Functional Role of Fire-derived Charcoal in Boreal Forest Ecosystem Processes

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Cover: Word clouds from this thesis generated by Wordle^{TM}. Photos of forest fire, post-fire forest, charcoal transversal cut and boreal landscape, respectively. (photos: N. Pluchon)

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Abstract

Charcoal is a natural product of wildfires which operate as a major natural disturbance in boreal forested ecosystems. This carbon (C)-rich material is present in most forest soils but its effects on ecosystem processes remain poorly understood. This thesis explores how charcoal, through its characteristics or traits, affects above- and belowground processes in the Swedish boreal forest by using laboratory mesocosm and glasshouse studies and a large field experiment. The relative importance of charring condition and species identity in determining charcoal traits was also investigated. These experiments covered a wide range of humus types, charcoal types and plant species in order to better understand the factors that determine the functional role of charcoal. With regard to aboveground processes, fire-derived charcoal promoted tree seedling growth but had only a minimal effect on seed germination, and plant community characteristics. Belowground processes such as humus decomposition and N mineralization rate were enhanced by the presence of charcoal, even though charcoal had minimal effect on microbial biomass and composition. Charcoal traits were shown to be affected primarily by species identity and to a lesser extent by charring conditions. The magnitude of charcoal effects was influenced by humus type, charcoal type and plant species identity. The mechanisms by which fire-derived charcoal affect ecosystem processes differed between above- and belowground processes; notably, while the effects of charcoal on aboveground processes were linked mostly to the direct input of phosphorus and especially PO_4^{3-} from charcoal, its effect on belowground processes were mostly determined indirectly through its impact on microbial specific activity. These findings suggest that charcoal is likely to play a role in boreal forest succession, plant-soil feedbacks and ecosystem C dynamics. Moreover, the impacts of charcoal in boreal ecosystems are relevant to better understanding the ecological consequences of forest management practices such as site preparation, prescribed burning, fire suppression and biochar addition. Overall, the findings described in this thesis show that charcoal is a significant component of the C cycle and one that can have strong impacts on boreal ecosystem processes.

Keywords: Charcoal, charcoal functional traits, fire, boreal forest, decomposition, plant growth, microbial community, fire, carbon

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Dedication

To my father, for having honoured his promise.

La pire ignorance, c'est de s'imaginer savoir ce qu'on ne sait pas. Socrate

Contents

List of Publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

I Pluchon N., Gundale M.J., Nilsson M.-C., Kardol P. & Wardle D.A. (2014). Stimulation of boreal tree seedling growth by wood-derived charcoal: effects of charcoal properties, seedling species and soil fertility. *Functional Ecology* 28, 766-775.

II Pluchon N., Vincent A.G., Gundale M.J., Nilsson M.-C., Kardol P. & Wardle D.A. The impact of mixtures of charcoal and humus type on decomposition and microbial communities in boreal forest. *Submitted manuscript.*

III Gundale M.J., Nilsson M.-C., Pluchon N. & Wardle D.A. The effect of biochar management on soil and plant community properties in a boreal forest. *Submitted manuscript.*

IV Pluchon N., Casetou S.C., Kardol P., Gundale M.J., Nilsson M.-C. & Wardle D.A. Influence of species identity and charring conditions on fire-derived charcoal traits. *Submitted manuscript*.

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1 Introduction

1.1 Boreal forest

Boreal landscapes form a circumpolar belt through northern Eurasia and North America. They cover about 1.25 billion km^2 which represent about 10% of the global land surface (Apps et al. 1993). The climate of these regions is characterized by strong seasonal variation with relatively low mean temperatures and short growing seasons, resulting in a forest cover dominated by coniferous vegetation (Bonan & Shugart 1989; Apps et al. 1993). With regard to terrestrial carbon (C) stock, boreal soils contain 200 Pg C globally and vegetation contains 64 Pg C globally, which corresponds to about 50% of the C presently in the atmosphere (Apps et al. 1993; Gower et al. 2001) and 6.4% and 8.7% of the terrestrial C stock worldwide in the soil and the vegetation respectively (Sabine & Heimann 2004). This reveals that boreal forests are relevant players in global C storage. The main natural disturbance in boreal landscape is wildfire, which acts as a major control of ecosystem processes such as nutrient cycling, decomposition and productivity (Bonan & Shugart 1989). Within the boreal zone the average fire return interval varies considerably, but is frequently in the order of 30 to 300 years (Flannigan et al. 1998; Carcaillet et al. 2007). In addition to its frequency, fire regime is also characterized by its intensity, which is defined as the energy released per unit time, and its severity, which is defined as the amount of organic matter consumed by fire (Schimmel & Granström 1996). Fire intensity is generally determined by the type of fire that occurs, i.e. surface fire is of low intensity while crown fire is of high intensity; a wide range of fire intensities occur in the boreal forest depending upon the species and forest structure. Fire severity, which varies greatly among forest type, ranges from the organic layer being almost unburnt to complete combustion of the organic layer, and the level of severity has major consequences for ecosystem properties and in particular nutrient availability (Bonan & Shugart 1989).

The Fennoscandian boreal forests represent about 5% of the total boreal area, which is about 61 million km^2 (Apps et al. 1993). Fennoscandian boreal forests are characterized by coniferous species, typically Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*) which have broad habitat occupancy. Birch (*Betula pubescens* and *Betula pendula*) is the dominant broad-leaved species, while aspen (*Populus tremula*), alder (*Alnus incana*), rowan (*Sorbus aucuparia*) and goat willow (*Salix caprea*) occur less abundantly (Hultén & Fries 1986; Esseen et al. 1997). The field layer consists mainly of dwarf shrubs such as heather (*Calluna vulgaris*) and crowberry (*Empetrum hermaphroditum*) on the driest sites and lingonberry (*Vacinium vitis-idea*) and bilberry (*V. myrtillus*) on mesic and moist sites (Hultén & Fries 1986; Esseen et al. 1997). The forest floor vegetation usually contains bryophytes such as the feather mosses stair-step moss (*Hylocomium splendens*) and big red stem moss (*Pleurozium schreberi*) which dominate in mesic sites and reindeer lichens (*Cladonia* spp) which dominate in drier Scots pine forests (Hultén & Fries 1986; Esseen et al. 1997). Large scale forest management which has taken place since the middle of 20th century in the Fennoscandian boreal forest has influenced both forest structure and species distribution, and has driven a decrease in deciduous cover (Hellberg 2004). Another consequence of the last century of forest management has been the virtual elimination of wildfire in many regions (Granström 2001). However, the long-term consequences of fire suppression on site productivity and biodiversity in the boreal forest ecosystems have been poorly studied.

1.2 Charcoal

Charcoal, also called pyrogenic or black C, is defined as the solid product of incomplete combustion of organic matter. Specifically, it is formed from heating wood, leaves or other biomass under limited supply of oxygen (O_2). The boundaries used to define charcoal structure are unclear and depend upon the technique used (i.e. hand picking, digestion by acids, etc.). As such, charcoal is part of a continuum from partially charred plant material to soot, and ultimately graphite. Along this continuum, the molecular structure is arranged from small cross-linked aromatic clusters to larger graphene sheets (Preston & Schmidt 2006). Fire affects 40% of the Earth’s land surface (Alexis et al. 2007) and charcoal is ubiquitous in terrestrial environments, with up to 45% of soil organic C being composed of charcoal (Forbes et al. 2006). In boreal forest, amounts of 1000-4200 kg ha^{-1} of charcoal have been measured

(Zackrisson et al. 1996; Ohlson et al. 2009), which account for up to 30% of total C of the forest floor (DeLuca & Aplet 2008). Charcoal production during forest fire is highly spatially variable and is a function of fuel loading, moisture and fire intensity (DeLuca & Aplet 2008). As such, charcoal conversion rates of 1-2% of total biomass or 1-10% of biomass consumed during a fire are generally reported (DeLuca & Aplet 2008). Of the charcoal that is produced following fire, a proportion is oxidised by subsequent fires, a proportion is degraded and the remainder is sequestered in soil; however to date these proportions have not been quantified (Preston & Schmidt 2006; DeLuca & Aplet 2008). The mean residence time of the sequestered charcoal in soil has been estimated between 3000 and 12000 years, which therefore makes it useful as part of the paleo record for vegetation reconstruction (DeLuca & Aplet 2008).

Charcoal is often described as a C-rich material that has porous structure and hydrophobic properties. When compared with soil, charcoal has a high water holding capacity, low bulk density and high cation exchange capacity (Lehmann & Joseph 2009), and also has a high potential for sorption of organic compounds (Zackrisson et al. 1996; Keech et al. 2005; DeLuca & Aplet 2008). These properties, together with the resistance of charcoal to decomposition, have led to a growing interest in using biochar, defined as intentionally carbonized organic matter used as soil amendment. The motivations for applying biochar technology include soil improvement (including the increase of soil fertility and productivity as well as pollution mitigation), waste management, climate change mitigation (through terrestrial sequestration of C) and energy production (Lehmann & Joseph 2009). Given the interest in biochar for these purposes, many recent studies have been performed to assess the effects of biochar application on different ecosystem components (Jeffery et al. 2011; Lehmann et al. 2011; Zimmerman et al. 2011; Biederman & Harpole 2013). It is well recognized that there is a need for further research, particularly in specific geographic areas and types of ecosystems that have been little studied, before the large scale application of biochar can be justified (Abiven & Andreoli 2011; Lehmann et al. 2011; Biederman & Harpole 2013). Properties of charcoal used for soil amendment have been shown to depend on both the starting material (i.e. feedstock and/or species of plant used to make the charcoal), and charring conditions (Keech et al. 2005; Lehmann & Joseph 2009). The production process of artificially produced charcoals, including biochar and activated charcoal, results in these materials having properties that may have some differences to charcoal naturally produced by wildfire (Lehmann & Joseph 2009). Thus, the conclusions drawn from studies using artificially produced charcoal may only be partly applicable to understanding the effects of charcoal in natural systems. Moreover, studies on the effects of naturally produced charcoal (e,g., derived from wildfire), particularly from contrasting types of woody materials, are scarce.

1.3 Effect of charcoal on ecological processes

A growing number of studies have investigated the effect of charcoal (or biochar) on aboveground and belowground processes in a variety of ecosystems. However, very few studies have focused on the effect of charcoal in fire-prone ecosystems outside of the boreal region and almost none outside of forested regions. Regarding aboveground processes, few studies have investigated the effect of charcoal on seed germination, and those have revealed either negative or neutral effects (Naydenov et al. 2006; Liao et al. 2014). Concerning plant growth, charcoal addition has been shown to cause an overall increase in plant productivity, though with effect sizes varying with target plant species, climate, soil type and charcoal properties (Jeffery et al. 2011; Biederman & Harpole 2013). In boreal ecosystems, Makoto et al. (2010; 2011) found that seedlings of *Larix gmelinii* responded positively to the addition of charcoal due to increased phosphate uptake from the charcoal surfaces by associated ectomycorrhizal fungi. Further, Wardle et al. (1998) found a positive effect of charcoal addition on *B. pendula* seedling growth, but in only one of the three soil types evaluated, which was most likely due to adsorption by the charcoal of allelopathic compounds that were present in high amounts in only that soil type. Charcoal has also been reported to adsorb allelopathic compounds which would otherwise impede plant growth, but with these effects varying depending on the structural traits of charcoal (Zackrisson et al. 1996; Keech et al. 2005; Gundale & DeLuca 2007).

Charcoal addition can impact soils through altering nutrient cycling and the decomposition of unburnt organic matter, with potential consequences for soil C storage. For instance, charcoal often has high concentrations of available nutrients, (e.g. NH_4^+, PO_4^- , Ca^{+2}, and Mg^{+2}) on its surfaces, which can have fertilization effects over short time-scales, i.e. months (Gundale & DeLuca 2006; Chan & Xu 2009; Jeffery et al. 2011). Charcoal has also been shown to enhance nutrient availability over longer time scales by enhancing nitrogen mineralization or nitrification (DeLuca et al. 2006) as a result of enhanced microbial growth and activity (Lehmann et al. 2011), and by reducing soil nutrient losses due to its high ion exchange capacity (Atkinson et al. 2010). Some studies have also reported a positive effect of charcoal on mineralization of native organic matter and loss of C (e.g., Hamer et al. 2004; Kuzyakov et al. 2009; Luo et al. 2011; Zimmerman et al. 2011), while other studies have demonstrated negative effects (Abiven & Andreoli 2011; Cross & Sohi 2011; Jones et al. 2011; Keith et al. 2011; Zimmerman et al. 2011) or neutral effects (Abiven & Andreoli 2011; Cross & Sohi 2011; Zimmerman et al. 2011; Bruun & EL-Zehery 2012). Further, a study from boreal forest systems showed an increased mass loss in humus-charcoal mixtures when compared with what was expected based on mass loss from charcoal and humus considered separately (Wardle et al. 2008a), although some of this loss may have come from the charcoal itself (see Lehmann & Sohi 2008; Wardle et al. 2008b).

Soil micro-organisms, which are key players in belowground processes through operating as primary decomposers, have been shown to be affected by charcoal addition in various ways (Lehmann et al. 2011). Some effects of charcoal on micro-organisms occur directly. For example, the pores in the charcoal serve as refugia for micro-organisms against predation (Warnock et al. 2007), and the surface of charcoal allows for the formation of biofilms (Lehmann et al. 2011) and adsorption and accumulation of nutrients and labile organic compounds (Lehmann et al. 2011). Sorption of organic matter can also occur within charcoal pores and this can restrict microbial access (Cross & Sohi 2011; Jones et al. 2011; Zimmerman et al. 2011). Charcoal also affects microbial communities more indirectly through modifying the physical and chemical soil environment (notably soil pH) (Pietikäinen et al. 2000; Lehmann et al. 2011), adsorbing and inactivating secondary compounds which would otherwise inhibit micro-organisms (Zackrisson et al. 1996), and altering the chemical signaling between plants and micro-organisms (Warnock et al. 2007). Many of these effects arise through the surface electrostatic properties of the charcoal that enables it to adsorb compounds and ions, and through its physical structure, including its porosity (Tryon 1948; Lehmann et al. 2011).

These studies reveal that charcoal affects ecosystem processes through many mechanisms which might differ in their consequences for soil fertility and C storage. Moreover, the effect of charcoal on both aboveground and belowground properties is likely to depend on the soil type, plant species and charcoal type, but very few studies have investigated how these factors impact on the ecological effects of charcoal. Furthermore, the majority of studies that have explored the ecological impact of charcoal have been performed in agricultural conditions (notably in the context of ‘biochar’), and confined to temperate or tropical systems, or have used charcoal that has not been derived from wood, which is the main charcoal source during wildfire. Therefore, it is crucial to address and better understand the effect of wood-derived charcoal on ecosystem processes in order to understand post-fire mechanisms in fire-prone ecosystems such as boreal forest.

1.4 Objectives

The overall aim of this thesis is to expand our understanding of the role of fire-derived charcoal in boreal ecosystems and the underlying mechanisms through which it affects key ecological processes both aboveground and belowground. This thesis covers charcoal effects on plant seedling establishment and growth, plant community structure and soil properties including microbial community composition and activity, as shown in Figure 1.

This thesis consists of four papers, and the questions addressed in each of these papers are:

I How does wood-derived charcoal influence the growth of seedlings of boreal tree species, and how does this effect depend on charcoal type, tree species and soil type?

II How does wood-derived charcoal influence humus decomposition and the soil microbial community, and how does this effect depend on charcoal type and soil type?

III How does wood-derived charcoal and soil mixing affect soil properties, seed germination and vegetation composition within a large scale stand-level field experiment?

IV How does charring condition and species identity of wood affect traits of fire-derived charcoal that may be of ecological importance?

In Papers I and II, the experiments were manipulated in mesocosms while the study in Paper III took place in field plots. The results reported in these papers will be collectively used to address the following three objectives:

(1) To determine the role of wood-derived charcoal in influencing aboveground processes such as germination, plant growth and plant community composition (Papers I and III).

(2) To assess the role of wood-derived charcoal in affecting belowground processes such as nutrient mineralization rate, soil organic matter decomposition and microbial community composition (Papers II and III).

(3) To evaluate the role of charcoal chemical and morphological traits in driving the aboveground and belowground effects of charcoal (Papers I, II and IV).

Addressing these objectives will collectively contribute to a better understanding of the combined effects of fire-derived charcoal on individual plants, plant and soil communities, and ecosystem functioning (Figure 1).

Exploring these effects in combination, along with the underlying mechanisms and sources of variability, will enable us to better understand the functional role of charcoal, and ultimately fire, in driving boreal ecosystem processes.

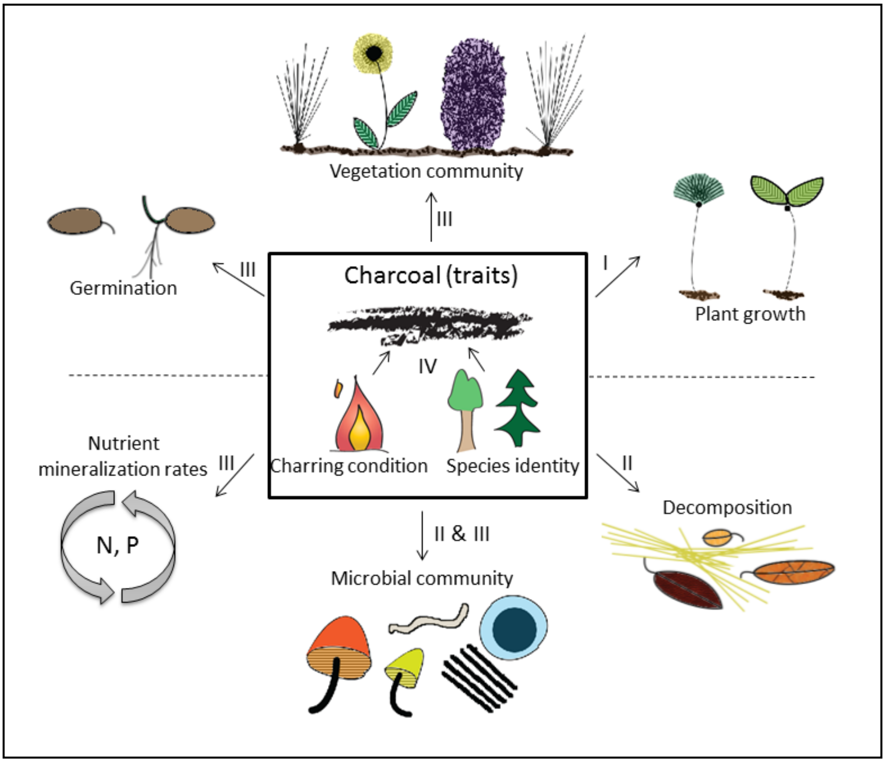

Figure 1. This thesis focuses both on the effect of wildfire-derived charcoal (through its traits) on aboveground and belowground properties and on how charring condition and species identity affects charcoal traits. Roman numerals relate to the four papers in the thesis.

2 Material and Methods

2.1 Experimental designs

In order to investigate the functional role of wood-derived charcoal on aboveground and belowground properties, experimental approaches have been used in controlled laboratory and glasshouse conditions in Papers I, II and IV and in the field in Paper III.

Paper I focussed on the effect of charcoal on plant growth, and on the underlying mechanisms, using a glasshouse pot experiment. As such, seedlings of four common boreal tree species, i.e. *B. pubescens*, *P. abies*, *P. sylvestris* and *P. tremula*, were each grown in each of two soil types amended with charcoal produced from one of nine boreal woody species or in a charcoal-free control. This glasshouse experiment was organized in a full factorial design (i.e., all possible 80 combinations of seedling species, soil type and charcoal type) set up as five replicate blocks, yielding 400 experimental units or pots. Charcoal was added to the soil at 3000 kg ha^{-1} or about 4.5% of total soil mass (dry weight basis), and was left to equilibrate for 50 days before planting pre-germinated seedlings. This amount of charcoal reflects the upper range of natural occurrence of charcoal in boreal soils (Ohlson et al. 2009). During the course of the experiment, seedlings were watered as needed and the temperature used was about 20°C, representing typical conditions in the northern Swedish boreal forest during the growing season (Jackson et al. 2011), with 16/8 h day/night light regime. After 70 days since planting, seedlings were harvested and roots and shoots were dried and weighed.

Paper II explored the effect of charcoal on humus decomposition and microbial communities in a laboratory incubation experiment. Here, mesh bags were prepared and were filled with (1) humus, (2) charcoal or (3) a 50:50 mixture of humus and charcoal (dry weight based); these were placed in 1L glass jars in a humus matrix. For this experiment, six humus types of contrasting fertility and charcoal produced from nine different woody plant species were used in a full factorial design (i.e., all two way combinations of humus and charcoal), with five replicate blocks (i.e., replicate jars) of all treatment combinations (and with a humus bag, a charcoal bag and a 50:50 mixed bag in each jar), yielding a total of 810 mesh bags distributed among 270 jars. Each mesh bag measured 8×4 cm and contained 2 g equivalent dry weight of material (i.e., charcoal, humus, or charcoal + humus) except for a subset which contained 4 g to allow enough material for additional analyses. The matrix of the jar was humus of the same type as that in the mesh bags, and had a moisture content of 60% of field capacity. The jars were covered by lids containing ventilation holes, and placed in a dark room for 9.5 months at 18°C. At harvest, the content of the mesh bags was dried and weighed to determine mass loss of the humus and/or charcoal. Further, a subset of the treatment combinations was subsampled before drying and analysed for substrate-induced respiration (SIR), which is a relative measure of active soil microbial biomass (Anderson & Domsch 1978), and phospholipid fatty acid (PLFA) analysis, which represents microbial community structure. This same subset of treatment combinations was also analysed using ^{13}C CP-MAS nuclear magnetic resonance (NMR) spectroscopy to determine the origin of lost material. For all measured variables, we calculated the expected value for the mixed (charcoal + humus) litter bag and compared this with the observed value from the mixture bag in each jar. This expected value was calculated for mass loss using the average of the mesh bags of pure humus and charcoal from the same jar (Wardle et al. 1997; Gartner & Cardon 2004; Wardle et al. 2008a). When response variables consisted of concentrations (i.e., for microbial measures, NMR data), the expected values were corrected by the differential mass loss that occurred in the humus and charcoal when decomposed separately (Wardle et al. 2008a).

In paper III, a stand-level field experiment was set up to study the effect of charcoal and soil mixing (which imitates silvicultural practices for site preparation in planting operations) on soil processes and plant community properties. Each of four treatments, i.e. control, soil mixing only, charcoal-only, and both charcoal and soil mixing, were applied to 22 × 22 m plots (or 0.05 ha), with six replicate blocks of all four treatments. Wood-derived charcoal was applied at a rate of 10 t/ha and soil was mixed down to 30 cm using an excavator, 1.5 years prior to the measurements (Figure 2). Moreover, pine seedlings of approximately 10 cm tall were planted in a 2 × 2 m grid pattern in all plots one year prior to measurements in a manner that represents conventional forestry practice. Soil nutrient concentrations and mineralization rates of ammonium, nitrate and phosphate were assessed at 2 soil depths (i.e. 0-

10 cm and 10-20 cm), both by analysing extracts of bulk soil and mixed bed ionic resin capsules and by conducting an *in situ* mineralization assay. Soil microbial community structure was measured using PLFA while SIR was used as a measure of active soil microbial biomass; both measurements were made at each of the two soil depths. Further, soil respiration was recorded on six occasions during the growing season, with approximately 3 weeks between each event. Plant community was assessed by estimating the total vegetation and graminoid cover, using point quadrat analysis. The survival of planted *P. sylvestris* seedlings was estimated by visual determination. Further, the germination rate of sown seeds of four boreal tree species, i.e. *B. pubescens*, *Pinus contorta*, *P. sylvestris* and *P. abies*, was investigated 15, 26, 48 and 92 days after sowing.

Paper IV explored the influence of wood from different tree species and charring condition on traits of charcoal that may be important in driving ecological processes. Charcoal from three boreal tree species, i.e. *B. pendula*, *P. sylvestris* and *S. aucuparia*, was produced under six charring conditions representative of natural fire conditions (Miyanishi 2001; Ryan 2002; Taylor et al. 2004) , i.e. 450°C for 45 min, 700°C for 10 and 15 min and 900°C for 5, 10 and 15 min, and replicated 5 times except for the 450°C treatment, which was replicated 2 times. Charring conditions were imposed by using a propane gas burner to allow accurate exposure time. A number of charcoal traits were then measured on each of the 84 resulting charcoal samples. Specifically, we measured density, micro-porosity and transversal porosity as representatives of structural traits and pH, electrical conductivity (EC), total N and P contents, NH_4^+, NO_3^-, and PO_4^{3-} concentrations as non-structural traits.

Figure 2. Setting up of the experiment used in Paper III in August 2011 showing the charcoal treatment (foreground) and other plots (background). *Photo: M. Gundale*.

2.2 Site description, sampling campaigns and charcoal production

The four studies are all focussed on boreal forest ecosystems with particular reference to Fennoscandia. As such, soil, wood and seeds needed for the four experiments came from northern Europe, with the exception of the *P. contorta* seeds (Paper III) which came from the boreal zone of North America. Figure 3 depicts locations of soil sampling and field set up for the different experiments.

2.2.1 Site description and soil sampling

For the experiments in Papers I and II, we collected soil from field sites. The six sites used in Paper II cover a wide range of soil fertility. These sites, ordered in terms of decreasing nitrogen availability, are:

1) Early-successional coastal forest dominated by alder (*A. incana*) (hereafter ‘Alder’ humus) (Figure 3A),
2) Open pine (*P. sylvestris*) forest with herbaceous vegetation (hereafter ‘Herbaceous’ humus) (Figure 3B),
3) Closed canopy Norway spruce (*P. abies*) forest with fern understorey (hereafter ‘Fern’ humus) (Figure 3C),
4) Birch (*B. pendula* and *B. pubescens*) forest (hereafter ‘Birch’ humus) (Figure 3D),
5) Open Norway spruce forest with ericaceous vegetation, notably crowberry (*E. hermaphroditum*) (hereafter ‘Ericaceous’ humus) (Figure 3E), and
6) Open pine forest with a lichen understorey (hereafter ‘Lichen’ humus) (Figure 3F).

The Herbaceous and Ericaceous humus was collected near Arvidsjaur (65°33’N, 18°36’E), the Fern, Birch and Lichen humus was collected near Vindeln (64°12’N, 19°42’E), and the Alder humus was collected in the vicinity of Umeå (63°50’N; 20°19’E) (Figure 3). About 50 L of each humus type was collected from the full depth of the organic horizon.

For Paper I, the two soil types came from the Herbaceous and Ericaceous sites. These two soil types were intended to be contrasting in terms of nutrient availability, with the Ericaceous site being more N limited and the Herbaceous site being more P limited. The sampling campaign took place in October 2010 when about 400L of each humus type was sampled to the full depth of the organic layer.

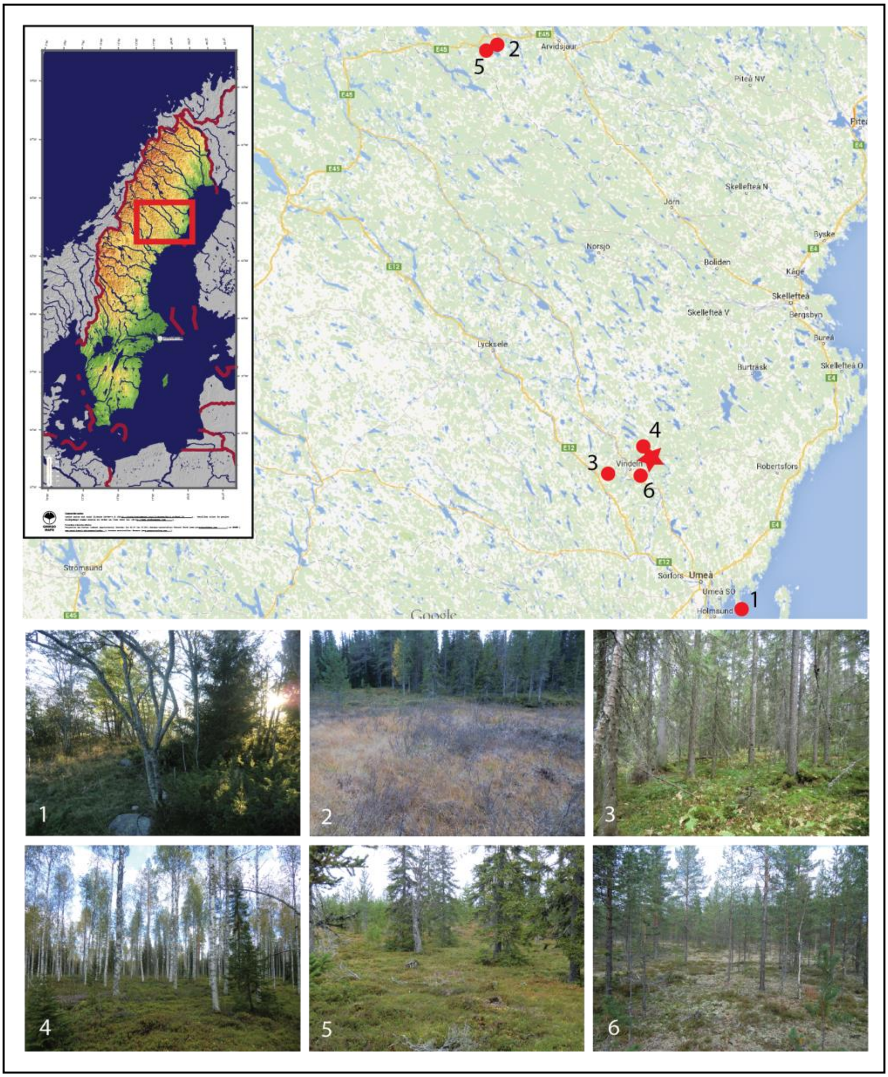

Figure 3. Location and pictures of the sites from which the soil was sampled for Papers I and II. The star point represents the location of the site used in Paper III. *Source of the maps: Google Maps® an GinkoMaps and photos: N. Pluchon*

The field site used for the work described in Paper III is situated in Vindeln, at Åheden research area within the Svartberget Experimental Forest (64°14´N, 19°46´E, 175 m above sea level). Soil at the site is a fine sandy Typic Haplocryod (FAO, Cambic Podzol) formed from silty glacial outwash sediments. The annual mean air temperature at the site is + 1.0° C and mean annual precipitation is approximately 600 mm, of which half falls as rain and half as snow. Snow usually covers the ground from the end of October to late April (Gundale et al. 2011). Prior to the start of the experiment, the experimental site was covered with a closed tree canopy consisting of ~60 year old *P. sylvestris*, which was established via natural regeneration. The understory vegetation consisted primarily of ericaceous shrubs, mainly *V. vitis-idaea* and *C. vulgaris*, and ground cover consisting of mosses and lichens (predominantly *P. schreberi*, *Dicranum* sp., C*ladina rangiferina* and *Cladina arbuscula* (Gundale et al. 2011).

2.2.2 Wood sampling and charcoal production

Wood used to produce charcoal in all papers except in Paper III was collected in the vicinity of Umeå (63°50’N; 20°19’E) from two coniferous species *P. abies* and *P. sylvestris* and the six deciduous tree species *B. pendula*, *B. pubescens*, *P. tremula*, *S. aucuparia*, *A. incana* and *Salix spp*. Wood from the ericaceous shrub *E. hermaphroditum* was collected at the “Ericaceous” site near Arvidsjaur.

The charcoal for Papers I and II was produced in a muffle furnace in the laboratory (Keech et al. 2005). Specifically, pieces of wood were covered by sand in an aluminium container, with an extra layer of aluminium foil covered by sand on the top. The container was placed in pre-heated muffle furnace at 450°C for 45 min. The container was then put outside to cool down for few hours and the resulting charcoal was sieved to retain fragments in the 0.8 - 1.5 mm size range. In Paper III, the charcoal was produced by a local company (Vindelköl AB, Vindeln Sweden), which sells and markets this material as “Terra Preta” for use as a soil amendment (www.vindelkol.se). The charcoal was made primarily from the wood and bark of *P. sylvestris*, and a small portion of *P. abies*. The charcoal for Paper IV was produced using an original set up consisting of an isolated gas flame fueled by propane gas, constrained in a barrel. The charring condition was a manipulated factor of this experiment and consisted of six conditions intended to reflect natural fire conditions: 450°C for 45 min, 700°C for 10 and 15 min and 900°C for 5, 10 and 15 min. The temperature was continuously assessed using thermocouple.

2.3 Methodological aspects

2.3.1 Soil analyses

Established techniques were used for measuring soil chemical properties. Soil pH was measured in a 1:4 ratio of soil to water for organic soil (Papers I and II) or in a 1:1 ratio for mineral soil (Paper III). A subsample of 10g (Papers I and II) or 20g (Paper III) of fresh soil was extracted with 50 ml 1 M KCl and analyzed for ammonium, nitrate, and phosphate concentrations by colorimetry on an AutoAnalyzer AA3 (SEAL Analytical, OmniProcess AB, Sweden). The *in situ* mineralization assay performed in Paper III used an additional soil sample which was incubated in a plastic bag for 2.5 months on site and measured following the same procedure. Moreover, mixed bed ionic resin capsules (PST1 capsules, Unibest, Bozeman, USA) were used in Paper III; these were placed in the field for the duration of the growing season (i.e. about 5 months), then extracted in 30 ml 1 M KCl and analyzed as described for soil samples. In Papers I and II, soil total carbon (C) and nitrogen (N) were additionally measured through dry combustion using a FLASH 2000 Organic Elemental Analyzer (Interscience, Breda, the Netherlands) and total phosphorus (P) using digestion followed by inductively coupled plasma optical emission spectrometry (ICP-OES) (Spark 1996). Soil electrical conductivity (EC) and cation exchange capacity (CEC) was measured in Paper I using a 1:4 slurry of deionized water to fresh humus and measuring Na and accounted for entrained Na with nitrite, respectively.

Total soil respiration (i.e. autotrophic and heterotrophic respiration combined) measurements were made in Paper III by installing cylindrical collars (25 cm diameter, 10 cm high). The CO_2 efflux was then measured by sealing the headspace within these collars by an opaque plexiglass lid fitted with a portable infrared gas analyzer (CARBOCAP model GMP 343, Vaisala, Finland). During each measurement, the headspace air temperature and CO_2 concentrations were recorded every 15 s for 3 min. Soil respiration within the headspace of each chamber was calculated using a linear regression of CO_2 concentration versus time, with the slope of the regression indicating the CO_2 efflux. Estimated values were subsequently adjusted for variation in headspace volume and air temperature, and converted to a soil surface area basis, resulting in units of µmol CO_2 m^{-2} s^{-1}, as described by Hasselquist et al. (2012).

In Papers II and III, the effect of charcoal on soil active microbial biomass was explored using SIR. To further investigate the soil microbial community structure, PLFA analysis was used as it has showed to be a robust and sensitive indicator of community composition, and because it provides a tractable means of quantifying relative abundances of different subsets of the soil microflora across large numbers of samples (Ramsey et al. 2006). For the PLFA measurements, we used 0.3 g (Paper II) or 1 g (Paper III) freeze dried soil which was then extracted and fractionated as described in Frostegård et al. (1991); larger amounts of soil were used for Paper III because the soil had a higher mineral content and less organic matter. Different types of PLFAs represent different components of the soil microflora such as gram-negative bacteria, gram-positive bacteria, fungi and actinomycetes. We used SIR as described by Anderson and Domsch (1978) as modified by Wardle (1993) and McIntosh et al. (2012). A fresh subsample of 1g (dry mass equivalent) (Paper II) or 20 g (Paper III) of material was placed into a 100 mL glass bottle and adjusted to 235% moisture (dry mass basis) (Paper II) or 125% (Paper III). Evolution of CO_2 between 1 h and 3 h after addition of 4 mL of glucose solution (60%) was determined by injecting 5 mL subsamples of headspace gas into an EMG-4 Gas Analyzer (ADC BioScientific, Hoddesdon, UK).

The C composition of the material inside each mesh bag from Paper II was determined using ^{13}C CP-MAS NMR spectroscopy using similar analytical methods to those used by Harrysson Drotz et al. (2010) and Erhagen et al. (2013). A subsample of 50–100 mg of soil at 40% moisture was packed into 4 mm zirconium oxide rotors and spun at 10 kHz ± 3 Hz in a 4–mm CP-MAS probe. The NMR spectra of the material were obtained with a Bruker Avance III 500 MHz spectrometer with a ^{13}C operating frequency of 125.76 MHz; the magic angle was adjusted to 54.7° using K79Br, and adamantane was used as an external chemical shift reference for carbon signals (38.5 and 29.4 ppm, respectively). Spectra were acquired using a 2.5 µs 1H 90° excitation pulse, followed by cross-polarization for 1.5 ms with ramped proton amplitude and 13C acquisition under SPINAL 64 1H decoupling at 100 kHz. A total of 4096 time domain points were collected at a spectral width of 50 kHz using 8000 scans with a relaxation delay of 1.5 s.

2.3.2 Trait measurements

The characterization of contrasting charcoal types, i.e. of charcoals produced from different species (Papers I, II and IV) or under different burning conditions (Paper IV), enables better understanding of the underlying mechanisms by which charcoal impacts on aboveground and belowground ecological processes. As such, a number of charcoal traits were measured in each of the four papers. Charcoal pH was measured in a 1:4 (Papers I, II and III) or 1:5 (Paper IV) slurry of deionized water with charcoal. A sample of 0.5g of charcoal was extracted with 5 ml 1 M KCl and analyzed for ammonium, nitrate, and phosphate concentrations by colorimetry on an AutoAnalyzer AA3 (SEAL Analytical, OmniProcess AB, Sweden). In addition, the total C concentration of charcoal was measured in Papers I, II and III through dry combustion using a FLASH 2000 Organic Elemental Analyzer (Interscience, Breda, the Netherlands). Total N was also measured through dry combustion (with the same analyzer) in Papers I and II and by using Kjeldhal digestion method in Paper IV. This Kjeldahl digestion method was also used to measure total P in Paper IV, while digestion followed by inductively coupled plasma optical emission spectrometry (ICP-OES) (Spark 1996) was used to measure total P in Paper I and II. In Papers I and II, the specific surface area (BET) was measured using the BET gas adsorption method (Brunauer et al. 1938) and CEC was measured by measuring Na. Charcoal density and transversal porosity (TP) was measured in Papers I, II and IV; density was measured using water displacement to estimate volume and a scale to measure the weight filling that volume, while the TP was derived from image analysis of a transversal section (as described by Keech et al. 2005) (Figure 4). Electrical conductivity was measured in Paper I using a 1:4 slurry of deionized water to charcoal and in Paper IV using a 1:15 slurry of deionized water to charcoal.

Some traits of wood prior to its conversion to charcoal have been measured in Paper I, i.e., total C, N, P, density and transversal porosity. The methodology used was the same as those used to determine charcoal traits described above.

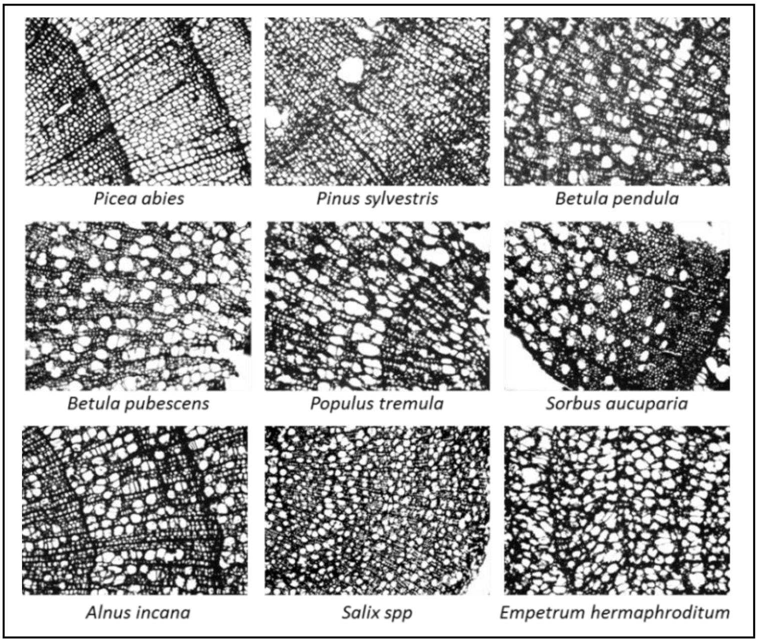

Figure 4. Microscopic pictures of transversal sections of wood-derived charcoal used to determined transversal porosity. All pictures are at the same scale and magnification (× 200). *Photo: N. Pluchon and S. Casetou*

2.4 Statistics

Different statistical analyses such as analysis of variance (AVOVA), correlation analyses, and multivariate approaches (i.e. multivariate analysis of variance (MANOVA) and principal component analysis (PCA)) were used to test the specific questions presented in each paper. Specifically, a multivariate analysis of variance (MANOVA) was run on the full traits data set to explore the overall effects of species identity and charring conditions on all 10 charcoal traits in Paper IV.

Univariate ANOVAs were used for analysing the data in each of Papers I-IV. In Paper I, a full factorial three-way ANOVA was used to test for the effect of seedling species, soil type and charcoal type and their interactions on plant above- and belowground biomass. In Paper II, a split plot model was first run with charcoal type and humus types as main plot factors and mesh bag content (i.e., charcoal alone, humus alone, or mixed) as a subplot factor to explore their effects and interactions on mass loss and microbial community attributes. Then, a factorial two-way ANOVA was used to test the effect of charcoal type and humus type and their interaction on the '(observed–expected)/expected' values for mass loss and microbial community attributes bags containing humus and charcoal mixtures. In Paper III, the effects of soil mixing and charcoal addition and their interaction were tested using a factorial two-way ANOVA, and for variables measured at both sampling depths, a split-plot model was used with soil depth included as an additional subplot factor. When measurements were made at different sampling events in Paper III (i.e., soil respiration), these were treated as a repeated measures term in the ANOVA. Further, for the germination data, seed species was also included as a subplot variable. In Paper IV, a factorial two-way ANOVA was used to test for the effect of species identity, charring conditions and their interaction on each charcoal trait. Block was always considered as random factor. When ANOVA revealed significant effects of any main factor, or interactions among factors, *post hoc* comparisons were performed using Tukey's tests at p=0.05 in Papers I, II and IV and Student-Neuman-Keuls tests in Paper III.

Principal component analysis (PCA) was performed on the full charcoal (and, in Paper I, wood) traits data set in Papers I and IV to summarize the large number of variables into fewer variables to further explore potential drivers of plant growth (Paper I) and the role of charring conditions and species identity on driving charcoal traits (Paper IV). In Paper II, PCA was performed on both PLFA and NMR analyses to describe community patterns in PLFA and pattern recognition of NMR spectra. In Paper III, plant community composition data were subjected to PCA. Axes scores of each of the first two (Papers I, II and

III) or four (Paper IV) principal components were then subjected to ANOVA as described above.

Correlation analyses using Pearson's correlation coefficients were used to identify relationships between charcoal traits and plant biomass in Paper I, and between mass loss and charcoal traits in Paper II. Nine independent data points represented each of the nine wood or charcoal types in both Papers I and II. In Paper IV, correlation analyses using Pearson's correlation coefficients were used to identify relationships among all possible pairwise combinations of the ten charcoal traits, with each of the 18 treatments serving as an independent data point.

All data were graphically analysed for assumptions of normality and homogeneity of variance, and were transformed when necessary to meet these assumptions. All statistical analyses were performed using MINITAB 16 (Minitab Statistical Software, State College, PA, USA) in Papers I, II and IV and IBM SPSS version 21 (Armonk, NY, USA) in Papers II and III.

3 Results and Discussion

This thesis investigates how charcoal, with particular focus on its traits, affects ecosystem processes occurring both aboveground and belowground (Figure 5). Papers I and III focussed on aboveground properties such as plant growth, seed germination and plant community composition. Papers II and III targeted belowground properties such as decomposition, microbial community composition, and nutrient cycling. Finally, the role of species identity and charring condition as drivers of charcoal traits were tested in Paper IV. A range of charcoal types, soil types and plant species was considered in the various studies in order to disentangle underlying mechanisms. The main findings of these studies and their implications are now discussed.

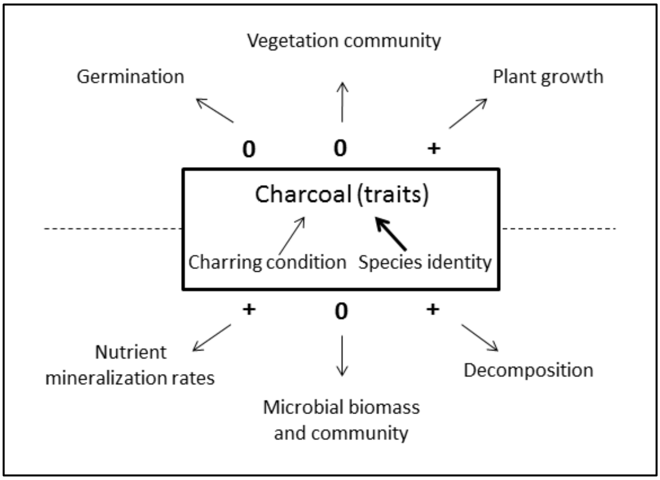

Figure 5. Summary of the drivers of charcoal traits (as shown by the width of the arrow within the central box) and of the overall directionality of effects of charcoal (‘-‘; ‘+’ or ‘0’) on some aboveground and belowground properties (Papers I-IV).

3.1 Effect of charcoal on aboveground processes

The response of germination rate of four common tree species to charcoal and soil mixing (which imitates silvicultural practices for site preparation in planting operations) was investigated in a field trial (Paper III). Charcoal did not show any effect on germination, either by itself or in interaction with soil mixing (Figure 5). A small number of other studies that have investigated the direct effect of wood-derived charcoal on seed germination in a laboratory setting have found negative impacts on germination (Naydenov et al. 2006). The unresponsiveness of germination to charcoal in Paper III suggests that other mechanisms at the field scale could over-ride direct effects of charcoal, such as availability of light and moisture. On the other hand, there was a positive effect of the soil mixing treatment on seedling establishment, which may be due to reduced competition from the ground layer vegetation for limiting resources such as light or soil moisture (Wardle et al. 2008; Thiffault et al. 2012; Stuiver et al. 2014). This highlights the importance of ground layer vegetation in determining the success of tree establishment success in boreal forests (Thiffault et al. 2013).

The early growth of tree seedlings from four species was investigated in two soils of contrasting fertility which were amended with charcoal from nine tree species in a greenhouse experiment (Paper I). Overall, charcoal addition had either neutral or positive effects on plant growth, with the magnitude of effects depending on tree species, charcoal type or soil type (Figures 5, 6). Positive effects of charcoal on boreal tree seedling growth have also been reported for *Larix gmelinii* (Makoto et al. 2010) and *B. pendula* (Wardle et al. 1998), as a consequence of P fertilization effects and adsorption of allelopathic compounds by the charcoal, respectively. In Paper I, increased seedling growth in the presence of charcoal occurred only in the most P-limited soil type (i.e. herbaceous) when compared with the most N-limited soil type (i.e. ericaceous). This suggests that charcoal alleviates P limitation in P-limited soils but does not contain sufficient N to alleviate N-limitation in N-limited soils (Makoto et al. 2010; Biederman & Harpole 2013). Further, the charcoal type which had the highest P concentration often had the greatest effect on seedling biomass, which suggests that charcoal types that have high concentrations of limiting nutrients, notably P, can have a strong fertilization effect on tree seedlings. Meanwhile, the seedlings of the two angiosperms (i.e. *B. pubescens* and *P. tremula*) showed greater responsiveness to the charcoal treatments than did the two gymnosperms (i.e. *P. sylvestris* and *P. abies*), which suggest that beneficial effects of charcoal inputs following fire on soil fertility (and especially P availability) may favor the initial colonization and establishment of angiosperms (Bond 1989; Linder et al. 1997; Fortin et al. 1999; Coomes et al. 2005). Further, because charcoal from the angiosperm species had the strongest positive effects on the growth of angiosperm seedlings, a positive feedback might exist whereby charcoal formed from angiosperm wood after fire may favor seedling establishment of angiosperms (Freschet et al. 2013).

At the plant community level, the effect of charcoal and soil mixing on ground-layer vegetation cover, species richness and species composition was investigated in a field scale experiment (Paper III). Of all measured plant community variables, only plant species richness responded to the presence of charcoal, and this effect was negative (Figure 5). On the other hand, soil mixing reduced graminoid and total plant cover, and promoted dominance by ericaceous shrubs. Because we found soil nutrient availability to be enhanced by charcoal application, these results suggest that ground layer vegetation was primarily controlled by disturbance rather than by nutrient availability over the time scale of this experiment. While charcoal has frequently been shown to positively affect plant growth and biomass in agricultural systems (Jeffery et al. 2011), the absence of effects found in our study may be because the effects of nutrient availability (and thus the effects of charcoal on nutrient availability) emerge only over longer time periods following disturbance, i.e., when standing plant biomass reaches a level at which competition for nutrients intensifies (Grime 1979).

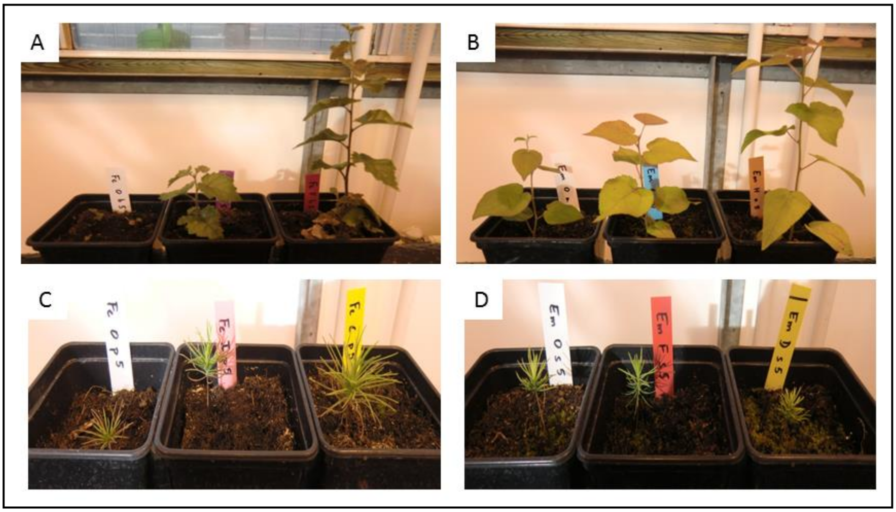

Figure 6. Growth of seedlings from *B. pubescens* (A), *P. tremula* (B), *P. sylvestris* (C) and *P. abies* (D) after 40 days (Paper I). Each picture of three seedlings shows the charcoal-free control on the left and amendment with different charcoal types in the centre and on the right.

3.2 Effect of charcoal on belowground processes

The effect of charcoal and soil mixing on soil nutrient availability and transformation rates was assessed in Paper III in a field scale experiment. The application of charcoal to soil increased NH_4^+ availability, but NO_3^- and PO_4^- were unresponsive. Although NH_4^+ accumulates within ash residues on the surface of fresh charcoal during the charring process (Gundale & DeLuca 2006), the observed increase in NH_4^+ in this experiment is unlikely due to charcoal acting as a source of NH_4^+. This is because the quantitative increase in NH_4^+ that we observed in the soil greatly exceeded the amount of NH_4^+ that was present in the added charcoal. Instead, this positive effect of charcoal on NH_4^+ is likely due to its effects on net N mineralization rates (Figure 5). Meanwhile the soil mixing treatment had a negative effect on N mineralization rates but a positive effect on NO_3^- availability. Positive initial effects of soil mixing on N mineralization rates have often been reported (Frey et al. 2003; Siira-Pietikäinen et al. 2003; MacKenzie et al. 2005; Piirainen et al. 2007) and these effects are usually transient (Piirainen et al. 2007); results shown in Paper III are consistent with this short term positive effect of mixing. Further, the higher extractable soil NO_3^- concentrations observed in response to soil mixing is consistent with this explanation, given that the NO_3^- pool would have originated from recent mineralization and nitrification activity (Stevenson & Cole 1999). Charcoal dampened many of the impacts of mixing on soil nutrient availability and nutrient transformation rates, for example through reducing the negative effect of soil mixing on N mineralization rates. The significant increase in soil PO_4^- in mixed soils with versus without charcoal could have been due to charcoal interfering with PO_4^- complexation with humic substances or Fe and Al ions (Lehmann et al. 2003; Topoliantz et al. 2005).

Decomposition of soil organic matter is a key process underpinning C and nutrient cycling (Cadisch & Giller 1997; Swift et al. 1979), and charcoal produced during a fire event is likely to interact with both existing and newly deposited organic matter. In Paper II, humus mass loss (i.e., humus decomposition), was assessed for all pairwise combinations of 6 humus types and 9 charcoal types in a laboratory experiment. Overall, mass loss from mixtures of charcoal and humus was greater than expected based on mass loss observed when the two components were not mixed (Figure 5). This accelerated C loss from soils caused by charcoal addition is consistent with some laboratory studies involving labeled charcoal (e.g., Hamer et al. 2004; Keith et al. 2011; Luo et al. 2011; Zimmerman et al. 2011) and a field study (Wardle et al. 2008a), but inconsistent with other studies revealing either neutral effects or retardation of C loss by charcoal (e.g., Kuzyakov et al. 2009; Abiven & Andreoli 2011; Cross & Sohi 2011; Jones et al. 2011; Zimmerman et al. 2011; Bruun & EL-Zehery 2012). Further, NMR analyses revealed that the accelerated mass loss observed in the mixed bags was mostly due to the loss of humus rather than charcoal. The magnitude of the synergistic effect of mixing humus and charcoal on mass loss differed among humus types but not among charcoal types, despite large physical and chemical differences among the charcoal types that were measured. Differences in these mixture effects among humus types could not be explained by soil nutrient availability, organic C content or pH. However, humus from the one site dominated by herbaceous vegetation (i.e., the ‘Herbaceous' site) showed a substantially stronger mixture effect than did humus from the other five sites. The vegetation characterizing the ‘Herbaceous’ site is characteristic of water discharge sites in the boreal landscape (Giesler et al. 1998), and humus collected from such sites may have properties that were not measured (e.g. those relating to structure or hydrology) which could have contributed to the strong mixture effects that we observed on mass loss.

The response of the microbial community to charcoal addition was explored in papers II (laboratory incubation) and III (field setting) using PLFA (to quantify the main soil microbial groups) and SIR (as a relative measure of total soil microbial biomass). In Paper II, the effect of mixing of charcoal and humus was additive (i.e. no difference between what was observed in the mixture versus expected in the mixture based on the components incubated separately) on the soil microbial biomass and on main microbial groups (i.e. gram+ bacteria, gram- bacteria, fungi and actinomycetes), while in Paper III the fungal to bacterial ratio was enhanced by the presence of charcoal (Figure 5). Nevertheless, the positive effect of charcoal on N mineralization rates in Paper III and humus decomposition in Paper II suggest that charcoal may have enhanced the effectiveness of the microbial community to mineralize N and C, for example through enhancing its specific activity (i.e., activity per unit biomass; Anderson & Domsch 1993). Additionally, microbial community level shifts might have occurred at a finer level of taxonomic resolution than that tested using PLFAs (Lehmann et al. 2011). Moreover, in the field, microbial biomass and soil bacteria and fungi were enhanced by charcoal when the soil had also been mixed (Paper III). These positive effects of charcoal on microbes at least in the field may have resulted from charcoal serving as a refuge enabling micro-organisms to avoid their consumers (Thies & Rillig 2009), enhancing availability of nutrients and labile organic matter for the micro-organisms (Steinbeiss et al. 2009; Luo et al. 2011; Zimmerman et al. 2011; Farrell et al. 2013), altering pH (Pietikäinen et al. 2000), sorption of allelochemicals (Zackrisson et al. 1996) and altering other soil properties

(DeLuca et al. 2006; Lehmann & Joseph 2009; Clough et al. 2013; Watzinger et al. 2014).

3.3 Traits and mechanisms

The studies from Papers I, II and III revealed that charcoal impacts on ecological processes through a variety of mechanisms. Further, Papers I and II explored how charcoal traits, influenced by species identity, may help explain several of the effects of the charcoal. Paper IV explored the sources of variability of these traits in terms of charring conditions and species identity.

The growth of tree seedlings was promoted by charcoal through increasing P availability (Paper I). Moreover, a significant increase in soil PO_4^{3-} in mixed soils with versus without charcoal was shown in Paper III. Charcoal might impact on P availability directly through releasing the PO_4^{3-} it contains, or indirectly by interfering complexation of PO_4^{3-} with humic substances or with Fe and Al ions (Giesler et al. 2005; Lehmann et al. 2003; Topoliantz et al. 2005). The charcoal traits involved in those mechanisms affecting P availability are PO_4^{3-} concentration, total P content, and adsorption capacity (as a result of its porosity). In fact, the biomass response of tree seedlings to 9 different charcoal types was strongly correlated with the PO_4^{3-} concentration of the charcoal, which was greater in charcoal produced from deciduous than from coniferous tree species (Paper I). Moreover, total P content, PO_4^{3-} concentration and micro-porosity of charcoal were shown to be affected by species origin but not by charring condition or their interaction (Paper IV). As such, P and PO_4^{3-} concentration in charcoal is largely reflective of tree species differences in the wood from which the charcoal is produced. It is recognized that woods of different tree species occupy different positions on the so-called ‘wood economic spectrum’, ranging from species with acquisitive traits (high nutrient content, low density, low tannins) to species with conservative traits (low nutrient content, high density, high tannins) (Chave et al. 2009; Jackson et al. 2013). Thus, the applicability of the ‘wood economic spectrum’ for assessing the effects of different wood species on decomposition and nutrient mineralization rates might have potential for predicting the relative effects of different charcoal types on tree seedling growth. These findings suggest that the potential for charcoal to enhance plant growth through promoting P availability would be greatest following low intensity fire (i.e. fires of low temperature) in stands dominated by deciduous species (Paper I; Makoto et al. 2011).

The decomposition of humus when mixed with charcoal was faster than expected when charcoal and humus were incubated separately (Paper II).

Moreover, N mineralization rate was enhanced by charcoal addition to soil (Paper III). The likely mechanism underlying this increased humus decomposition and N mineralization is the promotion by charcoal of microbial specific activity (i.e., activity per unit microbial biomass). Charcoal traits likely to be involved in influencing micro-organisms are micro-porosity, sorption capacity, nutrient content and pH (Thies & Rillig 2009; Lehmann et al. 2011). Micro-porosity, total P and PO_4^{3-} concentration were influenced by species origin, pH and NH_4^+ concentration were affected by charring condition, total N was affected both by species origin and charring conditions, and NO_3^- concentration was affected by the interactive effect of species origin and charring condition (Paper IV). Taken together, these results show that charcoal produced at high temperatures (> 500 °C) should have a higher pH and sorption capacity but fewer nutrients than charcoal produced at low temperatures, and that charcoal produced from deciduous species should provide more favorable conditions for microbes than charcoal from coniferous species (Paper I, IV; Lehmann & Joseph 2009). As such, charcoal from deciduous species could be expected to enhance microbial biomass and thus promote greater humus mass loss than would charcoal from coniferous species. However, in Paper II there was only additive stimulation of any microbial group caused by mixing of charcoal and humus, irrespective of charcoal type. Moreover, although four out of nine charcoal types promoted mass loss when mixed with humus, the magnitude of the increased humus mass loss was not affected by charcoal type (Paper II). Possible explanations as to why no differences were found among charcoal types could be either that the range of the traits among charcoal types was too narrow for differences to emerge, or that trait values for all charcoal types were below a minimum threshold required for promoting soil micro-organisms biomass.

While the effect of charcoal on aboveground processes are mostly linked to the direct input of P and especially PO_4^{3-} from charcoal, charcoal effect on belowground processes are mostly determined indirectly through its impact on microbial specific activity. These contrasting effects of charcoal on the different components of the ecosystem (notably above- versus below-ground) highlight the multiple mechanisms impacted by charcoal which are likely to have important implications at the ecosystem level, as will now be discussed.

3.4 Implications

In this thesis, fire-derived charcoal has been shown to promote seedling growth, humus decomposition and N mineralization rates in boreal forest ecosystem (Figure 5). The magnitude of these effects sometimes depended on the type of charcoal and thus its traits, which were frequently affected by species identity of the wood from which the charcoal was made as well as the charring conditions used. These results have several broader implications for the functioning of boreal forest ecosystems as will be now discussed.

The effect of fire-derived charcoal on increasing P availability (Paper I), N mineralization rates (Paper III), and humus decomposition (Paper II) suggest that the presence of charcoal can increase site nutrient availability, which can in turn positively affect plant growth (Paper I). Moreover, angiosperm tree seedlings were more responsive than gymnosperm seedlings to the effect of charcoal on soil fertility (Paper I; Bond 1989; Coomes et al. 2005). This suggests a potential role of fire-derived charcoal in determining the relative success of seedlings of different tree species during the initial stage of post-fire secondary succession, through promoting angiosperm tree species by enhancing P availability. Indeed, the two angiosperm species which were studied in Paper I are both important pioneers after fire (Linder et al. 1997; Fortin et al. 1999). However, despite generally increasing plant growth, charcoal did not affect seedling germination (Paper III), which suggests that the effects of charcoal differ in their effects on plant performance at different plant developmental stages. The increased growth response of angiosperm seedlings to charcoal was most pronounced when charcoal was produced from wood produced from angiosperm tree species (Paper I). This suggests a positive feedback whereby angiosperm trees produce charcoal after fire that promotes growth of angiosperm tree seedlings, and thereby points to a role of charcoal in reinforcing plant-soil feedbacks (see Freschet et al. 2013; Van Der Putten et al. 2013). Further, charcoal produced from wood that had traits associated with the ‘resource acquisitive’ end of the ‘wood economic spectrum’ (sensu Chave et al. 2009) promoted seedling growth more than did charcoal from wood that had traits associated with the more ‘resource-conservative’ end (Paper I). This suggests that the ‘wood economics spectrum’ influences the characteristics of charcoal produced from wood and the ecological effects of this charcoal. These findings, together with the insights regarding the source of variability of charcoal traits provided in Paper IV, may have potential for helping predict the post-fire consequences of charcoal in boreal forest ecosystems.

The results of this thesis are also relevant for understanding the ecological impacts of fire-derived charcoal in a forest management context. As such, forestry in the Fennoscandian region is characterized by the almost complete suppression of the natural forest fire regime (Granström 2001). This means that the disturbance generated by logging operations is not accompanied by inputs of charcoal. The improved soil fertility due to charcoal effects shown in this thesis (Papers II and III) suggest that without charcoal inputs, soil fertility could decline in managed forests, with the magnitude of this effect varying depending on soil type (Papers I and II). Some field-based and modelling studies have shown declines in soil fertility with fire suppression, with consequences for tree productivity; these effects may arise in part from the absence of charcoal and its beneficial effects (Peng & Apps 1999; Kang et al. 2006; Simard et al. 2007). Even if these effects should be expected to be lower for coniferous tree species which are less responsive to charcoal (Paper I) and which are more commonly used for pulp and timber production, the effects of charcoal could potentially have economic implications. Prescribed burning has been proposed for conservation purposes in order to preserve biodiversity components that are dependent of fire disturbance (Granström 2001). These prescribed fires are often low severity and only exert moderate effects on the humus layer while producing significant amounts of charcoal (Tanskanen et al. 2007). This thesis suggests that charcoal arising from prescribed burning has several potential benefits, including for conservation (Paper I; Van De Voorde et al. 2014) and for enhancing productivity by increasing soil fertility (Papers II and III) and promoting tree growth (Paper I).

There have been few studies on the ecological impacts of addition of fire-derived charcoal in forested ecosystems. In contrast, there has been significant recent focus on the ecological effects of addition of biochar (i.e., the carbonized form of any organic matter applied as soil amendment, primarily charcoal), particularly in agro-systems and in temperate and tropical environments (Gurwick et al. 2013). Many of the effects of fire-derived charcoal on ecological processes in forested settings that have been reported (including in this thesis) are generally in line with biochar effects shown in agroecosystems. These include neutral to positive effects on plant growth (Paper I; Jeffery et al. 2011; Biederman & Harpole 2013), on nutrient mineralization rates (Paper II; DeLuca et al. 2006; Lehmann & Joseph 2009; Clough et al. 2013) and on microbial biomass and activity (Papers II and III; Pietikäinen et al. 2000; Lehmann et al. 2011). On the other hand, while fire-derived charcoal in forests usually promotes soil organic matter decomposition (as shown in Paper II), reported effects of biochar on soil organic decomposition in agroecosystems are highly variable and include both negative and positive effects (Hamer et al. 2004; Kuzyakov et al. 2009; Abiven & Andreoli 2011; Cross & Sohi 2011; Jones et al. 2011; Keith et al. 2011; Luo et al. 2011; Zimmerman et al. 2011; Bruun & EL-Zehery 2012). This means that the effects of fire-derived charcoal in forests and of biochar addition in agroecosysytems may show similarities for some processes but not others, which could reflect partial differences in the ways by which charcoal addition affects the two types of ecosystems. Specifically, the high amounts of organic matter in boreal forest soils (especially in the humus layer) relative to those in temperate agroecosystems, combined with the differences between the two systems with regard to their soil microbial communities, may be important in driving differences in how charcoal affects ecological processes, especially belowground. Thus, the general patterns emerging from the extensive literature on the impacts of biochar in agroecosystems may be only partially applicable to understanding effects of charcoal in forests.

Charcoal is by definition a C-rich material and in this thesis it has been shown to interact with different components of the C cycle including those that drive ecosystem C inputs through plant production (Paper I) and C losses through mineralization (Papers II and III). Further, the effects of charcoal on different processes that comprise the overall C cycle are not unidirectional. Indeed, the observed increase in plant growth in the presence of charcoal suggests that more atmospheric C will be fixed into the vegetation (Paper I), while the increased organic matter decomposition indicates that previously stored C in soil will be released into the atmosphere (Paper II). Because of these counteracting effects, the overall effect of charcoal on total ecosystem C storage is unclear and further research is needed to quantify whether charcoal from wildfire will have a net positive or a negative effect on overall C storage. Moreover, the conversion of wood to charcoal is likely to fix atmospheric C in the ecosystem in the long term because the mean residence time for charcoal (i.e., 3000-12000 years) is several times that of wood (e.g. 500 years for pine wood) (Preston & Schmidt 2006; DeLuca & Aplet 2008). Therefore, charcoal affects turnover of belowground C in both directions, through accelerating the C cycle by increasing site fertility, and by slowing down the C cycle due to its recalcitrant nature. Direct quantification of the relative importance of these opposing processes is largely missing from the literature, and while attempts have been made through modelling (see Woolf et al. 2010), the balance between these processes is likely to depend on a variety of factors such as soil type, charcoal type, and plant species.

Conclusions

In this thesis, the effects of fire-derived charcoal have been investigated on both aboveground and belowground processes in order to characterize the role of fire-derived charcoal in boreal forest ecosystems. Further, a number of ecologically relevant chemical and morphological charcoal traits were measured, to explore the extent to which these traits could explain the observed effects of charcoal on ecological processes. Further, a range of charcoal types, soil types, plant species and scales of investigation were used in order to enable a more complete assessment of the functional role of fire-derived charcoal in Fennoscandian boreal forests. Using a range of methodologies, charcoal was found to have minimal effects on plant germination, plant community composition and microbial biomass, and to promote plant growth, organic matter decomposition and N mineralization rates. The magnitude of these effect depended on soil type, charcoal type and plant species. The most important mechanisms by which charcoal effects were manifested were related to fertilization through the direct input of P and PO_4^{3-} via charcoal, at least aboveground.

These findings help improve our understanding of the role of charcoal in boreal forest succession, plant-soil feedbacks and ecosystem C dynamics. Moreover, they are relevant to better understand the ecological consequences of forest management practices such as site preparation, prescribed burning, fire suppression and biochar addition. Overall, the findings described in this thesis have shown that charcoal is a significant component of the C cycle through its effect of the main components of this cycle, including both those relating to C inputs and C losses from the system. As such, these results suggest that charcoal, which can comprise up to 40% to total soil C in the boreal forest (DeLuca & Aplet 2008), could be responsible for increasing belowground C turnover by up to as much as 4.6%, at least within the time frame considered in this thesis. Moreover, these results are relevant to understand the ecological effects of charcoal and the underlying mechanisms for a range of situations, given the variety of plant, soil and charcoal types investigated. Finally, this work points to areas that would benefit from further research, including explicit quantification of the effects of fire-derived charcoal on the total ecosystem C balance, the importance of charcoal effects compared with those of other ecosystem drivers, the incorporation of the effects of charcoal into ecosystem (and C-cycling) models, and the ecological consequences of application of biochar in managed boreal forests. Long live charcoal research!

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