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Regeneration and vitality fertilization of infected stands

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Academic dissertation in Forest Pathology

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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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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 *Heterobasidion* 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 *Heterobasidion*. 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

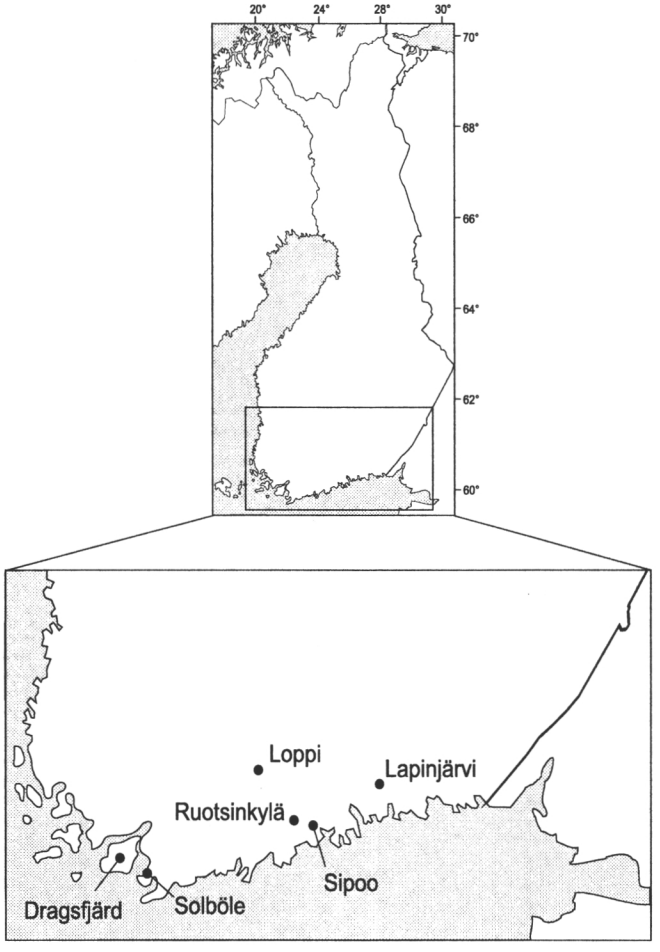


Fig. 1. Location of the experimental areas.

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 *Heterobasidion* 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.

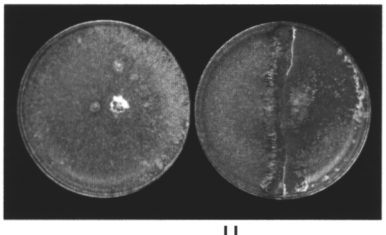
⇓

Wood samples

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

⇓

Pairing of pure cultures

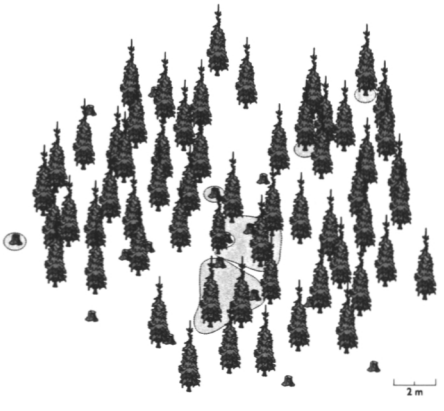


The genets of *Heterobasidion* on the experimental plot were identified on the basis of demarcation line formation (somatic incompatibility). Left: self pairing; right: pairing of two unrelated heterokaryons.

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 $p \leq 0.05$. 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 *Heterobasidion* 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

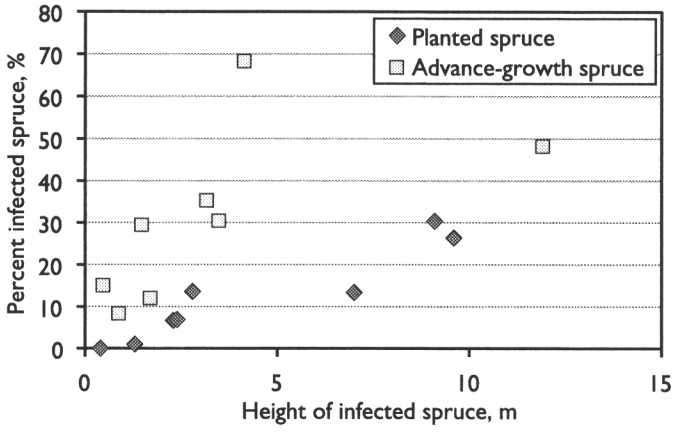


Fig. 3. Frequency of infected regeneration spruces in disease centres of Heterobasidion root rot in relation to tree height.

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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Paper I

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The spreading of the S type of *Heterobasidion annosum* from Norway spruce stumps to the subsequent tree stand

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Summary

The occurrence of *Heterobasidion annosum* in stumps and growing trees was investigated on 15 forest sites in southern Finland where the previous tree stand had been Norway spruce (*Picea abies*) infected by *H. annosum*, and the present stand was either Scots pine (*Pinus sylvestris*), lodgepole pine (*Pinus contorta*), Siberian larch (*Larix siberica*), silver birch (*Betula pendula*) or Norway spruce 8–53 years old. Out of 712 spruce stumps investigated of the previous tree stand, 26.3% were infected by the S group and 0.3% by the P group of *H. annosum*. The fungus was alive and the fruit bodies were active even in stumps cut 46 years ago. In the subsequent stand, the proportion of trees with root rot increased in spruce stands and decreased in stands of other tree species. On average, one S type genet spreading from an old spruce stump had infected 3.0 trees in the following spruce stand, 0.5 trees in lodgepole pine, 0.3 trees in Siberian larch, 0.05 trees in Scots pine and 0.03 trees in silver birch stand. Although silver birch generally was highly resistant to the S type of *H. annosum*, infected trees were found on one site that was planted with birch of a very northern provenance.

1 Introduction

The most common and economically most important decay-causing fungus of Norway spruce (*Picea abies* (L.) Karst.) in southern Finland is *Heterobasidion annosum* (Fr.) Bref. On average, *c.* 15–20% of the trees in mature stands are damaged by butt rot, mainly caused by *H. annosum*. Occasionally, the rot frequency can be 50% or greater (Tamminen 1985; Piri et al. 1990).

After final cutting, the fungus can survive for decades in stumps of infected trees (Holmsgaard et al. 1961; Schönhar 1973; Greig and Pratt 1976; Laine 1976). From old stumps, it spreads vegetatively via root contacts to neighbouring trees of the subsequent stand (Yde-Andersen 1970; Stenlid 1987; Capretti and Goggioli 1992). Strong evidence exists for the importance of the old spruce stumps as sources of infection in subsequent tree generations (Schönhar 1973; Yde-Andersen 1978). Based on the identification of the genets (i.e. the somatically compatible vegetative mycelia) of *H. annosum* in the current and previous Norway spruce stands in Sweden, Stenlid (1987) estimated that 65% of decayed trees in the present stand were infected from stumps of the previous spruce stand.

In northern Europe *H. annosum* consists of two intersterility groups, S and P. The main host of the S group is Norway spruce. About 90% of *H. annosum* strains isolated from mature spruce stands in southern Finland belong to the S group (Korhonen and Piri 1994). This type has also been found to kill seedlings of Scots pine (*Pinus sylvestris* L.) planted after a spruce stand (Korhonen 1978a; Jokinen and Tamminen 1979); on older pines or on

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other species of native trees it has been found only occasionally. In contrast with the S group, the P group has a wide host range, although its most important host is pine (KORHONEN 1978a; KORHONEN and PIRI 1994).

On sites infested by *H. annosum*, the following three factors have a major impact on the degree of infection in the next tree stand: (1) the type of *H. annosum* infesting the site, (2) its frequency and survival time in the stumps of the previous tree stand, and (3) the susceptibility of the tree species of the regenerated stand to the fungus.

To date, little detailed information is available about the spreading of *H. annosum* from the previous tree stand to the next in Finnish conditions. This understanding would be useful for the selection of tree species in forest regeneration. In this study the occurrence of *H. annosum* in trees of the present stand and in stumps of the previous stand was investigated and the vegetative spread of the fungus from the stumps to the trees of the present stand was estimated by identifying the genets of the fungus in the stumps and trees.

2 Materials and methods

All 15 stands studied are situated on old forest soil in southern Finland, in the Ruotsinkylä (60° 21′ N, 24° 59′ E) or Lapinjärvi (60° 36′ N, 26° 9′ E) experimental forests of the Finnish Forest Research Institute. The previous tree generation on the sites was Norway spruce, attacked by *H. annosum*. After clear-cutting, the infested sites were planted with Scots pine, lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Wats.), Siberian larch (*Larix sibirica* Ledeb.) or silver birch (*Betula pendula* Roth). The Norway spruce stands were regenerated naturally. Because some tree species become infected as saplings while others are not usually infected until the formation of heartwood has begun, the stands studied are composed of two age groups. The young-growth stands of Scots pine, lodgepole pine and birch were 8–14 years old and the middle-aged stands of spruce, larch, Scots pine and birch 25–53 years old. The middle-aged spruce and larch stands had been thinned in winter. Depending on the area of the stand compartment, the size of the sample plots in one stand varied from 0.04 to 0.3 ha. The characteristics of the stands studied are shown in Table 1.

Before sampling, all stumps and standing trees on the plots were mapped and the diameter of the stumps and trees (d.b.h.) was recorded. The wood samples were taken aseptically with an increment borer from the butt and three or four main roots of all standing trees in spruce stands. All the thinning stumps were investigated similarly in spruce and larch stands. The standing trees in larch, pine and birch stands were examined first for symptoms of *H. annosum* (foliage chlorosis, resin flow, reduced growth, fruit bodies), and the wood samples were taken only from roots and butts of dead and infirm trees. From all old stumps, pieces of rotten wood were removed for isolation of the decay fungus. Presence or absence of fruit bodies on each stump and tree sampled was also recorded.

In the laboratory the wood samples were placed on 2% malt agar substrate (2% w/v malt extract, 1.5% w/v agar) in Petri dishes. After 5–10 days' incubation at room temperature, the plates were examined for growth of *H. annosum* and other decay fungi. The genets of *H. annosum* on each study plot were identified by pairing the isolates from the previous and present stand in all combinations on malt agar plates (STENLID 1985). Infection was considered to originate from the previous stand in cases where the same genet was isolated both from old spruce stump and from the subsequent tree stand. Identification of the intersterility group of the genets was made with the aid of homokaryotic tester strains belonging to the S and P groups (KORHONEN 1978a). *Armillaria* species were also identified by means of mating tests (KORHONEN 1978b).

In this study a total of 712 old spruce stumps of the previous stand were investigated; 401 were from trees cut 9–15 years ago and 311 were from trees cut 26–46 years ago. A total

Table 1. **Some characteristics of the stands studied**

Plot	Location	Tree species	Regeneration	Site type	Age (years)	Area (a)	No. of stumps/trees investigated in previous spruce stand (n)	in present stand (n)
1	Ruotsinkylä	*P. abies*	natural	MT[1]	53	4.0	10	92
2	Ruotsinkylä	*P. abies*	natural	OMT[2]	45	6.0	37	126
3	Ruotsinkylä	*P. abies*	natural	MT	53	14.0	67	254
4	Ruotsinkylä	*P. sylvestris*	planted	MT	25	5.0	20	70
5	Ruotsinkylä	*P. sylvestris*	planted	MT	10	13.0	69	244
6	Ruotsinkylä	*P. sylvestris*	planted	MT	11	7.0	63	102
7	Ruotsinkylä	*P. sylvestris*	planted	MT	13	8.0	17	130
8	Ruotsinkylä	*B. pendula*[3]	planted	MT	37	17.0	103	336
9	Ruotsinkylä	*B. pendula*	planted	MT	10	30.0	82	495
10	Ruotsinkylä	*B. pendula*	planted	MT	9	13.0	73	277
11	Lapinjärvi	*L. sibirica*	planted	OMT	44	27.0	16	120
12	Ruotsinkylä	*L. sibirica*	planted	MT	26	7.0	32	57
13	Lapinjärvi	*L. sibirica*	planted	OMT	45	29.0	26	122
14	Ruotsinkylä	*P. contorta*	planted	MT	8	5.0	57	49
15	Ruotsinkylä	*P. contorta*	planted	MT	14	10.0	40	188

[1] *Myrtillus* type
[2] *Oxalis-Myrtillus* type
[3] Provenance: Northern Finland

of 2662 trees (2211 standing trees and 451 thinning stumps) of the present crop were investigated in the 15 stands.

All the calculations were performed using the BMDP program package (BMDP 1985).

3 Results

3.1 Occurrence of *H. annosum* and other wood-decay fungi in stumps of the previous spruce stand

The fungus most commonly found in Norway spruce stumps of the previous tree stand was *H. annosum*. It was isolated from 32.9% of the 9–15-year-old stumps and from 18.0% of the 26–46-year-old stumps. The great majority of the isolates (98.9%) belonged to the S intersterility group; only two out of 189 isolates belonged to the P group.

Active fruit bodies of *H. annosum* were detected on 11 out of 15 plots. The frequency of stumps with fruit bodies was 2.5% in the 9–15-year-old stumps group and 3.9% in the 26–46-year-old stumps group. Counting only stumps infected by *H. annosum*, 7.6% and 21.7%, respectively, had an active fruit body in these two age groups.

Although the frequency of spruce stumps infected by *H. annosum* decreased with increasing stump age ($r = -0.573$, $p < 0.05$), both viable mycelium and fruit bodies were found even in stumps cut 46 years ago. However, in the oldest spruce stand a few stumps were found with residues of old fruit bodies or old decay caused by *H. annosum* without any signs of fungal activity. In addition to age, the presence of *H. annosum* was also related to the size of the stumps; the proportion of infected stumps increased with increasing stump diameter ($r = 0.755$, $p < 0.05$). The mean diameter inside the bark of the spruce stumps, where the diameter was still measurable, was 28.9 cm (range 15.0–78.0 cm). *H. annosum* was found typically in middle-sized and larger stumps, which were almost totally colonized by the fungus. The frequency of fruit bodies did not correlate with the stump diameter.

Other fungi commonly isolated from old Norway spruce stumps were *Resinicium bicolor* (Alb. and Schw. ex Fr.) Parm. and *Armillaria borealis* (Marxm. and Korhonen). In contrast to *H. annosum*, *R. bicolor* typically occurred in small stumps and its frequency decreased with increasing stump diameter ($r = -0.817$, $p < 0.01$). The following decay fungi were also isolated in low numbers: *A. cepistipes* Velen., *Sistotrema brinkmannii* (Bres.) J. Erikss., *Fomitopsis pinicola* (Sw. ex Fr.) Karst., *Phlebiopsis gigantea* (Fr.) Jul., *Stereum sanguinolentum* (Alb. and Schw.: Fr.) Fr. along with several other unidentified basidiomycetes (Fig. 1).

3.2 Occurrence of *H. annosum* in the present stands

H. annosum was isolated from 197 out of the 2566 standing trees or stumps of recently thinned trees investigated. In addition, the fungus was isolated from 15 old thinning stumps.The incidence of the fungus varied considerably between the stands, depending on the current tree species. As in the previous tree generation, the S group was also dominant in the present stands regardless of the tree species. The P type was isolated only five times from spruce (three different genets), twice from larch (two genets) and once from birch (Table 2).

When comparing the decay frequency between the previous and present stands, it was found that the average frequency of *H. annosum* in the present spruce stands, which are not yet mature, was more than twice that in the previous mature spruce stands. On two sample plots out of three, however, the proportion of infected trees did not increase in the subsequent stand, although the number of infected trees on the plot increased (Table 2). On sites replanted with trees other than spruce, the percentage of infected trees decreased from

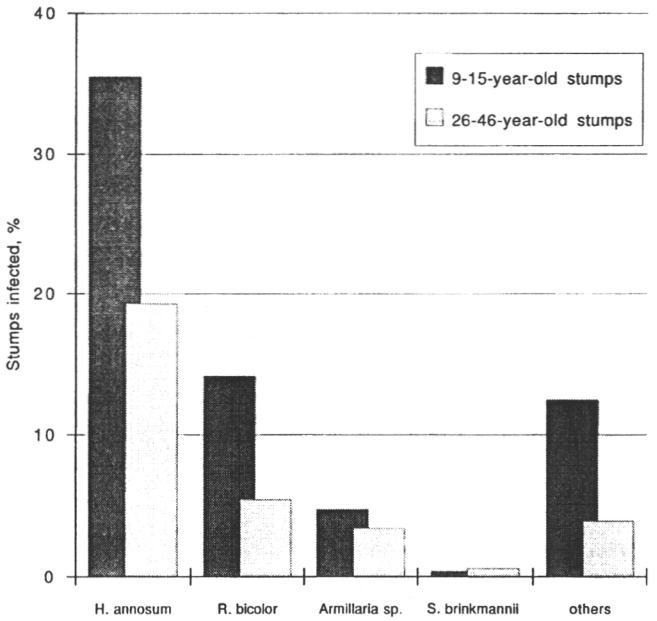


Fig. 1. Frequencies of basidiomycetes isolated from old Norway spruce stumps

the previous spruce stand to the next stand. In the stands of larch the decrease was 60%, in lodgepole pine 70%, in Scots pine 97% and in silver birch 99% (Fig. 2).

The average number of trees infected by a single genet of *H. annosum* in the current rotation was highest in the spruce stands (2.5 trees per genet). In the lodgepole pine stands the mean size of the genets was 2.0 trees, in the larch and Scots pine stands 1.2 trees, and in the birch stands 1.0 trees. The largest genet, including 28 trees of the present stand and three old stumps, was found in a spruce stand (Fig. 3). To date, this is the largest *H. annosum* genet found in Finland (Piri et al. 1990).

In the birch stands all the infected trees were attacked by a genet which was also isolated from a spruce stump of the previous stand. In lodgepole pine stands, the proportion of tree infection arising from old spruce stumps was 75.0%, in Scots pine stands it was 66.7%, in spruce stands 37.0% and in larch stands 19.3%. In spruce stands, the average number of trees infected from one infected spruce stump of the previous stand was 3.0. In lodgepole pine, larch, Scots pine and birch stands the corresponding values were 0.5, 0.3, 0.05 and 0.04, respectively.

A total of seven *H. annosum* genets were isolated from nine birch trees. Unexpectedly, six belonged to the S group infecting eight trees. However, five of these S group genets were collected in a stand that was planted with a very northern silver birch provenance (Kittilä, 67° 40′ N, 24° 50′ E). Because of the exceptional provenance, this stand was not included in the calculations presented above.

H. annosum was the only decay fungus identified consistently in the present stands. The next most frequently isolated decay fungi on growing trees and in stumps of recently thinned trees were the *Armillaria* species *A. borealis* (83% of *Armillaria* isolations) and *A. cepistipes*. In birch and Scots pine stands, *Armillaria* was even more common than *H. annosum*, infecting 3.9 and 1.5% of trees, respectively. In lodgepole pine, larch and spruce stands, the proportion of trees infected by *Armillaria* was 5.9, 5.3 and 1.6%, respectively. *R. bicolor* occurred frequently in older thinning stumps and was isolated from 9.2% of larch and 5.0% of spruce stumps.

Table 2. **Occurrence of *H. annosum* S and P type in the previous and present tree stands and frequency of trees infected from stumps of the previous stand**

	Previous tree stand Spruce stumps infected by *H. annosum*					Present tree stand Trees infected by *H. annosum*				Trees infected by *H. annosum* from old stump			
	S		P			S		P		S		P	
Plot	n	%	n	%	Tree species	n	%	n	%	n	%	n	%
1	2	20.0	0	–	*P. abies*	18	19.6	0	–	2	2.2	0	–
2	7	18.9	0	–	*P. abies*	19	15.1	0	–	15	11.9	0	–
3	10	14.9	0	–	*P. abies*	104	40.9	5	2.0	37	14.6	0	–
4	6	30.0	0	–	*P. sylvestris*	0	–	0	–	0	–	0	–
5	29	42.0	0	–	*P. sylvestris*	1	0.4	0	–	0	–	0	–
6	28	44.4	0	–	*P. sylvestris*	2	2.0	0	–	1	1.0	0	–
7	9	52.9	0	–	*P. sylvestris*	3	2.3	0	–	3	2.3	0	–
8	14	13.6	0	–	*B. pendula*	7	2.1	0	–	5	1.5	0	–
9	23	28.0	0	–	*B. pendula*	1	0.2	0	–	1	0.2	0	–
10	16	21.9	0	–	*B. pendula*	0	–	1	0.4	0		1	0.4
11	3	18.7	0	–	*L. sibirica*	18	15.0	0	–	4	3.3	0	–
12	10	31.2	2	6.2	*L. sibirica*	2	3.5	2	3.5	1	1.7	1	1.7
13	3	11.5	0	–	*L. sibirica*	9	7.4	0	–	0	–	0	–
14	11	19.3	0	–	*P. contorta*	9	18.4	0	–	7	14.3	0	–
15	16	40.0	0	–	*P. contorta*	11	5.8	0	–	10	5.3	0	–

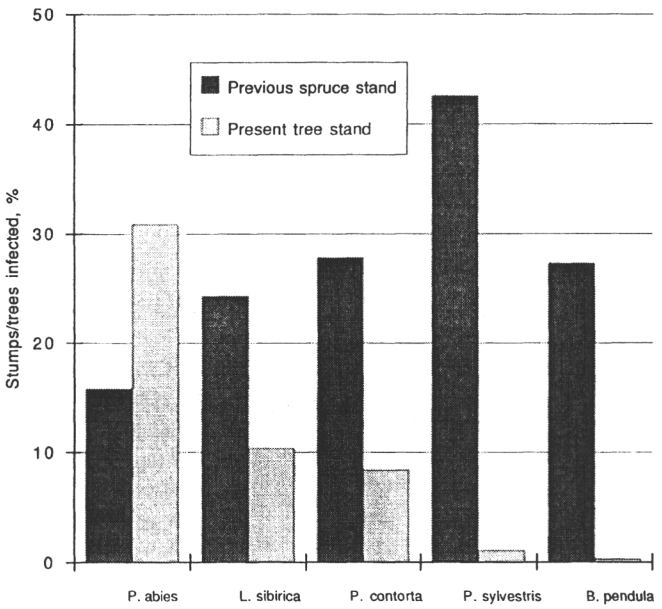


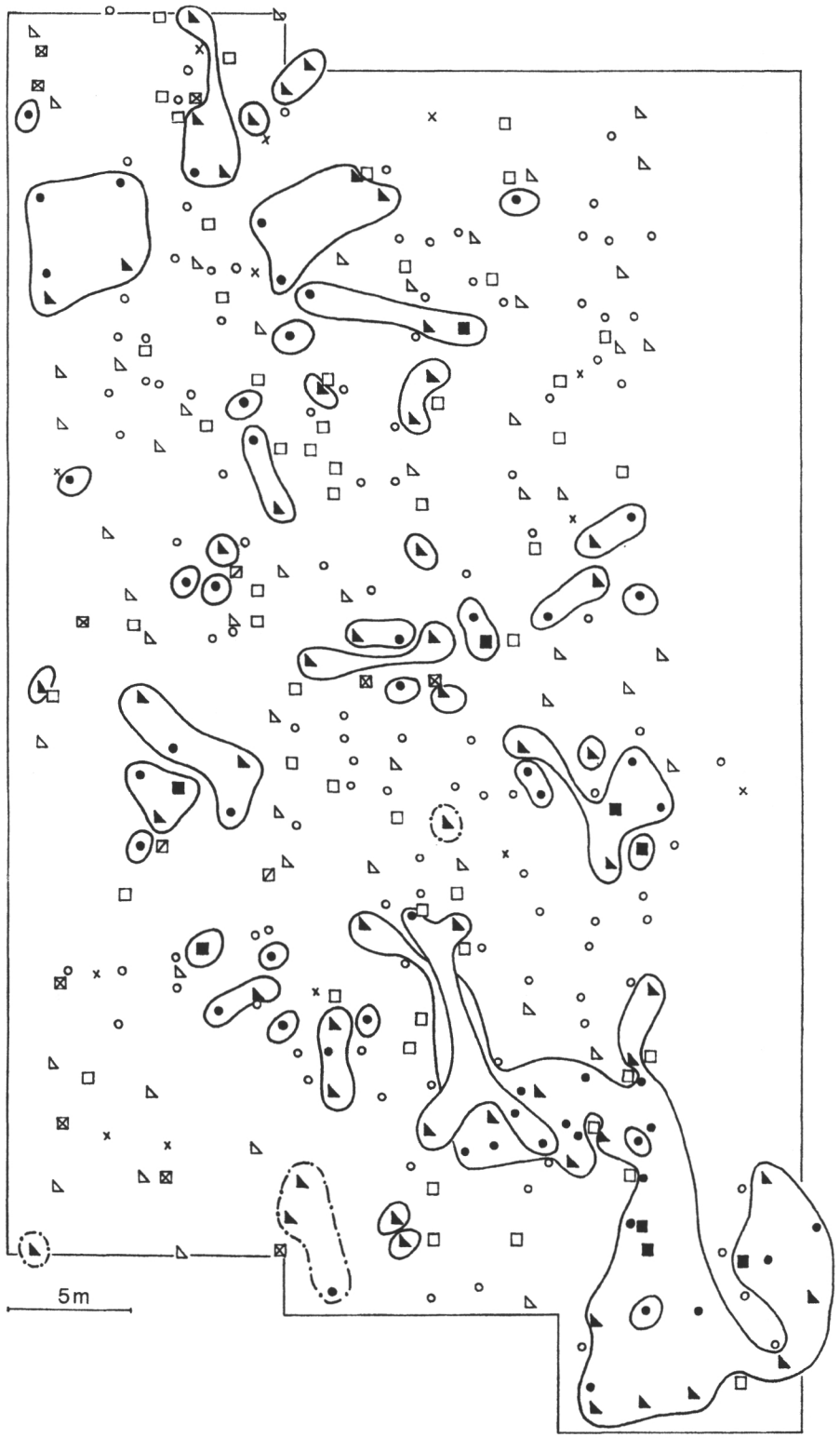
Fig. 2. Frequency of *Heterobasidion annosum* in the previous Norway spruce stands and in the subsequent stands of different tree species

4 Discussion

The oldest Norway spruce stumps investigated in this study were cut over 46 years ago. Because the mycelium of *H. annosum* was still alive in almost all stumps with signs of *H. annosum* decay, the fungus apparently can persist in an old stump for more than 50 years. After 40 years, however, *H. annosum* lives only in the interior of the largest stumps and the risk of vegetative spread of the fungus to surrounding trees is probably very small. Although the proportion of stumps colonized by *H. annosum* apparently decreases with increasing stump age, the correlation between decay frequency and stump age must be interpreted cautiously since the exact decay frequency of the stands at time of final felling is not known.

The maximum longevity of *H. annosum* in Norway spruce stumps has not previously been studied in the Nordic countries. However, to date, the longest documented survival of *H. annosum* in spruce stumps in southern Finland was 35 years (LAINE 1976). Under nearly comparable climatic conditions in Sweden, the fungus has been isolated from 28-year-old Norway spruce stumps (STENLID 1987). In Central Europe, where the decomposition of the stumps is more rapid than in Scandinavia, *H. annosum* has been found in spruce stumps cut *c.* 30 years earlier (HOLMSGAARD et al. 1961; SCHÖNHAR 1973; GREIG and PRATT 1976). The oldest stump with viable mycelium of *H. annosum*, a 68-year-old larch stump, was recorded in Great Britain (GREIG and PRATT 1976). Taking into account the slow decomposition of woody material in northern boreal forests, the longevity of *H. annosum* in Norway spruce stumps observed in this study is not surprising.

The stumps of large spruces, which are extensively colonized by *H. annosum* before felling, are particularly important infection sources in the subsequent tree stand. The low proportion of small stumps with *H. annosum* decay observed in this study may simply be due to the infrequent occurrence of the fungus in dominated and suppressed trees. It is also possible that, after felling of the tree, *H. annosum* is unable to compete with other decay fungi for the limited substrates in the stump. An incipient *H. annosum* infection in particular might be replaced by competing fungi.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In addition to the risk of infection by direct growth of the fungus through root contacts to the subsequent tree stand, the infected stumps increase the local inoculum level as sources of spore production that persist for decades. Although some spores can be spread by air currents over a distance of 500 km, a great majority of them are deposited within the stand (KALLIO 1970; STENLID 1994). The frequent presence of active fruit bodies (in every fifth infected stump over 25 years old) means an increased infection risk, particularly for trees growing close to a spore source. In older spruce and larch stands thinned once or twice, new genets of *H. annosum*, probably originating from spore infection during the life of the current stand, had already infected more trees than the old genets spreading vegetatively from stumps of the previous spruce stand.

Unfortunately, there is no information available about the exact decay frequency in the previous stands at time of final felling. Because of stump disintegration, the possibility of error in estimating the decay frequency of the previous stand increases as time passes since felling. Therefore, at least in the larch and spruce stands, the number of trees infected vegetatively from the previous stand generation is probably higher than presented in Table 2. The infection by spores of the stumps through the stump surface after final felling is also possible but unlikely, because all the cuttings in the stands studied had been carried out in the winter. Also, the total colonization of the stumps by *H. annosum* indicates that the infection was already present in these trees at the time of felling.

There is relatively little study material and it was collected from a restricted area; hence does not give complete answers to questions about the transfer of the S type of *H. annosum* to a subsequent tree stand. However, these experimental results are in quite good agreement with the earlier considerations based on the occurrence of the S type in different types of forests (KORHONEN and PIRI 1994).

Because of the variety of sampling methods used in this study, some caution is required when comparing the decay frequency of different tree species. Generally, the proportion of standing trees infected by *H. annosum* is underestimated. *H. annosum* frequency was determined most accurately in spruce stands where all standing trees were sampled. However, despite four or five bore-core samples taken per tree, some infected spruces (especially trees with incipient decay) remained undetected. In stands of other tree species samples were taken only from suspect trees with above-ground symptoms. This leads to underestimation of disease frequency, especially in larch stands. Unlike pine and birch, which show outwardly visible signs of disease at an early stage of infection, the disease is difficult to identify on larch. However, the error in the decay frequency of larch stands is reduced by the presence of thinning stumps, from which the decay is more reliably detected. Moreover, some additional bore samples were taken from growing larches close to old stumps colonized by *H. annosum*.

When planted on an infested site, Scots pine and silver birch proved to be the most resistant tree species. Because the susceptibility of Scots pine to the S group is confined to young trees between *c.* 5 and 25 years of age (KORHONEN 1978a; KORHONEN and PIRI 1994), it is unlikely that damage would continue in the stands studied.

A great majority of the earlier records on silver birches infected by *H. annosum* in Finland are of trees growing in a mixture with pine and attacked by the P group. Birches infected by the S group have very seldom been observed (KORHONEN and PIRI 1994). This study

Fig. 3. The genets of *Heterobasidion annosum* in a 53-year-old Norway spruce stand and in the stumps of the previous spruce stand. Present stand generation: white triangle, standing spruce; black triangles, standing spruce infected by *H. annosum*; white circles, spruce stump; black circles, spruce stump infected by *H. annosum*; cross, birch. Previous stand: white rectangle, spruce stump; black rectangle, spruce stump infected by *H. annosum*; crossed rectangle, birch stump; slashed rectangle, Scots pine stump. Trees containing the same S type genet are encircled by a solid line and trees containing the same P type genet are encircled by a broken line

shows that infection of birch by the S group is sometimes possible in areas where the birch grows close to the infected stump or the provenance is not well adapted to the site. In the stand regenerated with birch of very northern provenance, 47% of the trees were destroyed at the age of 40 years. In the majority of cases, the primary reason for mortality was no longer discernible. It appears possible that birches were attacked by *H. annosum* at an early stage of stand development. The number of infected trees may thus be greater than the seven trees observed. However, this case is exceptional and does not disprove the view that birch on a suitable site is very resistant to the S type of *H. annosum*.

A relatively high incidence of disease and effective vegetative spreading of the fungus from the previous to the following stand were observed in stands regenerated with lodgepole pine and Siberian larch. The high susceptibility of lodgepole pine to *H. annosum* has been reported by e.g. WAGN (1971, 1987) from a long-term field experiment in Denmark. Based on information about the condition of various lodgepole pine stands in Finland, VON WEISSENBERG (1975) regarded lodgepole pine as an unsuitable species for regeneration of spruce and pine stands infested by *H. annosum*. Unfortunately, the intersterility group of the fungus was not investigated in these earlier studies, although in the case of pine it was very probably P type. In an inoculation experiment by SWEDJEMARK and STENLID (1995), lodgepole pine seedlings showed moderate susceptibility to the P group and low susceptibility to the S group. The results of this study are in agreement with the field observations and suggest that young lodgepole pine is more susceptible than Scots pine to the S group of *H. annosum*.

Compared with other larch species, there are very few reports about the susceptibility of Siberian larch to *H. annosum*. Surveys in Russia show, however, that both *L. sibirica* and *L. sukaczewii* (Djil.) can suffer remarkable damage caused by *H. annosum* (NEGRUTSKIJ 1986; LEBEDEV and IVANOVA 1993). According to LAINE (1976), both young and mature Siberian larches can be attacked by the fungus. In a field experiment established on a site where diseased Scots pine (apparently infected by P type of *H. annosum*) was regenerated with different tree species, Siberian larch seedlings near infected pine stumps were killed soon after planting (KURKELA 1988). It is likely that the seedlings also become infected by the S type from old spruce stumps. Because in this study the disease incidence was determined only in mature larch stands, the proportion of infected trees in larch stands may be higher than the observed figure of 10.4%.

The tree species most heavily attacked by the S group of *H. annosum* in the present study was Norway spruce. Only on sites regenerated with spruce was the average frequency of infected trees clearly higher in the present compared with the previous spruce stand. On two sites having about the same rot frequency today, this will probably increase from the present figure and at the time of final cutting will be considerably higher than in the previous spruce generation. The frequency of infection by vegetative spread from the stumps of the previous spruce generation was six times higher in spruce stands than in lodgepole pine stands and 75 times higher in birch stands. Of all infected spruces, 37.0% were attacked by a genet originating from the previous tree generation. Although this is a minimum value, the proportion of trees infected from old stumps is unlikely to be as high as 65%, which, according to the model of STENLID (1987), is the probable rate of decayed trees infected from old stumps in spruce stands in Sweden. However, the lower rate of infection originating from old stumps in this study can at least partly be explained by the fact that the spruce stands were rather old (45–53 years) and established by natural regeneration, while the stands studied in Sweden were younger (25 and 28 years) and established by planting.

In this study only 1.1% of the *H. annosum* isolates collected from old Norway spruce stumps belonged to the P intersterility group. This is significantly less than the mean frequency of the P group in mature spruce forests of southern Finland. However, the low frequency of the P group is not necessarily a result of shorter or poorer survival of the P group in old stumps compared with the S group. It is more likely that the P group did not occur frequently in previous spruce stands on these sites. A high frequency of the P type

on Norway spruce appears to be connected with pine history on the site (KORHONEN et al. 1992; THOMSEN 1994). Unfortunately, little information is available on the history of the sites investigated.

The low frequency of the P group in the previous tree stand is also reflected in the low frequency of this group in the subsequent stand. Because the material of the this study did not include sites heavily infected by the P type, the results are not suitable for forecasting the development of infection on such sites which, however, are rather exceptional in southern Finland. In southern Sweden, VOLLBRECHT et al. (1995) investigated 40-year-old stands of several tree species established on a site where the previous tree species was Norway spruce heavily infected by the P type. Interestingly, new-growth Norway spruce was only moderately infected and Scots pine not at all.

The results of this study support the notion that Norway spruce stands infected by the S type of *H. annosum* can be safely regenerated with silver birch or Scots pine if that site is otherwise suitable for these tree species. In the case of pine, some mortality may occur in young plantations. If the site is regenerated to a pure spruce stand, losses caused by *H. annosum* tend to increase in the following spruce stand.

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Résumé

Passage du type S de Heterobasidion annosum des souches d'épicéa commun au peuplement suivant

La présence de *H. annosum* dans les souches et les arbres sur pied a été recherchée dans 15 sites forestiers du sud de la Finlande. Les peuplements précédents y avaient été de l'épicéa commun infecté par *H. annosum*, et les peuplements actuels étaient constitués de *Picea abies, Pinus sylvestris, P. contorta, Larix sibirica* ou *Betula pendula*, âgés de 8–53 ans. Parmi 712 souches d'épicéa des peuplements précédents examinées, 26,1% étaient infectées par le groupe S et 0,3% par le groupe P de *H. annosum*. Le champignon était vivant et les carpophores étaient actifs même chez des souches coupées depuis 46 ans. Dans les peuplements actuels, la proportion d'arbres avec pourriture racinaire augmentait dans les pessières et diminuait dans les peuplements des autres espèces. En moyenne, un même genet de type S avait infecté 3 épicéas à partir d'une souche, 0,5 *P. contorta*, 0,3 mélèzes, 0,05 pins sylvestres et 0,03 bouleaux. Bien que le bouleau soit généralement très résistant au type S de *H. annosum*, des arbres infectés ont été trouvés dans un site où une provenance très nordique avait été utilisée.

Zusammenfassung

Die Ausbreitung des S-Typs von Heterobasidion annosum von Fichtenstümpfen auf den nachfolgenden Baumbestand

In 15 Waldbeständen in Südfinnland wurde das Vorkommen von *H. annosum* in Stümpfen und in lebenden Bäumen untersucht. Dabei war der Vorbestand mit *H. annosum* befallene Fichte, und der aktuelle Bestand entweder *Pinus sylvestris*, *Pinus contorta*, *Larix sibirica*, *Betula pendula* oder *Picea abies* im Alter von 8–53 Jahren. Von 712 untersuchten Fichtenstümpfen des Vorbestandes waren 26,3% mit dem S-Typ und 0,3% mit dem P-Typ von *H. annosum* infiziert. Sogar in Stümpfen, die vor 46 Jahren geschnitten wurden, lebte der Pilz noch und bildete Fruchtkörper. In den Folgebeständen nahm der Anteil an infizierten Bäumen bei Fichte zu, bei den anderen Baumarten ab. Ein von einem alten Fichtenstumpf ausgehender S-Typ-Klon infizierte im Durchschnitt 3,0 Bäume des nachfolgenden Bestandes bei Fichte, 0,5 bei *Pinus contorta*, 0,3 bei *Larix sibirica*, 0,05 bei *Pinus sylvestris* und 0,03 bei *B. pendula*. Obwohl *B. pendula* im allgemeinen sehr resistent gegenüber dem S-Typ von *H. annosum* ist, wurden an einem Untersuchungsort mit gepflanzten Birken einer sehr nördlichen Provenienz infizierte Bäume gefunden.

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Paper II

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II

Infection of advance regeneration of Norway spruce by *Heterobasidion parviporum*

Tuula Piri and Kari Korhonen

Abstract: The incidence of *Heterobasidion* root rot in the advance regeneration of Norway spruce (*Picea abies* (L.) Karst.) was studied in nine stands at four different localities in southern Finland. The mean age of the unthinned advance regeneration on the 17 sample plots ranged from 14 to 44 years. On infested plots, the proportion of Norway spruce infected by *Heterobasidion* varied from 22.2 to 75.0% (mean 52.5%) in the overstory and from 1.8 to 68.2% (mean 21.1%) in the advance regeneration. The corresponding values on healthy-looking control plots were 0–6.7% (mean 5.9%) and 1.3–3.9% (mean 2.4%), respectively. Of the 138 *Heterobasidion* genets identified, 98.5% belonged to *Heterobasidion parviporum* Niemelä & Korhonen and 1.5% to *Heterobasidion annosum* (Fr.) Bref. s.s. The incidence of *Heterobasidion* root rot in advance regeneration was positively correlated with the mean size and age of the advance regeneration and the proportion of infected trees in the overstory and negatively correlated with the regeneration density. Vegetative spread through root contacts from overstory trees to the surrounding regeneration accounted for at least 53% of the *Heterobasidion* infections in the advance regeneration. The origin of the rest of the infections in advance regeneration remained unclear, but at least part of them may have started from spore infection on injured or dead roots. Our results suggest that, on sites infected by *H. parviporum*, advance growth of Norway spruce should not be used for regeneration even though the spruces look healthy and show no external signs of infection.

Résumé : L'incidence de la carie de racines causée par *Heterobasidion* chez la régénération préétablie d'épicéa commun (*Picea abies* (L.) Karst.) a été étudiée dans neuf peuplements situés dans quatre localités différentes du Sud de la Finlande. L'âge moyen de la régénération préétablie non éclaircie dans les 17 parcelles-échantillons variait de 14 à 44 ans. Dans les parcelles infectées, la proportion d'épicéa commun infectée par *Heterobasidion* variait de 22,2 à 75,0% (moyenne de 52,5%) dans l'étage dominant et de 1,8 à 68,2% (moyenne de 21,1%) dans la régénération préétablie. Les valeurs correspondantes dans les parcelles témoins où les arbres avaient l'air en santé étaient respectivement de 0–6,7% (moyenne de 5,9%) et 1,3–3,9% (moyenne de 2,4%). Des 138 souches d'*Heterobasion* identifiées, 98,5% correspondaient à *Heterobasidion parviporum* Niemelä & Korhonen et 1,5% à *Heterobasidion annosum* (Fr.) Bref. s.s. L'incidence de la carie de racine causée par *Heterobasidion* chez la régénération préétablie est corrélée positivement avec la dimension et l'âge moyens de la régénération préétablie ainsi que la proportion d'arbres infectés dans l'étage dominant et négativement avec la densité de la régénération. La propagation végétative du pathogène via les contacts racinaires à partir des arbres de l'étage dominant vers la régénération environnante explique au moins 53% des infections causées par *Heterobasidion* chez la régénération préétablie. L'origine des infections qui restent chez la régénération préétablie demeure incertaine. Cependant, quelques-unes au moins pourraient avoir été initiées par des spores sur des racines mortes ou blessées. Nos résultats montrent que, dans les sites infectés par *H. parviporum*, la régénération préétablie d'épicéa commun ne devrait pas être considérée comme telle même si l'épicéa semble en santé et ne montre aucun signe externe d'infection.

[Traduit par la Rédaction]

Introduction

Approximately every sixth mature Norway spruce (*Picea abies* (L.) Karst.) in southern Finland is damaged by butt rot. Almost 80% of the butt rot is caused by *Heterobasidion* (Tamminen 1985; Piri et al. 1990) consisting of two species: *Heterobasidion parviporum* Niemelä & Korhonen (= European S intersterility group of *H. annosum* s.l.) and *Heterobasidion annosum* (Fr.) Bref. s.s. (= European P intersterility group of *H. annosum* s.l.) (Niemelä and Korhonen 1998). The symptoms caused by these two species on spruce are very similar, and their relative frequencies in spruce forests of southern Finland are approximately 9:1 (Piri et al. 1990). Whereas *H. parviporum* is restricted almost only to spruce, *H. annosum* s.s. commonly attacks several tree species, pines in particular (Korhonen 1978; Korhonen et al. 1998). Other harmful root rot fungi of Norway spruce in Finnish forests, *Armillaria borealis* Marxmüller & Korhonen and *Armillaria cepistipes* Velenovský, infect fewer trees and affect less wood volume than *Heterobasidion* but may cause considerable losses locally. Like *Heterobasidion*, *Armillaria* also spreads into the next crop (Schönhar 1994).

After a diseased stand is felled, *Heterobasidion* can remain infectious in large spruce stumps for 40 years and spread to the next stand generation (Piri 1996). Consequently, the regeneration of infested sites may be a problem

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if the tree species is susceptible to the species of *Heterobasidion* that has infested the site (Stenlid 1987; Piri 1996).

The natural regeneration of Norway spruce has recently gained increased attention as a low-cost alternative to artificial regeneration. An important component of natural regeneration consists of advance growth. In naturally regenerated spruce stands in southern Finland, 60–80% of the trees have become established before the regeneration cutting (Hänninen et al. 1972; Räsänen et al. 1985). The most favorable places for the development of undergrowth are small, understocked openings, which, in mature spruce stands, are often a result of windthrow or the death of trees affected by root rot (Laine 1976). The health of the trees is an important factor when assessing their suitability in regeneration. However, detecting incipient *Heterobasidion* infection in the advance regeneration may be difficult.

Relatively little information is available about the susceptibility of young Norway spruce regeneration to root rot. Laine (1976) studied the occurrence of *Heterobasidion* in different host plants in Finland and only occasionally found the fungus on spruce saplings and young trees. Several other reports indicate that Norway spruces younger than 20–30 years of age, and with only a small proportion of heartwood in the stem, seldom become infected by *Heterobasidion* root rot (Rennerfelt 1957; Dimitri 1969; Werner 1973; Rieger 1995).

Moreover, naturally regenerated spruces are claimed to be less often and less severely affected by root rot than planted spruces (Weissen 1981; Graber 1996). The increased infection level in planted stands is supposed to be due to root damage during lifting in the nursery as well as damage caused by twisting or bending the roots during planting (Ouelette et al. 1971; Graber 1996). According to statistics collected by Falck (1930) in the Harz Mountains, the volume of butt rot was lower but the proportion of infected spruces higher in naturally regenerated than in planted spruce stands.

There are also investigations showing that advance growth of Norway spruce can be seriously infected. In Russia, near Moscow, 65% of the understory spruces were infected by *Heterobasidion* (Semenkova 1971). In Finland, Kangas (1952) investigated the root systems of young spruce wildings growing close to a decayed tree or stump and found that on the average 61% of the seedlings had root rot. In the majority of the infected seedlings the rot had reached the stem, and some seedlings were killed by the fungus. Kangas (1952) even suggests that root rot may prevent the regeneration of Norway spruce on heavily infested sites. Unfortunately, he did not describe the study material in a satisfactory way and identified the decay fungi only from a part of the material. Schönhar (1995) investigated the occurrence of primary infection in untended afforestation plantations of Norway spruce and found that suppressed spruces in particular became infected by *Heterobasidion*. Gramss (1992) reported that suppressed Norway spruces growing in the understory were more susceptible to colonization by inoculated wood-decay fungi, including *Heterobasidion*, than free-standing dominant spruces.

Current knowledge of the susceptibility of the advance growth of Norway spruce to root rot infection is insufficient for making the correct decisions in practical forestry. Utilization of the advance regeneration may increase the frequency of butt rot on heavily infected sites at least. In fact, mature spruce stands free of root and butt rot are exceptional in southern Finland. The present study was conducted to determine the level of root rot infection in advance regeneration stands on sites infected by *Heterobasidion*. The distribution of *Heterobasidion* genets on these sites was also examined to estimate the source of infection.

Materials and methods

Sample plots

The study was carried out on 17 sample plots established in nine Norway spruce stands at four different localities (Ruotsinkylä, 60°22′N, 24°29′E; Lapinjärvi, 60°40′N, 26°7–9′E; Sipoo, 60°28′N, 25°13′E; and Loppi 60°44′N, 24°29′E) in southern Finland. The experimental plots were situated in pure or mixed spruce forests in which a spruce understory had developed and the overstory was infested by *Heterobasidion*. Depending on the distribution of the advance regeneration, one to five circular sample plots were established in each stand. The plots averaged 20 m in diameter. Each sample plot contained 1–13 overstory trees or stumps colonized by *Heterobasidion*. Three of the plots (controls) were located in the healthy part of the stand where there were no signs of *Heterobasidion* root rot in the old rotation. In four of the stands the study was carried out before the removal of overstory trees, and in five of the stands after cutting. The time elapsed since final cutting varied from 1 to 5 years, except for Loppi where the advance regeneration had been released over 20 years earlier. The mean age of the overstory trees on the plots ranged from 60 to 118 years. The proportion of admixed tree species (silver birch, *Betula pendula* Roth; downy birch, *Betula pubescens* Ehrh.; and Scots pine, *Pinus sylvestris* L.) in the overstory varied from 0 to 72%. The sites were of the *Myrtillus* and *Oxalis–Myrtillus* forest site types, which are typical spruce sites in southern Finland (Cajander 1909). The stand characteristics are given in Table 1.

The average age of the advance-growth spruces varied from 14 to 44 years; average height, from 0.43 to 12.5 m (mean 2.8 m); and density, from 2200 to 53 400 trees/ha (mean 11 800). The proportion of admixed tree species on plots ranged from 4.6 to 69.4% (Table 1). Birch (*B. pubescens* and *B. pendula*) and rowan (*Sorbus aucuparia* L.) were the most common admixed tree species in the regeneration. White alder (*Alnus incana* (L.) Moench), European aspen (*Populus tremula* L.), and Scots pine occurred occasionally.

Measurements and sampling

The total growing stock and the stumps of varying age were mapped on each plot (Fig. 1). Seedlings smaller than 20 cm in height were excluded. Total height, diameter at stem base, and age of the advance-growth trees were recorded. The diameter and age of standing overstory trees (at breast height) and the stumps of cut overstory trees were determined. A total of 2199 advance-growth spruces and 243 standing trees or stumps of the previous tree generation were investigated. To determine the incidence of *Heterobasidion* infections, wood samples were taken aseptically with an increment borer from each overstory tree and stump of spruce and pine. In case the first sample taken from the butt was healthy, one or two additional samples were taken from different sides of the butt. If the cores taken from the butt were healthy, three to six main roots were sampled. Depending on the diameter of each root the sample core was taken at the point 20–40 cm from the root collar. The root system of all the advance-growth spruces was dug out by hand. In the laboratory the root systems were washed under running water and searched for lesions. Roots thicker than 3 mm in diameter were cut into 5-cm sections. The root sections were incubated in plastic bags at room temperature for about 1 month. The presence of *Heterobasidion* conidiophores and characteristic light-brown mycelial tufts of *Armillaria* spp. were examined

Table 1. Characteristics of the sample plots.

Sample plot	Plot No.	Site type[a]	Overstory: Spruce (%)[b]	Pine (%)	Birch (%)	Spruces infected by *Heterobasidion* (%)	Advance regeneration: Spruce/ha	Mean age of spruces (years)	Mixed tree species (%)[b]	Spruces infected by *Heterobasidion* (%)
Infected										
Sipoo	1.1	OMT	83.3	16.7	0	65.0	2 158	44	29.3	42.5
Sipoo	1.2	OMT	96.3	3.7	0	46.1	2 826	24	34.5	17.2
Lapinjärvi	2.1	MT	100	0	0	50.0	27 630	19	27.1	29.1
Lapinjärvi	2.2	MT	60.0	40.0	0	66.7	53 659	19	4.6	1.8
Lapinjärvi	2.3	MT	100	0	0	75.0	10 987	15	28.2	12.3
Lapinjärvi	2.4	MT	56.2	43.8	0	22.2	10 429	25	37.0	2.3
Ruotsinkylä	3.1	MT	60.0	0	40.0	33.3	9 153	40	13.2	30.4
Ruotsinkylä	4.1	MT	90.9	9.1	0	55.0	3 528	14	69.4	15.1
Ruotsinkylä	4.2	MT	76.0	24.0	0	47.5	6 646	16	68.3	15.0
Lapinjärvi	6.1	OMT	40.0	0	60.0	33.3	6 665	37	21.8	35.3
Lapinjärvi	7.1	MT	100	0	0	55.5	12 358	23	37.6	12.0
Ruotsinkylä	8.1	MT	38.9	38.9	22.2	71.4	4 531	32	43.7	68.2
Loppi	9.1	MT	85.7	0	14.3	66.7	3 331	40	21.8	53.5
Loppi	9.2	MT	57.1	14.3	28.6	75.0	2 241	35	42.8	41.7
Controls										
Lapinjärvi	2.5	MT	27.8	72.2	0	0	29 522	20	6.2	1.3
Lapinjärvi	5.1	MT	100	0	0	0	6 785	21	59.5	3.9
Lapinjärvi	5.2	MT	75.0	0	25.0	6.7	8 758	21	30.2	3.7

[a]Forest site types are according to Cajander (1909): OMT, *Oxalis–Myrtillus* type; MT, *Myrtillus* type.
[b]Values are percentages of the total number of trees.

weekly under a dissection microscope. Unidentified fungal cultures isolated from root sections were examined for clamp connections. The increment cores taken from overstory trees and stumps were cultured on malt extract agar (2% ME) and examined after 5–10 days for mycelia of *Heterobasidion* and *Armillaria*.

The distribution of *Heterobasidion* genets on each sample plot was identified with the aid of somatic compatibility reactions by pairing the fungal isolates collected from the same plot in all combinations on malt agar plates (Stenlid 1985). The distinction between *H. parviporum* and *H. annosum* s.s. was made with the aid of mating tests (Korhonen 1978).

Statistical analyses

Pearson's product–moment correlation analysis was used to determine the degree of association between all the studied variables (i.e., the proportion of infected spruce in regeneration and in the overstory; the proportion of spruce in regeneration and in the overstory; and the mean height, diameter, age, and density of the regeneration spruce). Multiple regressions based on a combination of independent variables were used to explain some of the variation of the dependent variable "percent infected spruce in regeneration." Logarithmic or square-root transformation was applied before the analyses to meet the prerequisites of distribution normality. Significance level in all tests was $\alpha = 0.05$. The tests were calculated with the programs included in the VAX/VMS 1990 version of the BMDP statistical package (BMDP, Inc. 1990).

Results

On the infested plots, *Heterobasidion* was by far the most frequent causal agent of root and butt rot. On average, 52.5% (range 22.2–75.0%) of the overstory spruce were infected by *Heterobasidion*. The proportion of advance-growth spruce infected by *Heterobasidion* varied from 1.8 to 68.2% (mean 21.1%). In the majority of the infected advance-growth spruce (78.7%), and especially in the young seedlings, *Heterobasidion* had colonized part of the root system but had not advanced up to the root collar. In 14.9% of the regeneration spruces the decay had spread into the stem, and 6.4% of the infected trees had been killed by the fungus.

On three healthy-looking control plots the proportion of infected spruces in regeneration was 2.6% (range 1.3–3.9%) (Table 1). However, the previous tree generation on the control plots had not been totally free of infection; on one plot *H. parviporum* was found in an old spruce thinning stump. On two other control plots, although *Heterobasidion* was not found in the old rotation, *H. parviporum* had infected some spruce seedlings in the regeneration.

Almost all the *Heterobasidion* genets (98.5%) proved to be *H. parviporum*. This species was isolated also from an old pine stump, which is unusual (Fig. 1). Only two *H. annosum* s.s. genets were found; both of them had infected one advance-growth spruce in each of two separate stands at Ruotsinkylä.

The second most common decay fungus was *Armillaria* spp. (*A. borealis* or *A. cepistipes*) isolated from 5.6% of the spruce overstory trees and 0.6% of the advance-growth spruces. Of all the cultures obtained from spruce advance regeneration, 85% represented *Heterobasidion*; 4%, *Armillaria* spp.; and 11%, other unidentified basidiomycetes with clamp connections.

The proportion of advance-growth spruce infected by *Heterobasidion* showed the strongest correlation with the mean height ($r = 0.712$, $p = 0.004$) and diameter ($r = 0.689$, $p = 0.006$) of the trees, indicating an increased infection rate with increasing tree size. The smallest spruce seedling infected by *H. parviporum* was only 27 cm high, had a diameter of 6 mm at stem base, and was 11 years old. The decay

Fig. 1. The genets of *Heterobasidion* on study plot 8.1. The mean age of advance-growth spruce was 32 years. Overstory: healthy spruce (□), spruce infected with *H. parviporum* (■), healthy pine (△), pine infected with *H. parviporum* (▲), birch (*); advance regeneration: healthy spruce (○), spruce infected with *H. parviporum* (●), deciduous trees (+). Trees containing the same genet are encircled by a line.

incidence also increased with increasing tree age ($r = 0.656$, $p = 0.011$). Significant positive correlation was also observed between the decay percentages in the overstory and regeneration ($r = 0.633$, $p = 0.006$). A weak but significant negative correlation was found between the infection rate and regeneration density ($r = -0.587$, $p = 0.027$); the proportion of infected trees slightly decreased with increasing density. The other stand characteristic variables showed no significant correlation with the incidence of *Heterobasidion* root rot (Table 2).

When combined, the variables "height of advance-growth spruces" and "percent infected spruces in overstory" accounted for up to 67% of the variation in "percentage of infected advance-growth spruces" ($R^2 = 0.674$, $n = 17$, $p < 0.005$, $y = 0.142 + 4.168x_1 + 0.364x_2$). The other independent variables were not included in the regression equation, because they were either highly correlated with tree height (i.e., tree diameter and tree age) or did not significantly increase the coefficient of determination (i.e., stand density).

The average number of trees infected by the same genotype of *Heterobasidion*, i.e., the mean size of the fungal genets, was three. Of the 138 identified *Heterobasidion* genets, 66.7% included only one tree. On the other hand, some large genets consisting of several trees from both tree generations were also found. The largest genet had infected 13 trees in the previous rotation and 33 trees in the regeneration. Overall, 53.3% of all the infected regeneration spruces were infected by a genotype that was also isolated from the overstory, indicating that the fungus has spread vegetatively through root contacts from the old generation to the surrounding regeneration. On average, each genet found in an overstory tree was also found in 2.4 regeneration trees. The spatial distribution of the *Heterobasidion* genets on one study plot is presented in Fig. 1.

Discussion

In the root rot centres, 21% of the advance-growth spruces were infected by *Heterobasidion*, almost all of them by *H. parviporum*. Typically the infection was restricted to a small part of the roots, and the young trees showed no visible aboveground symptoms of root rot. More than half of the decayed regeneration spruces (at least 53%) were infected through root contacts from the previous rotation.

To our knowledge, the genetic structure of *Heterobasidion* populations has not earlier been studied in unthinned naturally established Norway spruce stands. Studies in older, thinned Norway spruce stands have shown that the rate of secondary infection from old-growth stumps can vary considerably between individual stands. In three, 45- to 53-year-old naturally regenerated spruce stands in southern Finland, 11–79% of infections originated from the previous stand (Piri 1996). In about 30-year-old planted stands in Sweden, 52–73% of the decayed trees were infected by *Heterobasidion* (*H. parviporum* and *H. annosum* s.s.) originating from stumps of the previous generation (Stenlid 1987). In the present material, the proportion of secondary infections originating from the overstory may actually be greater than 53% because, in some cases, the fungus could have spread from small, currently fully decomposed thinning stumps to nearby regeneration. Moreover, some of the genets at the margin of the plot may originate from outside the study area, even if the risk was minimized by sampling all the trees and stumps bordering the plot.

At least some of those *Heterobasidion* genets that were isolated from the advance regeneration, but not from the previous rotation, have probably started from spore infections on injured roots. A close genetic relationship (unclear demarcation lines between paired mycelia) was frequently observed between these genets. This relatedness is probably a result of multiple infections by spores originating from the same fruit body. The importance of primary spore infection for the build-up of *Heterobasidion* root rot in advance regeneration is supported by the findings of Schönhar (1995), who found that suppressed spruces were susceptible to spore infection by *Heterobasidion*. The more superficial root system and more frequent root mortality of undergrowth spruces compared to other trees (Sirén 1951) may increase the risk of primary infection. The entry route for supposed primary infection was not thoroughly investigated in the present study. Dying roots are a possible infection route. All visible wounds on roots of advanced spruces were recorded, but they re-

Table 2. Correlation matrix (r value) between the percent advance-growth spruces infected by *Heterobasidion* (HeAR), percentage of overstory spruces infected by *Heterobasidion* (HeOS), mean age of advance regeneration (AgeAR), mean height of advance regeneration (HeightAR), mean diameter of advance regeneration (DiamAR), density of advance regeneration (DensAR), percentage of spruces of total number of trees in advance regeneration (SprAR), and percentage of spruces of total number of trees in overstory (SprOS).

	HeAR	HeOS	AgeAR	HeightAR	DiamAR	DensAR	SprAR	SprOS
HeAR	1.000							
HeOS	0.633**[a]	1.000						
AgeAR	0.656*	–0.047ns	1.000					
HeightAR	0.712**	0.179ns	0.844***	1.000				
DiamAR	0.689**	0.138ns	0.874***	0.994***	1.000			
DensAR	–0.587*	–0.217ns	–0.444ns	–0.443ns	–0.410ns	1.000		
SprAR	0.001ns	0.145ns	–0.499ns	–0.305ns	–0.341ns	–0.408ns	1.000	
SprOS	–0.292ns	0.087ns	–0.512ns	–0.483ns	–0.468ns	0.052ns	0.335ns	1.000

Note: ***, $p < 0.001$; **, $p < 0.01$; *, $p < 0.05$; ns, not significant ($p \geq 0.05$).
[a] $n = 17$; in all other cases $n = 14$.

vealed mostly infections of blue-stain fungi. Infections through sapling stumps are excluded because no precommercial thinnings had been carried out in the regeneration.

Correlation analysis revealed that size and age are the most relevant characteristics with respect to disease incidence in the advance regeneration of Norway spruce. The youngest 6- to 10-year-old seedlings were healthy, but the decay increased continuously as the seedlings became older. In Germany, Rieger (1995) investigated the predisposition of natural spruce seedlings to *Heterobasidion* root rot, mainly caused by *H. parviporum*, and found that seedlings younger than 10 years rarely became infected even when growing in close contact with *Heterobasidion* mycelium or fruit bodies. In accordance with our results, he also found that most of the infections on spruce seedlings were confined to a small part of the root system.

In contrast with our results, several earlier studies suggest that Norway spruces younger than 20–40 years are almost completely resistant to *Heterobasidion* (Rennerfelt 1957; Dimitri 1969; Werner 1973; Laine 1976). However, these studies did not deal with advance regeneration, and it is possible that advance regeneration suffering from competition may become infected at an earlier age and more seriously than free-growing trees, as stated by Gramss (1992) and Schönhar (1995). The substantially higher proportion of heartwood, which lacks active resistance to infection, in suppressed than dominant spruces (Sellin 1993) may increase the decay risk. Another possibility is that the resistance of young spruces was overestimated because, in most of the earlier studies, only the aboveground part of the tree was examined for infections and incipient infections in the roots may have been overlooked.

Investigations carried out in the Nordic countries have shown that an admixture of Scots pine or birch in mature Norway spruce stands slightly reduces the decay frequency of spruce (Rennerfelt 1946; Piri et al. 1990; Solheim et al. 1994). An investigation carried out in southern Finland showed that the average size of the fungal genets was slightly smaller in mixed than in pure spruce stands, indicating that admixed trees may restrict the vegetative spread of *Heterobasidion*, possibly by reducing the number of root contacts between spruces (Piri et al. 1990). So far, no information is available about the effects of other trees species on the root rot frequency of Norway spruce in the early stage of rotation. In our study material, no correlation was found between the proportion of admixed tree species and the incidence of *Heterobasidion* root rot. This is understandable because vegetative spread through root contacts was rather uncommon between advance-growth spruces. The mean size of the genets found only in advance regeneration was 1.4 trees. The situation should be different if tree species resistant to *H. parviporum*, i.e., broad-leaved trees, surround the diseased stumps up to a distance of several metres.

Our results indicate that, in southern Finland, where *Heterobasidion* root rot is a common disease of Norway spruce, special care should be exercised when regenerating spruce forest through advance growth. In practical forestry it is important to recognize the signs of *Heterobasidion* root rot in the previous tree generation. Advance growth of Norway spruce should not be used for regeneration on heavily infested sites even though the undergrowth trees look healthy, have good growth, and could otherwise provide a good starting point for the future stand. It is advisable to regenerate infected sites with birch or Scots pine, which are less susceptible to *H. parviporum* than Norway spruce. However, the change of tree species is not always possible. There is some indication that planted spruces could be more resistant than advance regeneration to *Heterobasidion* infection originating from the previous spruce generation (Vollbrecht and Stenlid 1999; Rönnberg and Jørgensen 2000), but more information is needed about the susceptibility of planted and sown Norway spruces to *Heterobasidion* root rot.

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Paper 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.

III

Early development of root rot in young Norway spruce planted on sites infected by *Heterobasidion* in southern Finland

Tuula Piri

Abstract: Root rot infections in Norway spruce (*Picea abies* (L.) Karst.) regeneration, planted after the clear-cutting of spruce on sites infested by *Heterobasidion*, were investigated on 21 experimental plots in eight 2- to 23-year-old plantations. *Heterobasidion* root rot became evident about 10 years after planting and the proportion of infected spruces increased steadily with plantation age. The average number of planted spruces infected per old decayed stump was 0.2 trees in 2- to 9-year-old plantations, 0.8 trees in 11- to 15-year-old plantations, and 1.8 trees in 20- to 23-year-old plantations. About 10 and 20 years after planting, 7 and 23% of the planted spruces in the disease centers were infected by *Heterobasidion*. *Heterobasidion parviporum* Niemelä & Korhonen, and *Heterobasidion annosum* (Fr.) Bref. s. str. caused 98 and 2% of the *Heterobasidion* infections in the previous spruce rotation, and 96 and 4% in the spruce regeneration, respectively. In all, 71% of the infected regeneration trees were attacked by a *Heterobasidion* genet that was also isolated from the stumps of the previous tree stand. *Armillaria* species (*Armillaria borealis* Marxmüller & Korhonen and *Armillaria cepistipes* Velenovský) were isolated from 7% of the planted spruces.

Résumé : Les infections causées par les champignons de carie de racines chez la régénération d'épicéa commun (*Picea abies* (L.) Karst.), plantée après que l'épicéa ait été coupé à blanc dans des sites infestés par *Heterobasidion*, ont été étudiées dans 21 parcelles expérimentales établies dans huit plantations âgées de 2 à 23 ans. La carie de racines causée par *Heterobasidion* est devenue évidente environ 10 ans après la plantation et la proportion d'épicéas infectés a augmenté régulièrement avec l'âge de la plantation. Le nombre moyen de plants d'épicéa infectés par vieille souche cariée est de 0,2 arbres dans les plantations âgées de 2 à 9 ans, 0,8 arbres dans les plantations âgées de 11 à 15 ans et 1,8 arbres dans les plantations âgées de 20 à 23 ans. Environ 10 et 20 ans après la plantation, 7 et 23 % des arbres plantés dans les centres d'infection étaient infectés par *Heterobasidion*. *Heterobasidion parviporum* Niemelä & Korhonen et *Heterobasidion annosum* (Fr.) Bref. s. str. ont causé respectivement 98 et 2 % des infections chez les épicéas de la révolution précédente et 96 et 4 % dans la régénération d'épicéa. En tout, 71 % des plants infectés parmi la régénération ont été attaqués par un genêt de *Heterobasidion* qui était aussi isolé des souches des arbres du peuplement précédent. Des espèces d'*Armillaria* (*Armillaria borealis* Marxmüller & Korhonen et *Armillaria cepistipes* Velenovský) ont été isolées de 7 % des plants d'épicéa parmi la régénération.

[Traduit par la Rédaction]

Introduction

Heterobasidion root rot is a serious threat when regenerating Norway spruce (*Picea abies* (L.) Karst.) stands in southern Finland. The majority (ca. 90%) of the cases of this disease in Finland are caused by *Heterobasidion parviporum* Niemelä & Korhonen (= European S intersterility group of *Heterobasidion annosum* s. l.). In some localities, especially on sites with a pine history, spruce can also be attacked by *Heterobasidion annosum* (Fr.) Bref. s. str. (= European P intersterility group) (Korhonen and Piri 1994; Niemelä and Korhonen 1998). On old spruce sites, where *Heterobasidion* root rot occurs abundantly, changing the tree species is the best method to control decay losses in the subsequent tree generation. Scots pine (*Pinus sylvestris* L.) and silver birch (*Betula pendula* Roth), which together with Norway spruce are the most important commercial tree species in Finland, are fairly resistant to *H. parviporum* and are recommended for the regeneration of infested sites (Korhonen 1978*a*; Piri 1996). In practical forestry, however, most spruce sites are too fertile for the production of high-quality pine timber. Furthermore, both birch and pine plantations are often impractical because of the high risk of browsing damage by elk (*Alces alces*) (Heikkilä and Raulo 1987; Lääperi and Löyttyniemi 1988). In such cases, Norway spruce may be the preferred tree species even on infested sites.

Several earlier investigations have demonstrated, however, that the incidence of *Heterobasidion* butt and root rot tends to increase in successive spruce rotations (e.g., Jørgensen et al. 1939; Holmsgaard et al. 1961; Schönhar 1973; Yde-Andersen 1978). More recent studies based on the identification of the fungal genets have also shown that the old infected stumps of the previous spruce generation may be important infection sources in the next rotation, and that young trees growing next to stumps from the previous rotation may suffer from butt rot already before the first thinning (Stenlid 1987; Piri 1996; Piri and Korhonen 2001).

Contrasting results have also been reported. Recent investigations in planted Norway spruce stands in southern

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Sweden and Denmark did not show any correlation between the incidence of butt rot in the present and previous spruce rotations. Even on sites heavily infected by *Heterobasidion*, less than 10% of the planted spruces showed visible decay at stump height at the first thinning (Vollbrecht et al. 1995; Vollbrecht and Stenlid 1999; Rönnberg and Jørgensen 2000). Consequently, Rönnberg and Jørgensen (2000) concluded that the transfer of *Heterobasidion* from the previous rotation is not an important factor in the buildup of infection in the subsequent rotation.

Whether the initial spreading of *Heterobasidion* into the subsequent spruce stand can be affected by the method of regeneration is not well understood. Some studies suggest that naturally regenerated spruces are less often and less severely affected by root rot than planted spruces (e.g., Weissen 1981; Graber 1996). On the other hand, advance-growth spruces, i.e., spruces established naturally under a spruce overstory before the regeneration felling, can be seriously infected by *Heterobasidion* (Semenkova 1971). In southern Finland, where advance growth forms an important part of the restocking material in naturally regenerated spruce stands (Hänninen et al. 1972), on average, 21% (max. 68%) of the advance-growth spruces under a decayed overstory were infected by *Heterobasidion* before the first thinning (Piri and Korhonen 2001). The utilization of advance regeneration may thus promote the spreading of *Heterobasidion* root rot to the next tree generation.

Several factors such as the decomposition rate of infected stumps (Kuhlman and Ross 1970; Kuhlman 1986; Piri 1996), competition with other decay fungi (Greig 1962), frequency of root contacts (Kuhlman 1973; Redfern 1984), age of the *Heterobasidion* genets (Stenlid and Redfern 1998), and physiological condition of the regeneration trees (Lindberg and Johansson 1992) may affect the spreading capacity of *Heterobasidion* root rot from the previous to the next tree generation. It is possible that suppression by the overstory increases the susceptibility of the understory trees to infection, and hence the spruce regeneration established after clear-cutting may be more resistant to root rot than advance-growth regeneration. So far, infection of free-growing regeneration, i.e., planted, sown, or from adjacent stand seeded stands, has not been studied under Finnish conditions. Owing to the differences in climatic conditions, forest site history, and study methods, the results obtained from planted stands in southern Sweden and Denmark (Vollbrecht et al. 1995; Vollbrecht and Stenlid 1999; Rönnberg and Jørgensen 2000) are indicative but not directly applicable in predicting the development of the disease in planted spruce stands in Finland.

The aim of this study was to investigate the early development of *Heterobasidion* root rot in young, unthinned spruce plantations established on infested sites after the clear-cutting of Norway spruce. To obtain detailed information about the spread of the disease from the previous spruce rotation, the origins and spatial distribution of the *Heterobasidion* genets were determined. Special emphasis was placed on incipient infections in the root system of young spruces.

Material and methods

Sample plots

A total of 24 sample plots were established in eight Norway spruce plantations in southern Finland. The plantations are situated in Solböle (59°58′N–60°02′N, 22°56′E–23°06′E), Loppi (60°14′N, 24°30′E), Sipoo (60°16′N, 25°28′E), Ruotsinkylä (60°14′N, 25°00′E), and Lapinjärvi (60°47′N–60°51′N, 26°08′E–26°09′E). The previous rotation on the sites had been Norway spruce infected by *Heterobasidion*. Following clear-cutting and site preparation (harrowing or, on a few sites, mounding), each site had been planted with 2- to 5-year-old, container or bare-rooted seedlings of Norway spruce. The planting density was 2000–2500 plants/ha.

The age of the experimental plantations ranged from 2 to 23 years (Table 1). Most of the plantations had been cleaned at least once, but no thinning had been carried out. Birch (*Betula pendula* and *Betula pubescens* Ehrh.) and rowan (*Sorpus aucuparia* L.) sprouts and seedlings were common mixed-tree species among the planted spruces. Naturally regenerated spruces and pines occurred on several of the plots. According to the Finnish classification, the sites were of the *Myrtillus* or *Oxalis–Myrtillus* site type (Cajander 1949).

Circular experimental plots were marked out in the disease centers around stumps that were affected by butt rot caused by *Heterobasidion*. As the aim was to include all the diseased spruces around an infected stump within the plot, the radius of the plots varied. To assure that this was in fact the case, at least one healthy tree was included between the outermost infected tree and the plot border. The radius of the circular plots varied from 5 to 10 m, and the number of infected stumps within a plot varied from 1 to 11 (mean 3.3). Twenty-one plots were located in disease centers, and three control plots (radius 5 m) were located in the healthy part of the plantations where no signs of infection had been observed in the earlier tree generation.

Measurements and sampling

All the standing trees more than 0.3 m in height and all the stumps on the sample plots were tagged. Tree species, origin (planted or natural), height, and location (direction and distance from plot center) were recorded for each standing tree, including naturally regenerated trees. In most of the plantations the planted spruces had been marked with a plastic stick at planting.

When such sticks were absent, the planted trees were distinguished from naturally regenerated trees on the basis of their location and size. Location, species, and diameter of the stumps of the previous tree generation were recorded within the plots and also on a 5 m broad zone around the plot. The total number of regeneration Norway spruces sampled was 764, of which 594 were planted and 170 were naturally regenerated.

The presence of *Heterobasidion* in the present and previous tree generation was determined by sampling all the coniferous trees and stumps on the plot. The root system of planted spruces younger than 20 years of age was dug out, washed, and examined for infections as described in Piri and Korhonen (2001). In over 20-year-old plantations three to five main roots of each standing conifer were excavated and wood samples (one to three samples from each root) were taken aseptically with an increment borer. The sample cores were taken at a point 10–40 cm from the root collar, depending on the diameter of the root. In addition to root samples,

Table 1. Characteristics of the sample areas.

Locality	No. of plots	Age of plantation (years)	Trees/ha: Planted spruces	Trees/ha: All conifers	Proportion of broad-leaved trees (%)	No. of planted spruces investigated	Planted spruces infected by *Heterobasidion* (%)	No. of planted spruces infected per decayed old stump	Planted spruces infected by *Armillaria* (%)
Solböle	1	2	2480	3106	48.0	11	0	0	0
Lapinjärvi	2	7	1445	3070	80.0	97	1.0 (0–2.4)	0.1	3.1 (0–5.5)
Solböle	3	9	2075	4845	75.2	30	6.7 (0–18.2)	0.3	10.0 (0–20.0)
Loppi	3	11	2220	2827	75.5	58	6.9 (0–20.0)	0.4	3.4 (0–5.6)
Lapinjärvi	1	15	650	650	33.3	22	13.6	0.8	18.2
Sipoo	3	20	2090	2820	43.5	97	13.4 (0–23.3)	1.2	2.1 (0–3.3)
Loppi	5	22	1470	2505	76.7	79	30.4 (12.5–76.9)	4.8	0
Ruotsinkylä	3	23	1435	1435	11.3	144	26.4 (11.9–39.1)	1.6	16.7 (6.5–28.2)
Controls									
Loppi	1	11	1897	1897	21.7	18	0	0	0
Sipoo	1	20	2355	2590	42	18	0	0	0
Loppi	1	22	1827	2538	63.8	20	0	0	0

Note: Values in parentheses are ranges.

two to four core samples were taken from different sides of the butt of the tree. Because the decay in old spruce stumps of the previous generation was already at an advanced stage, the stumps (butt and major roots) were sampled using an axe and a saw. The extent of decay in each stump was estimated visually as the proportion of stump wood colonized by *Heterobasidion* (typical white pocket rot) on the stump top and in the main roots.

The wood samples were transferred to 2% malt extract agar (MEA) in Petri dishes, incubated at room temperature, and examined microscopically for the presence of *Heterobasidion* and *Armillaria* mycelia at 3-day intervals. All the fungi growing out of the wood samples were subcultured on MEA. Unidentified fungal cultures were examined for clamp connections, but no further identification was made.

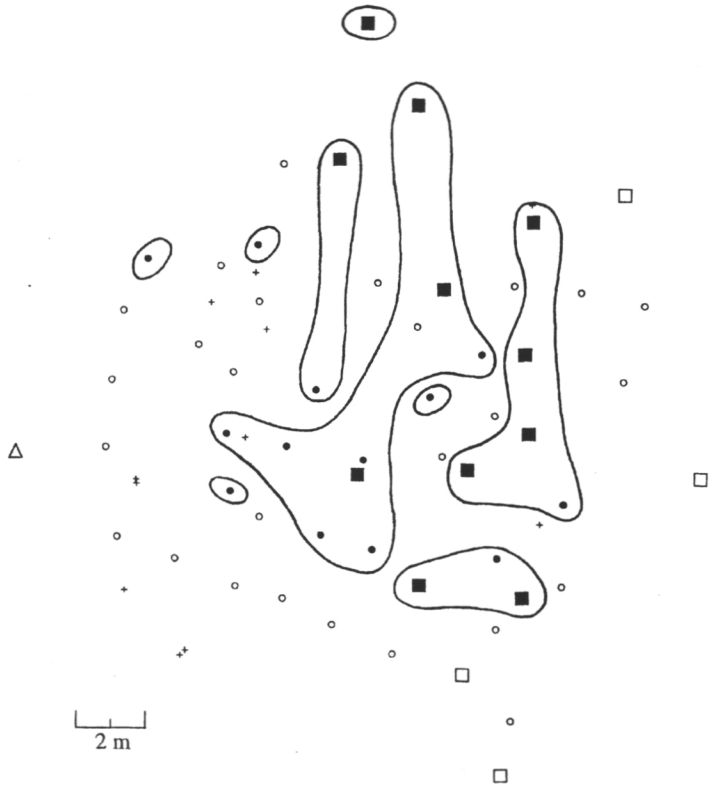
To estimate the upward extension of the decay in the tree stems, 22- and 23-year-old planted spruces were felled on seven plots in the Loppi and Ruotsinkylä experimental areas, and the extent of the decay column up the stem was measured. The measurements included the diameter of the decay at stump height, the highest point of visible discoloration, and the highest point of *Heterobasidion* mycelium.

The *Heterobasidion* genets present on each sample plot were identified with the aid of the somatic compatibility reaction (Stenlid 1985). First, all the fungal strains isolated from one tree or stump were paired with each other on MEA plates to determine whether one or more genotypes were present. After that, the isolates collected from the same sample plot were paired in all combinations to determine the size of the fungal genets (Fig. 1). The identification of *Heterobasidion* and *Armillaria* species was made with the aid of mating tests (Korhonen 1978*a*, 1978*b*).

Statistical analyses

The mean value of plots established in the same plantation was considered the experimental unit when assessing the correlations between both "percent planted spruces infected" or "number of spruces infected per decayed stump" and independent variables depicting stand characteristics (i.e., mean age and height of the planted trees and proportion of broad-leaved trees on the plot). The values of "number of spruces infected per decayed stump" were transformed ($x' = \log_{10}(x + 1)$) to normalize the data. The correlation between the diameter of the decay at stump surface and the height of the decay column in the stem was calculated from pooled data from each plot. Three 20- to 23-year-old stands (pooled data of 11 plots) were selected for analysing the relationship between the disease incidence of the previous and the present tree rotations. A decay index, $DI = x_1 + \ldots + x_n$, where x is the area of stump surface colonized by *Heterobasidion* (cm^2), and n is the number of infected stumps per plot (calculated per 0.01 ha), was used to describe the disease incidence in the previous rotation. The relationships were investigated using Pearsson's product–moment correlation analysis. Infection rates between planted spruces and naturally regenerated spruces were compared using the paired t test. The average number of spruces infected per decayed stump in different age-classes was compared using non-parametric tests (Kruskal–Wallis test followed by Mann–Whitney test). The significance level for all statistical tests was $P = 0.05$. The data were analysed in SPSS for Windows

Fig. 1. Genets of *Heterobasidion* in a 23-year-old spruce plantation. Stumps of the previous rotation: healthy spruce (□), spruce infected by *Heterobasidion* (■), healthy pine (Δ). Present stand: healthy, planted spruce (○), planted spruce infected by *Heterobasidion* (●), deciduous tree (+). Trees containing the same genet are encircled by a line. Not all healthy trees surrounding the genets are marked in the figure.



version 10.0 (SPSS Inc. 1999), and the plot maps were generated in Origin™ version 4.0.

Results

Heterobasidion was isolated from 15.8% of the planted spruces on the 21 sample plots established on disease centers. In plantations of age-classes 2–9, 11–15, and 20–23 years, *Heterobasidion* was isolated from 2.2, 8.8, and 23.4% of the planted spruces, respectively. No infections were found in planted spruces on seven plots (2–20 years old), even though they were growing close to old spruce stumps colonized by *H. parviporum*. In 28.2% of the infections, *Heterobasidion* was present in a part of the root system, but it had not reached the butt of the tree. In three cases (3.5%) the fungus had colonized the root system totally and killed the tree.

Of the 162 naturally regenerated spruces growing on infested plots, 8.6% were infected by *Heterobasidion*. Although the overall proportion of infected trees was lower among the naturally regenerated spruces than among the planted spruces, the paired test did not show any statistically significant difference in infection rate between the natural and planted spruces. No infected regeneration trees were found on the three control plots established in the healthy part of the stands.

Heterobasidion parviporum was the dominant species of *Heterobasidion* in all the stands. Its proportion was 98.4% in the previous rotation and 95.1% in the regeneration; the other cases were all *H. annosum* s. str. In addition to the spruces, *H. parviporum* was isolated from two Scots pine saplings and from one common juniper (*Juniperus communis* L.).

Decay caused by *Armillaria* spp. was found on 12 plots. Two *Armillaria* species were present: *Armillaria borealis* Marxmüller & Korhonen (83%) and *Armillaria cepistipes* Velenovský (17%). On six plots the number of planted spruces infected by *Armillaria* was higher than the number of spruces infected by *Heterobasidion* (Table 1). Altogether, *Armillaria* was isolated from 11.1% of the old spruce stumps, from 7.1% of the planted spruces (range 0–28.2%), and from 3.1% of the naturally regenerated spruces. No other basidiomycetes were isolated from the regeneration trees. The proportion of unidentified basidiomycetes in old stumps was small (total of 12 isolates).

The height of the decay column within the spruce stems was measured in 27 randomly selected infected trees on seven plots in 22- and 23-year-old plantations. The fre-

quency of infected trees on these plots varied from 11.9 to 76.9%. On average, visible decay had extended a distance of 170 cm up the stems of infected trees. The maximal distance was 350 cm. Mycelium of *Heterobasidion* was found approximately 30 cm in advance of the visible decay. The height of the stem decay correlated significantly with the cross-sectional area of the decay at stump height ($r = 0.800$, $P = 0.001$). In 25 stems the decay was caused by *H. parviporum* (mean height of the decay 174 cm), and in two stems by *H. annosum* s. str. (mean height 85 cm).

A total of 66 old spruce stumps were colonized by *Heterobasidion*. Only one *Heterobasidion* genotype was isolated from 65 stumps, but one stump was colonized by two different genotypes of *H. parviporum*. Both *Heterobasidion* and *Armillaria* were isolated from eight spruce stumps. Root rot had spread to the surrounding spruce regeneration (planted and naturally regenerated) from 58% of all the stumps infected by *Heterobasidion*. The corresponding figure was 62% for stumps infected by *Heterobasidion* alone, and 25% for stumps infected by both *Heterobasidion* and *Armillaria*.

A total of 71.1% of the planted spruces with a *Heterobasidion* infection were attacked by a genotype that was also isolated from stumps of the previous tree stand. The origin of the other infections in spruce regeneration could not be determined with any certainty. The mean number of trees and stumps infected by one genotype of *Heterobasidion* was 2.3, but 68% of the genets were limited to a single tree or stump. The largest genet detected included five old stumps and 10 planted spruces.

The mean height ($r = 0.938$, $P = 0.001$) and age ($r = 0.925$, $P = 0.001$) of the planted spruces showed the highest correlations with the frequency of *Heterobasidion* infection. Also the number of planted spruces infected by *Heterobasidion* per decayed stump of the previous rotation increased with increasing age ($r = 0.911$, $P = 0.002$) and height ($r = 0.912$, $P = 0.002$) of the stand (Fig. 2). For the whole material, the mean number of infected, planted spruces per decayed stump of the previous rotation was 1.24. The corresponding ratio was 0.2 in plantations of age-class 2–9 years, 0.8 in age-class 11–15 years, and 1.8 in age-class 20–23 years. The difference in disease frequency was statistically significant between age-classes 2–9 and 20–23 years, and between age-classes 11–15 and 20–23 years.

The relationship between the inoculum potential of the previous rotation, expressed as the stump surface area colonized by *Heterobasidion* per hectare, and the proportion of planted spruces infected by *Heterobasidion*, was calculated from data collected in three stands of about the same age (20–23 years). The infection rate tended to increase with increasing inoculation potential (Fig. 3). When the plot with an exceptional high infection frequency (76.9%) was omitted, the correlation was statistically significant ($r = 0.672$, $P = 0.047$). No relationship was found between the proportion of planted spruces infected and the proportion of mixed broadleaf trees growing in a spruce plantation, or between the proportion of infected spruces and density of the spruces.

Discussion

Our results indicate that, in Norway spruce plantations established on infested spruce sites in southern Finland, damage by *Heterobasidion* root rot begins about 10 years after planting, and that infection originating from the old rotation tends to increase steadily up until the first thinning. A number of other studies have also demonstrated that *Heterobasidion* root or butt rot has become firmly established in 10- to 20-year-old spruce regeneration (Rönnberg and Jørgensen 2000; Piri and Korhonen 2001). The conclusions that spruces younger than 20 or 30 years of age only occasionally become infected by *Heterobasidion* (Rennerfelt 1957; Dimitri 1969; Werner 1973; Laine 1976) apparently refer to sites where the inoculum potential of the previous rotation has been low.

In southern Finland, *Heterobasidion* is able to remain active in large spruce stumps for more than 40 years, and there is therefore a real risk of infection in the subsequent tree stand for several decades (Piri 1996). As the regeneration trees age, the length of their roots and hence the area occupied by the root system grows and the potential for root contacts and disease transfer also correspondingly increases. In our study, the incidence of *Heterobasidion* root rot correlated positively with both the age and size of the planted spruces. The slightly higher correlation with height may be attributable to the closer relationship between rooting radius and tree size than with tree age. In advance regeneration of Norway spruce, the frequency of *Heterobasidion* root rot correlated even more distinctly with the size than with the age of the trees (Piri and Korhonen 2001). In addition to tree age and size, the incidence of *Heterobasidion* root rot tended to increase with increasing infection potential of the previous rotation. A clear connection with the infection potential of the preceding rotation has also been found in planted stands in Sweden and Germany (Stenlid 1987; Schönhar 1973, 1990), as well as in naturally regenerated stands in southern Finland (Piri 1996; Piri and Korhonen 2001). In contrast, Rönnberg and Jørgensen (2000) found no correlation in Danish spruce plantations between the incidence of butt rot in the previous rotation at the time of final felling and in the next rotation at the time of the first thinning. Their study deals with butt rot in general, whereas other studies have concentrated on *Heterobasidion* root and butt rot, and the results may therefore not be directly comparable.

Expressed as an average of all the study plots, the number of planted trees infected by *Heterobasidion* was 1.2 times as great as the number of old decayed stumps of the previous rotation on the same site. This ratio increased as the plantation aged. No *Heterobasidion* infections were found in the youngest stand investigated (planted 2 years earlier). In the 20- to 23-year-old stands 1.8 planted spruces per old decayed stump were infected. It is likely that the ratio will increase further before the tree stands have reached the first thinning stage (i.e., dominant height of 13–15 m). In southern Finland, the recommended density of the final stock for Norway spruce is 450–550 stems/ha, and the recommended minimum density of planted spruces 1800 plants/ha (Hyvän metsänhoidon suositukset 2001). Assuming that 20% of the final stock are damaged by *Heterobasidion* butt rot, then, according to our results, about 20 years after planting 9.0–11.0% of the planted spruces of the following tree generation will be infected by *Heterobasidion*. At decay levels of 30 and 40% in the final stock, the proportion of infected spruces in the plantation would be 13.5–16.5 and 18.0–

Fig. 2. Relationship between the number of infected spruces per decayed stump (data transformed using $x' = \log_{10}(x + 1)$) and mean height of the planted spruces. Each point represents the mean of the plots established in the same stand.

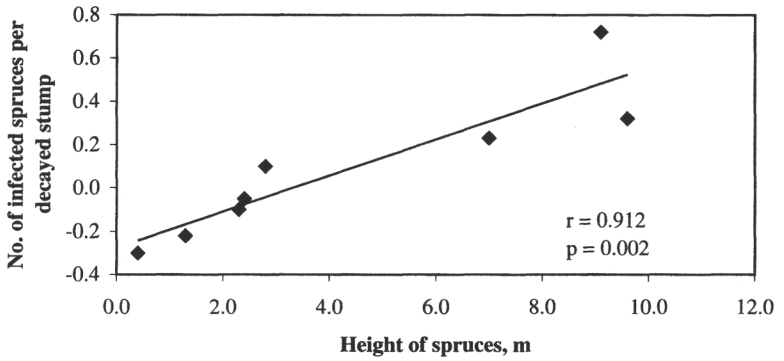
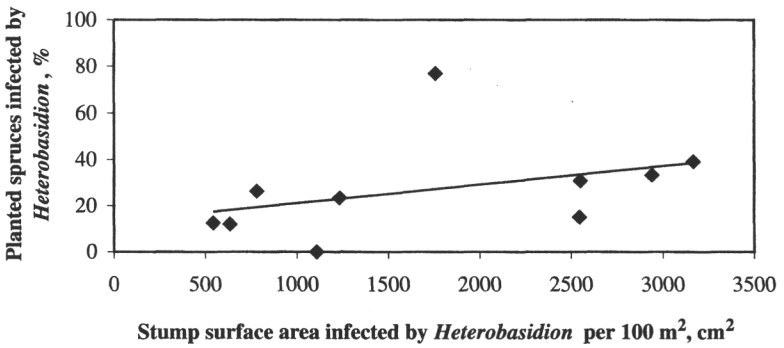


Fig. 3. Relationship between the disease incidence in the present spruce plantation (expressed as percent of planted spruces infected by *Heterobasidion*) and in the previous rotation (stump surface area colonized by *Heterobasidion* per 100 m^2). The age of the plantations varies from 20 to 23 years. Each point represents data for one study plot (N = 10). Owing to the exceedingly high value of an outlier (76.9%) the relationship is not statistically significant.



22.0%, respectively. However, when applying these results it is important to recognize that the frequency of spruce seedlings infected via an old decayed stump varies considerably. The reason why the fungus is able to spread from only some of the stumps to the regeneration remains largely unclear. The effect of competing fungi may be significant. Several fungi that infect spruce stumps, including *Armillaria* species, have been shown to be competitors of *Heterobasidion* (Holdenrieder and Greig 1998). In the light of this finding, our results suggest that the occurrence of *Armillaria* in the same stump with *Heterobasidion* may reduce the vegetative spread of *Heterobasidion*.

In advance regenerations of the same development stage, growing in similar conditions in southern Finland, the mean number of infected spruces per decayed stump was 4.5 (Piri and Korhonen 2001), whereas in the planted stands of this study it was 1.2. On the other hand, once infected, the spread rate of *Heterobasidion* root rot was faster in the planted spruces; the decay in these trees had frequently reached the butt of the tree (72% of all infections). In the advance-growth spruces, the majority of the infections were restricted to the root system (79%). The faster growth rate of *Heterobasidion* in the wood of planted spruces is probably due to the faster growth of the trees (Isomäki and Kallio 1974; Dimitri and Schumann 1989). Among planted spruces infected by *Heterobasidion*, 71% were infected by a genotype that was also identified from the previous tree generation. The corresponding figure in the advance regenerations was clearly lower, 53% (Piri and Korhonen 2001). Hence, it appears that advance-growth spruces are more susceptible to primary spore infection than planted spruces. Probably suppression by the overstory and periodic drought stress predispose the advance growth to spore infection (Lindberg and Johansson 1992; Schönhar 1995).

The fact that more rot has been found in stands established with a narrow spacing than in stands with wide spacing also points to the importance of root contacts in disease incidence in planted stands (Due 1960). Furthermore, stands established at narrow spacing are usually subjected to early and strong thinnings, which may later increase the frequency of spore infections (Venn and Solheim 1994). In our study the original planting density was rather similar in all the stands (2000–2500 trees/ha) but, later on, the density had decreased and at the time when the investigation was carried out it ranged from 650 to 2480 (mean 1813). However, no correlation was found between stand density and the inci-

dence of *Heterobasidion* root rot. Most of the missing spruces had apparently died soon after planting for reasons other than *Heterobasidion* root rot.

In the present study, the regeneration areas were harrowed before planting and the seedlings were planted on exposed mineral soil. Some of the stumps were partly lifted up by the harrow, which accelerates the drying of the stumps and conceivably may also diminish the spreading of disease. The production of fruit bodies may also decrease. Nevertheless, no effect of site preparation on the spread of the disease was observed. Neither did the study by Treschow (1958) in Denmark show any difference in infection rate between spruces planted 40–60 years earlier on deep-ploughed and non-prepared sites.

Because some of the plantations had been cleaned before our investigation, the study material is not very suitable for studying the effect of mixed tree species on the incidence of *Heterobasidion* root rot in a spruce stand. At the time of investigation the proportion of mixed broad-leaved trees (most of them sprouts) varied from 11 to 80% on the plots. No correlation was found between the root rot incidence in spruce regeneration and the proportion of mixed tree species in the plantations. A comparable result was obtained by Piri and Korhonen (2001) for natural spruce regenerations. The root system of broad-leaved trees may be too small during the first decades of growth, and the distribution of the trees may be too scattered for these factors to have any influence on the spread of the disease in young spruce regenerations.

After *Heterobasidion*, the most important agents of butt rot in spruce stands of southern Finland are *A. borealis* and *A. cepistipes* (Korhonen 1978*b*; Piri et al. 1990). These fungi were also frequent in the spruce plantations of this study. In contrast with *Heterobasidion* root rot, the frequency of *Armillaria* root rot was clearly higher in the planted than in the advance regenerations: 7.1 and 0.6%, respectively (Piri and Korhonen 2001). Our results are in agreement with the observations made by Graber (1996) in mature spruce stands in Switzerland: *Heterobasidion* was more common in naturally regenerated than in planted stands and, vice versa, *Armillaria* was more common in planted than naturally regenerated spruce stands. On the whole, butt rot damage in naturally regenerated spruce stands was less frequent and less serious than in planted spruce stands (Graber 1996). The reason for the frequent infection of planted spruces by *Armillaria* is probably due to deformations and injuries in the root system. Investigations in Newfoundland have shown that regardless of tree species and the number of infected stumps, trees in plantations established with bare-rooted stock are more susceptible to attack by *Armillaria* than those established by container planting or by direct seeding (Singh and Richardson 1973; Singh 1975).

As a conclusion of this and our earlier study (Piri and Korhonen 2001), we suggest that clear-cutting followed by planting is a better method to regenerate Norway spruce stands infected by *Heterobasidion* than utilization of advance regeneration established naturally under a spruce overstory. Up until the first thinning, the average frequency of regeneration trees infected by *Heterobasidion* apparently remains lower in planted than in advance-growth stands. Although the spreading of decay is more rapid in wood of planted trees, the difference may disappear after release cutting when the advance growth reaches the growth rate of free-standing trees. The losses caused by *Heterobasidion* in spruce plantations can obviously be diminished by avoiding planting spruce close to decayed stumps. A mixed plantation favouring birch or other broad-leaved trees in disease centers may be a recommendable alternative when regenerating spruce stands infected by *H. parviporum*.

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Paper IV

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IV

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Effects of vitality fertilization on the growth of *Heterobasidion annosum* in Norway spruce roots

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Summary

The effects of vitality fertilization on the growth of *Heterobasidion annosum* in roots of Norway spruce (*Picea abies*) were studied in a 53-year-old, naturally regenerated spruce stand in southern Finland. The fertilizer treatments were: (1), unfertilized control; (2), a compound fertilizer containing P, K, Ca, Mg, S, Cu, Zn and B; (3), as 2 with additional nitrogen; (4), as 3 with additional lime; and (5), a mixture composed on the basis of needle analysis, containing N, P, K and Cu. Three growing seasons after fertilization, four roots of eight trees in each treatment were inoculated with four different strains of *H. annosum*. Spread of the fungus from the inoculation point was determined after 12 months. Mean spread rates upwards in roots were 18.2, 25.6, 21.3, 26.0 and 29.8 cm/year in treatments 1, 2, 3, 4 and 5, respectively. These results suggest a tendency towards faster growth by *H. annosum* in fertilized trees. However, there was considerable variation in fungal growth at both the tree and root level and differences between treatments were not statistically significant.

1 Introduction

Butt rot is economically the most important disease of Norway spruce (*Picea abies* (L.) Karst.) in southern Finland. Approximately 80% of it is caused by *Heterobasidion annosum* (Fr.) Bref. (Tamminen 1985). Several factors influence the frequency of butt rot in spruce stands. These include various soil and site factors, stand management, stand age, variation in host resistance, and amounts of inoculum in and around the stand (e.g. Henriksen and Jørgensen 1953; Schlenker 1976; Troedsson and Nilsson 1980; Dimitri and Schumann 1989; Stenlid 1994).

Some studies suggest that air pollution can predispose spruces to damage by *H. annosum* (e.g. Schmidt 1985; Raddi et al. 1993). However, besides the host trees, pollutants also may affect the pathogen and rhizosphere fungi potentially antagonistic to *H. annosum* (Grzywacz and Wazny 1973; James et al. 1978; Kowalski et al. 1993). Grzywacz (1973) reported that the incidence of *H. annosum* in industrial areas in Poland was less in severely polluted pine forests than in forests experiencing only slight air pollution or none at all. On the other hand, Pearce and McLeod (1995) found no evidence for altered resistance to *H. annosum* in spruces exposed to sulphur dioxide and ozone.

Compared with central Europe, where most of the studies concerning pollution and annosum root rot have been conducted, atmospheric deposition of pollutants in Finland is less (Anttila and Tähtinen 1992). However, because of Finland's northern position, the ability of the ecosystems to tolerate pollutants may be low and is already of concern because the critical load of sulphur and nitrogen on forest soils is exceeded in southern parts of the country (Statistical Yearbook Of Forestry 1996).

One method to increase the vitality and tolerance of trees against pollutants is to counteract any nutrient deficiency and imbalance by applying nutrients to the forest (Hüttl and Fink 1988). These so-called vitality fertilizers tend to have low nitrogen content or are

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nitrogen-free. They may contain trace elements, as well as macronutrients. Some achieve long-term effects using slowly soluble compounds.

At present, little is known about the effect of vitality fertilization on annosum root rot. In the only study on this subject, WAHLSTRÖM and BARKLUND (1994) found that the growth rate of *H. annosum* in Norway spruce in south-western Sweden was slightly faster in trees treated with a vitality fertilizer than in untreated controls, but slower in trees exposed to excess nitrogen and sulphur.

Because vitality fertilization may become more common in forests where butt rot is a serious problem, it is important to understand how such fertilization may affect disease development. The objective of this study was to determine through inoculation experiments the growth rate of *H. annosum* in the roots of Norway spruce trees treated with four different compound fertilizers.

2 Material and methods

2.1 Fertilization treatments

The experiment was established in a 53-year-old, naturally regenerated stand of Norway spruce in Dragsfjärd (60°4′N, 22°23′E), on the south-western coast of Finland. The soil was a fertile sandy till (*Oxalis-Maianthemum* site type). Annual SO_4-S deposition in the area was 6.1 kg/ha and total nitrogen deposition 5.8 kg/ha (JÄRVINEN and VÄNNI 1993).

Twenty, 30 × 30 m plots were established. Each plot and its surrounding 5 m wide buffer strip received one of five randomly assigned treatments, yielding four replications of each treatment. Treatments were:

1 Unfertilized control.
2 A slowly releasing compound fertilizer: P 31, K 56, Ca 98, Mg 61, S 37, Cu 0.8, Zn 0.8 and B 1.3 kg/ha.
3 As in treatment 2, plus N 150 kg/ha (N 100 methylene urea and N 50 ammonium nitrate with lime; 27.5% N, 4.0% Ca and 2.2% Mg).
4 As in treatment 3, plus 1000 kg/ha granulated limestone (5% Mg).
5 Fertilization based on needle analysis: N 150 (ammonium nitrate with lime), P 40, K 80 and Cu 3 kg/ha.

The compound fertilizer used in treatments 1, 2 and 3 is a commercial product specifically developed for forest ecosystems subjected to nutrient imbalance caused by air pollution. The plots were fertilized immediately after thinning in the spring of 1991.

2.2 Inoculation of trees

Inoculum consisted of increment cores from stem wood of Norway spruce trees artificially inoculated with the S group of *H. annosum*. All *H. annsosum* isolates, representing four different strains, were collected from decayed Norway spruce stumps in southern Finland. Cores, 5 mm in diameter and 4 cm long, were soaked in distilled water and sterilized in an autoclave at 121°C for 1 h twice on two separate days. These sterile cores were placed onto 2-week-old malt agar cultures of *H. annosum* growing in Petri dishes and incubated for 4 weeks.

Two dominant or codominant, outwardly healthy trees in the buffer strip of each plot were inoculated. The trees varied in d.b.h. from 15.4 to 25.1 cm, and the diameter of the inoculated roots ranged from 3.0 to 19.0 cm. At the beginning of October 1993, three growing seasons after fertilization, four roots of every tree were inoculated with different strains of *H. annosum*. The inoculation point, about 30 cm out from the root collar, was cleared of soil, and the bark surface sterilized with diethyl ether. An inoculum core was placed aseptically in a radial hole made with an increment borer. The hole was immediately

sealed with grafting wax and the soil replaced. Root cores were taken to the laboratory and incubated on malt agar medium to detect possible pre-existing root infection by *H. annosum*. In total, 160 roots of 40 trees were inoculated, representing 32 roots of eight trees per treatment.

2.3 Harvest

Inoculated roots were harvested 12 months after inoculation and the development of the fungus was determined. Roots were cut at 10 cm intervals in both directions outward from the point of inoculation. Root pieces were washed in running water, incubated in plastic bags at room temperature for about 1 week, and examined with a dissection microscope for conidiophores of *H. annosum*.

Because of contamination or natural infection caused by *H. annosum* or other fungi, 28 roots were discarded. To keep the population of sample roots homogeneous, nine additional densely forked roots were excluded. The total number of roots included in the calculations was 123. The number of roots per treatments 1, 2, 3, 4 and 5 were 20, 23, 28, 26 and 26, respectively.

Tree growth was followed for 5 years after fertilization. Differences in mean volume growth, based on increment core measurements before and 5 years after fertilization, were calculated on the treated and control plots.

2.4 Statistical analysis

Analysis of variance (ANOVA) was used to test for differences in fungal growth rate among treatments. An ANOVA was also used to compare the volume growth of the trees.

For the other analyses the data was pooled across treatments before calculations. Mean growth of *H. annosum* in both directions outwards from the point of inoculum was compared by paired *t*-test. ANOVA was used to compare growth rates among different *H. annosum* strains. Correlation analysis was used to relate root and tree diameter to growth rate of the fungus in roots. Differences were judged to be statistically significant at $p \leqslant 0.05$. Analyses were performed using the BMDP STATISTICAL PACKAGE (1990).

3 Results

Nearly all (95.4%) of the 132 inoculated healthy roots were infected by *H. annosum*. Eleven roots had been infected prior to inoculation: five by *H. annosum* and six by *Armillaria* spp. There were no significant differences in infection levels among treatments.

Spread of the fungus in both directions from the inoculation point was slowest in the control trees (treatment 1) and most rapid in trees fertilized on the basis of needle analysis (treatment 5), extending 33.4 cm (range 5–65 cm) and 52.3 cm (15–100 cm), respectively. Spread of the fungus was between these values for the other treatments (Fig. 1). Because of the considerable variation in growth of the fungus on individual trees and among different roots on the same tree, the *F*-test detected no significant differences in mean fungal growth in roots among treatments ($\sigma = 0.05$, $p = 0.15$, d.f. = 19).

The maximum extent of mycelial colonization was 160 cm; 80 cm in each direction from the inoculation point. In 13% of the roots, *H. annosum* had extended less than 10 cm in both directions. Fungal growth was significantly ($p < 0.001$, d.f. = 120) faster towards the bole than away from it; 24.3 cm and 18.7 cm, respectively. There was a weak positive correlation between growth of the fungus and root diameter at the point of inoculation ($r = 0.235$, $p < 0.05$). Fungal growth in roots did not correlate significantly with tree d.b.h.

Differences in the growth rate among the four strains of *H. annosum* were not significant.

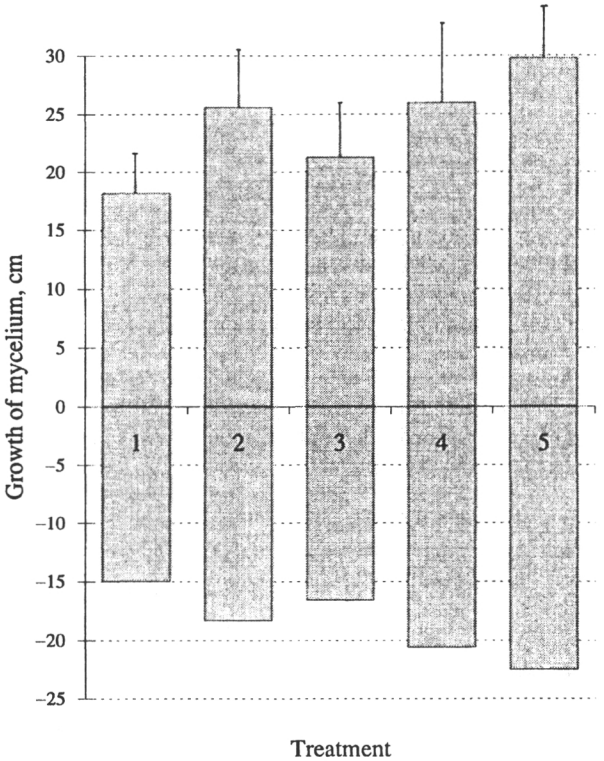

Fig. 1. Growth of *H. annosum* in roots of Norway spruce in different fertilization treatments. 1, control; 2, basic mixture (P, K, Ca, Mg, S, Cu, Zn, B); 3, basic mixture + N; 4, basic mixture + N + Ca; 5, a fertilizer based on needle analysis (N, P, K, Cu). Spread of *H. annosum* inwards (positive values) and outwards (negative values) in the root is shown. The *x*-axis represents the point of inoculation. Bars indicate the standard error of the mean for total spread. Differences between treatments are not statistically significant

Mean proximal growth of the fastest and slowest strains were 27.2 cm and 21.3 cm, respectively.

Fertilization based on needle analysis (treatment 5) increased, although not significantly, annual volume growth of trees by 1.5 m^3/ha. Volume growth in the other treatments did not differ from that on control plots (M. KUKKOLA, unpublished results).

4 Discussion

Variations in fungal growth among trees and among roots on a single tree was common in this study. Factors such as fungal strain and root diameter did not explain this variation. Differences in growth rate of *H. annosum* between individual trees and clones of Norway spruce have been reported elsewhere (e.g. VON WEISSENBERG 1975; DIMITRI and SCHUMANN 1989; HALLAKSELA 1993; SWEDJEMARK and STENLID 1996).

Perhaps variation in growth of *H. annosum* among roots of the same tree results from local and temporal differences in nutrient and water availability, which can affect the chemical and physiological processes in roots and alter decay resistance. LINDBERG and

JOHANSSON (1992) found that the resistance of wounded Norway spruce seedlings to *H. annosum* depends on the water potential in one or more of the woody roots.

Vitality fertilization did not increase the tolerance of Norway spruce to internal spread of *H. annosum*. On the contrary, there was a tendency towards faster growth by *H. annosum* in fertilized trees. Many of the previous investigations on the effects of fertilization on annosum root rot involved nitrogen fertilization; in most of these studies nitrogen fertilization increased the growth rate of *H. annosum* in spruce (e.g. DIMITRI and SCHUMANN 1989; ALCUBILLA et al. 1990). Three out of four vitality fertilizers used in this experiment contained nitrogen. The rate of fungal spread was slightly, but not significantly, slower in the treatment with additional nitrogen (treatment 3) than in the comparable treatment without nitrogen (treatment 2). The greater part of nitrogen used in treatment 3 was slowly soluble methylene urea and it is thus possible that nitrogen had not yet influenced fungal growth in the roots. In treatment 5, where fungal growth in roots was the most rapid, nitrogen was applied as water soluble ammonium nitrate. However, in an earlier study carried out in Finland, nitrogen (urea) fertilization showed no effect on the growth rate of *H. annosum* (LAIHO 1978).

The effect of nitrogen-free vitality fertilization on the growth rate of *H. annosum* was previously studied in Sweden (WAHLSTRÖM and BARKLUND 1994). Compared with this study, the annual deposition rate of nitrogen and sulphur was higher in the Swedish experiment. Composition of the fertilizer also differed. In both studies, however, the application of nitrogen-free vitality fertilizer slightly increased the growth of *H. annosum* in spruce wood.

Some reports (e.g. LAIHO 1983; DIMITRI and SCHUMANN 1989) indicate a positive correlation between tree growth and the spread of decay in stems of Norway spruce. In this study the treatment based on needle analysis (N, P, K, Cu) showed both the highest volume growth of trees and the highest growth rate of the fungus in roots. Other studies have shown that while fertilization improves tree growth, it does not necessarily decrease the resistance of trees to decay (SEIBT 1964; COWLING et al. 1969; YDE-ANDERSEN 1977; LAIHO 1978).

Since the inoculation method used allows *H. annosum* to bypass bark and sapwood, which contain most of the mechanical and biochemical defence mechanisms of the tree (LINDBERG and JOHANSSON 1991), this study primarily shows the impact of fertilization on development of *H. annosum* decay present in trees. It provides less information about the effect of fertilization on infection frequency, although infection of deep wounds may have some correlation with the inoculation method that was used. Consequently, overall effects of vitality fertilization on the incidence of butt rot requires further investigations.

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Résumé

Effet de la fertilisation sur la croissance de Heterobasidion annosum dans les racines de Picea abies

L'effet de la fertilisation sur la croissance de *Heterobasidion annosum* dans les racines de *Picea abies* a été étudié dans une régénération naturelle de 53 ans dans le sud de la Finlande. Les traitements ont été: (1) témoin non fertilisé, (2) fertilisation comprenant P, K, Ca, Mg, S, Cu, Zn et B, (3) fertilisation comme la seconde mais avec azote, (4) fertilisation comme la troisième mais avec calcaire, (5) un mélange ajusté en fonction des analyses foliaires, comprenant N, P, K et Cu. Après trois saisons de végétation,

quatre racines de 8 arbres dans chaque traitement ont été inoculées avec 4 souches différentes de *H. annosum*. L'extension du champignon à partir du point d'inoculation a été déterminée après 12 mois. Les croissances moyennes en direction du tronc étaient de 18.2, 25.6, 21.3, 26.0 et 29.8 cm/an dans les 5 traitements respectifs. Ces résultats suggèrent que chez les arbres fertilisés, la croissance du champignon a tendance à être plus importante. Il y avait cependant de très grandes variations entre arbres et entre racines et les différences entre traitements n'étaient pas significatives.

Zusammenfassung

Auswirkungen einer 'Vitalitätsdüngung' auf das Wachstum von Heterobasidion annosum in Fichtenwurzeln

Die Auswirkungen einer Düngung zur Förderung der Widerstandsfähigkeit von Fichten (*Picea abies*) gegen Immissionen ('Vitalitätsdüngung') wurde in einem 53jährigen, natürlich verjüngten Bestand in Südfinnland untersucht. Folgende Behandlungen wurden appliziert: (1) ungedüngte Kontrolle; (2) Komplexdünger mit P, K, Ca, Mg, S, Cu, Zn und B; (3) wie 2, aber zusätzlich N; (4) wie 3, aber zusätzlich Kalk; (5) Düngermischung aus N, P, K und Cu, zusammengesetzt nach Ergebnissen der Nadelanalyse. Drei Vegetationsperioden nach der Düngung wurden je 4 Wurzeln von 8 Bäumen in jeder Behandlung mit 4 verschiedenen *H. annosum*-Isolaten inokuliert. Nach 12 Monaten wurde die Ausbreitung des Pilzes von der Inokulationsstelle gemessen. Die mittlere proximale Ausbreitung des Myzels in den Wurzeln betrug 18.2, 25.6, 21.3, 26.0 und 29.8 cm/a in den Behandlungen 1, 2, 3, 4 und 5. Die Ergebnisse zeigen eine Tendenz zu schnellerem Wachstum von *H. annosum* in Wurzeln gedüngter Bäume. Es gab dabei jedoch eine beträchtliche Variation im Pilzwachstum sowohl auf der Ebene der Wurzel als auch des Baumes, die Unterschiede in den Behandlungen waren deshalb statistisch nicht signifikant.

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