, including Norway spruce, to damage by *Heterobasidion* (e.g. Domański 1978, James et al. 1980a, Schmidt 1985, Raddi et al. 1993). Both the susceptibility of the host

tree to infection and the growth rate of the fungus in a tree tend to increase as a consequence of air pollution (James et al. 1980a, 1980b, Raddi et al. 1993). One substantial effect promoting disease development is related to fungi antagonistic to *Heterobasidion*: mycorrhizosphere fungi inhibiting the growth of *Heterobasidion* were totally absent or were few in number in an area strongly polluted with industrial emissions, and were more frequent in an area free of excessive pollution (Kowalski 1989). Also colonization of pine stumps by competitors of *Heterobasidion* (*Trichoderma* spp. and blue stain fungi) was less in trees injured by photochemical air pollutants than in healthy trees (James et al. 1980b). On the other hand, direct effects of air pollution on the pathogen, such as reduced conidial production, germination and growth, have been reported; under field conditions, however, they appear to have little potential effect on the incidence of Heterobasidion root rot (Grzywacz and Wazny 1973, James et al. 1982). According to the model developed by James and Cobb (1989) for the mixed conifer forests in southern California, tree losses from Heterobasidion root rot are 6.5 times greater in stands severely damaged by air pollution than in stands only moderately or slightly damaged. Although a cold climate and relatively nutrient-poor soil are considered to intensify the harmful effects of air pollution on trees (Raitio 1990, Bäck 1994), there have been no observations of severe forest damage caused by pollutant emissions in Finland or in the other Nordic Countries (Lindgren et al. 2000, Ingerslev et al. 2001).

The Earth is now about 0.5° C warmer than it was 100 years ago, and a part of the observed temperature increase has been attributed to increased emissions of greenhouse gases and aerosols (Houghton et al. 1996). The natural variation in the climate is large in Finland. However, according to climate scenarios it is expected that the annual mean temperature may increase by 0.6–3.6° C (relative to 1961–1990) by 2050. It is also estimated the annual precipitation rate will increase (Carter et al. 1995). With increasing temperature, the distribution area of *Heterobasidion* may move farther towards northern Finland, while the damage due to root and butt rot may become more severe in southern Finland.

1.5 Possibilities of silviculture in disease control

"Control measures are, in fact, almost impossible once the fungus is below ground" Rishbeth 1949.

1.5.1 Stand regeneration

1.5.1.1 Mechanical soil preparation

Commercial clear cutting is a silvicultural system widely employed for the regeneration of Norway spruce forest in southern Finland. Following harvest, sites are usually prepared for planting by mechanical soil preparation such as harrowing, scarification and mounding or a combination of these techniques. Whether soil preparation has any effect on the incidence of Heterobasidion root rot in the subsequent spruce generation is not well known. In Denmark, Treschow (1958) did not find any difference in the infection rate between spruce planted 40–60 years earlier on deep-ploughed sites or on sites without soil preparation. Furthermore, no significant increase or decrease in decay incidence

was found in ploughed spruce sites in Germany (Seibt 1964), compared with unploughed sites. On the other hand, Redfern (1984) reported that the vegetative spread of *Heterobasidion* was influenced by the direction of the plough ridges: the spread was more frequent along the ridges than between ridges separated from each other by a furrow. It is not known whether the ploughing had an effect on the total disease incidence. Ploughing as a soil preparation method is, however, no longer used in Finland for aesthetic and other reasons.

Light soil preparation treatments such as harrowing and scarification may enhance the spread of the disease. According to Rönnberg and Vollbrecht (1999) there might be a risk that scarification, by distributing pieces of infected stump roots across the sites, increases the potential for *Heterobasidion* infection of young larch seedlings. On the other hand, soil preparation markedly improves the survival and early growth of spruce seedlings and increases a natural admixture of birch. In the majority of instances, mechanical soil preparation is a prerequisite for successful forest regeneration under Finnish conditions (Raulo and Rikala 1981, Kinnunen 1989, Mälkönen 2001).

1.5.1.2 Stump removal

Stump removal is a direct control measure to remove inoculum from infested sites and avoid carry-over of the disease to the new stand. In Great Britain, stump removal has proved to be an effective and useful method to control Heterobasidion root rot in heavily infected pine stands (Greig 1984, Greig et al. 2001). In Sweden, Stenlid (1987) found that the incidence of *Heterobasidion* infection significantly decreased on sites where stumps of the previous rotation had been removed and the soil was ploughed and sieved free of roots thicker than 5 mm prior to planting. Nevertheless, the frequency of decay caused by fungi other than *Heterobasidion* did not differ significantly between plots with or without stump removal. Results obtained in a tree species experiment in Denmark showed, however, that stump removal had little influence on the incidence of *Heterobasidion* root rot, although for most tree species it had a mitigating effect (Bornebush and Holm 1934, Yde-Andersen 1970). The reason for disease spreading was that some pieces of infected roots were left in the soil, from which the fungus may have spread to the next tree generation (Yde-Andersen 1970). Leaving the lifted stumps on a regeneration site apparently also reduce the effectiveness of stump removal as a control method of Heterobasidion root rot (Kurkela 2000).

Stump removal is an expensive control method, and because earlier there was no use for the lifted stumps, stump removal was not introduced into practical forestry in Finland (Kuitto 1984). During the last few years, however, there has been renewed interest in stump removal; the lifting process has been developed, and stumps are now utilized as a source of energy. As a result of these developments, and because the new technique enables site preparation without extra costs, the removal of stumps is considered to be economically justified even on healthy sites. Although even complete stump removal does not eliminate the source of infection entirely from the infested site, it reduces carry-over of the disease to the new stand. Thus, stump removal may become a practicable control procedure on infested spruce and pine sites where a change of tree species is not possible.

1.5.1.3 Prescribed burning

In southern Finland, Kallio (1965) studied the effect of prescribed burning on the aerial infection of Norway spruce stumps and found that burning strongly reduced stump infections on a clear cutting area. The control mechanisms provided by prescribed burning remained, however, largely unclear. Penttilä and Kotiranta (1996) observed that burning totally destroyed *Heterobasidion* basidiocarps and thus, at least in the short-term, burning reduces the incidence of local inoculum. It has also been shown that soil sampled from a burned area totally inhibits germination of *Heterobasidion* conidia (Kelley and Curl 1972). Furthermore, there is some evidence that burning increases soil microbial populations antagonistic to *Heterobasidion* (Froelich et al. 1978).

On the other hand, the severity of Heterobasidion root rot is related to soil pH and is more serious on alkaline than on acid soils (Rishbeth 1951b). Hence the temporarily alkaline conditions caused by burning (Viro 1969) may favour disease development. Factors such as root vigour and water-supply presumably affect the resistance of roots of young conifers to *Heterobasidion* (Rishbeth 1951b, Lindberg and Johansson 1992). On burned sites, where surface organic matter is destroyed and the roots easily suffer from drought, the young trees may be more susceptible to infection (Rishbeth 1949, 1951b). Rishbeth (1951a) also showed that basidiospores are able to germinate on freshly charred surfaces of pine trunks. The fungus then colonized the underlying unaffected tissues and the chance of establishment was possibly increased by the destruction of fungal competitors in the pine bark. Fire-damaged pine roots are the principal entry point for decay-fungi including *Heterobasidion* in pine stands (Littke and Gara 1986, Otrosina et al. 1995). These results indicate that the use of burning as a control measure against *Heterobasidion* may actually increase the incidence of the disease, depending on the site conditions, fungal flora, intensity of the fire, and other more or less unknown factors. More information is needed about the survival of *Heterobasidion* in spruce stumps after burning, as well as about the infection of the new spruce generation established on a burned site, in order to assess the effectiveness of prescribed burning as a control method against Heterobasidion root rot.

1.5.1.4 Tree species selection

When regenerating infested sites, the best method to avoid losses in the following tree generation is to cultivate a tree species that is resistant to the *Heterobasidion* species occurring on the site. On old spruce sites in southern Finland, where *H. parviporum* is the most frequent decay-causing agent (Piri et al. 1990, Korhonen and Piri 1994), regeneration with broad-leaved trees and Scots pine is recommended (Korhonen 1978a). Scots pine is not fully resistant to *H. parviporum* and some pines planted near decayed spruce stumps may become infected and die (Korhonen 1978a, Jokinen and Tamminen 1979). With increasing stand age, however, the resistance of Scots pine to *H. parviporum* increases and the spread of the disease in a pine stand is checked. On sites with a pine history *H. annosum s.str.* may predominate, also in Norway spruce stands (Korhonen et al. 1992, Thomsen 1994). In spruce stands infected by *H. annosum s.str.*, admixture of Scots pine and birch (*Betula pendula* Roth) are also at risk of infection. As a pure stand,

on the other hand, birch has proved to be very resistant to *H. annosum s.str.* under Finnish conditions. Apparently, *H. annosum s.str.* needs pine or spruce as a food base to be able to infect living birch. Aspen (*Populus tremula* L.) growing in a diseased conifer stand may become infected by *H. annosum s.str.*, but generally not by *H. parviporum* (Korhonen and Piri 1994, Kauhanen 2002).

Norway spruce is valuable as saw timber and pulpwood in Finland and, instead of changing the tree species, it may be economically more profitable to continue growing spruce even on relatively highly infested sites in spite of the fact that losses caused by root and butt rot cannot be avoided in the future spruce rotation. Norway spruce may also be the preferred tree species because most spruce sites are too fertile for the production of high-quality pine timber, and both birch and pine regenerations are often seriously endangered by browsing damage by elk (*Alces alces*) and other cervids (Heikkilä and Raulo 1987, Lääperi and Löyttyniemi 1988, Jalkanen 2001). The degree of infection by *Heterobasidion* of different tree species, including Norway spruce, that are regenerated on sites where the previous tree generation had been Norway spruce attacked by *Heterobasidion* is the main subject of this thesis.

Use of regeneration stock of a provenance adapted to local environmental conditions may increase the resistance of spruce to Heterobasidion root rot (McDonald 1990, Lindberg and Johansson 1992). In the future, the use of selected resistant individuals may be the most effective method for controlling *Heterobasidion* infections in Norway spruce forests (e.g. von Weissenberg 1980, Dimitri 1980, Swedjemark et al. 2001, Elfstrand et al. 2001).

Several Nordic studies concerning the effect of mixed tree species on butt rot incidence in Norway spruce support the idea that an admixture of Scots pine or birch in mature spruce stands reduces the spread of the disease and protects a proportion of the spruce from infection (Rennerfelt 1946, Enerstvedt and Venn 1979, Huse 1983, Piri et al. 1990, Lindén and Vollbrecht 2002). Due to the presence of resistant tree species the total production of sound wood is also greater in mixed stands than in pure spruce stands. The fact that the number of *Heterobasidion* inocula per unit area in the form of decayed spruce stumps is less in mixed than pure spruce stands may be of some importance for the following tree generation (Piri et al. 1990). So far, no information is available about the effects of other tree species on the root rot frequency of Norway spruce in the early stages of a rotation. The influence of naturally regenerated broadleaf trees on the early infection of advance-growth and planted spruce is treated in papers **II** and **III**.

1.5.1.5 Regeneration method

A few *Heterobasidion* studies deal with the relationship between regeneration method and disease incidence on Norway spruce. These studies are based on inventories made in mature spruce stands and show divergent results. According to Weissen (1981), naturally regenerated spruce is less often and less severely affected by Heterobasidion root rot than planted spruce. Based on material collected in Switzerland, Graber (1996) reported that, although the total butt rot damage was less in naturally regenerated spruce stands than in planted stands, butt rot caused by *Heterobasidion* was more common in naturally regenerated spruce stands. According to statistics collected by Falck (1930) in the Harz

Mountains, the volume of butt rot was lower but the proportion of infected spruce higher in naturally regenerated than in planted spruce stands. In Norway, no difference in total butt rot frequency or in the frequency of Heterobasidion butt rot was found between naturally established and planted spruce stands (Stamnes et al. 2000).

Advance-growth spruce developed under a spruce overstorey before the regeneration cutting form a major part of the plant stock (60–80 %) in naturally regenerated spruce stands in southern Finland (Hänninen et al. 1972, Räsänen et al. 1985). In Russia, Semenkova (1971) has shown that advance-growth spruce can be seriously infected by *Heterobasidion*. Other studies also support the view that suppressed spruce growing in the understorey are more susceptible to decay fungi, including *Heterobasidion*, than free-standing, dominant spruce (Kangas 1952, Schönhar 1995, Gramss 1992).

In planted spruce stands the risk of root rot infection is supposedly associated with root damage caused by lifting in the nursery, as well as with the damage caused by twisting or bending the roots during planting (Ouelette et al. 1971, Graber 1996). The decay risk associated with planting can be minimized by planting high-quality nursery stock adapted to the local environmental conditions, by careful working in the nursery and field, by using container seedlings instead of bare root seedlings, and by using correct planting techniques (Singh and Richardson 1973, Singh 1975, Thies and Russell 1984). Dense regenerations favour the spread of the disease as a result of competition stress and more frequent root contacts with adjacent trees. According to Külla and Lõhmus (1999), the formation of root grafts, which are a pathway for secondary infection, can be avoided by planting fewer than 2 500 plants per ha. The distance between trees should not be less than 1.5–2 m. In dense regenerations the number of thinning stumps will also be great and, consequently, the risk of stump infection will also increase (Due 1960, Redfern 1984, Venn and Solheim 1994, Johansson and Pettersson 1996). On the other hand, greater losses to *Heterobasidion* can be tolerated at higher planting densities than at lower densities (Greig 1984). Current management practice in Finland favours a spacing of 2.2 m, i.e. about 2 000 plants per ha (Hyvän metsänhoidon suositukset 2001), which appears to be low enough to hamper the vegetative spread of *Heterobasidion* in the early stages of stand development.

The results obtained by Möykkynen and Miina (2002) emphasize the importance of disease transfer from the previous to the next spruce generation. The presence of butt rot at the first thinning had a larger impact on the soil expectation values than the butt rot, which developed from stumps infected by airborne spores during the first thinning. Consequently, silvicultural measures that decrease the transfer of *Heterobasidion* to the next rotation of spruce are fully justified. Papers **II** and **III** of the thesis treat the effect of regeneration method on the transfer of Heterobasidion root rot from old spruce rotations to the subsequent spruce regeneration.

1.5.2 Logging operations and disease control

The extent of damage caused by *Heterobasidion* in Norway spruce stands is closely correlated with the frequency and intensity of thinning operations (Molin 1957, Venn and Solheim 1994). The risk of infection of freshly-cut stumps and wounds is high during the period when spores of *Heterobasidion* are present, i.e. from April to November in

southern Finland (Kallio 1970). The most effective means to eliminate the risk of stump and wound infection is to schedule the logging operations in the winter time when the temperature is below -5° C (Kallio 1970, Solheim 1994, Brandtberg et al. 1996, Möykkynen et al. 2000). Moreover, snow and frozen soil protect roots against logging injuries; the injuries are fewer and smaller than those inflicted in summer operations and, consequently, the decay starting from injuries advances less rapidly (Isomäki and Kallio 1974).

Rishbeth's elucidation of the importance of stumps as an infection route of *Heterobasidion* resulted in the development of control measures that reduce spore infection in harvested stands. Several biological and chemical control agents have been experimentally used against stump infection in Norway spruce stands, and a few of them have found practical use. In Finland, spore suspensions of *Phlebia gigantea* (Fr.) Donk (commercial name "Rotstop") or urea are recommended for use in summer thinnings of spruce and pine stands, as well as in final cuttings if the tree species is not changed. Urea, when applied as a 30 % solution immediately after cutting, reduces the infection rate of spruce stumps by approximately 86 % (Johansson and Brandtberg 1994). Urea per se is not toxic to *Heterobasidion*; the protecting effect is based on the high pH value of above 7 caused by the ammonia formed in the hydrolysis of urea (Johansson et al. 2002). Comparable or even better protection than given by urea has been obtained with the competing fungus *P. gigantea*, extensively used in practical forestry in Finland (Korhonen et al. 1994, Korhonen and Lipponen 1995). Its advantage over chemicals is that, apart from blocking the entry of *Heterobasidion* through the stump surface, *P. gigantea* grows down into the stump and thus, to some extent at least, also blocks the spread of *Heterobasidion* in the stump and roots (Korhonen and Lipponen 1995). Although the number of harvesting machines equipped with stump treatment devices, as well as the annually treated area, continues to increase, stump treatment is not yet a standard practice in Finnish forests. According to Möykkynen et al. (2000), stump treatment is profitable in the thinning of spruce (one thinning during a rotation) if the stump infection rate is above 10 %.

The effect of the number and intensity of thinning operations on disease incidence has been investigated in several studies. In general, few and light thinnings performed as late as possible during the rotation are recommended to control the incidence of Heterobasidion root rot (e.g. Henriksen and Jørgensen 1953, Venn and Solheim 1994, Vollbrecht and Agestam 1995, Möykkynen et al. 2000, Möykkynen and Miina 2002). Based on a simulation model and nonlinear stochastic optimization, Möykkynen et al. (2000) showed that, in Norway spruce stands exposed to infection by *Heterobasidion*, one thinning and a 6-year shorter rotation than normal resulted in the highest soil expectation value at a 3 % interest rate. Management without commercial thinnings was recommended by Vollbrecht et al. (1994) for slowing down disease development in spruce stands. An unthinned stand escapes primary spore infection, but the rate of secondary infection may also be reduced due to the fact that *Heterobasidion* spreads more slowly in the roots of living trees than in dead stump roots (Bendz-Hellgren et al. 1999). On the other hand, based on results of long-term studies in Germany, Schönhar (1997) recommends thinnings to prevent strong root and crown competition that increases susceptibility of Norway spruce to *Heterobasidion*. Külla and Lõhmus (1999) suggest

that the thinning of a Norway spruce stand should be completed before the formation of root grafts (i.e. before the stand age of 15–20 years) in order to reduce secondary spread of *Heterobasidion.* After that, no thinnings was recommended until the final harvesting.

The probability of stump infection decreases with decreasing stump diameter (Paludan 1966) and the risk of spore infection in stumps created in precommercial thinning seems to be small (Benz-Hellgren and Stenlid 1998). A Norwegian study showed, however, that under favourable conditions *Heterobasidion* may infect a high proportion (20.5 %) of precommercially thinned spruce stumps in the diameter class 6–7 cm (Solheim and Bjøre 1998). The spread of the fungus to adjacent trees is, anyway, not common in young spruce stands (Vollbrecht et al. 1995a, Külla and Lõhmus 1999) and, so far, treatment of precommercial thinning stumps has not been considered necessary in Finland or the other Nordic Countries.

The last opportunity to reduce losses in mature Norway spruce stands seriously affected by *Heterobasidion* is to shorten the rotation length (e.g. Graber 1996, Bendz-Hellgren et al. 1999). In practice, however, it may not be easy to assess the point when the production of sound timber is less than the decay rate. Simulation models like that constructed by Möykkynen et al. (2000; cited above) could be useful tools in making decisions about the application of control methods during stand development.

1.5.3 Nutrient management

Some Russian investigations have shown that combined NPK fertilization can increase the resistance of Scots pine to Heterobasidion root rot (e.g. Pasternak 1979, Fedorov et al. 1979, Raptunovich 1989). Novikov (1976) reported the same positive effect on fertilized Norway spruce. However, the influence of fertilizer treatments on forest health is complex and no generalizations can be made about whether the application of compound fertilizers increases or decreases the incidence of root and butt rot in conifer forests.

In Europe, a new type of forest fertilizer treatment, so-called vitality or reconditioning fertilization, designed to prevent or alleviate forest decline caused by air pollutants, was introduced in the late 1980s and at the beginning of 1990s (Huettl 1988, Huettl et al. 1990). The purpose of vitality fertilization is to improve the vitality and resistance of forest trees suffering from nutrient deficiencies and imbalances, to compensate for nutrients removed from the forest ecosystem by intensive biomass harvesting, and to counteract natural and anthropogenic soil acidification. Research on this topic has recently also been carried out in the Nordic countries (Andersson et al. 1998, Mälkönen 1998, Mälkönen et al. 2000). The fertilizers used in these studies have a low nitrogen content or are nitrogen-free, and may contain trace elements and macronutrients. They often consist of a mixture of fast- and slow-release compounds. Long-term fertilization effects as well as minimization of leaching losses, are achieved using slow-release compounds.

Only little information is available about the influence of different reconditioning fertilizers on the development of Heterobasidion root rot in Norway spruce stands. An inoculation experiment carried out in a compensatory fertilized Scots pine stand in south-eastern Finland showed, however, that application of N-free compound fertilizer may retard the development of Heterobasidion root rot in an infected pine stand. Furthermore, a slow-release compound fertilizer without supplementary limestone may also increase

the resistance of Scots pine to *Heterobasidion* infection (Piri 2000). The effect of a nitrogen-free vitality fertilizer on the growth rate of *Heterobasidion* in spruce roots has also been studied in Sweden. In this study, the mycelial growth was slightly faster in the roots of fertilized trees than in the roots of control trees (Wahlström and Barklund 1994). Study **VI** of this thesis deals with the growth rate of *H. parviporum* in the roots of Norway spruce treated with different vitality fertilizers.

2 Objectives of the thesis

The aim of the first paper was to determine the longevity of *Heterobasidion* mycelium in Norway spruce stumps after final felling and, further, the importance of old stumps as sources of infection in the subsequent tree generation consisting of Norway spruce, Scots pine, lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Wats.), Siberian larch (*Larix sibirica* Ledeb.) or silver birch (*B. pendula*). The frequency of the disease in the two tree generations was determined, and the transfer of the disease from old spruce stumps to the next tree generation was investigated by identifying genotypes of *Heterobasidion* occurring in the stumps of the previous spruce generation and in the diseased trees of the present generation.

The subject of papers **II** and **III** was the early development of Heterobasidion root rot in young, unthinned advance-growth and planted Norway spruce regeneration on sites infected by *Heterobasidion*. In order to clarify the effect of regeneration method on the transfer of Heterobasidion root rot from the previous spruce rotation and the role of admixed tree species in disease spread, the incidence of *Heterobasidion* infections as well as the origins and spatial distribution of the *Heterobasidion* genets were determined in consecutive spruce rotations.

The last study (paper **IV**) was carried out to elucidate how vitality fertilization affects the development of Heterobasidion root and butt rot in Norway spruce forests where the disease is a serious problem. The growth rate of *H. parviporum* in the roots of Norway spruce treated with four different vitality fertilizers was determined with the aid of inoculation experiments.

The main topics of the thesis are the transfer of *Heterobasidion* to the subsequent tree rotation and the effect of vitality fertilization on disease development, which are important aspects when devising silvicultural controls for this disease. Also, the routes and the rate of secondary spread of *Heterobasidion* in the course of a Norway spruce rotation are discussed.

3 Materials and methods

3.1 Sample plots (I, II, III)

A total of 90 sample plots were established in 32 different stands on forest soil in southern Finland (Lapinjärvi, Loppi, Ruotsinkylä, Sipoo and Solböle; Fig. 1). The sites were of the *Myrtillus* and *Oxalis-Myrtillus* forest site types, which are typical spruce sites in southern Finland (Cajander 1949). The previous rotation on each site had been Norway spruce infected by *Heterobasidion*. In study **I**, the infested sites were planted after clear-cutting with Scots pine, lodgepole pine, Siberian larch or silver birch or regenerated naturally with Norway spruce. The age of the planted stands varied from 8 to 44 years and the age of naturally regenerated spruce stands from 45 to 53 years. In study **II**, the
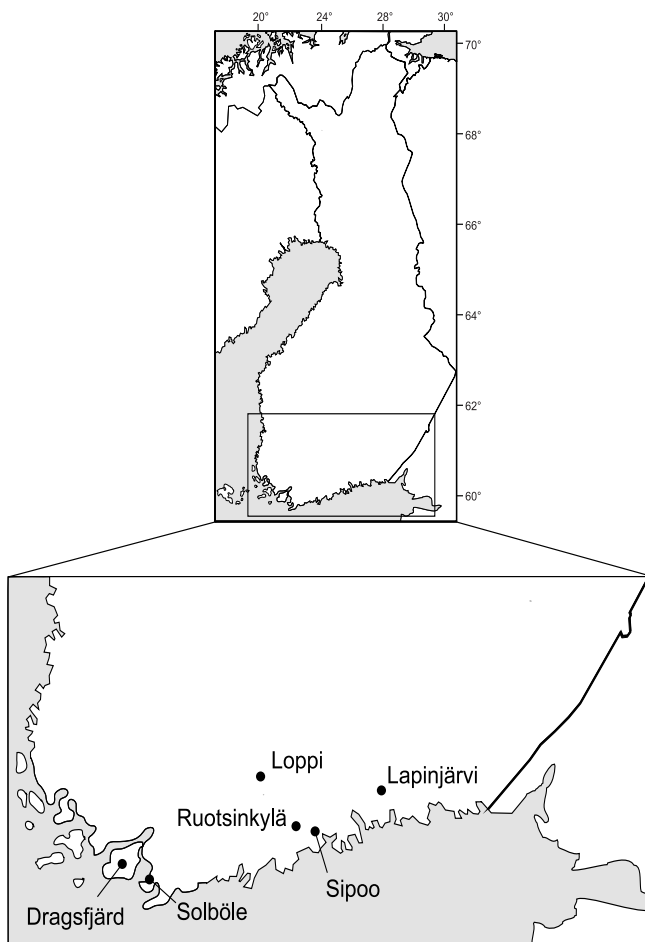
Fig.1. Location of the experimental areas.

regeneration consists of advanced-growth spruce developed under a spruce overstorey. In study **III**, the sites were planted after clear-cutting with Norway spruce. The mean age of the advance-growth spruce in study **II** varied from 14 to 44 years and the age of the planted spruce in study **III** from 2 to 23 years.

Some regeneration stands were cleaned (**I, III**) and two were thinned (**I**) before the investigation. No admixed tree species were left on the cleaned plots. On the uncleaned plots, the proportion of admixed tree species (naturally regenerated pine, birch (*B. pendula* and *B. pubescens* Ehrh.), rowan (*Sorbus aucuparia* L.), white alder (*Alnus incana* (L.) Moench) and European aspen (*Populus tremula*) varied from 5 to 80 percent.

The size of the sample plots in study **I** varied from 0.04 to 0.3 ha depending on the area of the stand compartment and the distribution of old rotation stumps infected by *Heterobasidion*. In studies **II** and **III**, circular plots were established in the disease centres. Individual disease centres (i.e. groups of infected trees) contained one to eleven colonized trees or stumps (on average three trees) of the previous rotation encompassing an area averaging 20 m in diameter. The control plots were established in the healthy part of the stand, where no signs of *Heterobasidion* infection had been observed in the earlier tree generation.

3.2 Measurements and sampling (I, II, III)

The total growing stock, including the stumps of the previous rotation, was mapped on all the regeneration plots. Seedlings shorter than 30 cm were ignored. Height, diameter at breast height or at stem base and age were recorded for the regeneration tree species, and height for the naturally regenerated admixed tree species. Species and diameter of all the stumps of the present and previous rotation were also recorded.

In the middle-aged, naturally regenerated spruce stands (**I**) wood samples were taken with an increment borer from the butt and 3–4 main roots of all standing trees and thinning stumps. In the planted larch, pine and birch stands (**I**) the core samples were normally taken only from trees showing external symptoms of infection (foliage chlorosis, reduced growth, resin flow, presence of basidiocarps) and from decayed stumps. Additional core samples were taken from larches growing close to infected stumps or trees in order to assure that as many infected trees as possible were detected.

The root systems of all the advance-growth spruce (**II**) and planted spruce younger than 20 years of age (**III**) were dug out and examined for infection. In the older stands of planted spruce (**III**), the samples were taken from butt and main roots with an increment borer. Boring is not as reliable method for detecting infected trees by as examination of the whole root system. It is therefore possible that older trees with very incipient infection have been classified as non-infected trees. In planted spruce, however, decay seems to advance rather rapidly and investigation of the root systems of young planted spruces showed that, except for a very few trees, the fungus had reached at least one of the main roots in all the infected trees. Healthy appearing wood cores were also cultivated on malt agar in order to check for incipient infections.

The samples from old conifer stumps of the previous rotation (**I, II, III**) and from overstorey trees (**II**) were taken with an increment borer or, in cases where the stump had advanced decay, with an axe and a saw. The presence or absence of basidiocarps on

each stump and tree sampled was recorded. The decay areas on the stump tops were described and used as an indication that the tree had been infected and colonized by *Heterobasidion* prior to being felled.

Wood samples were cultured on malt agar (2 % ME). Mycelia of *Heterobasidion* and *Armillaria* growing out of the wood samples were isolated. In addition to *Heterobasidion* and *Armillaria*, some other, frequently occurring basidiomycetes (*Resinicium bicolor* (Alb. and Schw. ex Fr.) Parm., *Sistotrema brinkmannii* (Bres.) J. Erikss., *Fomitopsis pinicola* (Sw. ex Fr.) Karst., *Phlebia gigantea* and *Stereum sanguinolentum*) were also isolated from old spruce stumps (**I**). The root systems of advance-growth spruce (**II**) and young planted spruce (**III**) were washed, cut into 5-cm-long sections and incubated in plastic bags for one to four weeks. Careful washing of the root samples with a brush under running water before incubation efficiently prevented the growth of suppressive moulds, such as *Trichoderma* and *Penicillium* species, on the samples. The root sections were microscopically examined for the presence of *Heterobasidion* and *Armillaria*, which were then isolated. No other basidiomycetes were found in the roots of young spruces.

A total of 5 625 regeneration trees and 1 119 old spruce stumps or standing trees of the previous tree generation were investigated.

3.3 Fertilization treatments (IV)

The inoculation experiment was carried out in a 53-year-old, naturally regenerated Norway spruce stand in Dragsfjärd, on the south-western coast of Finland (Fig. 1). The experiment consisted of five treatments: 1) unfertilized control, 2) compound fertilizer containing P, K, Ca, Mg, S, Cu, Zn and B, 3) compound fertilizer with nitrogen, 4) compound fertilizer with nitrogen and limestone, and 5) a stand-specific fertilizer based on needle and soil analysis containing N, P, K and Cu. The randomised plots (30 × 30 m in size) and a 5-m-wide buffer strip surrounding each plot were treated after thinning in spring 1991. There were four replications of each treatment.

3.4 Inoculation of trees (IV)

Three growing seasons after fertilization two dominant or codominant, healthy-looking trees on the buffer strip of each plot were subjected to artificial inoculation with *H. parviporum*. Inoculum cores were prepared by incubating sterile cores of spruce wood (c. 5 mm in diameter and 4 cm long) on a 1-month-old malt agar culture of *Heterobasidion* for 4 weeks. Four different heterokaryotic isolates of *H. parviporum* were used. Four roots of every tree were excavated and each of them was inoculated with a different isolate at about 30 cm from the root collar. The mean diameter of the roots at the inoculation point was 8.5 cm (range 3.0–19.0 cm). The inoculation was made by inserting a core colonized with *H. parviporum* aseptically into a radial hole made with an increment borer. The hole was sealed with grafting wax and the soil replaced. Root cores were taken to the laboratory and checked for possible pre-existing root infection. In all, 32 roots of eight trees per treatment were inoculated.

3.5 Harvesting (IV)

Inoculated roots were harvested 12 months after inoculation. In the laboratory, the roots were cut at 10-cm intervals in both directions outward from the point of inoculation. The root sections were washed, incubated in plastic bags for about one week and examined for conidiophores of *Heterobasidion*. Isolations were made from each wood section infected by *Heterobasidion*. Thirty-seven roots were excluded from the study material because of contamination or natural root infection, or abnormal root structure. Thus, the final number of roots per treatment varied from 20 to 28. To determine the effect of fertilization on tree growth, increment cores were taken at breast height five years after fertilization.

3.6 Use of somatic incompatibility tests in the studies

In order to obtain detailed information about the transfer of *Heterobasidion* from the previous spruce stand to the next tree generation, the frequency, spatial distribution and size of *Heterobasidion* genets on the study plots were identified with the aid of somatic incompatibility tests (**I**, **II**, **III**). Infection was considered to originate from the previous stand in cases where the same genet was isolated both from old spruce stumps or overstorey trees and from the subsequent tree stand. Somatic compatibility tests were also performed in the fertilization experiment (**IV**) to confirm that the genotype of *Heterobasidion* isolated from an inoculated root was the original one. In the test, two isolates were placed 1 cm apart on malt extract agar (MEA), incubated at room temperature for 3–5 weeks and the occurrence or absence of a demarcation line was recorded (Stenlid 1985).

3.7 Identification of *Heterobasidion* and *Armillaria* species with mating test

The species of *Heterobasidion* and *Armillaria* were determined with the aid of the Buller phenomenon (Raper 1966, Korhonen 1978a, 1978b). Heterokaryotic isolates of *Hetero-basidion* were paired with 2–3 homokaryotic tester strains of both *H. parviporum* and *H. annosum s.str.* on 2 % malt extract agar. The pairings were examined after about 3-weeks incubation at room temperature. In a compatible pairing the homokaryotic tester strain turns to heterokaryotic; this was indicated by the appearance of clamp connections and by a change in the mycelial morphology of the tester.

Diploid isolates of *Armillaria* were paired with three haploid tester strains (monospore isolates) from each of the species *A. borealis* (Marxmüller & Korhonen), *A. cepistipes* Velenovský and *A. ostoyae* (Romagnesi) Henrik, and the mating reactions were recorded after 3–4 weeks incubation time. A change in the external appearance of the tester from whitish and fluffy to brown and flat indicates diploidization of the tester and a compatible pairing (Korhonen 1978b).

A diagram of the experimental procedures is presented in Figure 2.

Experimental plot

The total growing stock including trees of the present tree generation, and stumps of the previous rotation were mapped and sampled.

Wood samples

The mycelium of *Heterobasidion* growing out of wood samples was isolated.

Pairing of pure cultures

The genets of *Heterobasidion* on the experimental plot were identified on the basis of demarcation line formation (somatic incompatibility). Left: self pairing; right: pairing of two unrelated heterokaryons.

Heterobasidion species of each genet was determined.

Map of *Heterobasidion* genets

A map showing the spatial distribution of *Heterobasidion* genets on the experimental plot was prepared. Trees and stumps within the grey area are infected by the same *Heterobasidion* genet.

Fig.2. A diagram of the experimental procedures carried out on a study plot established in a planted, 22-year-old Norway spruce stand.

3.8 Statistical analyses

The relationships between disease incidence and independent variables depicting stand characteristics were investigated using Pearsson's product-moment correlation analysis. Variables describing disease incidence in this analysis were percent trees or stumps infected by *Heterobasidion* or *Armillaria*, and percent stumps with *Heterobasidion* basidiocarps. Variables describing stands characteristics were age, height and diameter of the trees, age and diameter of stumps, proportion of admixed trees and stand density. Correlation analysis was also used to determine the association between the disease incidence of the previous and present tree rotations (**II** and **III**), between the diameter of the decay at the stump surface and the height of the decay column in the stem (**III**), and between the growth rate of *Heterobasidion* and diameter of the tree (**IV**). In correlation analyses performed on the material of planted stands, the mean value of plots established in the same even-age plantation was considered the experimental unit (**III**). In advance-growth stands, in contrast, the study material was pooled before making calculations because of heterogeneity of tree age and size within and between plots in the same stand (**II**). Multiple regressions based on combinations of independent variables were used to explain some of the variation of the dependent variable (percent infected advance-growth spruces) (**II**).

Infection rates between planted and naturally regenerated spruces (**III**), as well as the growth rate of *Heterobasidion* from the inoculation point towards the trunk and towards the root tip (**IV**), were compared using the paired *t* test. Further, the *t* test was used to analyse the difference in the diameter distribution of stumps colonized by *Resinicium bicolor* and *Heterobasidion* (**I**). The average number of spruce infected per decay stump in different age classes was compared using non-parametric tests (**III**). The effects of different treatments on the growth rate of *Heterobasidion* (using mean values of fungal strains) were tested by analysis of variance (ANOVA) (**IV**). ANOVA was also used to compare the volume growth of trees among treatments and the fungal growth rate among different *Heterobasidion* strains (**IV**). Logarithmic or square-root transformation was applied before the analyses to meet the prerequisites of distribution normality. The significance level in all tests was p ≤ 0.05. The analyses were performed using the BMDP statistical package (BMDP, Inc. 1990) (**I**, **II**, **IV**) or SPSS for Windows 10.0 (SPSS, Inc. 1999) (**III**).

Detailed information about materials and methods can be found in original publications **I**-**IV**.

4 Results and discussion

4.1 Survival of *Heterobasidion* in spruce stumps after final felling

The results (**I, II, III**) showed that in most stumps of timber-size spruces, which had been attacked by Heterobasidion root rot before final felling, the fungus was able to remain viable for at least 20 years after harvest. Laine (1976) recorded the fungus in a 35-year-old spruce stump, but *Heterobasidion* can survive for a considerably longer time in large spruce stumps (diameter over 40 cm). In the present work, active mycelium and basidiocarps of *Heterobasidion* were isolated from Norway spruce stumps that had been felled 46 years earlier. No older stumps were investigated. The mycelium isolated from the oldest stumps appeared vigorous, which suggests that, in southern Finland, the fungus can persist in large spruce stumps even for 50 years or more. In Great Britain, viable *Heterobasidion* has been found in a 68-year-old larch stump (Greig and Pratt 1976), which is the maximum longevity of *Heterobasidion* in a conifer stump recorded in Europe. In the present studies, all the cuttings had been carried out in the winter and infection by spores through the stump surface after final cutting is unlikely. Also, the total colonization of stumps by *Heterobasidion* and the fact that several old stumps belonged to the same genet, indicate that the stumps were already infected at the time of clear-felling. Infection of several stumps by spores of the same genotype is extremely unlikely, although it is possible through conidial infection. Some insects breeding in stumps, such as *Hylobius abietis*, have been found to transfer conidiospores of *Heterobasidion* for short distances (Nuorteva and Laine 1968, Nuorteva and Laine 1972, Kadlec et al. 1992). However, the inoculum transferred by an insect is very small and it is questionable whether the mycelium is able to compete with other fungi and colonize the stump. The proportion of asexual conidiospores in the air spora seems to be low in Finland (Kallio 1970,1971, Möykkynen 1997). However, the possibility that a freshly cut stump would be infected by heterokaryotic conidiospores released by wind or rain from an adjacent colonized spruce stump cannot be wholly excluded. No signs of such conidial infection (based on size and location of the fungal colonies) were found in our studies.

Basidiocarps of *Heterobasidion* were frequent on older stumps, in which the fungus had grown out from the central parts of the stump wood and penetrated the bark. Active basidiocarps were found in 7.6 % of the 9- to 15-year-old stumps and 21.7 % of the 26- to 46-year-old stumps colonized by *Heterobasidion* (**I**). Because the frequency of active basidiocarps in stumps appears to be high at the time of first thinning, and because the majority of the spores are deposited in the immediate surroundings within the stand (Kallio 1970, Stenlid 1994a, Möykkynen et al. 1997), the old stumps may considerably increase the risk of spore infection in the subsequent rotation, especially if no stump treatment is carried out in summer cuttings.

4.2 Disease transfer into the subsequent spruce regeneration

The present studies showed that root contacts are an important means of *Heterobasidion* transfer from old stumps to the surrounding spruce regeneration. As juvenile stands become older, root systems enlarge and more contacts develop between colonized stump roots and the roots of the surrounding regeneration. On the other hand, the risk of disease transfer from old stumps through root contacts decreases with time due to the decomposition of stump roots. In unthinned regeneration stands (mean height over 2 meters), the fungus had spread vegetatively from one decayed overstorey tree or old stump on the average into 3.8 advance growth spruce trees and 1.1 planted spruce (**II**, **III**; data not shown). The distance between colonized stumps and regeneration trees is an important factor determining regeneration tree infections. In dense advance-growth regeneration (11 800 trees/ha), where the average distance between trees is only ca. 0.9 m, the probability of root contacts and disease transfer is considerably higher than in sparsely planted stands with a distance of ca. 2.4 m (1 800 trees/ha).

Investigation of the genotypes of *Heterobasidion* indicated that the regeneration trees were mostly infected by direct growth of the fungus from the old stumps. In contrast, this kind of disease transfer between regeneration spruce was uncommon or, at least in the youngest stands investigated, it did not occur at all (**II**, **III**). In thinned, middle-aged spruce stands the average number of trees infected from one old stump was 3.0 (**I**). In those 45- to 55-year-old stands where most of the old stumps were already ineffective, the *Heterobasidion* genets mainly expanded from tree to tree in the current rotation.

On the whole, the rate of disease transfer from old stumps into the regeneration varied widely from plot to plot. On seven plots in the planted regeneration (25 % of all study plots), no infections were found in planted spruce even though they were growing close to an old spruce stump colonized by *Heterobasidion*. This would suggest that the coexistence of *Armillaria* in the same stump diminishes the vegetative spread of *Heterobasidion* to the surrounding regeneration. Of the stumps colonized by *Hetero-basidion* alone, 62 % showed secondary spread into adjacent trees, whereas from stumps colonized by both *Heterobasidion* and *Armillaria* the percentage was clearly lower, 25 % (**III**). No detailed observations on the decay pattern of *Armillaria* in stump wood were made in this study, but obviously *Armillaria* colonizes the outer root tissues and thereby restricts the contacts of *Heterobasidion* with adjacent root systems (Greig 1962, Morrison and Johnson 1978). Also, *Resinicium bicolor* was common in the old spruce stumps (**I**/Fig.1). The diameter distribution of stumps colonized by *R. bicolor* differed statistically significantly (p < 0.01) from that of stumps colonized by *Heterobasidion*. In contrast to *Heterobasidion*, *R. bicolor* typically occurred in small stumps and its frequency decreased with increasing stump diameter. Consequently, the effect of *R. bicolor* on the secondary spread of *Heterobasidion* may not be as significant as that of *Armillaria*.

The effect of soil properties on disease transfer has been investigated by Redfern (1984, 1998), who showed that both survival of *H. annosum* in inoculated Sitka spruce (*Picea sitchensis* (Bong.) Carr.) stumps and the infection of surrounding trees was greater on mineral soils than on peat soils. According to Redfern (1984), soil factors which

influence the frequency of root contacts may have an important effect on spread of the disease. In the present studies, the investigated stands were located on rather similar (podzolic) till soils, and no further attempts were made to analyse the effect of different soil factors on spread of the disease.

4.3 Secondary versus primary infection in relation to the regeneration method

Of all the *Heterobasidion* infections, the proportion of secondary infections from the previous rotation through root contacts was 71 % in planted spruce regenerations (**III**) and 53 % in advance-growth regenerations (**II**). The structure of *Heterobasidion* genets (i.e. the ratio of secondary infection to primary infection) has, so far as I know, not been studied earlier in young, unthinned, naturally regenerated spruce stands. In a Swedish study (Stenlid 1987), the rate of secondary infection from previous rotations in planted, unthinned spruce stands was of the same order (52–79 %) as that in the planted stands of the present study (**III**). Undoubtedly, all the infection sources of the previous rotation cannot be found during sampling and therefore the figures for vegetative disease transfer from old stumps presented in these studies are probably somewhat lower than the actual values. The likelihood of underestimating the proportion of secondary spread from old stumps increases with time passed since final felling.

The reason for the higher proportion of primary infection in advance-growth regeneration compared with that in planted stands remained partly unclear. The same methods were used in both studies, and therefore the results obtained in advance-growth and planted stands should be comparable (**II, III**). The inoculum potential of spores is small compared with that of a vigorous mycelium, and therefore there must be some other factors that predispose roots to spore infection. In advance-growth regeneration this could be the superficial root system that often suffers from drought (Sirén 1951). Furthermore, understorey trees are often stressed as a result of reduced light and nutrients, which may lower their ability to resist primary infection. Some earlier studies support the result that suppressed trees are more susceptible to primary infection by *Heterobasidion* than free-standing trees (Gibbs 1967, Schönhar 1995).

The total frequency of Heterobasidion root rot was generally higher in advance regeneration than in planted stands of the same tree size (Fig. 3). In both types of regeneration, the decay frequency correlated positively with the tree size and age of the regeneration, as well as with the disease incidence of the previous rotation.

Several earlier studies have demonstrated that the incidence of Heterobasidion root and butt rot tends to increase in successive spruce rotations (e.g. Jørgensen et al. 1939, Holmsgaard et al. 1961, Schönhar 1973, Yde-Andersen 1978). It has been also shown that the old infected stumps are important infection sources in the next spruce rotation (Stenlid 1987, Schönhar 1973, 1990). However, recent Nordic studies dealing with the incidence of butt rot in planted spruce stands did not show any correlation between the incidence of butt rot at final felling of spruce stands and the incidence of butt rot at first thinning of the subsequent spruce stands (Vollbrecht and Stenlid 1999, Rönnberg and Jørgensen 2000, Rönnberg et al. 2003). The spore infection of healthy stumps at clear
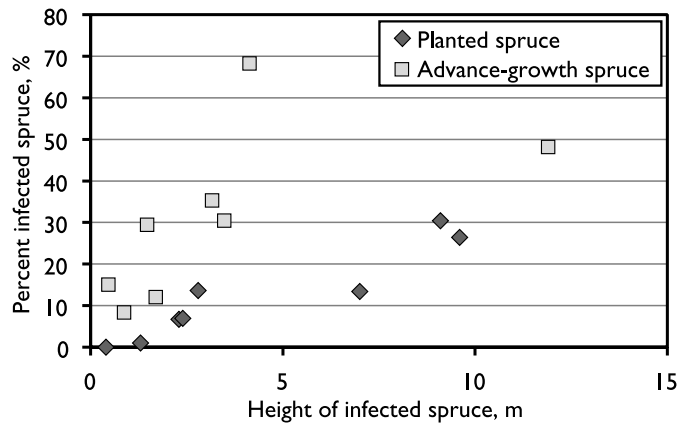
Fig. 3. Frequency of infected regeneration spruces in disease centres of Heterobasidion root rot in relation to tree height.

felling and subsequent transfer of *Heterobasidion* to planted spruces has been suggested as a factor that can diminish the correlation in decay incidence in successive spruce generations (Rönnberg and Jørgensen 2000, Rönnberg et al. 2003). In our studies, all the cuttings had been carried out in winter when infection of healthy stumps by spores is unlikely under Finnish conditions. Compared to Finland, decomposition of old colonized stumps is faster in Denmark and southern Sweden, which may restrict the vegetative spread of *Heterobasidion* to the next rotation. Furthermore, the studies mentioned in the above deal with butt rot in general, mainly based on the visual examination of stump surfaces, whereas the present studies have been carried out in *Heterobasidion* centres and are focused on the identification of individual *Heterobasidion* genets. Consequently, the results obtained in Denmark and Sweden may therefore not be directly comparable with our results.

4.4 Disease development in individual trees in relation to the regeneration method

In advance-growth spruce, *Heterobasidion* had typically colonized only a small part of the root system. Only in 21 % of the infected advance-growth spruce had the decay advanced up to the root collar or the tree had been killed by the fungus. In the majority of the infected planted spruce (72 %) the decay had spread into the stem. In the 22- to 23-year-old plantations, the mean extension of visible decay was 170 cm and the maximal extension 350 cm.

The faster growth rate of *Heterobasidion* in the wood of planted spruce as compared with advance-growth spruce is probably due to the faster growth of the planted trees (Isomäki and Kallio 1974, Dimitri and Schumann 1989) and, consequently, the rate of spread of decay in advance growth spruce may increase after release cutting. The wide growth rings in fast-growing wood probably directly accelerate the spread of decay.

Other factors such as moisture content and chemical composition of the wood may, however, be involved (Courtois 1970, Isomäki and Kallio 1974). The slow advance of *Heterobasidion* in advance-growth spruce may also be due to spore infection; the low inoculum potential of spores may retard disease development at least in its early stage (Gibbs 1967).

4.5 Transfer of *Heterobasidion* into the regeneration of other tree species

H. parviporum is by far the dominant species of *Heterobasidion* on old spruce sites in southern Finland. In the present studies (**I-III**), 99.6 % (out of a total number of 671) of the *Heterobasidion* infections in trees and stumps of the previous spruce rotation were assigned to *H. parviporum* and 0.4 % to *H. annosum s.str*. The high frequency of *H. parviporum* in the previous stand was also reflected in the high frequency of this species in the subsequent stand, although most of the replanted tree species are considered to be highly resistant to *H. parviporum* (Korhonen 1978a, Swedjemark and Stenlid 1995). The infection potential of old spruce stumps is high and, consequently, even tree species with a low susceptibility to *H. parviporum* may become infected when planted on a site where the previous spruce rotation had been attacked by *Heterobasidion*. If these tree species are not well adapted to the site, the damage caused by *H. parviporum* may be extensive. In the present study, a silver birch provenance poorly adapted to the site showed considerable root rot damage although *B. pendula* is normally highly resistant to *H. parviporum* (**I**).

The age of the stands is a decisive factor when assessing the susceptibility of various tree species to decay caused by *H. parviporum*. In pine, *H. parviporum* causes root decay leading to the mortality of seedlings and pole-sized trees, whereas older pines appear to be able to prevent the infection (Korhonen 1978a, Korhonen and Piri 1994). In Norway spruce and Siberian larch, *Heterobasidion* causes a typical butt rot and the disease incidence tends to increase during the course of a rotation (Laine 1976). Both young and mature silver birch (*Betula pendula*) may have decay caused by *Heterobasidion* but, so far, birches infected by *H. parviporum* have rarely been observed in Finland (Korhonen 1978a, Korhonen and Piri 1994).

Compared to Norway spruce, the transfer of Heterobasidion root rot into the other tree species was considerably less. The average number of regeneration trees infected per old spruce stump colonized by *Heterobasidion* was 4.5 trees in the advance-growth regenerations and 1.2 trees in the planted spruce stands (**II, III**). In the lodgepole pine, Siberian larch, Scots pine and silver birch stands the corresponding values were 0.5, 0.3, 0.05 and 0.04, respectively (**I**). Of all the regeneration trees infected by *Heterobasidion*, the proportion of trees infected vegetatively from old stumps was 67 % in the Scots pine stands, 85 % in the lodgepole pine stands, and 78 % in the birch stands. In the older larch and spruce stands, which were thinned before the investigation, the corresponding values were only 19 % and 37 %, respectively. Thinning operations increase the incidence of primary infections. However, the likelihood of missing inoculum sources of the previous rotation is also greater when the interval since final cutting is longer. Small, rapidly

decomposed stumps have a small root system and are often colonized by other decay fungi such as *Resinicium bicolor* and may therefore not be of great importance for disease transfer. Nevertheless, some of the genets in the present stands that were assumed to have developed via spore infection may, in fact, have originated from decomposed stumps of the previous rotation.

In middle-aged, naturally regenerated spruce stands, the frequency of trees infected by *Heterobasidion* in present stands (30.9 %) was almost twice that in the previous stands (15.8 %) (**I**/Fig.2). Although the decay frequency of the previous stand may have been underestimated due to disintegration of some small stumps, the disease incidence in the present spruce rotation will continue to increase to the end of the rotation and, consequently, a trend towards increasing disease incidence in consecutive spruce generations seems likely.

On sites replanted with tree species other than spruce, the overall percentage of infected trees decreased from the previous to the next stand. Silver birch and Scots pine proved to be the most resistant tree species when planted on sites infested by *H. parviporum*. Although some pine and birch became infected from old stumps, the further spread of the disease from tree to tree seemed to be uncommon. According to earlier studies, the susceptibility of Scots pine to *H. parviporum* is restricted to young trees between the age of about 5 and 25 years (Korhonen 1978a, Korhonen and Piri 1994), and it is unlikely that damage would continue in the studied Scots pine stands. Also mature birch, even when growing as an admixed tree with decayed Norway spruce, appears to be resistant to *H. parviporum* (Piri et al. 1990). Stumps of birch do not seem to be vulnerable to spore infection (Bendz-Hellgren 1997). Both silver birch and Scots pine thus appear to be good choices when regenerating a site infested by *H. parviporum*.

In unfavourable conditions, when not adapted to the site, birch can be more severely attacked by *H. parviporum*. In the present study, 2 % of the birches of a very northern provenance (Kittilä, 67°40'N, 24°50'E) were definitely colonized by *H. parviporum* at the age of 40 years when planted in southern Finland (Ruotsinkylä, 60°21'N, 24°59'E). The actual amount of damage can be considerably greater, because 47 % of the birch were killed and it is likely that *Heterobasidion* had also killed birches at the earlier stage of development. Because of the exceptional provenance, this stand was not included in the calculations.

Lodgepole pine and Siberian larch were more susceptible than Scots pine and birch to *H. parviporum*. Further damage can be expected to occur in lodgepole pine stands, because the studied stands were rather young (8 and 14 years). The present decay frequency in the larch stands may be underestimated, because it is difficult to detect the disease on larch on the basis of external symptoms, and samples were not taken from all the standing trees. The disease incidence in larch stands will also probably increase during the course of a rotation. However, possible damage caused by *Heterobasidion* in the seedling stage was no longer recognizable at the time of the investigation. Field studies have shown that young trees of *Larix decidua* Mill., *Larix kaempferi* (Lamb.) Carr. and *Larix* x *eurolepis* Henry are susceptible to *H. annosum s.str*. (Vollbrecht et al. 1995b, Vollbrecht and Stenlid 1999, Rönnberg et al. 1999, Greig et al. 2001). Based on an inoculation experiment carried out under greenhouse conditions, seedlings of *Larix* x *eurolepis* and *L. kaempferi* were found to be susceptible to both *H. annosum s.str*. and *H.*

parviporum (Swedjemark and Stenlid 1995). No distinction has earlier been made between *Heterobasidion* species attacking Siberian larch. Kurkela (1988) reported mortality of Siberian larch seedlings planted on a site where the previous stand had been Scots pine attacked by Heterobasidion root rot; in this case the larch seedlings were most likely attacked by *H. annosum s.str*. In the present study, both *H. parviporum* and *H. annosum s.str.* were isolated from Siberian larch, but *H. parviporum* was the more frequent species in both the previous and present tree generation (**I**/Table 2).

4.6 Effect of admixed tree species on spread of the disease

The effect of admixed tree species on the root rot frequency of spruce at the early stage of stand development was studied in both advance-growth and planted stands. The proportion of admixed trees (by number) on the advance-growth plots varied from 5 to 69 %, and on the planted plots from 11 to 80 %. The most frequent admixed tree species were naturally regenerated birch (*B. pendula* and *B. pubescens*) and rowan (*S. aucuparia*). No correlation was found between the proportion of infected spruce and the proportion of naturally regenerated broadleaf trees either in the advance-growth stands or in the planted stands. It should be noted, however, that some of the planted stands had been cleaned before the investigation, and the present stand composition might thus be misleading when assessing the importance of admixed tree species on spread of the disease (**II**, **III**).

An earlier investigation carried out in mature spruce stands showed that the average size of the *Heterobasidion* genets was slightly smaller in mixed than in pure spruce stands, indicating that admixed trees may restrict the vegetative spread of the fungus, possibly by reducing the number of root contacts between spruce trees (Piri et al. 1990). In the studied spruce regenerations, vegetative spread between young regeneration spruce was infrequent. Furthermore, considering that young broadleaf wildings were distributed very unevenly on the study plots and their root systems were rather small, the influence of admixed trees on the vegetative spread of *Heterobasidion* on the investigated sites was insignificant (**II**, **III**).

More important than the proportion of admixed tree species in the regeneration is their location in relation to the infected stumps. In planted spruce stands, Heterobasidion root rot is transmitted to the regeneration trees mainly by means of mycelial spread from old stumps, and the trees growing inside the rooting area of the stumps have the highest risk of infection. Calculations based on distribution maps of *Heterobasidion* genets showed that a 2.5-meter-wide, spruce-free area around colonized stumps would have decreased the number of infected trees in the planted spruce stands by 50 %. With a radius of three and four meters, the decrease in infection would have been 60 % and 80 %, respectively (**III**, data not shown). Thus, disease transfer into the subsequent spruce stand can be markedly restricted if no spruce are planted near stumps colonized by *Heterobasidion*, and the disease centres are regenerated with broadleaf trees. In advance-growth stands where the distribution of infected trees was more scattered than in planted stands, possibly due to frequent spore infections, leaving a protective area around stumps would be less effective. Because advance growth most readily develops in small stand openings, which

are often disease centres of Heterobasidion root rot, careful consideration is required when using advance-growth spruce in regeneration.

4.7 Root contacts versus root grafts in disease transfer

Heterobasidion is reported to be transmitted by root contact and by root grafts. Contact between roots arises when two roots touch each other. Roots are considered functionally grafted when they are connected by common bark, phloem, cambium, and xylem tissues (Epstein 1978). In living roots of Norway spruce, *Heterobasidion* is typically confined within the central part of the root (Gibbs 1968, **IV**). Radial spread into living sapwood is limited due to the accumulation of phenolic inhibitory substances in a zone surrounding the heartwood (Shain 1971). A low oxygen supply induced by high wood moisture content is also an important limiting factor in the growth of *Heterobasidion* in the sapwood of living trees and freshly cut stumps (Worrall and Parmeter 1983, Cwielong et al. 1993, Bendz-Hellgren and Stenlid 1998). The anatomical structure of root wood with dense growth rings also acts as a physical barrier that limits inward, radial spread of the fungus (Johansson and Theander 1974, Tippett and Shigo 1981, Garbelotto et al. 1997a). The transfer of *Heterobasidion* between living trees may thus be mainly limited to functional root grafts, which enable the fungus to grow from the xylem of infected roots to the xylem of healthy roots. Dead roots of living spruce have been shown to be a potential point of infection (Dimitri 1969b), and contacts between the dead roots of living trees may be responsible for disease spreading in stands with extensive root mortality, e.g. in stands established on old agricultural land (Swedjemark and Stenlid 1993, Stenlid and Redfern 1998). So far, no experimental evidence is available for this kind of spreading under field conditions in forest soils.

After the tree is cut and its active defence fails, decay begins to expand outwards from the centre of the root. When the fungus has breached functionally intact sapwood and cambial tissue, it is also able to spread into the surrounding trees through looser, non-grafted root contacts. Consequently, root contacts most probably play an important role in spread of the disease from stumps and dead trees to adjacent healthy trees. The fact that the roots of young trees prefer to grow along the channels of decaying or already decayed old roots (Laitakari 1927) may also increase the probability that a regeneration tree contacts the inoculum and becomes infected from the previous rotation.

4.8 The size of *Heterobasidion* genets during the course of a spruce rotation

In young, unthinned spruce regenerations the mean size of the *Heterobasidion* genets (without trees of the previous rotation) was 2.1 trees in the planted stands and 2.6 trees in the advance-growth stands (**III**, **II**; data not shown). In the middle-aged spruce stands the average size of the genets (including thinning stumps) was of about the same order, i.e. 2.5 trees (**I**). Similar results have been obtained in Sweden and Norway, where the mean size of the genets in thinned spruce plantations varied from 1.0 to 2.5 trees (Stenlid 1985, Venn and Solheim 1994).

In the final cutting stands in southern Finland the mean size of the *Heterobasidion* genets was 1.8 trees, and most of the genets (61 %) had infected only one tree (Piri et al. 1990). In a 60-year old Norway spruce stand in Lithuania, the average number of trees infected by a single fungal genet was also small (1.5 trees) and about half of the genets included only one tree (Vasiliauskas and Stenlid 1998). Somewhat larger genets containing on an average 3.6 trees were identified in a 120-year-old spruce stand in Sweden (Stenlid 1985). In fact, the size of the genets (by number of trees) in the final-cutting stands is underestimated because most of the thinning stumps infected by *Heterobasidion* are already decomposed by the end of the rotation. On the other hand, thinning operations may increase primary infection resulting in the establishment of new genotypes in the forest, which reduces the average size of the genets in middle-aged and mature stands.

A Swedish investigation carried out in thinned spruce stands one and seven years after thinning showed that the genets of *Heterobasidion* established through spore infection were confined either to a single thinning stump (90 % of all genets) or had spread to only one or two adjacent trees (10 %) (Swedjemark and Stenlid 1993). The presence of *Heterobasidion* in a stump root at the contact point with a root of a growing spruce did not ensure the transfer of the fungus to the tree root. In Sitka spruce stumps inoculated with *Heterobasidion* spores in Scotland, only 22 % of the contacts between a colonized stump root and the tree root had resulted in disease transfer 8 years after stump infection. Transfer was always associated with viable mycelium at the bark surface and a broad, firm contact (Morrison and Redfern 1994). There is no information available on how often or how rapidly a spore infection in a stump spreads to an adjacent tree under Finnish conditions. Neither is it known how living stumps, connected with adjacent trees through root grafts, affect disease spreading.

Overall, the clonal studies carried out in Norway spruce stands of varying age do not indicate that *Heterobasidion* would easily spread as mycelium between living spruce. This might simply be due to a scarcity of functional grafts necessary for disease transfer. The probability of root grafts and contacts depends on site factors, including soil depth, stoniness and slope, and on stand factors, including tree diameter at breast height and stand density (Yli-Vakkuri 1953, Bloomberg and Reynolds 1982, Reynolds and Bloomberg 1982). There is no detailed information about the frequency of functional root grafts in mature spruce stands on mineral upland soils in Finland. In mature, naturally established pine stands in southern Finland, approximately 21–28 % of the trees were grafted (Yli-Vakkuri 1953). Compared to pine, spruce has a wider horizontal root system, and in spruce stands the frequency of grafted trees may be higher than that in pine stands (Laitakari 1927). Investigations made in Estonia and Denmark revealed that 25–38 % of planted mature spruce are interconnected by root grafting (Holmsgaard and Scharff 1963, Külla and Lõhmus 1999). In a row culture of Norway spruce with a 2 × 2 m planting density, the first root grafts were formed when the stand was 24 years old (Külla and Lõhmus 1999). Most of the root grafts develop between spruce trees when the stand is 30–60 years old (Holmsgaard and Scharff 1963). Assuming that the tree-to-tree spread of *Heterobasidion* is mainly confined to root grafts and approximately one third of the spruce are functionally grafted and, further, that only a small proportion of the grafts actually function as an infection route, the vegetative growth of *Heterobasidion* between living trees might not be an effective means of disease transfer. The situation may be

different when the fungus spreads from a dead tree or stump into a living tree, in which case also less developed root contacts are sufficient for the disease to transmit. Considering that the growth rate of *Heterobasidion* in stump roots is almost three times that in the roots of living trees, felling of infected trees may substantially promote and accelerate the spread of Heterobasidion root rot in Norway spruce stands (Bendz-Hellgren et al. 1999).

As shown in studies **I**, **II** and **III**, the size of the *Heterobasidion* genets in the previous rotation may be reflected in the size of the genets in the subsequent rotation. A number of large genets found in a spruce stand are probably derived from the previous tree generation, where the genet had infected several trees or stumps. In the present studies, a few exceptionally large genets were detected. One of them included three old stumps of the previous tree generation, as well as 14 thinning stumps and 14 standing trees of the present tree generation. Because the stumps of the previous rotation were already over 40 years old, it is highly likely that more than three trees of the previous rotation had been infected by the same genet (**I**). Another large genet included 13 trees of the previous tree generation and 33 advance-growth trees (**II**). In a planted stand, representatives of a large genet were isolated from five old stumps of the previous tree generation and from 10 planted spruce (**III**).

If the vegetative spread of *Heterobasidion* from the previous to the subsequent tree stand can be prevented or appreciably reduced, for instance by establishing a protective area around infected stumps or by stump removal, and if the spore infection in the current rotation can be effectively controlled, cultivation of consecutive spruce rotations should be possible without increasing losses caused by butt rot.

4.9 Growth of *Heterobasidion* in roots of vitality-fertilized spruces

In the present study, vitality fertilization did not increase the resistance of Norway spruce to internal spread of *H. parviporum*. In fact the result seemed to be quite the opposite: there was a tendency for increased growth of the fungus in the roots of fertilized trees. The growth rate of the fungus was slowest in the unfertilized control trees (on an average 33 cm in twelve months). *H. parviporum* had advanced most rapidly, i.e. 52 cm per year, in trees given the stand-specific fertilization based on needle analysis (treatment 5) containing N, P, K and Cu (**IV**/Fig.1). Diagnostic foliage analysis has proven to be one of the most powerful tools for determining the current nutrient status in trees and the possible need for fertilization (Linder 1995). The results of the present study suggest, however, that the optimal nutrient status of Norway spruce may be different depending on the practical purpose of the fertilization. Fertilization focused on increased stand productivity does not necessarily ensure increased tolerance to *Heterobasidion*.

Fertilization based on needle analysis was the only treatment that showed increased annual volume growth of the trees. The accelerated advance of *Heterobasidion* decay in that treatment may, at least partly, be due to increased tree growth. A positive correlation between tree growth and the spread of decay in wood has been observed both in mature (Laiho 1983, Dimitri and Schumann 1989) and young Norway spruce (**III**). According

to Entry et al. (1991), trees that are growing rapidly may allocate more carbon to sugar and cellulose synthesis and less carbon to compounds with defensive functions, such as lignin, phenolics, and tannins. Also, the anatomical structure of fast-grown wood with wide growth rings enhances the growth of fungal mycelium (Courtois 1970).

Because the rates of decomposition and nitrogen mineralization are low in boreal coniferous forest soils, the availability of mineral nitrogen is normally the factor restricting tree growth on mineral soils (Kukkola and Saramäki 1983). Despite a certain amount of nitrogen deposition, nitrogen is still the major growth-restricting nutrient in Finnish forests. Needle analysis in the present study also indicated a shortage of nitrogen in experimental trees.

Nitrogen fertilization is generally regarded as a risk factor as regards Heterobasidion root rot. It can increase the damage caused by *Heterobasidion* in three ways at least: 1) it increases the crown of the tree in relation to the roots (Helmisaari and Hallbäcken 1999, Smolander et al. 2000), exposing the tree to increased swaying in the wind and subsequent root damage, 2) a high nitrogen content of the wood accelerates the rate of spread of the fungus (Aguinagalde and Cerny 1974, Alcubilla et al. 1988), and 3) nitrogen increases tree growth and this, as stated above, makes the spread of *Heterobasidion* easier (Dimitri and Schumann 1989, Alcubilla et al. 1990). On the other hand, in unfertilized Norway spruce trees growing on sites of medium-to-good nutrient and moisture regimes (*Myrtillus*-type) in central Finland, the nitrogen content in the wood was not related to the vertical spread of *Heterobasidion* in spruce stems (Ekman and von Weissenberg 1981). Proper fertilization, although improving tree growth, does not necessarily decrease the resistance of trees to decay. Nitrogen (urea) fertilization of Norway spruce had no effect on the growth rate of *Heterobasidion* in a Finnish experiment (Laiho 1978). Comparable results have also been obtained elsewhere (Seibt 1964, Cowling et al. 1969, Yde-Andersen 1977).

The availability of nitrogen for a tree and its effect on disease depends *inter alia* on the form and solubility of the fertilizer. In treatment 5, in which the growth rate of *Heterobasidion* was the highest, nitrogen was added in the form of water-soluble ammonium nitrate, whereas in the other treatments (containing nitrogen) two thirds of the nitrogen was in the form of slow-release methylene urea. Because the period between fertilization and inoculation was only three growing seasons, decomposition of methylene urea and the release of nitrogen may not yet have influenced fungal growth in the spruce roots. It is also possible that the effect of urea fertilization on the growth rate of *Heterobasidion* is less than the effect of ammonium nitrate. Furthermore, other unknown factors may contribute more to spread of the disease than the application of nitrogen.

In the 1990s, the nitrogen oxide emissions were falling slowly. In 2000, nitrogen oxide emissions totalled approximately 236 000 tonnes in Finland and were about 10 kg N ha^{-1} along the southern coast of Finland (Ympäristötilasto 2002). Although carefully balanced N fertilization may not greatly influence the development of *Heterobasidion* in standing spruce, we cannot exclude the possibility that N deposition could, if it continues at the present level, in the long term promote the spread of Heterobasidion root rot in spruce stands in the most exposed areas in southern Finland.

The sum of many interacting factors associated with the pathogen, host, environment, and time determines how a disease is affected by nutrition management. The inoculation

experiment was carried out only on one site and the conclusions presented in this work are partially speculative, and require confirmatory experiments. Further work is needed to clarify the long-term effects of vitality fertilization on the development of Heterobasidion root and butt rot. However, the results of the present study are consistent with the results obtained in a comparable experiment carried out in south-western Sweden (Wahlström and Barklund 1994). Although site conditions and composition of the fertilizers used in the Swedish and Finnish inoculation experiments were somewhat different, both studies showed that the growth rate of *Heterobasidion* was slightly faster in Norway spruce treated with a nitrogen-free vitality fertilizer compared to the untreated controls. Thus, vitality fertilization with nitrogen-free fertilizers or fertilizers with a low nitrogen content does not seem to help in reducing the damage caused by Heterobasidion root rot in infested spruce stands.

5 Conclusions

The control of Heterobasidion root and butt rot in Norway spruce forests in southern Finland is an important consideration for the sustainable management of regenerating stands. Heterobasidion root and butt rot is expressly a disease of the site. Old spruce stumps colonized by *Heterobasidion* are important infection sources in the subsequent tree stand. The fungus can persist in the wood of large spruce stumps for more than 40 years and is able to transfer vegetatively through root contacts into the surrounding regeneration of any susceptible tree species. In addition to the direct transfer through root contacts, basidiocarps developing in decayed stumps increase the risk of spore infection in the subsequent tree stand for several decades.

Changing the tree species is an important method to reduce the damage caused by Heterobasidion root rot on infested sites. Silver birch and Scots pine were the most resistant tree species on sites infested by *H. parviporum*. If regeneration trees are poorly adapted to the site, resistant species may, however, suffer from considerable damage caused by *Heterobasidion*. Regeneration of infested sites with exotic tree species, lodgepole pine or Siberian larch, does not eradicate *H. parviporum* from the site. Both tree species become infected from old spruce stumps. However, damage caused by *H. parviporum* remains lower in subsequent lodgepole pine and Siberian larch stands than in a subsequent Norway spruce stand.

Advance regeneration of Norway spruce established naturally in disease centres of Heterobasidion root rot proved to be relatively seriously infected by *H. parviporum*. If the advance growth is used in the regeneration of a new spruce generation there is a danger of increasing decay frequency. Planted spruce of the same size was infected to a lesser degree. Because most of the infections in the planted spruce occurred through root contacts from the old stumps of decayed trees, the transfer of *Heterobasidion* to the regeneration trees can be decisively reduced if no spruce are planted near infected stumps, and the regeneration of resistant broadleaved trees is encouraged around them.

In a mature Norway spruce stand infected by *H. parviporum*, treatment with nitrogen-free or low-nitrogen vitality fertilizers did not improve the resistance of the trees to Heterobasidion root rot. On the contrary, in the short term the growth rate of mycelium of *H. parviporum* tended to be slightly faster in roots of fertilized trees than in those of unfertilized control trees. Although differences in disease development between the control treatment and fertilization treatments were not statistically significant, extra caution is needed when fertilizing Norway spruce stands suffering from Heterobasidion root rot.

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