Effects of Sustainable Management Practices on Fine-root Systems in Willow *(Salix viminalis, S. dasyclados)*, Grey Alder *(Alnus incana)* and Norway Spruce *(Picea abies)* Stands

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Abstract

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Fine roots of trees can be sensitive indicators of environmental change. This thesis analyses the response of tree fine-root (<1 and <2 mm in diameter) systems in deciduous and conifer stands to different sustainable management regimes. Separate studies were conducted in plantations and in natural stands of the Baltic Sea region. Clones of *Salix viminalis* and *S. dasyclados* in an unfertilised short-rotation forestry (SRF) plantation in Estonia (58°42′N, 26°55′E) were studied to compare the decomposition dynamics of fine roots, and the amount, structure and species diversity of associated ectomycorrhizal (EM) communities. The level of EM colonisation was estimated in stands of *Alnus incana* (Sweden, Estonia). The effect of granulated wood ash (GWA) on the distribution, morphology and chemistry of fine roots was analysed in a *Picea abies* stand in SW Sweden (56°33′N, 13°13′E), a site exposed to high acid deposition.

The fine roots of *S. dasyclados* were a more recalcitrant substrate for decomposition (k=0.162) than those of *S. viminalis* (k=0.325), because of the higher initial concentration of acid detergent lignin of the former. The N in decomposing fine roots was retained in the system, as indicated by its decrease and immobilisation in the substrates. The level of EM was high in studied *Salix* spp. and *Alnus incana* roots. *Salix dasyclados* was characterised by a higher proportion of colonised root tips (94%) than *S. viminalis* (75%). Nine EM fungal taxa were identified in *Salix* spp. roots in SRF – a relatively low diversity compared with established forest ecosystems.

The long-term effect of GWA on fine roots of *Picea abies* was mainly revealed in decreased necromass (1-2 mm root fraction), in decreased specific root length, and in increased P/N and Ca/N proportions by mass (1-2 mm). Fine-root biomass (<1 mm) was significantly greater in the lower humus in the GWA treatment, but this did not affect the total biomass in the whole soil profile. Wood ash in granulated form and in the long term caused only modest changes in the fine-root system, and can be used as a compensatory fertiliser in *Picea abies* stands.

The results are applicable for maintaining sustainable forest ecosystems.

Keywords: fine roots, decomposition, acid detergent lignin, ectomycorrhiza, short-rotation forestry, granulated wood ash, vertical distribution of fine roots, specific root length, nutrient/N ratios

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Tõnnile ja Ukule

Contents

Introduction

Appendix

Papers I – V

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

I. Püttsepp Ü., Lõhmus K., Koppel A. Decomposition of fine roots and α-cellulose in a short rotation willow (*Salix* spp.) plantation on abandoned agricultural land (manuscript)

II. Püttsepp Ü., Rosling A., Taylor A. F. S. Ectomycorrhizal fungal communities associated with *Salix viminalis* L. and *S. dasyclados* Wimm. clones in a short- rotation forestry plantation (accepted in: Forest Ecology and Management)

III. Püttsepp Ü., Lõhmus K., Persson H., Ahlström K. Effect of granulated wood ash application on fine-root distribution and morphology in an acidified Norway spruce (*Picea abies* (L.) Karst.) stand in SW Sweden (manuscript)

IV. Püttsepp Ü., Lõhmus K., Persson H., Ahlström K. Effect of granulated wood ash on fine-root chemistry in an acidified Norway spruce (*Picea abies* (L.) Karst.) stand in SW Sweden (manuscript)

V. Granhall U., Lõhmus, K. Püttsepp, Ü., Ostonen I. - “Mycorrhizae in *Alnus incana*” (accepted in: Riparian Alder Forests: their importance as buffer zones and bioenergy sources. Eds. Ü. Mander, K. Lõhmus. Kluwer Academic Publishers, in prep.)

Introduction

Background

The belowground part of a tree can be roughly seen as a mirror image of the aboveground system, with its specific morphology and function in the soil environment. A tree root system belowground consists of coarse and fine branches – the coarse roots and the fine roots. The coarse roots function mainly as support organs and as long-distance transport pathways, and the fine root network, in association with mycorrhizal fungi, functions as an organ for nutrient and water uptake. The fine roots are usually the high-order laterals that make up most of the surface area of the root system (Waisel & Eshel 2002). A symbiotic association between fine roots with primary structure and mycorrhizal fungi forms the main nutrient-absorbing organ (Smith & Read 1997). Large quantities of carbohydrates are allocated to the fine-root and mycorrhizal system (Olsthoorn & Tiktak 1991). Through continuous development and interaction with the soil environment, the belowground part of trees forms a highly heterogeneous and dynamic network in a forest soil. While young rootlets develop, the older parts senesce and eventually die. The dead roots become soil organic matter, which undergoes decomposition and further mineralisation, processes that are influenced by abiotic factors and soil organisms. An appreciable amount of the photosynthetically fixed carbon will be incorporated via roots into the soil carbon pool (Atkinson 1992).

Sustainable management of forests as natural resources is beginning to attract wider public attention. Man-made stresses, such as expanding deforestation, air pollution and climatic change leave footprints on the global forest ecosystem. Extensive timber production and regionally high atmospheric pollution influence the forests in the Baltic Sea region. The southern parts of Sweden, Finland and Norway have received high loads of acidic deposition since the mid-1950s, in consequence of increased emissions from motor vehicles, industry and agriculture (Andersson et al. 1997, Bertills & Näsholm 2000). Although nutrient uptake by trees can have a natural acidifying effect on forest soils, the environmental risk comes mainly associated with anthropogenic factors. Increasing amounts of nitrogen via airborne deposition have a fertilising effect on temperate and boreal forest ecosystems, which otherwise are limited by nitrogen availability. This can result in an increase in aboveground tree growth and a decrease in fine root biomass, which implies a considerable shift in the functional equilibrium of the shoot : root ratio (Olsthoorn & Tiktak 1991). Reduced uptake capacity (i.e. a reduced fine root system) and increased aboveground demand for water and nutrients, can increase the susceptibility of the stand to drought and nutrient deficiency (Olsthoorn & Tiktak 1991). The maintenance of balanced inputs and outputs and the recirculation of nutrients in an ecosystem are fundamental principles of sustainable forestry (Saarsalmi 2001, Sverdrup & Stjernquist 2003).
Wood ash has a good acid-neutralizing capacity and the ability to provide the soil with base cations (Eriksson 1998, Saarsalmi 2001). Wood ash has been proposed for practical use to counteract soil acidity and to compensate for losses of calcium and other nutrients (Högbom et al. 2001). An increased production of energy from

biomass, such as forest residues and short-rotation crops, will result in the accumulation of end products, including wood ash. The recycling of wood ash, by returning it to the forest, may be an environmentally sound way of solving the practical problems of deposition of that highly alkaline material. However, along with the advantages, experimental results have sometimes shown negative effects, e.g. accelerated formation and leaching of NO_3^- after the addition of wood ash (Högbom et al. 2001). The consequences of adding wood ash to forest ecosystem and its effects on the fine-root system of trees are complex, and are not yet fully understood.

Fast-growing broadleaved trees are widely cultivated in short-rotation forestry (SRF) plantations for renewable energy. The amount of CO_2 bound in the harvestable biomass approximately equals that released by combustion after few years' growth (Hall & House 1994). The closed carbon cycle of the SRF economy makes it a valuable alternative to fossil fuels. In the long term, different non-fossil fuel options will be used in the world's energy system. Naturally, the interest of the SRF industry is largely focussed on the processes that affect the production of the aboveground crop. An understanding of belowground processes, e.g. of the symbiotic associations between the fine roots and soil fungi, decomposition of root-litter, etc., is important in any attempt to optimise fertiliser amounts, and in estimates of the carbon sequestration by SRF systems.

This thesis focusses on mycorrhizal fine-root systems of trees in various sustainably managed plantations, and covers the vertical distribution of fine roots, their morphology, biomass and necromass, and estimates of their chemistry in regimes that involve compensatory fertilisation, as well as investigations of fine-root decomposition and of root–fungal associations.

Tree fine-root system

Both conceptual and methodological difficulties are involved in root-system studies (Vogt et al. 1993). Tree root systems spread laterally to a great extent and intermingle; connection between different individuals may occur by grafting (Vogt et al. 1993, Külla & Lõhmus 1999). In contrast to the boles and crowns, the individuals in root systems are difficult to distinguish without the use of special methods (Vogt et al. 1993). Roots of different size have different functions (Helmisaari 1991). Fine, non-woody tree roots are responsible for nutrient acquisition, mycorrhiza formation and most exploration of the soil (Brundrett et al. 1990). No standard size class or operational definition of a fine root exists, and the classification criteria vary from study to study (Hendricks et al. 2000). Commonly, fine roots have been defined on the basis of diameter, such as <1 mm and/or <2 mm in diameter. Within a given diameter class, roots with different function and structure occur in different proportions. Even the <1 mm diameter class is highly heterogeneous, in that it consists of primary and secondary root structures. Moreover, one species may have a 'finer' average fine-root compartment than another. King et al. (2002) stated that much of what has been termed 'fine roots' in the literature is probably a mix of static and dynamic root fractions. Berg and McClaugherty (2003) suggest that fine roots should be defined to include root tips and small-diameter roots without secondary growth. The diameter-based classification can thus increase the risk of lumping together the roots of primary and secondary structure, with different functional importance. A rough interpretation of the results can still be made. As can be seen from the results of the current study (papers III, IV), there was a marked difference in chemical composition and morphology between the root fractions <1 mm and 1–2 mm in *Picea abies*. Nutrient concentrations vary with plant tissue and age (Helmisaari 1991). Nutrient concentrations decrease in roots with increasing diameter, especially for N, P, K and Mg (Helmisaari 1991, Persson et al. 1995). Fe and Al accumulate in fine roots, exceeding several times their concentration in needles (Vogt et al. 1987, Helmisaari 1991).

Observations with minirhizotrons have demonstrated a highly dynamic behaviour of the fine-root fraction. The roots of *Pinus taeda* <1 mm in diameter, were far more dynamic in their length production and mortality than those of diameter 1-2 mm; of those fractions, almost 80% of the root length occurred in the diameter fraction <1 mm (King et al. 2002). In the present thesis, the length of *Picea abies* fine roots in the <1 mm diameter class was approximately eleven times that in the 1-2 mm diameter class (paper III).

Owing to their dynamic character, a large amount of resources is allocated to the fine roots of trees. Vogt et al. (1990) estimated the fine-root production in coniferous stands to lie in the range 1,200–12,230 kg ha^{-1} yr^{-1}. Of the total net primary production (NPP) in various coniferous ecosystems, 5–73 % was annually allocated to fine roots (Vogt et al. 1990). When the soil profile is considered, the majority of fine roots occur in the upper few centimetres, e.g. 48 % of *Pinus sylvestris* roots in the 0–2.6 cm FH layer (Persson 1980).

The fine-root systems of *Salix viminalis* and *S. dasyclados* clones, *Alnus incana* and *Picea abies,* were studied in the present thesis. Brundrett et al. (1990) described the root system of the Salicaceae as heterorhizic (separate long and short lateral roots) ‘with several orders of straight long roots bearing crooked, narrow short roots (0.15-0.25 mm wide) that gradually taper to an even narrower apex (0.08-0.15 mm wide).’ Those short roots which establish ectomycorrhizal (EM) associations are usually shorter and substantially thicker than non-mycorrhizal laterals (Brundrett et al. 1990). Both *Picea abies* and *Alnus incana* are also known to have heterorhizic root systems.

Fine roots as ecological indicators

Fine roots are to some extent more sensitive indicators of forest nutritional status than is provided by foliar analysis (Vogt et al. 1993, Genenger et al. 2003). The spatial distribution of fine-root biomass in the soil is well related to the availability of nutrients and water. For example, as an adaptation tactic to drought, fine-roots can redistribute to deeper soil horizons (Persson et al. 1995a). Different fertilisers can affect the biomass growth and necromass of fine roots. Liming can result in a smaller biomass and a larger necromass of the fine roots of *Picea abies,* compared with the control, while nitrogen fertilisation can result in increased fine-root biomass when it is applied on a nutrient-poor site (Helmisaari & Hallbäcken 1999).

The effects greatly depend on the amount and form of a fertiliser (Persson & Ahlström 1994), as well as on the site conditions, species and the age of the stand. The chemical composition of plant tissues, including fine roots, reflects the soil composition at the particular site and the ability of the plant to accumulate or exclude excessive uptake of certain elements (cf. Ericsson 1994). Nutrient imbalances may occur in soils when one or more nutrients becomes greatly available, while the trees cannot use them owing to other limitations, e.g. other nutrients (Binkley & Högberg 1997). In addition to the effects driven by atmospheric deposition, natural acidification of the root zone occurs when the plant uptake of cations (charge) exceeds the uptake of anions (charge). If plant material is returned to the soil as litter, the release of the base cations counterbalances the uptake caused by acidification (Wild 1995). Intensive harvesting of forest (whole-tree harvesting) leads to a reduction of soil base saturation (Olsson et al. 1996).

Indices derived from fine-root morphology, such as length-to-weight ratio or specific root length (SRL), and from fine-root chemical composition (e.g. nutrient weight proportions in relation to nitrogen (where N = 100%), Ca/Al molar ratio) can sensitively reflect changes in soil qualities. At low soil pH and low base saturation, the molar ratio of base cations to Al in fine roots becomes a critical parameter. The threshold conditions for potential forest impacts from Al stress have been estimated as a Ca/Al molar ratio lower than 0.2 in fine roots as a threshold for moderate risk, and a ratio lower than 0.1 as the threshold for high risk (Cronan & Grigal 1995).

The <1 mm diameter fraction of fine roots reacts more readily to changes in the soil environment, since it contains the majority of nutrient-absorbing surface. In the present thesis, the proportion by weight of fine roots <1 mm in diameter, of the general fraction of all fine roots <2 mm in diameter, increased slightly (non-significantly in biomass, significantly in necromass) in the treatment with granulated wood ash, compared with the control.

Decomposition

Dead plant material, the plant litter – mainly leaves, wood and fine roots – undergoes decomposition in all natural ecosystems. The decomposer communities – fungi, bacteria and invertebrate animals - perform the mineralisation of essential elements and the formation of soil organic matter (Swift et al. 1979). Climate, edaphic conditions, decomposer communities and the quality of litter or substrate are important factors that control the rate of the decomposition process. The litter quality comprises chemical and physical properties, which determine the accessibility of the litter to degradation (Ågren & Bosatta 1996). Substrate quality is changed by the activity of the decomposer organisms, and this change itself modifies the future activity of the decomposers in a 'feedback manner' (Swift et al. 1979). Litter decomposition is a direct source of CO_2 to the atmosphere; approximately half of the annual CO_2 output from the soil is accounted for by mineralization (Coûteaux et al. 1995). The quality indices used to analyse root litter are similar to those used for leaf litter, including mineral nutrient concentration, the concentration of secondary compounds, and ratios of C : nutrient and nutrient : nutrient (Silver & Miya 2001). However, root litter tends to be more heterogeneous – possessing fractions with differing stabilities – than is leaf litter (Silver & Miya 2001).

Fine roots decay in the same place as they die, being already in close contact with the saprophytic microorganisms (Berg & MacClaugherty 2003). Fine-root litter input is comparable with the amounts of foliar litter fall (Berg & McClaugherty 2003). From the perspective of a forest ecosystem, fine-root mortality plays a key role in biogeochemical cycling (Pregitzer 2002). Fine-root litter is characterised by relatively high lignin and nitrogen content; since most fine roots of trees are mycorrhizal, the mycorrhizal compartment influences the chemical composition of fine roots (Brandes et al. 1998, Berg & McClaugherty 2003). Litterbags are widely used to study mass loss in fine-root decomposition (Camiré et al. 1991, Lõhmus & Ivask 1995, Berg & McClaugherty 2003, Silver & Miya 2001), and were used in the present thesis (paper I).

Although green leaves and fine roots are among the most nutrient-rich plant tissues (Ericsson 1994), they may differ in decomposition pattern and rate (Berg & McClaugherty 2003). Some of the differences between fine-root litter and leaf litter, which influence their decomposition patterns, are as follows:

- The chemical composition and structure of fine roots changes with diameter and with the function of the roots; this makes the fine-root substrate very heterogeneous when classified on a diameter basis; leaf litter is more homogeneous;
- Mycorrhizal colonization contributes to fine-root chemistry by increasing nutrient concentrations, especially of N and P (Langley & Hungate 2003). Fungal structures in roots contain chitin, a recalcitrant compound, which causes slower decomposition of roots heavily colonized by mycorrhiza (Langley & Hungate 2003);
- Microbial decomposition can be relatively more important for fine roots because of their placement in the soil than for the leaf litter on the soil surface (Silver & Miya 2001);
- Substrate quality tends to be the dominant factor in controlling patterns in the decomposition rates of fine roots at a global scale, while the decomposition of leaf litter tends to be more highly correlated with climatic factors, especially temperature. This is because soil can serve as a buffer to roots and decomposers, while leaf litter is exposed to extremes of temperature and precipitation on the surface of the soil (Silver & Miya 2001);
- The growing and dying cohorts of a fine-root population can occur in close proximity, and present a direct feedback to the nutrition of an individual plant. Rapid nutrient release and uptake can occur in microenvironments concomitantly with root decomposition, which differs from the decomposition of aboveground tissues (Langley & Hungate 2003).

Ectomycorrhiza

Mycorrhizal associations between plant roots and symbiotic fungi are ubiquitous in most terrestrial ecosystems. In boreal and temperate forests, commonly formed by the tree families Betulaceae, Pinaceae, Fagaceae and Salicaceae, most of the fine roots are ectomycorrhizal, which is the main nutrient-absorbing organ (Read 1991). The distal root tips of the laterals in a tree fine-root system are the primary infection points for mycorrhizas (Pregitzer 2002). Amongst several mycorrhizal types, in the ectomycorrhiza a mycelial structure, the mantle (or sheath) encloses the rootlet, and hyphae penetrating inwards between the cells form a complex intercellular system, the Hartig net (Smith & Read 1997). Common to all mycorrhizas, the extramatrical mycelium extends out to the soil, exploiting an immense soil volume for nutrient uptake and mobilisation. Nutrient transfer between the plant and fungus occurs bidirectionally at the interface of the cells of the root cortex and the Hartig net. The soil-derived nutrients are exchanged for carbohydrates from the host plant. Ectomycorrhizal fungi increase the uptake rate of nutrients by increased physical access to soil, change the chemistry and alter the bacterial community of the mycorrhizosphere (Simard et al. 2002). Brandes et al. (1998) estimated that extramatrical mycelium contributed 73% of the total N and 76% of the total P uptake of *Picea abies* seedlings, resulting in increased dry weight, increased N and P concentration and content in mycorrhizal plants. It has been demonstrated that ectomycorrhizal fungal hyphae can also transport divalent cations such as Mg to their host trees, e.g. *Picea abies* (Jentschke et al. 2000).

Species from the genera *Salix*, *Eucalyptus*, *Populus, Alnus* can form dual mycorrhizas, where ecto- and arbuscular mycorrhizas are present in the same root system. In *Alnus*, arbuscular mycorrhiza was present only in seedlings, replaced later by dominating ectomycorrhiza (Arveby & Granhall 1998). Arbuscular mycorrhiza is characterized by branched fungal structures within the root cortical cells.

The effect of management activities such as ploughing, fertilisation, herbicide and fungicide application or conversion to non-native plant species, on mycorrhizal communities is poorly understood (Simard et al. 2002). Herbaceous arable crops associate commonly with arbuscular mycorrhiza. Helgason et al. (1998) compared the diversity of arbuscular mycorrhizal communities, and found a lower diversity on arable sites compared to that of woodlands. Pointing to the broad host range of some arbuscular mycorrhizal taxa, Helgason et al. (1998) related the low mycorrhizal diversity rather to the agricultural practices than to the monoculture *per se*. In the *Salix* plantation studied in the present thesis, a relatively low ectomycorrhizal diversity was found (paper II), although the studied blocks had been out of intensive management for seven years. Arbuscular mycorrhiza was not found in *Salix* in that 7-year-old plantation. Ectomycorrhizal fine-roots of *Salix* are illustrated in Fig. 1.

Short-rotation forestry

In the search for an alternative to fossil fuels, the sustainability of energy systems and environmental concerns have become the main driving forces since 1980s

(Gustafsson 1994). The term ‘short-rotation forestry’ (SRF) or ‘energy forestry’ mainly implies fast-growing deciduous trees or shrubs, such as *Salix*, *Populus*, *Alnus*, *Eucalyptus*. Apart from the reduction of greenhouse gases, the production of energy crops contributes to sustainable development. Abandoned agricultural land can be used for growing energy crops, preferably in combination with waste recycling, adding an environmental effect as well as a positive effect on employment (Christersson & Sennerby-Forsse 1994). Research in the field of energy forestry started in Sweden already in the 1970s. In the conditions of agricultural overproduction in the 1990s, *Salix* plantations became more frequent in fertile Swedish farmlands, as crops for bioenergy production. Biomass from SRF is used in district-heating plants, and the residual ash can be re-used as fertiliser.

In scientific co-operation between the Swedish University of Agricultural Sciences (SLU) and various Estonian research institutions, the first experimental energy-forest plantations were established in Estonia in 1993-1995 (Koppel et al. 1996). In the present thesis, studies on *Salix* fine-root decomposition and ectomycorrhizal associations were conducted in one of the Estonian SRF plantation of *Salix*.

Makeschin (1994) points to the positive effects on the soils of former agricultural land that results from afforestation with energy forest. The physical structure of the soil is usually improved, due to the absence of cultivation and of the frequent passage of heavy machinery; and the content of carbon and nitrogen, as well as microbial biomass and soil biodiversity, increase in the upper soil layer in the long term (Makeschin 1994, Jug et al. 1999). Owing to the change of land-use, the soils under SRF stands are in transition from arable to forest characteristics. Leaf and root litter production give rise to an increasing C/N ratio in such soils (Jug et al. 1999). Forest soils have a higher N retention capacity value than arable soils, because of their higher C/N ratio (Ågren & Bosatta 1996). The C/N ratio in the soil of the studied SRF plantation (Saare, Estonia) were 12.1 in *Salix viminalis* and 13.5 in *S. dasyclados* plots (paper I). These values surpass slightly the average value (C/N 10) for agricultural soils in temperate regions, but remain still low in C supply and may be limiting for microbial growth (Rowell 1994).

Wood ash as compensatory fertiliser

According to Eriksson et al. (1998), ca. 200,000 tons of wood ash are produced in Sweden annually. An environmental risk arises from its deposition as landfills, giving a highly alkaline pH when dissolved in (rain) water (Eriksson et al. 1998). During combustion of woody biomass, a large proportion of S and N is gasified, while the majority of nutrients (Ca, K, P, Mg, Mn), trace elements and the acid-neutralising capacity remain in ash (Steenari & Lindqvist 1997, Eriksson 1998). The unsustainable base-cation balance in forest soils, which results from whole-tree harvesting, acid deposition or both, can be counteracted by recirculation of wood ash (Lundborg 1998, Saarsalmi et al. 2001). Wood-ash treatment has been shown to increase soil pH, causing a mineralisation pulse and an increase in nitrate-reductase activity in the fine roots (Genenger et al. 2003b). Given its

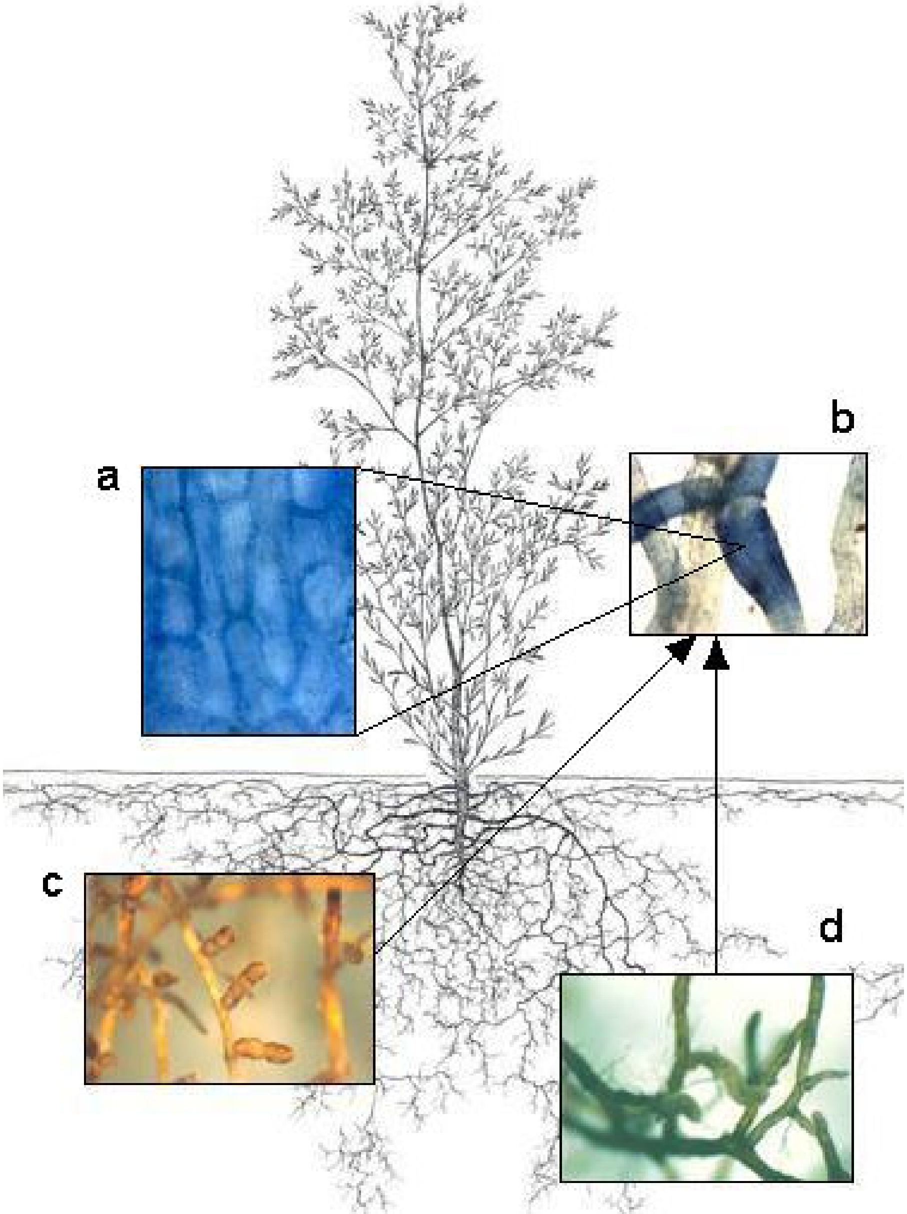

Figure 1. Ectomycorrhiza in *Salix viminalis* roots (photos). a) Hartig net between cortex cells, 1000 x; b) ectomycorrhizal tissues on the root apart from the tips, 400 x; c, d) different morphology of ectomycorrhizal roots of *Salix*, 10 x. On the background *S. purpurea*, from Kutschera & Lichtenegger (2002); photos by A. Taylor (b), Ü. Püttsepp (a, c, d).

alkalising character, the effects of wood ash on the soil environment and biota are to some extent similar to the effects of liming. Lime has been widely used to counteract soil acidification, although there is a risk of increased leaching of nitrate (Högberg et al. 2000). However, the effect of wood ash on the forest ecosystem are not well studied, and conclusions about its long-term effect are lacking (Persson & Andrén 1999).

The changes in forest soil are related to the dose and form of wood ash applied (Perkiömäki & Fritze 2002, Genenger et al. 2003a). Compacted wood ash dissolves more slowly than loose ash; therefore the latter can induce more changes at the same application rate (Perkiömäki & Fritze 2002). Stabilisation of wood ash before spreading is necessary, to avoid the risks of dust, salt effects, pH shock and burning damage to vegetation (Steenari & Lindqvist 1997). Positive effects of hardened wood ash treatment in aboveground organs of trees have been demonstrated, such as increased concentrations of P, Ca and K in the needles of *Picea abies* (Arvidsson & Lundkvist 2002). The effects of wood-ash treatment on soil chemistry (pH, base saturation) and on fine roots has been reported to occur mainly in the upper 0-5 cm of the soil (Clemensson-Lindell & Persson 1995, Arvidsson & Lundkvist 2003). In the present thesis, the long-term effect of wood ash on fine roots of *Picea abies* was recognised even in the deeper mineral soil layers (paper III). That the effect of hardened wood ash can last long, was seen by increased microbial activity detected 18 years after treatment (Perkiömäki & Fritze 2002). Ectomycorrhiza may act in mobilising nutrients from wood ash (Mahmood et al. 2001, Mahmood et al. 2002). Hagerberg & Wallander (2002) showed a considerable increase in ectomycorrhizal mycelium biomass following wood-ash amendment.

The number of studies on the effect of wood ash on fine roots is rather scarce (Persson & Ahlström 1994, Clemensson-Lindell & Persson 1995, Genenger et al. 2003a, b). Alkalizing compounds have shown to increase the concentration of essential cations (Ca, S, Mg, K) and to raise the Ca/Al ratio in fine roots of Norway spruce (Persson & Ahlström 1994). Persson & Ahlström (1994) used loose wood ash, and recorded a significantly higher soil pH in the wood-ash treatment than in the control, in contrast to the study in the present thesis (papers III, IV). Among different alkalizing compounds tested, peat ash had a negative effect on root development (Persson & Ahlström 1994). The experiment by Genenger et al (2003a) resulted in a strong effect on fine-root element concentrations, after loose ash was applied in two consecutive years.

Three years after granulated wood ash was applied on the Skogaby site in SW Sweden, the fine-root biomass of *Picea abies* decreased and the specific root length (SRL) increased significantly, compared with that in control plots (Clemensson-Lindell & Persson 1995). The result of the present work on the same site indicated that no change has occurred in total fine-root biomass, and a significantly decreased SRL in 0-5 cm of the top soil, although an increase in SRL in the <2 mm root fraction could be seen in the lower soil horizons.

Objectives of the work

The general aim of the study was to analyse the fine-root related processes in forest ecosystems under sustainable management practices. The specific aims were:

- to compare the decomposition dynamics of fine roots of *Salix viminalis* and *S. dasyclados* clones in non-fertilised SRF plantation, an ecosystem in transition from agricultural to forest;

- to compare the amount, structure and species diversity of ectomycorhizal colonisation in *Salix viminalis* and *S. dasyclados* clones in a non-fertilized SRF plantation, and to estimate the level of ectomycorrhizal colonisation in *Alnus incana* under different management regimes;

- to estimate the response of fine-root distribution, morphology and chemistry to the improved nutrient supply from granulated wood ash in a *Picea abies* stand exposed to high acid deposition.

Material and methods

Fine roots were defined as <1 mm in diameter (papers I, II, V). In studies III and IV the fine roots were defined as <2 mm in diameter and subdivided into <1 mm and 1-2 mm diameter classes.

Studies I and II were carried out in an experimental 6-year-old *Salix* plantation for short rotation forestry in Saare, Estonia. Two *Salix* clones were studied, clone 78183 of *Salix viminalis* and clone 81090 of *S. dasyclados* (Swedish clone numbering system). For simplicity, these clones were referred to by their species names in the present work, which does not imply that the results apply to the species as a whole. Studies III and IV were carried out on the Skogaby experimental site, a 31-year-old Norway spruce (*Picea abies*) plantation in SW Sweden. Six planted sites in Sweden and five sites in Estonia (one planted, four natural) were sampled for mycorrhizal analysis of *Alnus incana* (V).

Ectomycorrhizal colonisation and decomposition of fine roots were studied in non-fertilised blocks of the *Salix* SRF plantation. The mycorrhiza in *Alnus* was studied both in fertilised (N, P, K, Ca, ash) and non-fertilised treatments. Granulated wood ash (GWA) treatment was applied to evaluate the effect on fine-root distribution, morphology and chemical composition in a Norway spruce stand (III, IV).

A soil-coring method was used to collect the fine-root material for ectomycorrhizal analysis (II, V) and for the analysis of fine-root morphology, distribution and chemical composition in response to wood ash application (III, IV). The fine roots used in the decomposition study originated from ingrowth-cores (I).

The litterbag technique (I) was used to study fine-root decomposition (Berg 1984, McClaugherty et al. 1984, Lõhmus & Ivask 1995). Decomposition of fine roots of *Salix viminalis* and *S. dasyclados* was studied during one year of incubation in the densely rooted 0-10 cm of soil. The dynamics of ash-free mass, of the N content, AD lignin and AD cellulose was analysed in the decomposing fine-root substrate. In parallel, sheets (50 × 10 × 1 mm) of α-cellulose were incubated to estimate the dynamics of the cellulose decomposers' activity. The dynamics of ash-free mass, and the dynamics of the N and AD cellulose content, were analysed in α-cellulose.

Ectomycorrhizal colonisation was analysed by morphological characters, and estimated as proportions of root tips, length colonised or both (II, V). The proportions of different fungal structures in the fine roots were estimated (II) by means of the magnified intersection method (McGonigle et al. 1990). Taxonomic identification of ectomycorrhizal fungi (II) was performed by amplifying the ITS region of the fungal rDNA by the polymerized chain reaction (PCR) and subsequent sequencing (Gardes & Bruns 1993).

The roots of *Picea abies* were sampled by soil coring (inner diameter 4.5 cm) to 50 cm depth of the mineral soil. Fine-root biomass, necromass (g m^{-2} or kg ha^{-1}), and length (m m^{-2}) of the live fraction (<1 mm, 1-2 mm) were calculated on the basis of the core cross-sectional area. The vertical distribution of roots was studied on a 1-cm-depth scale, both in the humus layers and in the mineral soil. Specific root length (SRL) was calculated as length to mass ratio (Ostonen et al. 1999). Fine-root chemical composition was analysed in <1 mm and in 1-2 mm root diameter classes, in the top-humus 0-2.5 cm, in the lower humus below 2.5 cm and in the mineral soil. In addition to element concentrations and content in the fine roots, the ratios of nutrient/N, Ca/Al and (Ca+Mg)/Al molar ratios were calculated. Soil and root chemical composition was analysed by different methods, described in the individual papers. For each study, the statistics used are explained in the individual papers.

Results and discussion

Papers I, II, V.

Ectomycorrhizal (EM) colonisation was high in both clones of *Salix* in the studied short rotation forestry plantation. However, *Salix viminalis* was characterised by significantly lower EM colonisation (75% of root tips colonised) and higher decomposition rate (k=0.325) than *S. dasyclados* (respectively 94% and k=0.165). The main difference in the fine-root qualities between the studied *Salix* clones, which influenced the decomposition rate, was found in AD lignin concentration. The decomposition patterns of AD lignin were clearly different. The content of the AD lignin fraction increased in *S. viminalis* root litter (initially 25%) while it remained unchanged in *S. dasyclados* root litter (initially 35%) during a one-year period of incubation in litterbags. The dynamics of N content was similar for both clones during decomposition. It was characterised by an initial decrease and a subsequent immobilisation phase. High N immobilisation, to 0.35% from the initial 0%, was observed in the decomposing α-cellulose after 300 days' incubation, indicating that the soil potential for cellulose decomposition was not a limiting factor. A soil C:N ratio of 12.1–13.5 remained, which was in a range higher than that of agricultural systems and lower than that of forest ecosystems.

The diversity of the fungal taxa associated with *Salix* roots was low. The most common associate was *Phialophora finlandia*, which typically inhabits the roots of a wide range of host plants (Jumpponen & Trappe 1998). Species of Tomentelloid fungi and of the genus *Cortinarius*, which commonly are found in established forests and *C. saturninus* in parks (Deacon & Fleming 1992, Hansen & Knudsen 1992) were also identified in *Salix* roots.

Ectomycorrhiza was the dominant mycorrhizal type in *Alnus incana* older than five years. In two natural riparian middle-aged *Alnus incana* stands, 89% and 67% of the fine-root system (<1 mm) was ectomycorrhizal.

Papers III, IV.

The long-term effect of granulated wood ash (GWA) on fine roots of *Picea abies* was mainly revealed by decreased necromass (1-2 mm root fraction), in decreased specific root length (<1 mm, 1-2 mm, in topsoil of 5 cm), and in increased P/N weight proportion (1-2 mm). Since the P/N ratios were in the lower part of the optimum range in this study, < 10 (Brække 1994, Knecht & Göransson 2004), the slight improvement could indicate an ameliorating effect of GWA. Although the total fine-root biomass in the whole soil profile was not affected by GWA, a shift towards higher biomass in the lower humus occurred in the GWA plots. That biomass increase brought about an increase in total content of P in the fine roots and a decrease in P and N concentrations. Nitrogen concentrations decreased relatively more than P concentrations, giving rise to the increase in the P/N ratio. The increased Ca/N ratio may indicate an excess uptake of Ca, because the ratio (>20) was far above the suggested optimum 2–4 (Brække 1994, Knecht and Göransson 2004).

The molar ratios of Ca/Al and (Ca+Mg)/Al in the fine roots decreased with the GWA treatment, but remained above the risk level (>0.2, Cronan & Grigal 1995).

The vertical distribution of the relative biomass of the fine roots (<2 mm in diameter) showed a trend towards more uniform distribution on the GWA plots in the 0–5 cm soil layer, as compared with the control, where a distinctive partitioning between the upper 0–2.5 and 2.5–5 cm soil layers occurred.

Total biomass and root length (estimated down to 50 cm depth) did not differ significantly between control (C) and granulated wood ash (GWA) treatment plots in any fine root fraction. Biomass values for the <2 mm diameter fraction were 256 ± 20 (SE) g m^{-2} and 258 ± 25 (SE) g m^{-2} in C and GWA respectively. The fine-root length occurred predominantly in the <1 mm fraction, 1900 ± 176 (SE) m m^{-2} on C plots and 1644 ± 192 (SE) m m^{-2} on the GWA plots. Necromass was significantly higher on C plots only in the 1–2mm root fraction.

The root fractions <1 mm and 1–2 mm in diameter differed in their response to GWA. The impact of GWA on root morphology, on specific root length (SRL), occurred particularly in the finest, <1 mm root fraction and in the topsoil, while the necromass, live/dead ratio and P/N, Ca/N weight proportions were affected in the 1–2 mm root fraction. The smaller SRL in GWA may have resulted from higher root tissue density, greater root diameter or both.

The granulated wood ash used was characterised by a slow release of elements. However, the effects detected on fine roots, although modest, may refer to improved nutrient availability. The decrease in necromass can probably be related to higher decomposition rates on the GWA plots, to extended life span of the fine-roots or both. The latter is supported by the decrease of SRL on the GWA plots, because roots with a longer lifes pan usually have higher tissue density.

Conclusions

- The fine roots of *S. dasyclados* are a more recalcitrant substrate for decomposition than the fine-roots of *S. viminalis*, as the decomposition of the latter was more rapid, during the first year of incubation. In the short term, the fine-root litter of *S. dasyclados* contributes more than that of *S. viminalis* to carbon sequestration in soil.
- Ectomycorrhizal (EM) fungal diversity in the short rotation forestry plantation of *Salix viminalis* and *S. dasyclados* was low, featuring an agricultural system, but some taxa such as *Cortinarius* spp. and tomentelloid fungi (family Thelephoraceae) are more commonly encountered in established forests.
- The clone (or tree species) may primarily determine the level of EM colonisation in *Salix*, but the local soil nutrient status may also influence colonisation.
- Six years after its establishment on abandoned agricultural land, the soil ecosystem of the unfertilised *Salix* plantation can be characterised as transitional towards forest soil.
- Application of granulated wood ash (GWA) in *Picea abies* stand on acidic podzol-type soil had a modest effect on root distribution, morphology and chemistry.
- The decreased fine-root necromass was more clearly an effect of GWA, while the biomass redistribution may have been an interaction effect between GWA and the thicker humus layer.
- Specific root length decreased with the long-term effect of GWA; the mechanism may be related to increasing root diameter, higher root tissue density or both.
- The vertical distribution of fine roots and morphology indices can indicate the effect of granulated wood ash more unequivocally than root chemistry

parameters, since a shift in the former (e.g. biomass) can affect the latter (e.g. element concentrations).

- Different diameter fractions of fine roots react to the environmental changes with different sensitivity. The <1 mm fraction is highly heterogeneous in structure and function, hence variability in that fraction may hide a treatment effect.

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