Root Rot in North-Temperate Forest Stands: Biology, Management and Communities of Associated Fungi

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Abstract

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The aim of the present thesis was to study the biology and to evaluate possible means of silvicultural control of tree root pathogens *Heterobasidion* spp., *Armillaria* spp. and *Rhizina undulata*. First investigated option was the prevention of *Heterobasidion* spp. by establishing mixed coniferous-deciduous tree plantations, which would allow thinning delay and thus the absence of stumps that are main infection courts for the pathogen. Results showed that full prevention can be achieved, and that mixed stands also produced a better yield than pure plantations. During the second experiment it was demonstrated that the treatment of stumps with biological (Rotstop) and chemical (urea) control agents can also effectively prevent the *Heterobasidion* infections, and that the biological control is more environmentally friendly than the chemical. Furthermore, the prevention of loss in forest areas that already were heavily infested by *Heterobasidion* spp. was investigated. It was shown that in such areas the pathogen persists in root systems of killed trees for decades and readily attacks replanted deciduous trees, e.g. birch. Despite that, the results indicated clearly that the loss could be minimised by replanting the infested sites with more resistant tree species. The investigations of root rot in declining stands of ash led to a hypothesis that saprotrophic behaviour of weakly pathogenic *Armillaria cepistipes* has been shifted to aggressive pathogenic by some predisposing factor (-s) (possibly - water stress) after at least 20–30 years of latent presence in the area. Population studies of root pathogens in infested sites led to discovery of large territorial clones (up to 50–55 m in diameter) of *H. annosum* s.s. and *A. cepistipes*. In case of *R. undulata*, the evidence of strict both dispersive and territorial clonality was revealed for this species, showing a potential airborne dispersal of the fungus over at least 40 km. Finally, the results of this work showed striking differences between the fungal communities present in stems of healthy, declining and dead trees, indicating that fungal species in wood of living trees change along with changes in tree condition.

Keywords: *Armillaria*, disease control, fungal community, *Heterobasidion annosum*, population structure, *Rhizina undulata*, silviculture, wood-inhabiting fungi.

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Contents

Appendix

Papers I-V

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

I. Lygis, V., Vasiliauskas, R., Stenlid, J. & Vasiliauskas, A. 2004. Silvicultural and pathological evaluation of Scots pine afforestations mixed with deciduous trees to reduce the infections by *Heterobasidion annosum* s.s. *Forest Ecology and Management 201*, 275-285.

II. Vasiliauskas, R., Lygis, V., Thor, M. & Stenlid, J. 2004. Impact of biological (Rotstop) and chemical (urea) treatments on fungal community structure in freshly cut *Picea abies* stumps. *Biological Control 31*, 405-413.

III. Lygis, V., Vasiliauskas, R., & Stenlid, J. 2004. Planting *Betula pendula* on pine sites infested by *Heterobasidion annosum*: disease transfer, silvicultural evaluation, and community of wood-inhabiting fungi. *Canadian Journal of Forest Research 34*, 120-130.

IV. Lygis, V., Vasiliauskas, R., Larsson, K.-H. & Stenlid, J. Fungal infections to stems of *Fraxinus excelsior* in declining stands, with particular reference to *Armillaria cepistipes*. Submitted manuscript.

V. Lygis, V., Vasiliauskas, R. & Stenlid, J. Clonality in the postfire root rot ascomycete *Rhizina undulata*. Submitted manuscript.

Introduction

Wood-inhabiting fungi

Wood-inhabiting fungi are an inconspicuous but ecologically important component of forest ecosystems that contribute significantly to the biodiversity. The association of fungi with damaged or diseased trees has been known since old times: occurrence of fruitbodies or other fungal formations on wood clearly pointed to the tight relationship between fungi and wood as a substrate. Wood-inhabiting fungi are of great economical and ecological importance: they act as causal agents of tree decline; they cause root rot and stem decay; they spoil wood products by decomposing or staining these... Also, those fungi are the most important agents in the nutrient turnover (cycling) in the forest ecosystems.

The presence of fungi also within sound-looking trees was suspected already by founders of forest pathology (*e.g.* Hartig, 1882), and thereafter confirmed by early microscopical studies (*e.g.* Lewis, 1924). On the other hand, even for a long time after these studies, it was often assumed that the internal environment of healthy tree tissues represent practically aseptic conditions (*e.g.* Sivak & Person, 1973). More recently, three main lines of research have radically changed this assumption. First, plant pathologists have documented the presence of some tree pathogens, ascomycetes in particular, in or on healthy trees (*e.g.* Butin, 1986; Barklund, 1987; Carroll, 1988; Chapela, 1989). Second, taxonomically-oriented mycological studies have shown that aerial organs of healthy trees, particularly leaves and twigs, can be extensively colonised by inconspicuous fungi with endophytic affinity (Carroll, 1988). Third, mycological studies focusing on the ecology of wood-decomposing and tree-pathogenic fungi strongly pointed to the existence of a latent phase in the life history of these organisms (Bassett & Fenn, 1984; Chapela, 1989). A number of studies have shown that the presence of fungi in living, sound-looking woody tissues is common, detected in 30–100% of apparently healthy samples from different parts of a tree (*e.g.* Butin, 1986; Barklund, 1987; Barengo *et al.*, 2000; Papers **I** & **III**).

Wood-decaying fungi have always been the subject of intensive studies, especially those that cause root rot and stem decay of trees. This work gives insights into population biology and possibilities of disease management. At the same time it describes the diversity and substrate preferences of many less known fungal species found in wood of living, declining, dead trees and stumps on forest sites subjected to management. This group of fungi has received little attention until recently. In aerial tree parts, extensive studies over the last decades have focused on fungi on leaves and needles (*e.g.* Kowalski, 1982; Petrini, 1991; Helander *et al.*, 1994; Müller & Hallaksela, 1998; Barengo *et al.*, 2000; Müller *et al.*, 2001), shoots, twigs and branches (*e.g.* Barklund & Kowalski, 1996; Sieber, 1989; Petrini & Fisher, 1990; Barengo *et al.*, 2000). Several studies were performed to reveal communities of fungi inhabiting fine non-ectomycorrhizal roots of forest trees and shrubs (*e.g.* Holdenrieder & Sieber, 1992; Ahlich & Sieber, 1996). Despite several investigations of fungal communities in stems,

larger branches or roots of living trees (*e.g.* Basham, 1966; Roll-Hansen & Roll-Hansen, 1979; Huse, 1981; Fisher & Petrini, 1990; Fisher *et al.*, 1991; Hutchison, 1999), knowledge on this group of fungi is still very limited.

Heterobasidion *spp.*

The basidiomycetous wood-decay fungi of the genus *Heterobasidion* (*Heterobasidiomycetes, Russulales, Bondarzewiaceae*) are, in economic terms, the most important pathogens of conifer trees in north temperate forests. They cause heart rot in spruce, fir, larch, and mortality in pine and some other species, including broadleaves. Estimated yearly losses inflicted by the pathogen amount to 790 million € for Europe alone (Woodward *et al.*, 1998). The fungi enter stands mainly following colonisation of freshly cut surfaces of conifer stumps by airborne basidiospores (Rishbeth, 1951; Chase & Ullrich, 1983), although living trees (of genus *Picea* and *Tsuga* in particular) can also be infected through stem or root wounds (Isomäki & Kallio, 1974; Redfern & Stenlid, 1998). Following establishment, vegetative mycelia of the pathogen grow down to woody root tissues and infect neighbouring healthy trees via root contacts (Rishbeth, 1949, 1951). As *Heterobasidion* may persist and remain active in stumps for decades (Rishbeth, 1951; Greig & Pratt, 1976; Piri, 1996, Stenlid & Redfern, 1998), the disease readily spreads into trees of the next forest generation planted on infested sites (Yde-Andersen, 1970; Stenlid, 1987; Piri, 1996, 2003).

Heterobasidion occurs in several intersterility groups (biological species) that have different host preferences (Korhonen, 1978b; Korhonen *et al.*, 1992). Of the three European intersterility groups, P (pine), S (spruce) and F (fir), two, namely P and S, occur in forests of north-eastern Europe. Besides pine, the P group (=*H. annosum* (Fr.) Bref. s.s.) attacks many other trees, especially when they grow in mixed stands with pine, or on sites with a pine history (Korhonen *et al.*, 1992; Korhonen & Piri, 1994). In particular, *Picea abies* (L.) Karst. and *Juniperus communis* L. are very susceptible to *H. annosum* s.s. Deciduous trees can also be attacked, especially *Betula pendula* Roth. (Korhonen *et al.*, 1998a). The S group of the fungus (=*H. parviporum* Niemelä & Korhonen s.s.), almost exclusively occurs on *P. abies* in Europe (Korhonen *et al.*, 1998a).

In eastern Europe, *H. annosum* s.s. causes dying in Scots pine (*Pinus sylvestris* L.) stands 4–5 years after first thinnings, often resulting in open areas of up to 0.5 ha (Fig. 1). These areas are non-productive and may comprise thousands of hectares on a country-wide scale (Vasiliauskas, 1989). The attacks are particularly destructive in young pine plantations, established on former agricultural lands (Delatour *et al.*, 1998; Fiodorov, 1998). The susceptibility of pine to *H. annosum* s.s. tends to decrease with age, and in the older stands attacks of the fungus seldom result in tree death (Vasiliauskas, 1989; Stenlid & Redfern, 1998).

Fig. 1. Heterobasidion disease centre in a stand of *Pinus sylvestris*, thinned 40 years ago (Vilnius forest enterprise, Paneriai forest district (eastern Lithuania, Paper **III**)).

Armillaria *spp.*

Among fungal pathogens that spread vegetatively in soil, species of the genus *Armillaria* (*Agaricomycetidae, Agaricales, Marasmiaceae*) have received particular attention (Guillaumin *et al.*, 1996); root rot caused by this genus is a major disease of woody plants, attacking various species of coniferous and broadleaved trees. Being a natural component of a forest mycoflora, *Armillaria* is nevertheless able to significantly affect the structure and function of forest ecosystems (Shaw & Kile, 1991).

Armillaria can establish in new areas by spore dispersal (primary spread) (Guillaumin *et al.*, 1994; Smith *et al.*, 1994). Secondary spread occurs by mycelial expansion at points where infected roots come into contact with healthy ones, or through the spread of rhizomorphs, which are able to grow through soil (Redfern, 1978). Established genets of *Armillaria* spp. (the term "genet" is defined as all the mycelium produced by vegetative means following an initial sexual mating event) may persist in a stand for several decades or centuries, and their mycelia may eventually spread over large areas (*e.g.* Shaw & Roth, 1976; Korhonen, 1978a; Smith *et al.*, 1992; Rishbeth, 1991; Dettman & Van der Kamp, 2001; Ferguson *et al.*, 2003). All species belonging to this genus can survive saprophytically in woody substrates in soil (Redfern & Filip, 1991). The prominent role of *Armillaria* species in root rot diseases results from their extensive natural distribution in the stress-affected forests and their primary infection of, or epiphytic presence on, many root systems prior to the advent of stress. The fungus is thereby able to take advantage of changed circumstances to spread quickly from existing infections or establish new ones (Kile *et al.*, 1991).

In Europe two species, namely *Armillaria mellea* (Vahl: Fr.) Kumm. and *A. ostoyae* (Romagnesi) Herink, are regarded to be highly pathogenic and able to act as primary pathogens causing lethal disease (Gregory *et al.*, 1991; Kile *et al.*, 1991). Four other pathogenic European species, *A. cepistipes* Velen., *A. gallica* Marxm. & Romagn., *A. borealis* Marxm. & Korhonen, and *A. tabescens* (Scop.: Fr.) Emel are less pathogenic, although they sometimes play a prominent role in tree dieback and decline diseases (Guillaumin *et al.*, 1993). Previous investigations (Legrand *et al.*, 1996; Rigling *et al.*, 1998; Marxmüller & Holdenrieder, 2000; Prospero *et al.*, 2003) have shown *A. cepistipes* to be one of the most common *Armillaria* species in Europe. *Armillaria cepistipes* is generally considered to behave similarly to *A. gallica*, a species which is categorised, according to field observations and inoculation experiments, as a weak pathogen, showing a low ability to infect the roots of healthy trees (Rishbeth, 1982; Guillaumin *et al.*, 1985, 1989; Prospero *et al.*, 2004).

Rhizina undulata

Rhizina undulata Fr. (*Discomycetes, Pezizales, Helvellaceae*) is a cosmopolitan ascomycete that colonises burned forest areas and causes root rot and group dying to conifer seedlings (Hartig, 1900; Brooks, 1910; Weir, 1915), and 15–60-yr-old conifer trees (Gremmen, 1961; Murray & Young, 1961). *Rhizina undulata* prefers acidic sites and germination of its dormant ascospores in the soil is activated by the heat of the fire (Jalaluddin, 1967a, b). The pathogen is able to spread both by airborne ascospores and by mycelial growth in the soil from tree to tree (Hartig, 1900; Laine, 1968; Phillips & Young, 1976).

Characteristic for this fungus is circular distribution of its fruitbodies, the focal point being placed in the periphery of burned areas (Butin & Kappich, 1980). The ability of the pathogen to grow saprotrophically, ramifying through the soil and attacking roots of conifers with which it comes in contact (Brooks, 1910; Weir, 1915; Murray & Young, 1961), may result in groups of up to 100 killed trees within areas of 0.04–0.1 ha (Murray & Young, 1961). Recurrence of fire is not necessary for radial progression of tree mortality (Murray & Young, 1961; Tainter & Baker, 1996). However, after 4–7 years further spread of *R. undulata* comes to a stop and most infection centres stabilise (Murray & Young, 1961; Sato *et al.*, 1974; Phillips & Young, 1976; Vasiliauskas, 1999).

Forest management and root diseases

Several considerations need to be made by forest managers when dealing with disease problems. Firstly, forest managers must critically evaluate disease impact to ensure that the level of loss justifies control (Hagle & Shaw, 1991). Secondly, they must understand the biology and ecology of the causal fungi (Kile *et al.,* 1991). This understanding also improves knowledge of disease development in natural stands and forest plantations. Advances in our ability to identify the pathogenic species accurately, determine their relative pathogenicities, and model

the disease process provide us with a sharper image of disease problems, and should allow a more systematic evaluation of control options.

Three of the studies in this thesis were done in order to evaluate forest management practices aimed to prevent the infections (**I** & **II**) and to minimise the damaging effect (**III**) of one of the most important forest tree pathogens,- *Heterobasidion* spp. A study of Paper **I** focus on the possible options to escape the disease by planting a species mixture rather than a pure stand of a susceptible conifer. In Paper **II**, an efficiency of biological (Rotstop^{TM}) and chemical (urea) stump treatments against the establishment of *Heterobasidion* spp. infections on freshly cut spruce stumps is evaluated. A study of Paper **III** evaluates the possibility to prevent further loss caused by the root rot in pine plantations established on former agricultural land by sanitary fellings. Two other tree pathogens, *Armillaria* spp. (**IV**) and *Rhizina undulata* (**V**) are also discussed with the regard to possible control means.

Escaping the disease

Silviculture

When a pathogen is established within a plant or forest stand, it is usually too late to prevent loss. Forest monitoring, planning and proper silvicultural management should help to achieve the highest economical effect when fighting the tree diseases and to prevent the pathogens from entering the healthy stands (*e.g.* Hagle & Shaw, 1991; Korhonen *et al.*, 1998b). Silvicultural practices can be used to regulate species composition, tree spacing, maintain biological diversity, reduce the risk for insect pest build-up on selected tree species and increase host vigour (*e.g.* Houston, 1981; Korhonen *et al.*, 1998b). Selection of proper sites for establishment of new plantations is one of the most important options in disease control (*e.g.* Korhonen *et al.*, 1998b). Once the stand is established, the main entry courts into an uninfested site by *Heterobasidion* spp. and *Armillaria* spp. are fresh stump surfaces and larger stem or root wounds (Redfern & Filip, 1991; Korhonen & Stenlid, 1998; Redfern & Stenlid, 1998), indicating that silvicultural operations, and tree felling in particular, pave the way for new infections and build-up of disease. The challenge of forest management is to harvest the forest and still to avoid the infections.

The most destructive outbreaks of *H. annosum* s.s. are observed in pure young (up to 40-year-old) plantations established in high initial densities on former agricultural soil following several pre-commercial thinnings (Vasiliauskas, 1989; Delatour *et al.*, 1998; Fiodorov, 1998). To escape the infections, one possible option is to delay thinnings to the latest possible period of stand development and thin as few times as possible (Vasiliauskas, 1989). This was the initial idea behind the 25-year-old experimental plantations in central Lithuania (**I**), where Scots pine trees were sparsely planted in different mixture schemes with deciduous species such as *Robinia pseudoacacia* L., *Amorpha fruticosa* L. and *Betula pendula* Roth. (Fig. 2). *Betula pendula* was chosen because, similarly to Scots pine, it is a timber producing species on poor sandy soils. *Robinia pseudoacacia* and *A. fruticosa* were chosen because (1) during the early stages of plantation development they

eliminate grass competition; (2) neither species compete with pine since their tops commonly freeze down during the Lithuanian winters; (3) both species are nitrogen fixers able to improve a nitrogen nutrition in soil; (4) the root exudates of *R. pseudoacacia* and *A. fruticosa* have significant negative effect on the growth of *Heterobasidion* spp. culture *in vitro* (Vasiliauskas, 1989). The objectives of study performed for Paper **I** were twofold. The first aim was to estimate tree and stand characteristics in previously mentioned plantations after 25 years, with particular attention to quality of their timber and current thinning requirements. The second aim was to identify the community of wood-inhabiting fungi in planted pines, focusing the attention on possible infections by *H. annosum* s.s.

When preventing disease caused by *Armillaria* species the main strategies are: eliminating the inoculum, avoiding abiotic and biotic stresses, and promoting good health condition (vigour) of trees in a stand. According to Hagle & Shaw (1991), the following silvicultural means should be considered: (1) selection of proper/uninfested sites for the new plantations, (2) cultural modifications (mixed stands), (3) utilisation of resistant or tolerant tree species, genotypes, or rootstocks, if known that are compatible with other necessary values as *e.g.* productivity, (4) maintenance of the general health of the forest by preventing damage from abiotic and biotic stresses, and detrimental human activities. In natural forests, local tree species grown in natural mixtures and densities may resist the disease even though they are known hosts for the local species of *Armillaria*. In forest plantations (especially monocultures), however, trees are more prone to infections (Hagle & Shaw, 1991).

The root pathogen, *R. undulata*, has received far less attention than *e.g. Heterobasidion* or *Armillaria*, although its impact on coniferous plantations around burned areas has been widely acknowledged (Murray, 1955; Murray & Young, 1961; Ginns, 1974; Phillips & Young, 1976; Vasiliauskas, 1999). As with most soil-borne pathogens, the main task in keeping forest plantations free of disease is prevention of the infection, *i.e.* fungus must not enter the site or should be kept from becoming active. Damage caused by *R. undulata* can be prevented if no fires are lit in or near the plantations (Murray & Young, 1961). If fires are unavoidable, separation of the burned areas from the adjacent plantations by ditches or similar barriers must be ensured (Gremmen, 1958; Phillips & Burdekin, 1982). If site conditions allow, cultural modification could also be considered: when establishing new plantations, deciduous trees should be planted on burned areas instead of susceptible conifers. As a means of biological control of *R. undulata,* using mycorrhized outplanting material could be recommended: in laboratory tests a number of ectomycorrhizal fungi have exhibited strong antagonism towards this pathogen (Zak & Ho, 1994).

Stump treatment

Harvesting trees provides *Heterobasidion* spp. with suitable substrate in form of tree stumps. Intensively managed, regularly thinned, even-aged pure plantations of conifers and the increased demand for timber have favoured the infections and

spread of *Heterobasidion* spp. in conifer stands over the last decades (*e.g.* Rennerfelt, 1946; Vasiliauskas, 1989; Bendz-Hellgren, 1997; Rönnberg, 1999).

Starting with early experiments of Rishbeth (1959, 1963), biological and chemical treatment of the fresh stump surfaces proved to be crucial in prevention of the aerial infections by *Heterobasidion* spp. on uninfested conifer sites (Holdenrieder & Greig, 1998; Pratt *et al.*, 1998). In this way, use of such treatments could reduce spore infections on the fresh stumps by 90–95% (Korhonen *et al.*, 1994; Pratt, 1994; Thor, 1997). Consequently, the method was developed for routine use in forest management programs. At present, over 200,000 ha of forest are subjected to stump treatment in Europe each year (Thor, 2003). Among the products available for stump protection, the biocontrol agent *Phlebiopsis gigantea* (Fr.) Jül. (Rotstop^{TM}) is applied on about 56%, and chemical compound of urea ($CO(NH_2)_2$) on about 42% of the area (Thor, 2003). The efficiency of stump protection against *Heterobasidion* spp. is reported to be about similar for the both products (*e.g.* Thomsen, 2003; Thor & Stenlid, 2005).

Knowledge of the early patterns of establishment of *Heterobasidion* spp. on surface of treated stumps could provide more insight into the mechanisms of disease control. So far, little is known about the mode of action of Rotstop in controlling aerial stump infections by *Heterobasidion* spp., but hyphal interference and competition for space are thought to be involved (Holdenrieder & Greig, 1998; Pratt *et al.*, 1998). The mechanism of urea treatment involves enzymatic splitting of urea by ureases in the fresh sapwood of stumps, leading to an elevated pH that is toxic to *Heterobasidion* spp. (Johansson *et al.*, 2002). During the study of Paper **II**, the infections of the fresh Norway spruce stumps by *Heterobasidion* spp. were examined with regard to the treatments applied (Rotstop and urea).

Minimising the loss if the infection already occurred

There are several options to minimise the losses caused by root rot in conifer stands and avoid damage in the future: (1) removal of the infected stumps (reduction of inoculum potential) (Hagle & Shaw, 1991; Korhonen *et al.*, 1998b), (2) cultivation of resistant tree species in the following stand generations (Hagle & Shaw, 1991; Vollbrecht *et al.*, 1995; Piri, 1996) or in mixed stands (Vasiliauskas, 1989; Korhonen *et al.*, 1998b), (3) reducing the incidence of abiotic and biotic stresses that affect general forest health (Hagle & Shaw, 1991; Korhonen *et al.*, 1998b), and (4) application of chemical and biological methods (curatives) (Hagle & Shaw, 1991).

Heterobasidion spp.

Of the above-listed ways, two are regarded as the most effective in fighting *Heterobasidion* spp. that is already established on the site: (1) the removal of the infected stumps - an effective but expensive method, and (2) the cultivation of resistant tree species in the following stand generations that can clean the site of pathogen inoculum (Korhonen *et al.*, 1998b). If a stand is infected by *H. parviporum* s.s., which almost exclusively occurs on *P. abies* in Europe (Korhonen *et al.*, 1998a), a change in tree species on the infested site could be a

good option (Piri, 1996, 2003; Korhonen *et al.*, 1998b). This option, however, is more problematic in the case of stand infection by *H. annosum* s.s., which has a wide host range (Korhonen *et al.*, 1992, 1998b).

Generally, deciduous tree species are regarded to be less susceptible than conifers to *Heterobasidion* root rot (Vasiliauskas, 1989; Korhonen & Stenlid, 1998; Korhonen *et al.*, 1998b). Only a few observations of attacks by this pathogen have been made in pure birch stands (Laine, 1976; Piri, 1996). This was the initial idea behind a 25-year-old experimental plantations in eastern Lithuania (**III**), where silver birch (*Betula pendula*) was planted on sites infested by *Heterobasidion*. The main goals of growing birch were: (1) to sustain a tree cover of the forest, (2) to achieve timber production on sites with poor soil conditions, and (3) to increase the diversity of soil microorganisms, including possible antagonists to *Heterobasidion* (Vasiliauskas, 1989). To date, little information is available on spread of root rot from a previous tree stand to the next, especially when those are composed of different tree species. This understanding is essential for selection of tree species for the next forest generation on the infested sites.

Armillaria spp.

As regards control of *Armillaria* root disease, we still lack convenient, cost-effective methods, and, while our biological knowledge about this pathogen has increased markedly since the time of Hartig, the efficiency of control measures, with some exceptions, has not improved very much (Schütt, 1985; Hagle & Shaw, 1991). The main problems with controlling this fungus are associated with a low degree of host (substrate) specialisation (Redfern & Filip, 1991), an impressive longevity of persistence on infested sites (Smith *et al.*, 1992; Ferguson *et al.*, 2003), the strong saprotrophic survival and the ability to form the most highly organised rhizomorphs of any fungus (Redfern & Filip, 1991). The matter is complicated here also because *Armillaria* is known as a natural component of the mycoflora of native forests, causing endemic disease, disease that is constantly present to a greater or lesser extent in a particular place (Van der Plank, 1975; Kile *et al.*, 1991), and several *Armillaria* species of different pathogenicity may occur on the same site (*e.g.* Legrand *et al.*, 1996; Prospero *et al.*, 2003). The long co-existence of hosts and pathogens in natural forests favours a state of balance. However, since environmental conditions do not remain constant, especially in managed forests, fluctuations in disease levels (local epidemics) can occur (Wargo & Harrington, 1991).

Tree roots constitute the major source of inoculum for *Armillaria*, but logging debris may also be colonised and act in the same way (MacKenzie & Shaw, 1977). Established on the larger food base, *Armillaria* is able to spread and occupy new territories very efficiently. From this perspective, a removal of the inoculum potential (the food base) is usually mentioned among the most effective means of disease control (Hagle & Shaw, 1991). However, only complete removal of the woody material or even sieving of soil can clean the site from the inoculum, and that obviously makes this method too costly to be extensively applied in forest plantations (Hagle & Shaw, 1991).

Change in tree species from susceptible to more resistant could also be a decision on infested sites, and the use of healthy, vigorous outplanting material should always be promoted. Some other ways of control as soil fumigation, application of fungicides (curatives) on living trees are in most cases applicable in orchards, parks or amenity plantings, but not in forest plantations, because such operations are costly and because reliable information on the expected economic gains is lacking (Hood *et al.*, 1991).

Rhizina undulata

When controlling root rot disease caused by the postfire ascomycete *R. undulata*, a rather short period of disease activity (4–7 years) must be taken into account. After this period, most disease centres stabilise (Murray & Young, 1961; Sato *et al.*, 1974; Phillips & Young, 1976; Vasiliauskas, 1999). However, even after the spread of *R. undulata* stops, immediate reforestation by coniferous seedlings should be avoided as some inoculum may persist in roots of stumps and surrounding healthy-looking trees (Hagner, 1960).

Infection of regeneration by *R. undulata* develops from the periphery of burned sites. Within this concentric activation zone, the presence of dying roots of recently fire-killed or cut coniferous trees promotes an active saprophytic colonisation and vegetative increase by the fungus. Seedlings planted in this zone during the first few years after the fire are likely to become infected, whereas natural regeneration or plantations established by sowing often escape this fate through delayed root contact with the inoculum, which, in itself, begins to dissipate with time (Gremmen, 1971; Tainter & Baker, 1996).

Thinnings should not be carried out in the vicinity of active disease foci. It reduces the number of possible survivors. It also tends to increase the transpiration rate of trees that have, or will have, damaged roots, thus reducing their chances of survival. Finally, thinning provides a source of food material in the form of stumps and fresh root systems which greatly encourages the spread of *R. undulata* (Murray & Young, 1961).

Why is it important to investigate population structure of a pathogen?

A population genetics approach is widely used to understand the ecology and epidemiology of fungal tree pathogens, especially for those species that spread vegetatively in soil (Guillaumin *et al.*, 1996). The size, distribution and density of fungal genets provide information on mode and frequency of establishment and growth of individual mycelia, and their intraspecific interactions. Such knowledge could then be related to the establishment of infections and disease spread, permitting the refinement of epidemiological models and approaches to management (Worrall, 1994). Using the phenomenon of somatic incompatibility (*e.g.* Korhonen, 1978a; Stenlid, 1985; Guillaumin *et al.*, 1996; Malik & Vilgalys, 1999), it is possible to identify genetically distinct secondary mycelia of the same species coexisting within a population. Intraspecific pairings on agar media are

widely applied for the determination of the structure of fungal populations; this method is still popular because of its simplicity and straightforward results.

During the last decades, the population structure of several basidiomycetes has been studied, including that of *Heterobasidion* spp. (*e.g.* Stenlid, 1985), *Phellinus weirii* (Murrill) Gilb. (*e.g.* Hansen & Goheen, 2000), *Fomitopsis pinicola* (Sw.) P. Karst. (Högberg *et al.*, 1999), *Resinicium bicolor* (Alb. & Schwein.) Parm. (Kirby *et al.*, 1990), *Suillus bovinus* (Fr.) Roussel (*e.g.* Dahlberg & Stenlid, 1990), and *Armillaria* spp. (*e.g.* Legrand *et al.*, 1996). Until recently, population studies of ascomycetes have been mainly directed towards species regarded as microscopic, and their population structures have been therefore viewed from an angle of "genetic diversity vs. dispersive clonality" (Anderson & Kohn, 1995; Correll & Gordon, 1999). Nevertheless, more recent investigations on wood-inhabiting species have shown that individual mycelia of some ascomycetes, *e.g. Daldinia loculata* (Lev.) Sacc. and *Sarea resinae* Kuntze (even despite microscopic fruitbodies of the latter), might be rather large and expand 2–3 m within living tree stems (Johannesson *et al.*, 2001; Vasiliauskas *et al.*, 2001). In contrast to the above-mentioned fungi with a resource-unit-restricted growth manner, pathogens investigated in this thesis (*H. annosum* s.s., *A. cepistipes* and *R. undulata*) grow in soil, thus the space for their vegetative spread over forest areas is potentially unlimited. Regarding *H. annosum* s.s., *A. cepistipes* and *R. undulata*, this could provide information on the number of individuals that colonise certain forest areas, as well as on their growth rates, physical boundaries and size.

Aims of the work

The overall aim was to study the biology and possible means of silvicultural control of the economically important root pathogens *Heterobasidion* spp., *Armillaria* spp. and *Rhizina undulata*. More specifically, the objectives were:

- to investigate the efficiency of forest management, performed to prevent the infections (**I** & **II**) and the further loss caused by *Heterobasidion* spp. (**III**) on conifer sites.

- to investigate the population structure and persistence of *Armillaria cepistipes* (**IV**), *Rhizina undulata* (**V**) and *Heterobasidion annosum* s.s. on infested sites, and the transfer of the latter to a new forest generation (**III**).

- to assess the impact of biological (Rotstop) and chemical (urea) treatments on biodiversity in communities of non-target fungi in freshly cut Norway spruce stumps (**II**).

- to identify the community of wood-inhabiting fungi in investigated *Pinus sylvestris*, *Betula pendula* and *Fraxinus excelsior* stands, focusing on possible disease-causing agents (**I**, **III** & **IV**).

Materials and methods

Study sites, fieldwork and sampling

Plantations of P. sylvestris *mixed with deciduous trees (Paper **I**)*

The experimental plantations of mixed Scots pine (*Pinus sylvestris*) - deciduous tree species (*Robinia pseudoacacia* L., *Amorpha fruticosa* L. and *Betula pendula* Roth.) were located in central Lithuania, Kaunas region. Non-thinned, 25-year-old plantations were initially established on former arable land in five planting schemes, representing different tree mixture and spacing patterns (Fig. 2). Planting schemes and other characteristics of the plantations at the time of their establishment are presented in Table 1.

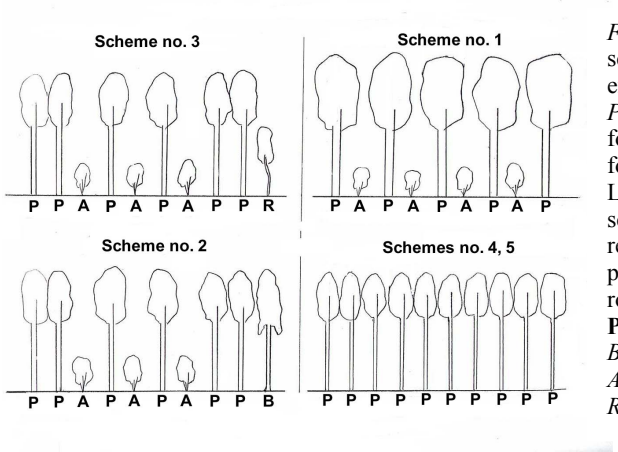

Fig. 2. Five planting schemes used in the experimental plantations of *Pinus sylvestris* in Dubrava forest enterprise, Kačerginė forest district (central Lithuania, Paper **I**). Each scheme is represented by repeatable fragments of pine rows' alternation with rows of other tree species. **P**: *Pinus sylvestris* L.; **B**: *Betula pendula* Roth.; **A**: *Amorpha fruticosa* L.; **R**: *Robinia pseudoacacia* L.

Table 1. *Characteristics of the experimental plantations of* Pinus sylvestris *at the time of their establishment (Dubrava forest enterprise, Kačerginė forest district (central Lithuania, Paper **I**))*

No. of planting scheme[a]	Spacing (m),[b] between × within rows	Planting density (trees/ha)	
		all species	P and B only[c]
1.	1.5 × 1.20	5,500	2,750
2.	1.4 × 1.25	5,700	4,000
3.	1.2 × 1.25	6,700	4,000
4.	1.4 × 1.25	5,700	5,700
5.	1.0 × 1.00	10,000	10,000

[a] Scheme numbers as in Fig. 2.
[b] The same spacing for all tree species within the scheme.
[c] **P**: *Pinus sylvestris* L.; **B**: *Betula pendula* Roth.

Few disease centres of *H. annosum* s.s. were observed in an adjacent pine stand, about 30–100 m away from the investigated plantations (Fig. 3), although within

the plantations no external signs of the root rot (fruitbodies, decay, resin-soaking or fungal pustules (according to Greig, 1998)), or any other disease were visible. Dead or declining pines within the plantations were observed occasionally, forming no clusters; most of them were suppressed by the inter-tree competition.

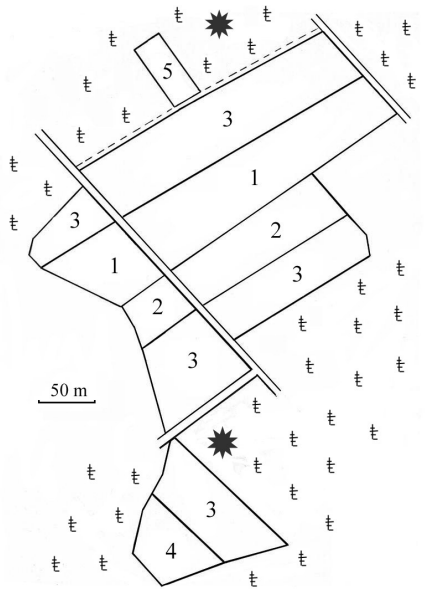

Fig. 3. Distribution of planting schemes in the experimental plantations of *Pinus sylvestris* in Dubrava forest enterprise, Kačerginė forest district (central Lithuania, Paper **I**). Black stars indicate disease centres of *Heterobasidion annosum* s.s. See Fig. 2 and Table 1 for the scheme numbers.

Eleven permanent measurement plots (20 × 20 m) were established to evaluate quantitative and qualitative tree and stand characteristics in the plantations after the 25 years of growth. Superficial parts of root systems of 53 randomly selected declining pines were investigated in detail by digging them up. Pieces of the roots that looked infirm or were resin-soaked, as well as wood cores, extracted from the root collars by means of an increment borer, were transported to the laboratory and subjected to a fungal isolation on Hagem agar media (Stenlid, 1985). For more detailed mycological investigations within the plantations, cores of wood were extracted also from root collars of 150 sound-looking pine trees.

Thinned P. abies *plantation with biological (Rotstop) and chemical (urea) stump treatment (Paper **II**)*

The study of Paper **II** was conducted in a 33-year-old *Picea abies* plantation, located near Kristianstad in Skåne, southern Sweden. In October 2001, a discrete plot within the plantation was thinned by a harvester, equipped with device for mechanized stump treatment that ensured the coverage by a protective agent at the same time as a tree was cut off (Thor, 1997). The treatment was done either with Rotstop™ *Phlebiopsis gigantea* strain (Kemira OY, Finland), or with 35% aqueous solution of urea (Hydro Kemi AB, Sweden). In another part of the thinned plantation, stumps were left as untreated controls.

Seven weeks after felling the spruce trees, 1–2 cm thick wood discs were taken with a chainsaw from the tops of the stumps. A total of 63 stumps were sampled:

21 treated with Rotstop, 21 with urea, and 21 untreated. Neither of them had any visual symptoms of pre-established butt rot. The cut discs were individually labelled, put into plastic bags and stored at +5 °C for four weeks. After the storage, the pieces of wood (about 5 × 5 × 10 mm in size) were taken for fungal isolations from the lower surface of those discs. At least five samples were taken from each stump - one from central, two from random intermediate, and two from random outer parts of the disc. Any area of discoloured wood observed on disc surface was subjected to additional sampling.

The presence of *Heterobasidion* spp. was recorded from the occurrence of conidiophores on lower surfaces of wood discs after one week of storage at +20 °C in moist conditions (Thor, 1997; Bendz-Hellgren & Stenlid, 1998). All areas occupied by the conidiophores were marked. Consequently, both the number of colonies and the colonised area were estimated.

Betula pendula *on pine sites infested by* H. annosum *s.s. (Paper **III**)*

The sites represented three *Heterobasidion* disease centres in 50–60-year-old Scots pine (*Pinus sylvestris*) stands located in eastern Lithuania, Vilnius region. Pure plantations of Scots pine were established in 1940–1950 on former agricultural land with a sandy soil, corresponding to *Vacciniosa* forest site type (Karazija, 1988). The stands were thinned in 1960–1965, and spread of the pathogen from infected stumps into surrounding trees took place within 4–5 years resulting in pine dieback and open areas in the stand. Three disease centres (each of about 0.2 ha in size) were clear-felled in 1973–1974 and replanted with silver birch (*Betula pendula*) in 1975, which was subsequently thinned in 1996.

An evaluation of qualitative and quantitative tree and stand characteristics of those three birch plantations was carried out in permanent measurement plots (one per birch plantation, dimensions 20 × 20 m). Mapping, numbering and sampling of trees and stumps included both replanted birch and surrounding pines from the previous generation. In total, 310 living birch trees, 58 dead standing or uprooted birch trees, 133 thinning stumps of birch were sampled in three permanent sample plots (one sample plot per stand). Also, seven dead birch trees bearing fruitbodies of *Heterobasidion* were sampled from outside of the sample plots. In addition, 49 dead pine trees, 21 dead juniper trees (*Juniperus communis*) and 1 dead willow tree (*Salix cinerea* L.) was mapped, numbered and sampled from inside or at the closest possible distance to the investigated birch plantations.

Superficial parts of root systems of all sampled dead trees and stumps as well as of randomly selected 118 living birch trees were investigated in detail. An effort was made until any sign of root rot disease (fruitbodies, decay, resin-soaking or fungal pustules) has been found. The presence of decay or other symptoms typical to *Heterobasidion* (according to Greig (1998)) was recorded. For the fungal isolation, cores of wood were extracted by means of an increment borer from the root collars of all mapped trees and stumps making a total of 579 wood samples. The obtained wood samples were transported to the laboratory and subjected to a fungal isolation on Hagem agar media (Stenlid, 1985).

Declining F. excelsior *stands of northern Lithuania (Paper **IV**)*

The study was carried out in declining mixed-aged (20–60-year-old) *Fraxinus excelsior* stands located in northern Lithuania, Biržai region. The decline in those stands was first observed in year 2000, one year prior to the study. For every tree, we estimated the diameter at breast height (1.3 m), crown density reduction (defoliation), the presence of disease signs such as tarry spots or dead bark, and the occurrence at the stem base of mycelial fans and rhizomorphs typical to *Armillaria* spp. (according to Morrison *et al.* (1991)). Mapping, numbering, measurement and sampling of trees were carried out in three discrete permanent sample plots (about 0.15 ha in size each), each consisting of 70 ash trees that represented three different categories of health condition: sound looking, declining and dead.

All mapped 210 ash trees were sampled at the root collar by means of an increment borer. Preferentially, the sampling was done pointing the borer to fresh necroses in order to isolate fungi that could primarily be associated with the tissue death. The collected bore cores, pieces of *Armillaria* mycelial fans (maximum 10 × 10 mm in size) and rhizomorphs (about 15-mm-long) that were also collected when available, were transported to the laboratory and subjected to a fungal isolation on Hagem agar media (Stenlid, 1985).

Burned areas infested by R. undulata *(Paper **V**)*

Five *Rhizina undulata* infection foci bearing numerous fruitbodies were investigated in three localities on the Curronian Spit in western Lithuania (Fig. 4). The areas represented over-100-year-old stands of mountain pine (*Pinus mugo* Turra.) growing on sandy soils. The stands were partly clear-cut 2 years prior to the study, with concurring slash burning. A total of 141 fruitbodies were collected and mapped around five discrete fireplaces: three sites in Preila locality (128 fruitbodies), one site - in Smiltynė locality (8 fruitbodies), and one site - in Juodkrantė locality (5 fruitbodies).

Pure cultures of *R. undulata* were isolated directly from hymenium of the fruitbodies on Hagem agar media (Stenlid, 1985; Vasiliauskas & Stenlid, 2001). Ascospores were collected by spraying the surface of the fruitbodies with sterile water (Vasiliauskas & Stenlid, 2001). For germination, the ascospores were spread on Hagem agar media in Petri dishes, and incubated at 37 ºC for 72 h to break dormancy (Jalaluddin, 1967a). Single germinating ascospores were subcultured on three different types of media: Hagem agar, vegetable juice agar and yeast extract agar (Vasiliauskas & Stenlid, 2001).

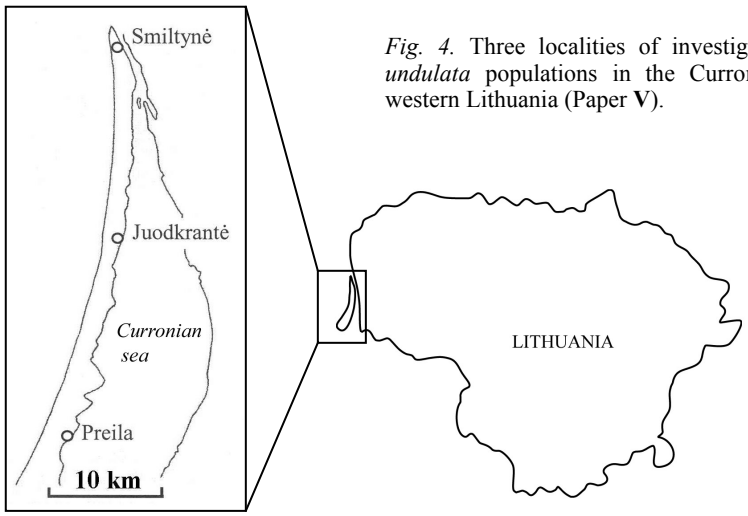

Fig. 4. Three localities of investigated *Rhizina undulata* populations in the Curronian Spit of western Lithuania (Paper **V**).

Identification of fungi

All obtained fungal isolates were distributed into groups based on mycelial morphology. The representatives of each group were selected for DNA extraction, PCR amplifications and DNA sequencing procedures that followed established protocols (Kåren *et al.*, 1997). The ribosomal ITS region was sequenced using two primers (ITS1 and ITS4) for every specimen (White *et al.*, 1990). All fungal identifications were made including and combining culture morphology, sequence checking against available databases (the NCBI BLAST database (Altschul *et al.*, 1997), the database of the Dept. of Forest Mycology and Pathology at the Swedish University of Agricultural Sciences, Uppsala, and the basidiomycete database of the Dept. of Systematic Botany at the Göteborg University, Göteborg), and the ecology of certain species. In addition, species that were producing spores in pure culture were identified with the assistance of mycologists at the Central Bureau of Fungal Cultures (CBS) in Utrecht, the Netherlands.

In addition to the results obtained by sequencing of the ribosomal ITS region, the determination of *Heterobasidion* (**III**) and *Armillaria* (**IV**) intersterility group (biological species) was based on the ability to heterokaryotize known homokaryotic tester strains and, either to form clamp connections (**III**) (Korhonen, 1978b; Stenlid & Karlsson, 1991), or to change the morphology of a tester (**IV**) (Guillaumin *et al.*, 1991). All the haploid tester strains used are stored at the culture collection of the Dept. of Forest Mycology and Pathology at the Swedish University of Agricultural Sciences, Uppsala.

Somatic incompatibility tests

The distribution of *H. annosum* s.s. (**III**), *A. cepistipes* (**IV**) and *R. undulata* (**V**) genets (clones) on the infested sites was identified with the aid of somatic incompatibility reactions. The fungal isolates were paired in all possible

combinations, including self-pairings as controls, on 9-cm Petri dishes containing either Hagem agar media (**III** & **IV**) (Stenlid, 1985; Vasiliauskas & Stenlid, 1998), or vegetable juice agar (**V**) (Vasiliauskas & Stenlid, 2001). In studies of Papers **III**, **IV** and **V**, representatives of the obtained genets (clones) from the different plots were also paired in all possible combinations. If the reactions were not clear, the pairings were repeated two to five times. During study of Paper **II**, somatic incompatibility tests were performed with all isolates of *P. gigantea*, in an effort to check genetic relationships within the wild type population, as well as to compare the wild types with the original Rotstop *P. gigantea* strain.

Interactions between two mycelia were regarded as compatible and the strains were classed as genetically identical when a continuous mycelial mat was formed between the isolates, corresponding to that of self-pairing controls. Antagonistic types of mycelial interactions (demarcation line) following contact were classed as incompatible, and the tested strains in such cases were classed as genetically different from each other. The results of the tests were projected on the constructed maps. Maximum linear extent of a genet (vegetative clone) was determined as the maximum spatial distance between two compatible isolates (*e.g.* Dettman & Van der Kamp, 2001). Mapping of the fungal genets was based on observations that genets of the same species are strongly antagonistic, and that spatial overlapping by different fungal genets in the field is unlikely (*e.g.* Prospero *et al.*, 2003).

Results and discussion

Forest management and root diseases

Escaping the disease: silvicultural and pathological evaluation of mixed P. sylvestris-*deciduous trees' plantations (Paper **I**)*

In spite of the occurrence of *H. annosum* s.s. disease centres in adjacent stands and the generally hazardous site conditions (**I**), we found no external signs (fruitbodies or typical symptoms) of *Heterobasidion* infections in the investigated mixed pine-deciduous tree plantations. Furthermore, detailed examination of the superficial root systems of the declining pines and fungal isolations did not show the presence of the root rot disease either. Lack of entry points in form of fresh thinning stumps very likely was the crucial factor that prevented the infection.

The results of study performed for Paper **I** showed that dense planting does not lead to higher yield than lower densities, but instead to actual and potential losses; densely stocked plantations at the age of 25 years (Table 1) already needed urgent thinnings according to thinning programs currently required by Lithuanian forestry regulations (Juodvalkis *et al.*, 2000). The reduction of individual tree parameters as well as the volume of stand per hectare was not compensated by the higher number of surviving trees. Moreover, an intense competition resulted in high level of tree suppression and decline. In the intensive production-based forestry, higher

initial density of pure Scots pine stands is desirable as in the dense stands a production of high quality timber increases (Persson, 1976, 1977; Uusvaara, 1985; Kellomäki, 1986; Prescher & Ståhl, 1986; Huuri *et al.*, 1987). However, the gain achieved by dense spacing must naturally be weighed against the additional cost of planting and pre-commercial thinnings (Prescher & Ståhl, 1986), as well as the risk of getting infections by root rot at a young age.

In contrast, sparse planting and intercropping with deciduous trees increased stand productivity and allowed thinnings to be delayed. For example, the most sparsely planted scheme no. 1 at the age of 25 years was by 27% more productive than the most densely stocked pure control scheme no. 5 (Table 1, Fig. 2). A positive effect on the growth of pine could also be achieved by improved nitrogen, and possibly phosphorus nutrition provided by the nitrogen-fixing species *A. fruticosa* and *R. pseudoacacia* (*e.g.* Boring & Swank, 1984; Gillespie & Pope, 1990). Certain qualitative traits of individual pine trees (stem taper, size of crown and branches, self-pruning) were adversely affected by the sparse stocking, but in general those traits still remained acceptable from a silvicultural point of view.

Biological and chemical control of Heterobasidion *(Paper **II**)*

In temperate forests, when thinning a coniferous stand under periods of high *Heterobasidion* spore spread, biological or chemical stump treatment should be considered. During the study of Paper **II**, the efficacy of stump treatment against the infections by *Heterobasidion* spp. was investigated. The investigation revealed a high incidence of the pathogen on Rotstop-treated and on control *P. abies* stumps, 76.2 and 85.7% of them were infected, respectively. In the Rotstop treatment, the number of stumps infected by *Heterobasidion* and the number of colonies per stump did not differ significantly from those observed in untreated controls, however, the biological treatment reduced significantly both the size of the individual colonies of *Heterobasidion* spp., and colonised stump area. This was in good agreement with other related studies (Thor, 1997; Thomsen, 2003).

It is known that the size of mycelial colonies is a major factor influencing the competitive success among wood-inhabiting fungi (Holmer & Stenlid, 1993; Boddy, 2000). Also in stumps of spruce, the penetration of *Heterobasidion* spp. into deeper layers has been shown to depend on initial size of a colony, and small colonies seldom progressed into infection of root systems (Morrison & Redfern, 1994; Thomsen, 2003). In the present study, the Rotstop *P. gigantea* strain successfully competed with and seemingly restricted spread of the pathogen already at the initial stages of fungal community establishment.

In general, the results of study performed for Paper **II** demonstrated that the Rotstop application: (1) lead to establishment and dominance in stumps of the applied strain of *P. gigantea*; (2) did not prevent initial multiple infections of freshly cut stump surfaces by *Heterobasidion* spp.; (3) reduced significantly further spread of the pathogen; (4) allowed the colonisation of stumps by many other species of fungi; and (5) restricted the substrate availability for their growth (including *Heterobasidion* spp.).

The application of urea, as distinct from the Rotstop, completely prevented the colonisation of stumps by *Heterobasidion* spp. soon after the wood was exposed. As demonstrated in the recent study by Johansson *et al.* (2002), basidiospores of the pathogen are unable to germinate and mycelia are unable to survive on wood treated with urea because of raised pH levels. Moreover, in the study of Paper **II**, urea also reduced incidence of other basidiomycetes in the stumps. Thus, it is very likely that urea has a similar effect on basidiomycetes other than *Heterobasidion* spp., including *Armillaria* spp.

Is planting of birch on pine sites infested by H. annosum *s.s. a good silvicultural option? (Paper **III**)*

Based on externally visible symptoms and the results of fungal isolation, a high proportion of *B. pendula*, *P. sylvestris* and *J. communis* trees and stumps in the investigated stands were infected by *Heterobasidion* spp. An unexpected result was that birch, regarded as a rather resistant species, became as heavily infected. It was found that after the diseased pines have been felled, *Heterobasidion* remained to a large extent in the root systems thereby sustaining the inoculum at the site. This very likely resulted in the high mortality rates of the replanted birch and the comparably low vigour of the individual trees.

The yield of the investigated birch plantations at the age of 25 years was rather low (45.0–76.1m^3/ha), lower than would be expected in healthy areas according to standard growth models of birch stands (Juodvalkis *et al.*, 2000). This productivity was determined by low stand densities (mortality rate of birch during the past 25 years comprised 55%) and generally thin stems. Some loss could also be due to careless selection of the birch outplanting material used in the plantations, and extremely poor site conditions.

Despite the low yield and rather poor quality of the investigated plantations, cultivation of birch on infested sites may still be a good option; the maintenance of forest environment as well as the production of firewood are the substantial benefits on such poor site conditions. Using improved outplanting material could possibly increase the sustainability and economical potential of such plantations. The outplanting material could be improved, on the one hand, by selection (breeding) of the most productive (or of high stem quality) birch genotypes (*e.g.* Malcolm & Worrell, 2001), and, on the other hand - by using birch material proved to be more resistant to *Heterobasidion* as was demonstrated with Norway spruce in the studies by Dimitri (1982) and Swedjemark (1995).

Armillaria cepistipes – *a serious pathogen of ash stands? (Paper **IV**)*

In ash (*Fraxinus excelsior*) stands investigated during the study of Paper **IV**, about 60% of ash trees were declining, about 30% were dead and only about 10% were classed as sound-looking. Based on external signs, mycelial fans, and wood decay characteristic for *Armillaria* (Morrison *et al.*, 1991), it was concluded that at least 97.6% of the investigated trees (including sound-looking ones) were colonised by

this pathogen. Moreover, the presence of *Armillaria*-like rhizomorphs was recorded on every examined tree, regardless of its condition.

In the study of Paper **IV**, *A. cepistipes* was found to be the dominant fungus in all tree health categories, as it was most commonly observed and isolated from stem bases of sound-looking, declining and dead trees. This was to a certain extent surprising, since *Fraxinus* seems to be an uncommon host to *Armillaria* (*e.g.* Sokolov, 1964). Moreover, *A. cepistipes* is generally considered to be a weak pathogen, only capable of slow infection to roots of healthy trees (Rishbeth, 1982; Guillaumin *et al.*, 1985, 1989, 1993; Gregory *et al.*, 1991; Prospero *et al.*, 2004). In the study sites (**IV**), active decay caused by *A. cepistipes* was consistently recorded on a great majority of the investigated trees, thus the fungus likely contributed to and accelerated the decline of the investigated stands.

On the other hand, it is unlikely that the attacks by *A. cepistipes* was the primary cause of the decline. It is generally accepted that *Armillaria* spp. are opportunistic pathogens able to invade hosts weakened by certain stress factors (Wargo, 1977; Singh, 1983; Entry *et al.*, 1986). Moreover, the results of study performed for Paper **IV** indicated that *A. cepistipes* was present on the investigated sites for at least 20 years without causing serious tree mortality. Among the stress factors that could be involved in the ash decline, an increased frequency of dry years and a lowered level of ground water are usually mentioned (Juodvalkis & Vasiliauskas, 2002; Skuodienė *et al.*, 2003). It must therefore be stressed, that in the investigated sites the drainage system, built about 20 years prior to the study, could contribute to water stress (deficit), from which the ash stands have likely been suffering in the recent years. Thus, this example possibly illustrates how "positive" forest management practices can adversely affect a future stand, *i.e.* a disturbed state of balance between a host and a pathogen can cause unpredicted consequences.

Population biology of *H. annosum* s.s., *A. cepistipes, R. undulata* (Papers III-V) and artificially distributed *P. gigantea* (Paper II)

Transfer of H. annosum *s.s. to a new forest generation (Paper **III**)*

In the study of Paper **III**, somatic incompatibility tests were performed with 139 heterokaryotic isolates of *H. annosum* s.s. revealing an extensive territorial clonality of the pathogen. In total, 31 genets of *H. annosum* s.s. were found on the investigated sites. The three largest clones consisted of 30, 18, and 10 isolates and covered areas up to 25, 32 and 48 m across, respectively. It was not uncommon for a clone to cover areas that encompassed both *P. sylvestris* (previous), and *B. pendula* (present) forest generations; of 103 birch trees and stumps yielding heterokaryotic *H. annosum* s.s. isolates, 41 (or 39.8%) were attacked by fungal genets shown to originate from the previous generation of pine.

A high number of *H. annosum* s.s. clones that colonise more than one host tree and a generally large size of those clones indicate an efficient expansion of the fungus from tree-to-tree (*e.g.* Piri *et al.*, 1990). As the stumps of the diseased pines have not been removed, it is difficult to say to what extent the birch contributed to

the expansion of individual *H. annosum* s.s. clones. Nevertheless, the estimated rate of the fungal spread (at least 0.6 m/year) did not conflict with results obtained in other *Heterobasidion* population studies in pine stands (Stenlid & Redfern, 1998).

Fresh stump surfaces of thinned birch do not seem to be important entry courts for *Heterobasidion* infections as there were only few small-sized clones of the pathogen occurring in 4-year-old birch stumps and/or trees that could have root contacts to these stumps. The rate of mycelial spread from the birch stump surface to the root systems of adjacent trees for *Heterobasidion* is not known, and it is unclear if it takes place at all (Redfern & Stenlid, 1998). Even if it occurs, it would be improbable for this fungus to spread through birch roots at a rate of more than 1 m per 4-year period (according to Stenlid & Redfern (1998)). So, most likely, the fungus was initially spread in pine, and then transferred to birch via multiple pine stump-replanted birch infections. The results of study performed for Paper **III** therefore showed that *H. annosum* s.s. is able to persist in root systems of diseased trees for decades and readily attack birch replanted on infested sites.

Armillaria cepistipes*; a shift from saprotrophic behaviour to pathogenic (Paper **IV**)*

In the study of Paper **IV**, somatic incompatibility tests with a total of 150 heterokaryotic *A. cepistipes* isolates revealed an extensive territorial clonality of the pathogen; 28 genets were identified on three sample plots occupying 0.45 ha (about 62 genets per hectare). Such a high diversity, as well as the presence of small, scattered genets in the investigation plots might indicate frequent infections by basidiospores through stumps made during the pre-commercial thinnings (Rishbeth, 1991; Worrall, 1994). A high number of *A. cepistipes* clones that have colonised more than one host tree and generally large size of those clones indicated an efficient expansion of the fungus from tree-to-tree.

Based on the size of the largest *A. cepistipes* genets (up to 55 m across) found in the study of Paper **IV**, and known mycelial growth rates for *Armillaria* in north-temperate forests (about 0.3–1.6 m/year (Shaw & Roth, 1976; Rishbeth, 1991; Smith *et al.,* 1992; Legrand *et al.,* 1996; Peet *et al.,* 1996)), it was reckoned that the fungus was present on the investigated sites for at least 20 years before the ash decline started to occur. The finding of one genet, which was split into two spatially separated ramets by a forest road that had also been built 20 years ago, further supported this conclusion. It was therefore hypothesized that latent saprotrophic behaviour of *A. cepistipes* had been shifted to the pathogenic by some predisposing factor (-s) after 20–30 years of presence in the stands, leading to decline of *F. excelsior*.

Territorial and dispersive clonality in R. undulata *(Paper **V**)*

In the study of Paper **V**, somatic incompatibility tests identified fourteen distinct genets of *R. undulata*, thirteen of which were represented by 2–48 strains, and three were encountered in 2–4 different sites (a maximum distance between the

sites - 40 km). Occurrence on spatially separated sites of the same genotype of the fungus clearly indicated a presence of dispersive clonality in *R. undulata* populations and potential airborne dispersal of the fungus over at least 40 km.

On a local scale, clusters of genetically identical fruitbodies occupied discrete territories, implying territorial clonality (the largest genotype covered an area 7 m across). However, the possibility cannot be excluded that several genetically identical (sib-related) ascospores might have germinated in the vicinity, independently resulting in genetically identical fruitbodies. This event, for example, looked likely for one of the genets, where two fronts of *R. undulata* fruitbodies were advancing in different directions from opposite sites of one fireplace. Cases, when territorial clonality is mixed with dispersive clonality in fungal populations, have previously been reported (Anderson & Kohn, 1995).

The results of study performed for Paper **V** showed that both dispersive and territorial clones are characteristics of natural populations of *R. undulata*. Studies of *R. undulata* populations on even larger geographical scale might provide interesting results on spatial distribution of the genets of the fungus.

Tracking an artificially distributed P. gigantea *in thinned stands (Paper **II**)*

In the study of Paper **II**, somatic incompatibility tests with the 23 *Phlebiopsis gigantea* strains isolated from the Rotstop-treated *P. abies* stumps indicated that all the strains were genetically identical among themselves and to the original Rotstop *P. gigantea* strain. At the same time, all the strains were different from the wild *P. gigantea* strain isolated from an untreated stump. Shortly, this study has demonstrated that following the Rotstop treatment, a single dispersive clone of *P. gigantea* can be artificially distributed over large forest areas.

Communities of wood-inhabiting fungi (Papers I-IV)

In studies of Papers **I-IV**, a high diversity of wood-inhabiting fungi was found, including pathogens, endophytes and saprotrophs. Sampling and isolation from dead, declining and apparently healthy trees of 4 different species resulted in 1196 fungal strains representing 190 distinct operative taxonomic units (OTU). Of those OTUs, 47 were basidiomycetes, 133 ascomycetes and deuteromycetes, and 10 zygomycetes. Of the 190 OTUs, 147 (or 77%) were identified at least to a genus level. Therefore, a significant part of the fungal community remained unidentified, both as species and functional groups, thus providing a potential for the future work. It is also worth noting that in most cases the sampling effort had not exhausted the existing diversity of wood-inhabiting fungi, indicating that in case of more extensive sampling many more species could be found.

Most of the identified basidiomycetes are commonly fruiting on dead wood in northern European forests, and are generally considered as decomposers of dead wood (Ryvarden & Gilbertson, 1993, 1994). Therefore, it was quite surprising to find such species as *Bjerkandera adusta* (Willd.: Fr.) Karst., *Trametes hirsuta*

(Wulfen) Pilát, *Merulius tremellosus* Fr., *Fomitopsis pinicola* (Sw.) P. Karst., *Inonotus radiatus* (Fr.) Karst., or *Xerula* sp. in living stems of pine (**I**), birch (**III**) and ash (**IV**). A possible negative impact of those species on tree health cannot be excluded. Even less is known about the role played in pathological processes by numerous isolated microfungi. Over 70% of the identified asco- and deuteromycetes are commonly encountered fruiting on dead substrates (for references see Stewart *et al.* (1988)), some, however, are regarded as potential tree pathogens (*e.g. Nectria haematococca* Berk. & Broome (Anamorph: *Fusarium solani* (Mart.) Appel & Wollenw.), *Nectria radicicola* Gerlach & L. Nilsson (Anamorph: *Cylindrocarpon destructans* (Zins.) Scholten), *Phoma exigua* Desm., *Botryosphaeria stevensii* Shoemaker (Anamorph: *Diplodia mutila* (Fr.) Mont.) (Sinclair *et al.*, 1987; Unestam *et al.*, 1989; Przybył, 2002)). Their occasional occurrence at the stem bases does not exclude the possibility of a more widespread pathogenic behaviour in roots or crowns of the investigated trees.

An interesting finding was a marked difference in fungal communities in sound-looking, declining and dead trees (stumps). Consequently, the Sorensen similarity coefficients (Magurran, 1988; Krebs, 1999) were generally low, indicating that principally different fungi inhabited trees of different health categories within the stands investigated. Striking differences in fungal community structure noted among sound-looking, declining and dead pines (**I** & **III**), between living and dead birches (**III**), and among sound-looking, declining and dead ashes (**IV**) indicated that fungal species in wood of living trees change along with changes in tree condition. The change in the species composition in a sequence "healthy-declining-dead tree" could occur due to less restricted external infections on the declining or dead trees, where newcomers tend to replace species that were resident in apparently healthy stems. According to ecological strategies of the fungi (Cooke & Rayner, 1984), in the tree stems, the "ruderal" species should have been replacing "stress-tolerant" ones, but we may only hypothesize on that, since many species remained unidentified and/or their biology is largely unknown.

In study of Paper **II**, the impact of biological (Rotstop) and chemical (urea) treatments on biodiversity in communities of non-target fungi in freshly cut Norway spruce stumps was assessed. The stump treatment led to a decrease in species richness both in Rotstop-treated (by 15%) and in urea-treated (by 19%) stumps. Despite being very close in estimates of species richness, Rotstop-treated and urea-treated stumps differed markedly from each other in structure of fungal community. Stumps that have been subjected to the biological compound (Rotstop), were colonised mainly by the same species that occurred naturally in untreated stumps. By contrast, chemical treatment (urea) strongly promoted stump colonisation by asco- and deuteromycetes, led to a significant decrease of zygomycetes, and almost completely eliminated basidiomycetes thus showing a low resemblance to a natural community.

Future prospects

Already in the late eighties numerous experiments have been set to find out if there is any effect of admixed deciduous tree species and the initial spacing on the incidence of the annosum root rot in coniferous plantations. According to Vasiliauskas (1989), Davidenko & Nevzorov (1978) and Negrutskii (1986), some stand models are able to reduce the incidence of *Heterobasidion* spp. infections and extent of the caused damage significantly. The resistance of experimental pine plantations investigated during study of Paper **I** could also be tested by monitoring tree condition and spread of the disease following artificial infections (through the thinning stumps) by a known strain of *H. annosum* s.s.

The persistence of artificially distributed (following stump treatment) Rotstop *P. gigantea* strain in nature should be investigated (this could be done also on sites investigated during the study of Paper **II**). We need to know, if this strain is able to form fruitbodies on treated stumps and disperse viable basidiospores to the environment. Moreover, it is necessary to estimate the extent to which the spores mate with individuals of the resident *P. gigantea* populations and what impact does it have on intraspecific genetic diversity.

There is an old and aching problem in eastern Europe,- replanting of forest sites (pine sites growing on poor soils in particular) infested by *Heterobasidion* spp. An option of growing birch on infested pine sites was offered (**III**), although the performance of birch was not satisfactory enough. Therefore, search of disease-resistant *P. sylvestris* and *B. pendula* genotypes (the two main timber-producing species on poor sandy soils) could be another logical step.

As mentioned in the study of Paper **IV**, the stress factors that have weakened Lithuanian *F. excelsior* stands making them prone to infections by weakly pathogenic *Armillaria cepistipes*, are unclear and possibly complex. Those "predisposing factors" could be investigated more thoroughly from the pathological point of view, focusing also on fungal infections to tree crowns (according to Przybył (2002), P. Barklund (personal communication)).

During study of Paper **V**, a spatial distribution of *Rhizina undulata* genets was investigated on small and medium geographical scales, however studies of this fungus' populations on a larger geographical scale might provide more information on biology and ecology of this interesting ascomycete as well as of other homothallic fungi. Molecular techniques should be employed to study genetic relationships and variation among the different strains and genets of *R. undulata*.

Finally, to contribute to knowledge on the diversity of wood-inhabiting fungi it is important to continue species identification and updating of the existing sequence databases. A possible negative impact on tree health by many fungal species found during studies of Papers **I**, **III** and **IV**, and especially by those that were found in healthy-looking wood (basidiomycetes in particular), cannot be

excluded, providing a potential for further taxonomy- and pathology-oriented studies.

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