

Ecosystem Functioning and Plant-Soil Interactions in Forests

Influences of quality and diversity of resources

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Abstract

The aim of this thesis was to investigate the role of resources in driving ecosystem processes and in influencing soil- and plant communities in boreal and temperate forests, through four complementary experimental studies. In the first study, plant and soil microbial responses to the quality and diversity of added organic substrates from boreal forests were investigated. The substrate-diversity effects were greatest for plants and depended on the presence of high-quality substrates. In the second study, the impact of fire disturbance in boreal forests on litterfall composition and decomposition rates was assessed along a fire chronosequence, by collecting litterfall data and performing a litterbag experiment. Time since last fire reduced tree litterfall quality by increasing the proportion of twigs (low-quality litter) in the litterfall and this resulted in a decline in overall litter decomposition rates. In the third study, effects of resource availability on the performance of coexisting boreal tree seedlings were examined by growing seedlings in pots with low- and high fertility soil under different light filters. The growth and mycorrhizal colonisation of seedlings in response to light and soil conditions differed between species, which affected the relative competitive abilities of the seedling species. In the fourth study, impacts of different canopy tree species on tree seedling recruitment and soil communities were assessed by planting seedlings in stands of native and invasive tree species in temperate forests. Treatments were applied to test for effects of mycorrhizal connections and root competition from canopy trees on seedling performance. Tree seedlings were unaffected by root competition and mycorrhizal treatments, but both seedlings and soil organisms were strongly affected by canopy species identity through influences on the microenvironment. In combination, these studies demonstrate different mechanisms for how resources may influence nutrient dynamics, soil communities and tree seedling recruitment in forests, i.e. through regulating decomposer activities and decomposition rates, nutrient cycling, mycorrhizal colonisation, plant growth, and through influencing feedbacks between soil- and plant communities. These studies are also relevant for a better understanding of global change issues such as impacts of invasive species, biodiversity loss, and increased carbon sequestration.

Keywords: Boreal forest, decomposition, litter-mixing, light, mycorrhiza, microbial community, plant productivity, regeneration, substrate-induced respiration, tree seedling

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Appendix

Papers I-IV

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

I. Dehlin, H., Nilsson, M.-C. & Wardle, D.A. 2006. Aboveground and belowground responses to quality and heterogeneity of organic inputs to the boreal forest. *Oecologia* in press (published online) DOI: 10.1007/s00442-006-0501-5.

II. Dearden, F.M., Dehlin, H., Wardle, D.A. & Nilsson, M.-C. 2006. Changes in the ratio of twig to foliage in litterfall with species composition and consequences for decomposition across a long term chronosequence. Accepted in *Oikos*.

III. Dehlin, H., Nilsson, M.-C., Wardle, D.A. & Shevtsova, A. 2004. Effects of shading and humus fertility on growth, competition and ectomycorrhizal colonization of boreal forest tree seedlings. *Canadian Journal of Forest Research* 34, 2573-2586.

IV. Dehlin, H., Peltzer, D.A., Wardle, D.A., Allison, V.J., Yeates, G.W. & Nilsson, M.-C. 2006. Tree seedling growth and soil community structure in forest stands of invasive and native tree species. *Manuscript*.

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Introduction

Ecosystem functioning

Ecological processes such as decomposition, cycling of nutrients and carbon, and primary (plant) production are essential for the functioning of both aquatic and terrestrial ecosystems (Chapin III *et al.* 2002; Begon *et al.* 2005). During the decomposition process a variety of organic substrates of different quality, mainly dead plant material but also remains of consumer organisms and animal faeces, are broken down and nutrients are released. These nutrients exist both in inorganic and organic forms that vary in their availability to plants; when available these nutrients can be taken up by plants and stored in plant biomass, and then in due course return to the soil as organic matter. In this way, resources are cycled in the system and productivity is maintained. Carbon (C), the main constituent in plants and the energy source for the decomposers, is also cycled by being extracted from organic matter by decomposers and released to the air as respiration [carbon dioxide (CO₂)], and taken up by plants through photosynthesis. Other ecosystem processes, such as competition between plants or soil organisms, herbivory, predation, and disturbance are also important for determining the structure and dynamics of communities and ecosystems (Begon *et al.* 2005). The organisms performing ecosystem processes are strongly affected by the quality and availability of resources. In forest ecosystems, decomposition and nutrient cycling are carried out by soil organisms in the decomposer (belowground) subsystem, and plants in the producer (aboveground) subsystem. The aboveground and belowground subsystems are closely linked, and influence each other in various ways, and hence also the outcome of ecosystem processes (Wardle 2002). To understand ecosystem functioning it is therefore necessary to consider both subsystems, and the interactions between them.

Increasing the knowledge of the mechanisms and processes that maintain ecosystem functioning, and learning how organisms interact with each other and with their physical environment to perform these functions, is important for several reasons. In terms of forest ecosystems, we can get a better understanding of forest and regeneration dynamics, which may contribute to sustainable forest management. Also, from a global change perspective, this knowledge is important for predicting how forest ecosystems can resist and recover from events such as biodiversity loss, invasive species, global warming and pollution. Further, by studying C sequestration in the aboveground biomass and soil, we can learn about the role in forests in the global C storage and source–sink balances.

The role of resources in the functioning of forest ecosystems

Resources have a fundamental role in all ecosystems, as the quality, diversity and quantity of resources present influence the abundance and species composition of plants, animals and soil organisms, as well as ecosystem processes rates (e.g. fluxes of C and nutrients and ecosystem productivity) (e.g. Grime 2001; Begon *et*

al. 2005). In forest ecosystems, resources comprise of solar radiation (light), CO₂, water and nutrients.

Differences in light conditions caused by shading vegetation have large impacts on growth and competitive interactions between tree species in forests (Messier *et al.* 1999; Paper III). Likewise, soil nutrient availability has important effects on plant species composition in forests. For example, in boreal forest reserves in which soil fertility increased (and in which nitrogen (N) concentrations increased from 0.80% to 2.03%), there was shift in tree species from *Pinus sylvestris* to *Picea abies*, and in understory species from dwarf shrubs to grasses and herbs (Paper III).

The aboveground forest subsystem

The plant community largely determines the quantity and quality of resources that are deposited to the soil. In terrestrial ecosystems, a large portion (50-99%) of the plant tissue is shed as litter (McNaughton *et al.* 1989), and the remainder is eaten by herbivores and subsequently respired or returned to the soil as animal faeces or remains of consumer organisms. Plant species differ vastly in the quality of litter they produce. The chemical and physical properties (i.e. quality, or decomposability) of substrates returned to the soil is regarded as the most important factor influencing microbial activity and decomposition rates in ecosystems (Swift *et al.* 1979). Evidently, the higher the quality of the substrate, the more attractive it is for the decomposers and the faster it is decomposed. High-quality substrates often contain high concentrations of the macronutrients N and P and easily degradable sugars and aminoacids, and low concentrations of more recalcitrant materials such as lignin and polyphenols (Swift *et al.* 1979). Macronutrients (or ratios of C: N and N: P) often limit decomposition rates in the early stages of decomposition (from months to a few years) (Berg 2000), whereas the concentration of lignin (or ratios of lignin: C and lignin: N) is often related to decomposability in the later stages of decomposition (Berg & McCaugherty 2003). Deciduous tree species usually have higher-quality foliar litter than do evergreen tree species (Cornelissen 1996). In Paper II, the N concentrations were 1.06% for the deciduous *Betula pendula*, and 0.62% and 0.70% for the conifers *P. sylvestris* and *P. abies*, respectively (Paper II); however, intraspecific litter quality may vary depending on site characteristics such as soil fertility.

The belowground forest subsystem

The forest soil is inhabited by an extremely diverse community of soil organisms, which together constitute the soil food-web. The major groups of soil organisms are microorganisms/microbes (bacteria and fungi), microfauna (<0.1 mm bodysize: nematodes, protozoa, and rotifers), mesofauna (0.1-2 mm bodysize, e.g. mites, springtails and enchytraeids) and macrofauna (>2 mm body size, e.g. earthworms, beetles and millipedes) (Swift *et al.* 1979). The soil microbes (particularly fungi) are the primary decomposers of organic matter in forests, and are uniquely able to break down and release the nutrients from complex carbohydrates (e.g. cellulose, hemicellulose and lignin). It has been estimated that soil microbes can carry out more than 95% of the decomposition in boreal forests

(Persson *et al.* 1980). Soil fauna have important roles in decomposition and nutrient cycling through feeding on microbes and on each other, and through altering the physical structure of plant litter and soil (Wardle 2002; Hättenschwiler & Gasser 2005; Schädler & Brandl 2005).

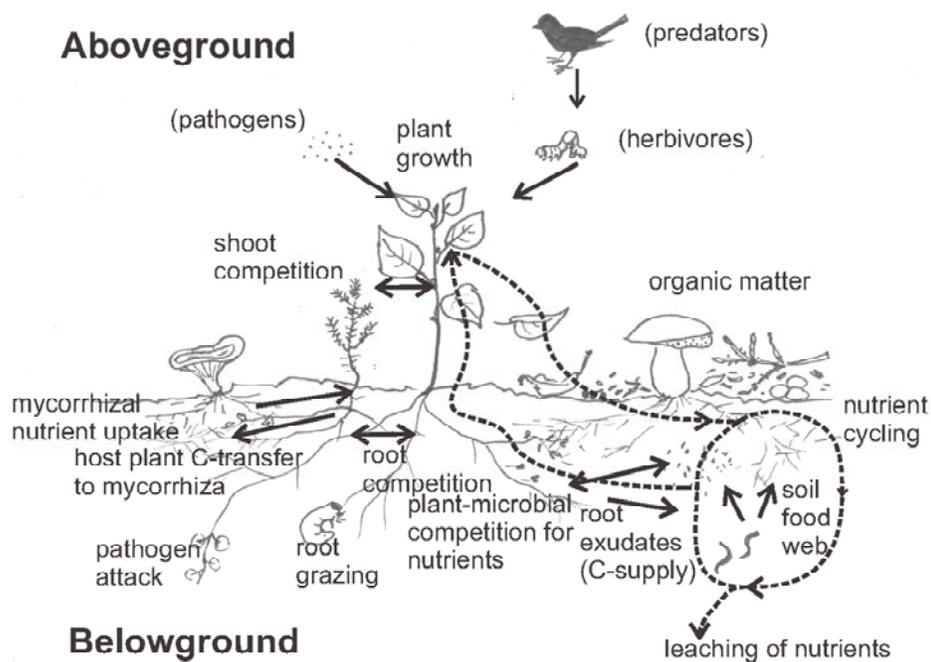


Figure 1. Interactions between the aboveground and belowground ecosystem components and their influences on ecological processes. Briefly, plant litter and other dead organic material are broken down by decomposers, which mainly consist of soil microbes (fungi and bacteria). The nutrients and carbon (C) released from decomposition are then cycled within the soil food-web (microbes and soil fauna), and taken up by plants or leached out of the system. Plants influence the soil community by supplying resources of different quality through the production of litter and the release of root exudates, and by providing mycorrhizal fungi with C. They also, to some extent, compete with microbes for nutrients. The soil community in turn influences plants through releasing plant-available nutrients during the decomposition process, competing for nutrients, enhancing plant nutrient-uptake via mycorrhiza and by the effects of root feeding fauna and pathogens.

Aboveground-belowground links

The aboveground and belowground subsystems interact in several ways (Figure 1), and aboveground-belowground feedbacks play an important role in controlling ecosystem processes (Wardle *et al.* 2004). Plant species determine the energy (C) and nutrient resources available for soil organisms, by adding litter or C compounds (through rhizodeposition) of different quality to the soil. Plants may also influence the community composition of microorganisms (e.g. Molina *et al.* 1992; Bardgett *et al.* 1999) and root associated organisms such as nematodes through root litter and root exudates (Yeates 1993). The decomposer subsystem in turn influences plants through determining the supply of plant-available soil nutrients, and thereby indirectly regulates plant growth. Another link between the aboveground and belowground systems involves mycorrhizal fungi, and their symbiotic relationship with plants. Even though mycorrhizal fungi usually are less able than saprophytic fungi to decompose organic matter, they are likely to affect decomposer activities through influencing the growth of plants, and to some (unknown) extent through competing with other soil organisms for nutrients (Schimel & Bennet 2004). Root pathogens and root feeding soil fauna may also exert direct negative impacts on plant growth through consuming nutrients and C and reducing plant root uptake capacity (Westover *et al.* 1997).

Diversity of organic resource inputs

The importance of biodiversity for ecosystem functioning has been an intensively studied subject the last decades, because of concerns about the increased rates of species extinctions world-wide. Losses of biodiversity are likely to have negative impacts on ecosystem processes, at least if we assume that species, or similar groups of species, have different roles in maintaining ecosystem functioning. Studies from plant communities have found a positive relationship between species diversity and ecosystem (plant) productivity (Loreau *et al.* 2001), but less is known of effects of plant species diversity on the functioning of the soil community.

A reduced diversity of organic resources in forests, for example as results from forest management promoting monoculture stands, may affect ecosystem processes. Studies have shown that substrates that decompose in mixtures with other substrates may have different decomposition rates, and alter microbial activity or biomass, relative to when they are decomposed in isolation (reviewed by Gartner & Cardon 2004). Further, it has been hypothesized that a greater diversity of organic substrates may increase microbial diversity by increasing the number of niches available for microbes, and that this could have positive influences on decomposition rates and nutrient cycling through resource complementarity and increased microbial efficiency (Hooper *et al.* 2000). However, only a few researchers have attempted to test this hypothesis (e.g. Griffiths *et al.* 2000; Bonkowski & Roy 2005), and no clear evidence exists. The knowledge of whether quality and diversity of organic residues affects plant nutrient up-take, growth and interactions between the plant- and soil subsystems is scarce. This is despite responses of the belowground community to resources

being likely to create feedbacks through influencing nutrient uptake and growth of seedlings.

The few existing studies on effects of substrate diversity on plant recruitment or performance have involved plant or moss litter and have shown either neutral or negative effects of substrate diversity (Nilsson *et al.* 1999; Quested *et al.* 2003; Quested and Eriksson 2006). These effects depended on the species composition of the mixture, and also on the site the litter was placed on. Further, studies on effects of substrate diversity have almost exclusively focused on leaf litter (but see Paper I), although many other organic substrates occur in forest ecosystems, such as twigs, vertebrate faeces and sporocarps.

The mechanisms behind the effects of substrate diversity on ecosystem processes are often unclear, but these are likely to involve nutrient transfer among substrate types, improved microclimate or habitat diversity and presence of stimulatory or inhibitory compounds. Substrate-diversity effects may also be influenced by interactions among soil fauna (Gartner & Cardon 2004; Hättenschwiler *et al.* 2005).

The role of fire for resource quality and decomposition rates

Fire is the primary natural disturbance in many forest biomes, including boreal forests where fires have occurred frequently (return intervals of 30-250 years are common) (Zackrisson 1977; Swetnam 1996; Niklasson & Granström 2000). Anthropogenic fire suppression has occurred in many forested areas the last two centuries; in Swedish boreal forests fires have been actively suppressed the last 130 years (Zackrisson 1977). Fire is well known to have important influences on successional dynamics, forest structure and tree species composition. Studies of a long-term fire chronosequence in northern Sweden has shown that absence of fire may lead to changes in tree species and litter composition, and reductions in soil fertility, decomposition rates, and tree productivity, eventually leading to ecosystem decline (Wardle *et al.* 1997; 2003; DeLuca *et al.* 2002). The main reason behind the large impacts of fire is its rejuvenating effects on ecosystem processes, by increasing soil pH, decomposition, and nutrient release (Zackrisson *et al.* 1996; Wardle *et al.* 1998; Pietikäinen *et al.* 2000). Fire-produced charcoal has an important part in determining the positive effects of fire, through its ability to adsorb and deactivate secondary compounds that often occur in high concentrations in late-successional boreal forest soils and which are inhibitory for nutrient acquisition and growth of tree seedlings (Wardle *et al.* 1998). Absence of fire may also reduce litter quality and cause a shift in plant composition to species that produce lower quality litter (e.g. Bradshaw 1993; Wardle *et al.* 2003). Recent data showed that the proportion of twigs (low-quality litter) increases in the litterfall with time since fire (Zackrisson *et al.* 1996; Wardle *et al.* 2003), which may also have a role in retarding decomposition in absence of fire through altering

the quality of the total litterfall (investigated in Paper II).

Influences of light and soil fertility on tree seedling regeneration

Light and soil fertility are important factors determining competitive interactions between plants in forests, since plant species differ in their resource requirements and have different strategies for avoiding or tolerating resource-limitation (Grime 1979). Regenerating tree seedlings under the canopy or in treefall gaps are exposed to shade from canopy trees and other vegetation; this reduces both the quantity and the quality of light through differential uptake and reflection of radiation of different wavelengths (Björkman 1981; Ballaré 1999). Plants may respond to shading by neighbours by growing taller to escape the shade; this response is more pronounced for light-demanding early-successional tree species that are able to quickly colonise gaps (Gilbert *et al.* 2001). Late-successional species are more shade-tolerant and can often survive and grow slowly in shade for extended periods, before they overtake shade-intolerant species later in succession. Soil nutrient availability influences photosynthetic capacity, resource allocation and growth rates of plants (Field & Mooney 1986). Thus, both shading and soil fertility are important factors in competitive interactions between plant species. Although it is well-known that tree species perform differently at forest sites depending on the soil- and light conditions, competitive interactions between the seedlings of coexisting Swedish tree species under varying conditions have not been investigated. By studying such interactions we can get a better insight into forest regeneration dynamics and the factors that determine the composition of forests stands.

Effects of resources on the mycorrhiza of forest trees

Resource-availability has an important role in the formation of mycorrhiza, which is an at least 400 million year old association (symbiosis) between plants and fungi (Simon *et al.* 1993; Remy *et al.* 1994; Redecker *et al.* 2000). Mycorrhizas are a normal part of root function for about 90% of all seed plant species in the world (Molina *et al.* 1992), and are highly important for nutrient up-take for plants in nutrient-poor soils such as the boreal forest soils (Smith & Read 1997). Ectomycorrhiza (EM) is the type of mycorrhiza formed with boreal tree species, for which the fungal symbionts mainly consists of Basidiomycetes or Ascomycetes; many of these are common edible fungi such as Slippery jack or “smörsopp” (*Suillus luteus*), or deadly fungi like the fly agaric or “flugsvamp” (*Amanita muscaria*). Many temperate trees also form EM, including the southern hemisphere eucalypts (*Eucalyptus* spp.) and southern beeches (*Nothofagus* spp.).

Ectomycorrhizal fungi are in several ways more efficient than tree roots at taking up nutrients, for example through the production of enzymes that degrade recalcitrant organic material and by the mycorrhizal hyphae that provide an up to 60 times larger surface area for nutrient-uptake than do roots (Simard *et al.* 2002).

Several studies have found that EM colonisation (e.g. Nylund 1988; Arnebrant 1994) and mycelial growth (Nilsson & Wallander 2003; Nilsson *et al.* 2005) are

higher in low than in high nutrient-availability. Shading by vegetation (Nylund 1988; Ekwebelam & Reid 1983), or browsing by herbivores (e.g. Gehring & Whitham 1994; Markkola *et al.* 2004) may reduce EM colonisation through reducing the amount of the C assimilated in plants through photosynthesis. Mycorrhizal fungi largely depend on the supply of C from plants to support their growth, and about 10-50% of the C produced by plants may be allocated to EM fungi (Simard *et al.* 2002). However, the largest effects of changes in nutrient availability (Lilleskov *et al.* 2002) and photosynthates (Gehring & Whitham 2002; Saikkonen *et al.* 1999) is likely to be through alteration of the EM community composition.

Both experimental and field studies have provided evidence that C and nutrients may be transferred from canopy trees to seedlings via a common mycorrhizal network (consisting of all mycorrhizal hyphae in the soil that are interconnected and linked to the trees) (Simard *et al.* 2002; Simard & Durall 2004), although the importance of this transfer for seedling growth and establishment has not yet been investigated. Also, the net impact of canopy trees on tree seedlings through facilitation (mycorrhizal resource transfer) and resource competition is unclear.

Objectives

This thesis focuses on ecological effects of quality and diversity of resources (nutrients) present in the forest humus or in the litter layer, and of varying quality and quantity of light resources that are likely to be encountered by tree seedlings in forests. These resources are essential for key ecosystem processes (such as decomposition, nutrient cycling, plant biomass production), and therefore play an important role in influencing soil- and plant communities. In the research projects underlying this thesis, ecosystem and community processes in both the aboveground and belowground subsystems were studied. As these subsystems are closely linked, considering them together should enable a better insight into mechanisms behind ecosystem functioning. The ultimate aim of this thesis was to improve the current knowledge on mechanisms behind the functioning and structure of forest ecosystems, with special emphasize on aspects involved in nutrient dynamics (decomposition and nutrient cycling) and tree seedling recruitment (growth and competitive interactions).

The main questions for this thesis were:

What influences do quality and diversity of litter and other organic resources returned to the soil have on ecosystem processes in the plant- and soil subsystems (Papers I-II)?

How does fire disturbance (time since last fire) affect litter quality, litterfall composition, and decomposition rates (Paper II)?

How do varying light- and soil fertility conditions under canopy trees affect growth, interspecific competition and mycorrhizal colonisation of tree seedlings (Papers III-IV)?

What impacts do native and non-native canopy species have on the abundance and community structure of soil communities, and tree seedling growth and survival (Paper IV)?

Material & methods

Studied forest ecosystems

Swedish boreal forests including the island fire chronosequence

The study systems for Papers I-III were situated in the northern boreal zone of Sweden that is dominated by coniferous forests, in an area extending from 64° to 66° North and 17° to 20° East. These sites were situated in late-successional forest reserves (Papers I and III) or on lake islands forested with late-successional trees (Paper II), where the extent of anthropogenic disturbance is limited. Late-successional stages of boreal forests are characterized by thick humus layers and strong N-limitation (Swift *et al.* 1979). The Swedish boreal forests have few abundant tree species of which the conifers *P. sylvestris* and *P. abies* are the dominant species. *Betula pendula* and *B. pubescens* are the most common deciduous species, but species like *Populus tremula*, *Sorbus aucuparia*, *Salix caprea* and *Alnus incana* are also encountered. The ground vegetation is dominated by the dwarf shrubs *Vaccinium myrtillus*, *V. vitis-idaea* and *Empetrum hermaphroditum* and the feather moss *Pleurozium schreberi* on low- to medium-fertility sites, and by herbs such as *Geranium sylvaticum* and grasses such as *Dechampsia flexuosa* and *Melica nutans* on fertile sites (Paper III). For Paper II, a study system involving 30 forested islands of varying sizes situated in lakes Uddjaure and Hornavan (Wardle *et al.* 1997), which were formed by the retreat of land ice 9000 years ago, was used. The islands differ in fire disturbance as larger islands have been struck by lightning causing wildfires more frequently than smaller ones. Time since fire and island size is related to many ecosystem properties on the islands, such as plant composition, plant litter decomposition, and tree biomass (Wardle *et al.* 1997; 2003; Wardle & Zackrisson 2005).

New Zealand temperate forest

The study system for Paper IV was situated in the temperate zone dominated by broadleaved evergreen forests, in a mountain region of central South Island of New Zealand (171°24'E, 43°58'S; 900-1100 m above sea level). This region is characterised by steep soils that are extremely prone to erosion, and by deforestation through human impacts (Ledgard & Baker 1980). The native forest is dominated by *Nothofagus solandri* var. *cliffortioides* (mountain beech), which occurs in mountain areas throughout most of New Zealand (Wardle 1984). This species often forms monospecific stands that have very little ground vegetation

(Wardle 1984). Non-native tree species that have been introduced for forest plantations, erosion control and shelterwood are abundant throughout the east-coast of the South Island, including the area for our field site (Ledgard & Baker 1980; Ledgard 2001).

Study designs

All Papers included in the thesis were based on experimental studies, although Paper II also included monitoring of litterfall in the field. The experiments were conducted under controlled light and temperature conditions in a climate chamber or greenhouse (Papers I and III), outside in a climate similar to that in the field (Paper II), or in the field (Paper IV). The experiments were set up in randomized complete block designs (Papers I-II) or in hierarchical (nested) designs (Papers III-IV). For all experiments, pots or tubes made up mesocosms (experimental units) that were exposed to different treatments. For studies I-III, pots were filled with forest soil and were planted with tree seedlings and/or were amended with organic substrates that were added singly or in mixtures. The substrates were mixed with the soil (Paper I) or put in litterbags and buried into the soil (Paper II). The pots were planted with single tree species, except for Paper III where two-species mixtures were included to measure competitive interactions between seedlings. Light filters that alter both light intensity and light quality were used to simulate natural light environments in forests (Paper III), i.e. shade in canopy gaps or shade from surrounding vegetation (Lee filters, Hampshire, England). For Paper IV, a combination of trenching treatments (trenched and untrenched plots) and mesh treatments (tubes with or without mesh that allow mycorrhizal hyphae but not roots to pass through) were applied to examine how canopy trees affect seedling nutrient supply through root competition and mycorrhizal networks. The duration of the experiments was 6-19 months; hence only the relatively short-term effects of resource quality and diversity were studied.

Measurements

Plant attributes

Total-N and total-C concentrations of seedlings (Paper I) were determined using an elemental analyser (Soil Science Laboratory, Swedish University of Agricultural Sciences). Mycorrhizal colonization was assessed under 40 x magnification, on root subsamples (Paper III) or on whole root systems along line transects (Paper IV). Root length and the number of root tips of seedlings (Paper IV) were assessed using a scanner and computer software from WinRHIZO (Régent Instruments Inc., Québec City, Canada). Measurements of tree seedling biomass production (Papers I, III and IV) are described under Processes.

Soil community attributes

Soil microbial community structure was assessed using the catabolic response profile (CRP) method (Degens & Harris 1997; Degens 1998) (Paper I), which describes the potential of the microbial communities to catabolise different organic

compounds. In short, 16 different organic compounds and water were added individually to soil subsamples kept in different air-tight containers, and the CO₂ released from microbial activities during three hours was measured for each container by injecting a gas sample from that container's head-space into an Infrared gas analyser. Ordination analyses were performed on the CRP-data to describe differences in microbial catabolic community structure between substrate and plant treatments. Microbial catabolic diversity was obtained for the CRP-data using the Simpson-Yule evenness index (Magurran 1988), measured as $1/\sum p_i^2$, where p_i is the respiration response for an organic compound i as a proportion of the total respiration summed across all compounds (Degens 1998). The microbial respiration response to water (i.e. soil basal respiration) and glucose (i.e. substrate-induced respiration) were used as measures of microbial activity and microbial biomass, respectively (Papers I and IV) (Anderson & Domsch 1978). The ratio of soil basal respiration to substrate-induced respiration (i.e. the metabolic quotient) was used as a relative measure of microbial carbon-use inefficiency (Anderson & Domsch 1985). To study nematode abundance and assemblages (Paper IV), nematodes were extracted from soil sub-samples using a tray method (Yeates 1978). The total number of nematodes was recorded live, and later in preserved samples the nematodes were divided into genera and six functional groups (Yeates 1993).

Processes

Decomposition of litter was measured as the % loss of litter biomass after incubation in humus for 19 months. Plant biomass (production) was assessed by determining the dry mass of shoots and roots at harvest after drying in 60-70 °C for 48 h. To be able to quantify the change in biomass production from the time of planting to harvest (Paper IV), initial seedling biomass was estimated by height-biomass regressions, by measuring heights and dry biomass of 40 additional seedlings of each species. Tree seedling survival was assessed at the time of harvest (Paper IV). Interspecific competition among seedling species was assessed by comparing the performance of each seedling species in planted singly in pots to those planted in mixtures with seedlings of another species (Paper III). An additive design was applied keeping the number of seedlings of each species (i.e. two) constant in all pots, which allowed for determining indices of competitive intensity and competitive balance (Wilson 1988).

Other measurements

All studies involved some measurements of chemical characteristics of the soil and organic substrates used, e.g. N, C, P, ammonium, nitrate, soluble P and pH. For the greenhouse studies, measurements of temperature, light quantity [Photosynthetically Active Radiation (PAR)] and light quality [The ratio of red to far-red light (R: FR)] (Paper III) were made. Study IV included measurements of soil organic C, light transmission (% PAR), soil moisture, soil nutrients and soil pH.

Statistics

Treatment effects were usually evaluated using analysis of variance (ANOVA), followed by post-hoc tests (Tukey's, Tukey-Kramer or Least Significant Difference) when treatments were significant at $P \leq 0.05$. The mycorrhizal variables in Paper III were analysed with the non-parametric Kruskal-Wallis test. Pearson's correlation coefficient or the non-parametric Spearman's rank-order correlation were used for the correlation analyses. Students *t*-tests were used to test for synergistic effects of diversity of litter or organic substrates (Papers I-II), where observed and expected values of each mixture were compared. The expected values for a mixture were based on the average value of the response variables in the corresponding single litter/substrate treatments. The data for the microbial and nematode communities was analysed with multivariate analysis of variance (MANOVA) (Paper I) and Principal Components Analysis (PCA) followed by ANOVA of the PC scores (Papers I and IV) to describe differences in soil community structure between treatments. The data analyses were performed in SPSS 11.5 or, for the mixed model analyses in Papers I and IV, in SAS statistical package using the MIXED or GLIMMIX procedures.

Summary of papers

Paper I. *Aboveground and belowground responses to quality and heterogeneity of organic inputs to the boreal forest*

Previous studies on ecological effects of organic resources returned to the soil have focused on leaf litter, despite the fact that other resource types constitute a major part of the total resource input, and the majority of these studies have concentrated on effects on the belowground community. In this study, I investigated how quality and heterogeneity of different organic resources commonly returned to the soil in boreal forests affect the activity and community structure of decomposers (soil microbes), and plant nutrient uptake and growth. I set up a greenhouse experiment, where six organic substrates (wood, charcoal, berries, sporocarps, vertebrate faeces and leaf litter) were added singly or in mixtures of two, three and six resource types to pots containing forest soil (with or without tree seedlings of *Betula pendula* Roth). When substrates were added singly, nutrient-rich substrates (faeces and sporocarps) or substrates with high sugar-content (berries) had the largest positive effects on microbial basal respiration (BR), substrate-induced respiration (SIR) and microbial metabolic quotient (qCO_2). Mixing of substrates had no synergistic effects (i.e. the effects could be explained by the microbial response to the single-substrate additions) on BR or SIR, but decreased qCO_2 or altered the microbial community structure for specific combinations of substrates. In contrast to the niche complementarity hypothesis, microbial catabolic diversity was not stimulated by greater diversity of resources. For seedlings, the effects of single substrates were either neutral or negative; the growth inhibition in some treatments largely resulted from microbial competition for nutrients. Substrate mixing enhanced seedling nutrient-uptake and

growth for all mixtures containing sporocarps and leaf litter. Overall, the effects of resource heterogeneity were stronger for plants than for microbes, and synergistic effects only occurred when nutrient-rich substrates were present within the substrate mixtures. The results show that the quality of, and interactions among, a wide range of resource types returned to the soil has a role in influencing ecosystem functions such as nutrient cycling and plant productivity.

Paper II. *Changes in the ratio of twig to foliage in litterfall with species composition and consequences for decomposition across a long term chronosequence.*

Absence of disturbance by fire, e.g. through anthropogenic fire suppression, may have large influences on boreal forests, by altering tree species and litterfall composition, soil fertility, decomposition rates and plant productivity. Previous studies of 30 islands in the boreal zone of Sweden differing in fire regime have shown that absence of fire has caused shifts in plant species composition towards species that produce lower-quality litter, and an increase in the proportion of twigs (i.e. low-quality litter) to foliage in the tree litterfall. Using litter from the same islands, a decomposition experiment was set up to investigate the hypothesis that the increased twig proportions with increasing time since last fire would negatively affect overall litter decomposition rates by reducing net litter quality and through impairing decomposition of associated foliar litter. The natural proportions of litterfall from *Betula pendula* (birch), *Pinus sylvestris* (pine) and *Picea abies* (spruce) found on each islands was used to prepare litterbags comprising three mixtures (all foliar litters, all twig litters and all twig plus foliar litters), and up to six monotypes with all the above litter types found on a particular island added singly. Further, the twigs found in the litterfall on each islands was sorted by tree species to investigate the influence of tree species identity on the increased proportion of twigs in the litterfall. The proportion of twigs of *P. abies* increased and twigs of *P. sylvestris* decreased with time since fire, similarly to the shift in dominance of these tree species on the islands. There was no effect of time since fire on N and P concentrations of individual twig and foliar litters. There was a negative effect of time since fire on decomposition rate for the foliage-twig mixtures, but not for the other litter treatments. However, twig litter did not inhibit the decomposition of foliar litter within these mixtures. The reduced decomposition rate in the foliage-twig mixture from the islands with the longest absence of fire was therefore due to the increased proportion of twigs in the mixtures from these islands. The results suggest that, with prolonged absence of fire, the increase of twig proportion in the foliage-twig litterfall for *P. abies* combined with the shift in dominance in the forest canopy by this species may be important in contributing to reduced decomposition rates in boreal forest soils.

Paper III. *Effects of shading and humus fertility on growth, competition and ectomycorrhizal colonisation of boreal forest tree seedlings.*

In this study, I investigated how patterns behind seedling growth, interspecific competition, and mycorrhizal colonization are related to nutrient- and light conditions in forests and species-specific plant strategies for coping with or

avoiding resource limitation. I set up a climate-chamber experiment where seedlings of three coexisting tree species, *Pinus sylvestris* (pine), *Picea abies* (spruce) and *Betula pendula* (birch), were planted in pots filled with humus of high or low fertility and placed under light filters simulating low to moderate vegetation shade. Seedlings of the early-successional species, *P. sylvestris* and *B. pendula*, increased their stem height in response to shade, which may enable these species to pre-empt space and capture new light resources in canopy gaps or when shaded by surrounding vegetation. *Betula pendula* seedlings were most responsive to shade, and this response was influenced by humus fertility; seedlings had the highest stems under the high level of shade in high-fertility humus. Growth of seedlings of the late-successional *P. abies* was not affected by shade. Interspecific competition among pairwise combinations of the three species was greater in high than in low fertility humus, but was not altered by shade. *Betula pendula* seedlings were the strongest competitors among species and strongly suppressed the coniferous seedlings, especially in high-fertility humus. Mycorrhizal colonization of seedlings of all species was highest in low-fertility humus, but was unaffected by shade treatments. This study demonstrates species-specific responses of coexisting seedling species to varying light and humus fertility and to presence of neighbours, which are important for the relative recruitment abilities of coexisting tree species and ultimately for the species composition of developing forests.

Paper IV. *Tree seedling growth and soil community structure in forest stands of invasive and native tree species.*

In this Paper, I investigated influences of non-native canopy species on tree seedling performance and the abundance and structure of soil (nematode) communities relative to native canopy species. For tree seedlings, mechanisms likely to affect seedling growth and survival were separated, i.e. nutrient competition, facilitation of carbon- and nutrient uptake through a common mycorrhizal network, and modification of light- and soil conditions by canopy trees. Seedlings of two tree species invasive to New Zealand, *Pseudotsuga menziesii* (Douglas fir) and *Pinus contorta* (Lodgepole pine) and of the native *Nothofagus solandri* var. *cliffortioides* (mountain beech) were planted in PVC tubes in single-species stands of each of these tree species. Effects of root competition and mycorrhizal connections from trees was separated by root trenching and by the use of tubes with or without a fine mesh allowing mycorrhizal hyphae, but not roots, to pass through. Seedling survival and growth was generally higher in stands of *N. solandri* var. *cliffortioides* than in stands of the non-native species. Root trenching and mesh treatments had no effect on any of the seedling species. This indicates that changes in the growth environment was the main factor affecting seedling performance in different stand types; I explain the negative impacts on seedlings in stands of non-native species with reduced light availability and poorer soil conditions created by the canopy species. Seedlings in *P. menziesii* stands had lower mycorrhizal colonisation than in stands of the other species, which is likely a result of the low light levels under canopies of this species. Soil nematode abundance and diversity was highest in stands of *N. solandri* var. *cliffortioides*, and nematode assemblages differed between stand types. The negative effects on nematodes in stands of non-native species relative

to native stands are probably explained by the lower availability of organic C and microbial biomass in these stands providing less resource for the nematodes. This study shows that established stands of non-native tree species may affect both tree seedlings and soil communities through modifications of the microenvironment.

Results & Discussion

Quality and diversity of organic substrates

Quality

It is well-known that litter from different plant species decompose at different rates and may have different impacts on microbial activity and plant growth (Swift *et al.* 1979). The majority of studies on effects of litter on plants have found negative effects of litter on plant growth and recruitment, especially when high amounts of litter are present (reviewed by Xiong & Nilsson 1999), although some studies have found that litter may enhance plant growth, for example through increasing nutrient-availability (Qested *et al.* 2003; Brearly *et al.* 2003).

Effects of litter species identity on decomposition rates have been observed for boreal forest plant and moss litter, although the nature of these effects depended on soil and site properties (Nilsson *et al.* 1999; Wardle *et al.* 2003). However, Nilsson *et al.* (1999) found no effects of litter species identity on soil microbial activity, biomass or plant growth. In Paper I, effects of quality of leaf litter and other substrate types found in the boreal forest on aboveground and belowground ecosystem properties and processes were investigated. I found that type of substrate added affected the performance of both soil microbes (positively or neutrally) and plants (negatively or neutrally). The effects of substrate quality were strongest for microbial parameters. Addition of substrates generally enhanced microbial activity and biomass and decreased microbial carbon-use inefficiency. Further, there were differences in microbial parameters, including microbial catabolic community structure, between substrate types. Substrate quality was also an important driver of decomposition rates, as the % mass loss of the foliar and twig litters of *P. sylvestris*, *P. abies* and *B. pendula* in monotypic litterbags differed (Paper II). The differences in decomposability could not be predicted from the initial N and P concentrations of either the foliar or twig fractions of the litter, showing that decomposability of litter from these tree species were controlled by other chemical or physical attributes (c.f. Hoorens *et al.* 2003). However, as expected, the low-quality twig-litter generally had lower decomposability than the foliar litter. In Paper I, substrate N concentrations largely reflected the effects of individual substrates on microbial parameters, likely because there were large differences in N-concentration among substrates. Microbial performance was also associated with presence of labile or recalcitrant C sources in the substrates; for example, microbial biomass was promoted by the addition of berries that had high concentrations of labile sugars. Although boreal soils are rich in organic C, soil microbes may still be energy-limited by poor C-

quality of the soil substrates (e.g. Flanagan & van Cleve 1983; Jonasson *et al.* 1996). However, although the traditional view is that microbes are more limited by C than N (Schimel & Weintraub 2003), several studies suggest that microbes may mainly be limited by N (Schimel & Weintraub 2003; Nordin *et al.* 2004; Mack *et al.* 2004). In this light, the strong microbial immobilisation observed after addition of some of the organic substrates in Paper I suggests that microbes were N-limited.

The effects of addition of individual substrates on tree seedling growth were either negative or neutral (Paper I). As microbial biomass was generally promoted by addition of substrates, and plant biomass was not, the nutrients released from decomposition were likely immobilised in microbial biomass and thereby unavailable to plants (Zak *et al.* 1990). The substrates may also have had negative effects on seedlings through altering soil moisture conditions (e.g. Sydes & Grime 1981). For example, decomposition of the fungal substrate caused water-logging that probably reduced oxygen availability and thereby impaired seedling growth and increased seedling mortality. The reduced seedling growth in pots with *Empetrum hermaphroditum* berries may partly have resulted from high amounts of polyphenols being released and inhibiting seedling nutrient uptake and growth (c.f. Hättenschwiler & Vitousek 2000).

The importance of diversity

The presence and direction of non-additive (i.e. synergistic or antagonistic) effects of substrate diversity are largely dependent on the component substrates in the studied mixtures. In the published literature, decomposition rates and microbial activity are more frequently stimulated than impaired by mixing of substrates (Gartner & Cardon 2004). The few existing studies on plant responses to substrate diversity show neutral or positive effects on plant growth (Nilsson *et al.* 1999; Quedsted *et al.* 2003).

Overall, there was little influence of substrate diversity on the belowground community and decomposition processes. In Paper I, substrate mixing increased microbial C-use efficiency and/or induced changes in microbial community structure for the substrate combinations that also supported the highest plant biomass. Mixing foliar litter (Paper II) slightly increased decomposition rates (i.e. the mixtures decomposed faster than expected based on the decomposition of component monospecific litters), but mixing litters of very different quality (twigs and foliage) had no non-additive effects on decomposition. These results are in line with the majority of litter mixing studies, which have found increased or neutral effects of litter mixing on decomposer activity (reviewed by Gartner & Cardon 2004). That few effects of litter mixing were observed in Paper II may be because the “natural” proportions of the component litter types were used, in contrast to most other studies that have used equal proportions (Gartner & Cardon 2004). This may have made it more difficult to detect non-additive effects. For example, Scowcroft (1997) found an increased decomposition rate of litters in mixtures when using equal proportions of different litters, but not when using the natural proportions. However, the use of natural proportions of litter types better

mimics what occurs in the field, and is therefore more appropriate for examining potential effects of interactions between different litters that occur in the field.

There is little evidence of effects of litter or substrate diversity on microbial community structure. The two existing studies on EM community responses to mixing of leaf litters showed either no non-additive effect of litter-mixing (Jonsson *et al.* 2006), or a change in the dominant EM morphotypes in single versus mixed litters (Conn & Dighton 2000). In study I, mixing of substrates induced effects on microbial community catabolic structure (CRPs) for some substrate combinations relative to when substrates were added individually; this shows that substrate-mixing may stimulate certain catabolic activities performed by the microbes. In this light, substrate-mixing may potentially also promote nutrient release from the substrates, and this may explain some of the positive effects on nutrient cycling and plant growth that were observed in this study. As non-additive effects only occurred when seedlings were present, these catabolic activities likely involved mycorrhizal fungi or microbes associated with plant roots. Further, in Paper I, substrate diversity did not increase microbial catabolic diversity (measured with the Shannon-Wiener evenness index), contrary to the niche complementarity hypothesis (Hooper *et al.* 2000; Wardle 2002). In fact, the substrate treatments that supported the greatest seedling and microbial biomass had the lowest microbial diversity among treatments. This is similar to earlier findings that high N availability may increase the dominance of competitive species and thereby reduce microbial diversity (Stahl & Christensen 1992; Lilleskov *et al.* 2002). However, no differences in “catabolic richness” were found among treatments, which may be because I only measured catabolic responses to common, easily degradable substrates.

Our results in Paper I showed that organic substrate diversity had positive impacts on seedling growth if mixtures contain nutrient-rich substrates. The substrate combinations that gave the highest seedling biomass were those that contained the relatively recalcitrant *B. pendula* leaf litter and nutrient-rich sporocarps. Since these substrates very commonly occur together in the litter layer in forests, it is possible that microorganisms may be adapted to decompose these mixtures. This may result in an efficient decomposition and nutrient cycling, and much plant-available nutrients. In study I, the presence of sporocarps greatly stimulated the microbial biomass, and this would have promoted decomposition of other lower-quality substrates. This is consistent with studies showing that higher quality litter can enhance decomposition of co-occurring litter (e.g. Chapman *et al.* 1988; McTiernan *et al.* 1997; Quested *et al.* 2003). Based on the current knowledge, whether effects of resource diversity on plants occur depend both on the composition of the mixture and environmental conditions. In general, diversity of substrates *per se* appears to be less important for ecosystem processes than is the composition of the mixtures, as diversity effects usually saturate at low levels of diversity (2-3 components). The results from Paper I indicate that the presence of higher-quality substrates, such as litter from deciduous tree species, animal faeces and fruitbodies of fungi may be important for stimulating decomposition processes in boreal forests, and that this may consequently enhance nutrient release and plant productivity. A more heterogeneous forest is also likely to

promote biodiversity, especially of consumer organisms, by providing resources for organisms with different resource requirements.

Effects of fire disturbance on litter quality and decomposition rates

The results from Paper II show that the proportion of twigs (low-quality litter) in the foliar-twig litterfall may increase with prolonged absence of wildfire. The contribution of twigs in the litterfall was greatest on the smallest islands that had burned on average 3250 years ago, largely as a result of the increasing dominance by the late-successional *P. abies* with time since fire (Wardle *et al.* 1997), and an increase in the proportion of twigs in the litterfall from that species. The increased amount of twigs in the litterfall of *P. abies* may partly be explained by smaller needle size and retention of needles for longer periods relative to twigs as a response to decreasing ecosystem productivity with time since fire (Jalkanen *et al.* 1995; Reich *et al.* 1996). The reduced humus quality (i.e. reduced pH and microbial activity and biomass and increased concentrations of phenolics and immobilized N) with time since fire (Wardle *et al.* 2003) did not influence decomposition rates and there were no differences in chemical litter quality of foliage or twig litter with time since fire, in line with the findings of Wardle *et al.* (2003). Further, mixing twig litter with foliar litter (in the proportions that they co-occurred on the islands) had no effects on overall decomposition rates (discussed under Substrate effects). The increased proportion of twigs of *P. abies* in the litterfall, combined with an increased dominance of this species, may therefore contribute to reduced decomposition rates in boreal forests following long-term absence or suppression of fire (Paper II). Hence, the absence of fire and the increasing dominance by *P. abies* in boreal forests may have negative effects on overall forest productivity, as the low-quality litter of this species may impair decomposition rates (and thus nutrient release from the litter), thereby reducing forest productivity in the long-term. Allowing naturally ignited wildfires to burn, or using prescribed burning as a management method, may therefore be important both for promoting ecosystem processes and for maintaining forest dynamics and biodiversity. Further, the increased proportion of low-quality litter in the absence of fire may also contribute to an increased accumulation of C in the humus, by slowing down decomposition and C cycling. Considering that the boreal forest occupies 29% of the global forested area (Goldammer & Furyaev 1996), this could have significant impacts on global C-storage.

Impacts of light- and nutrient conditions on regeneration and mycorrhizal colonisation of tree seedlings

Seedling regeneration

Light is a major driver of forest successional dynamics (i.e. the structure of forest stands), and the light environment in gaps and in forest understories is critical for growth and establishment of tree species (e.g. Kuusela 1990; Kuuluvainen 1994; Messier *et al.* 1999, but see Steijlen *et al.* 1995; Zackrisson *et al.* 1995). As tree species differ in their light requirements, a change in light environment through

gap formation, wildfire or clear-cutting may change the relative advantage of different tree species, usually through favouring more light-demanding species (Coates 2002). Tree species response to light is also influenced by nutrient availability (Catovsky *et al.* 2002; Ekwebelam & Reid 1983; Latham 1992). The results from Paper III show that seedlings of coexisting early- and late successional tree species in boreal forests respond differently to shade and to nutrient-availability, and this influenced competitive interactions between species. This in turn may affect future species compositions of the stands. In this study, the growth and competitive dominance of the early-successional and fast-growing species *B. pendula* was enhanced in fertile compared to infertile soils. Long-term effects of these seedling interactions are difficult to predict, but results obtained from a forest dynamics model (SORTIE) indicate that increased N-availability for regenerating seedlings may lead to an increased dominance of early successional species in gaps (Catovsky *et al.* 2002). However, to be able to better predict and explain long-term effects of interactions between seedling species in different light- and soil-fertility conditions in boreal forest, interactions between the coexisting tree species need to be followed for a longer period than the duration of the experiment (Paper III). There are of course also many other factors that are involved in the recruitment of tree seedlings in a forest stand, such as the characteristics of the gap to be colonised (e.g. size and presence of other plants), the dispersal abilities of species, the timing of dispersal, and presence of suitable microsites for establishment (Grubb 1979; Kuuluvainen 1994). In the boreal forest, competition from understory vegetation is also likely to be severe (Jäderlund *et al.* 1996; Cater & Chapin 2000).

Paper IV also demonstrates species-specific responses of tree seedlings to different light and soil conditions as created by different (native and non-native) canopy species. Differences in light transmission among the canopy species was the major factor determining seedling growth. The high growth of the light-demanding *P. contorta* in stands of the native *N. solandri* var. *cliffortioides* with lower light transmission than stands of *P. contorta* may also have been influenced by soil characteristics, such as soil moisture and soil microbial biomass.

The absence of effects of root competition from canopy trees or by access to mycorrhizal networks on seedling growth (Paper IV), are in contrast to studies that have found positive effects on seedling growth and survival of reduced root competition (root trenching) (Coomes & Grubb 2000; Platt *et al.* 2004), and mycorrhizal connections with canopy trees (Onguene & Kuyper 2002). In our study, the different canopy species had very different influences on the growth of tree seedlings through differential alteration of light and soil conditions, which may have overruled any effects of root competition or mycorrhizal networks. In addition, the seedlings used in our study were relatively small and were enclosed in tubes that limited root contact, and this may have reduced the response to trenching and mycorrhizal treatments relative to larger and naturally established seedlings. It is possible that effects of the root trenching and mycorrhizal treatments would have been detected if the experiment had been run for a longer than 1.5 years, or if the seedlings had been planted under more open canopies (or canopy gaps) permitting faster growth. Hence, there is much more to be

understood about the generation dynamics in forests, especially concerning the importance of C and nutrient transfer via mycorrhizal networks in the regeneration of different tree species.

Mycorrhizal colonisation

Previous laboratory and field studies have shown decreases in EM colonisation (Nylund 1988; Arnebrant 1994) or mycelial growth (Nilsson & Wallander 2003; Nilsson *et al.* 2005) in response to increased nutrient-availability in boreal forests, and this demonstrates the importance of mycorrhizas in nutrient-poor soils (Tuomi *et al.* 2001). Consistent with this, the results from Paper III show that seedlings of all the studied tree species had a higher EM colonisation in low-fertility than in high-fertility soils. However, opposite patterns have been found for arctic soils where nutrient-limitation is more extreme (Clemmensen *et al.* 2006), indicating that growth of the EM mycelium may be N-limited in these ecosystems. Anthropogenic N-deposition may therefore have large effects on mycorrhiza, and nutrient dynamics, in the arctic. Further, studies from boreal forests have shown that N-fertilisation or anthropogenic N-deposition may induce shifts in ectomycorrhizal community structure (Lilleskov *et al.* 2002; Nilsson & Wallander 2003).

In Paper III, neither seedling growth nor mycorrhizal colonisation was affected by the reduced light transmission under the shade treatments that were applied (corresponding to 29% and 32% of PAR). In Paper IV, mycorrhizal colonisation of seedlings was lower under *P. menziesii* canopies (0.5% PAR) than under canopies of *N. solandri* var. *cliffortioides* (5.1% PAR) or *Pinus contorta* (13.3% PAR) where the colonisation was close to 100%. Thus, these results indicate that EM colonisation may be limited under conditions of deep canopy shade, but that it is largely unaffected by light levels higher than 5% PAR. This is in contrast to studies showing that EM colonisation may be reduced under intermediate levels of shade because of C-limitation (e.g. Ekwebelam & Reid 1983). However, Zhou and Sharik (1997) showed that ectomycorrhizal colonisation of *Quercus rubra* seedlings grown in the field was highest at intermediate levels of shade (48-56% PAR). They found that nutrient- and water availability increased with decreasing canopy cover, indicating that responses of mycorrhizal colonisation to shade in forests may also be affected by concomitant changes in soil conditions.

Effects of canopy species on soil communities

Invasion by introduced (non-native) plant species may have large impacts on ecosystem processes and soil- and plant community structure, through altering resource supply, nutrient cycles, hydrology, habitats, microclimate, and fire regimes (reviewed by Levine *et al.* 2003; Wolfe & Klironomos 2005). Previous studies have found that non-native plants have altered abundance and community structure of soil organisms, including nematodes (Wolfe & Klironomos 2005; Yeates & Williams 2001). In line with these, large differences in soil nematode abundance and assemblages were found between stands of non-native (*Pseudotsuga menziesii* and *Pinus contorta*) and native (*N. solandri* var.

cliffortioides) tree species (Paper IV). The nematode abundance was 14-22 times higher in native stands than in non-native stands, and the nematode assemblage contained more predatory and less fungal feeding nematodes. I explain these differences in terms of effects of canopy species on the resources available to nematodes and their prey in the soil, i.e. soil C and the soil microbial biomass. Resource-supply has been shown to regulate the abundance of many trophic groups of soil organisms through “bottom-up” controls (Wardle & Yeates 1993). The observed differences in C and microbial biomass between the tree species likely result from species-specific properties of the trees such as productivity (NPP), the extent of nutrient depletion of the soil, litter quality and rhizodeposition (Wardle 2002). Further, different microbial communities (particularly EM communities) supported by the tree species may induce different C-flows to the soil.

There were also some effects of tree species on the soil community in Paper I. Presence of *B. pendula* seedlings altered microbial CRPs and catabolic diversity, and also had some influences on the microbial response to litter treatments as shown by differences in CRPs. These effects are likely due mostly to relatively easily degradable carbon sources released from the roots (rhizodeposition) changing the composition of carbon substrates available for microbes, and thus altering the interactions between substrates and microbes (Wardle *et al.* 2003).

Some methodological considerations

Soil microbial community structure and diversity

An advantage with the CRP method (Degens & Harris 1997), which was used for characterizing the microbial communities (Paper I), is that it summarizes the functional characteristics of all microorganisms present in the soil. Other community-level physiological profile (CLPP) methods, which are based on culturing of organisms (e.g. BIOLOG®), are biased towards those microorganisms that can be easily cultured (i.e. only about one percent, and mainly bacteria) and that grow fast (Nannipieri *et al.* 2003). The CRP method also enables measurements of microbial diversity; “catabolic richness” (the number of substrates added that induce a response in the microbial community) and “catabolic evenness” (describes the distributions of the measured catabolic activities in the soil). However, it should be mentioned that the ecological relevance of these diversity measures is not known, e.g. whether a soil community with high catabolic evenness is more “natural” or efficient than one with low evenness. A disadvantage with the CRP-method is that it is quite time-consuming especially when many carbon compounds are tested (Leckie 2005).

The CRP method gives no information about what organisms are present in the soil, as it only considers the functional aspects of the microbial community. Thus, to also be able to describe the microbial community at a taxonomic level and to connect different catabolic functions to specific organisms or groups of organisms, the CRP method needs to be combined with other (particularly molecular-based) methods that can identify specific taxa or groups of organisms. However, as the

studies that have used this method indicate, the CRP method is useful for discriminating between soil communities under different plant species, soil types or resources present in the soil (e.g. Orwin *et al.* 2006; Paper I).

Plant interspecific competition

I used an additive design to assess interspecific competition, with two seedlings of the same species present in both pots with monocultures and in pots with two-species mixtures (i.e. the total number of seedlings were two in monocultures and four in mixtures) (Snaydon 1991). This design allows for determining indices of competition such as “intensity of competition” and “competitive balance” (Wilson 1988), and serves to keep intraspecific competition constant in all pots (by using the same number of individuals of each species), so that interspecific competition is not confounded with intraspecific competition (e.g. Snaydon 1991; Gibson *et al.* 1999). This differs from replacement (or substitution) designs, where the total number of seedlings in mixtures and monocultures is held constant while the proportions of each species are varied (de Wit 1960). Replacement designs have been commonly used in competition experiments but have been strongly criticized for confounding interspecific with intraspecific competition (Connolly 1986; Gibson *et al.* 1999; Joliffe 2000). Additive designs have received less criticism than replacement designs (Snaydon 1991; Gibson *et al.* 1999), but they have been criticised for confounding competition with species density or frequency (i.e. relative proportions of the competing species) (Gibson *et al.* 1999). To avoid these confounding factors I could have applied a response-surface design where the densities of both species are varied independently (Firbank & Watkinson 1985; Law & Watkinson 1987; Gibson *et al.* 1999). However, this approach would be intractable for use in multi-factorial experiments such as those that I performed, because the number of experimental units required would be immense.

The initial size of seedlings may have a large impact on the results of competition experiments. To try to control for size bias, I used seedlings of similar ages and, within species, sizes. To further reduce bias, it is also possible to include initial size of seedlings as a covariate in the mixed-model ANOVA used to test for competitive interactions, along the lines of the approach that I used in Paper IV.

Conclusions

This thesis demonstrates how light, soil fertility and different types of organic inputs to the soil may influence decomposition processes and growth, competitive interactions and mycorrhizal colonisation of tree seedlings in boreal and temperate forests. It describes a role for not just leaf litter but also other organic inputs in influencing below- and aboveground properties and processes, and shows that long-term absence of disturbance may result in an increased proportion of low-quality twig litter in the litterfall and a decline in initial decomposition rates. The results also demonstrate how species-specific responses of young boreal tree seedlings to light- and humus conditions may affect their competitiveness when

growing in gaps or under forest canopies, and shows that species identity of canopy trees may have impacts on regeneration of tree seedlings through influencing microclimatic conditions. The impacts of canopy species is also shown belowground, where the abundance and assemblages of soil organisms (nematodes) differed greatly between stands of native and non-native species, reflecting differences in soil organic C status and microbial biomass among the species. Furthermore, this thesis indicates that mycorrhizal colonisation is to a large extent regulated by soil fertility (at least under controlled conditions), but that effects of shade from canopy trees was only apparent in conditions of deep shade in the field.

In the studies underlying this thesis, I considered responses of both the aboveground and belowground subsystems to variations in resource availability (light and nutrients), with the intention of mimicking different conditions that may be encountered by tree seedlings and soil organisms in forest ecosystems. I identified several ways that resource availability affected interactions between the above and belowground subsystems. The quality and diversity of organic substrates returned from aboveground had large effects on decomposer activities and decomposition rates, and the belowground community affected plants by determining the plant-available nutrients (the nature of these aboveground feedbacks depended on the quality and diversity of substrates added). Presence of tree seedlings also affected the response of the microbial community to organic substrates, either through root exudates or through mycorrhizal fungi. Furthermore, canopy tree species influenced several belowground properties (microbial activity and biomass, the abundance and assemblages of soil nematodes and the mycorrhizal colonisation of tree seedlings) through altering light- and soil conditions. Aboveground, shade from canopy trees affected seedling growth and interspecific interactions between tree seedlings, and these effects were influenced by soil fertility.

This thesis is also relevant to several aspects of human induced global change through studying the consequences of organic substrate diversity, invasive tree species, and fire suppression for ecosystem functioning. Briefly, I found that diversity of aboveground resources entering the soil may enhance tree seedling productivity, that invasive tree species can have large negative impacts on the abundance of soil organisms and the establishment of tree seedlings, and that the reduced quality and decomposition rate of the tree litterfall in the prolonged absence of fire in boreal forests may contribute to an increased carbon sequestration through increased accumulation of organic matter.

Ultimately, these studies in combination demonstrate how key components of ecosystem functioning in forests may be affected by resource availability. The studies also identify clear linkages between the aboveground and belowground forest systems, and show how these may influence nutrient dynamics, plant productivity and tree seedling recruitment. This shows the value of using a combined aboveground-belowground approach for studying how forest ecosystems function and how they may respond to factors such as global warming, biological invasions and different forestry management practices.

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