Soil fertility and charcoal as determinants of growth and allocation of secondary plant metabolites in seedlings of European beech and Norway spruce

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ABSTRACT

Climate-change is predicted to drive a migration of European beech (Fagus sylvatica) into the boreal Norway spruce (Picea abies) zone. Still, the mechanisms underpinning beech success on novel soils is little understood. Further, projected increasing summer temperatures will increase risk of fire and subsequent charcoal deposition. Here we investigate how soil type and presence of charcoal affect growth and key plant traits of beech and spruce seedlings.

Beech and spruce seedlings were grown in pots with forest soils of beech- or spruce origin to which beech- or spruce derived charcoal was added. Concentrations of phenolic compounds, carbon (C) and nitrogen (N) were analysed separately for root, stem, and leaf tissues.

Our spruce forest soil contained more N than the beech forest soil, and both beech- and spruce seedlings grew bigger in spruce forest soil. Beech seedlings also had overall lower tissue concentrations of phenolic compounds when grown in spruce soil. For both species, shoots and roots displayed opposite phenolic responses. The addition of charcoal had no effect on growth, while effects on phenolic compounds were largely idiosyncratic.

Our results indicate that beech expansion is not limited by soil factors in the study area, nor is it facilitated by increased levels of charcoal.

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1. Introduction

European beech (Fagus sylvatica L., deciduous angiosperm) and Norway spruce (Picea abies (L) Karst., evergreen gymnosperm) are two late successional and shade-tolerant tree species that dominate the forests over large areas in Northern Europe. At present, their distributions are becoming increasingly sympatric as climate warming is causing the temperate vegetation zone to shift northwards into the boreal spruce forest (Hickler et al., 2012; Saltré et al., 2014). The distribution of species is driven by phenology (Chuine, 2010; Hänninen, 2016), which imply that both light (quantity and quality) and temperature come into play. Today, the temperate zone meets the boreal zone in South-central Norway where beech has its northern distribution limit. Beech spread substantially in Scandinavia from the Bronze Age (Bjune et al., 2013; Fries, 1965), and probably expanded further north than present during the early medieval period (Björkman, 1997). Lower temperatures, the rapid southward spread of spruce, as well as increasing human impact on the landscapes, pushed the beech back towards south and west (Fries, 1965). During the last half of the 20th century, beech stands in Norway was largely substituted by planted spruce after logging. At present, we observe that beech rapidly spreads into the spruce plantations, which may be due to both less intensive forest management and a warming climate. This may probably happen so fast because it is already adapted to the light climate in this region through its presence as small populations in the area for thousands of years (Bjune et al., 2009, 2013). Together, the projections and observations suggest that huge areas of Norwegian spruce dominated ecosystems will go through fundamental transformations due to the northwards expansion of beech.

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To the best of our knowledge, no earlier studies have investigated the role of soil fertility for the establishment of beech in spruce dominated forests. However, as soil fertility strongly influences species-specific tree growth rates and secondary metabolism, which in turn are decisive for interactions in the forest ecosystem, we foresee that soil fertility will play a key-role as a driver of the interactions between beech and spruce. We also foresee that plant defence mechanisms will be a vital part in these interactions as soil fertility influences the defence strength in tree seedlings (e.g. Keski-Saari and Julkunen-Tiitto, 2003; Randriamanana et al., 2014).

Trees produce large quantities of carbon-based secondary compounds (CBSC) with various functional roles such as herbivore deterrents (Bryant et al., 1983; Coley et al., 1985; Dübeler et al., 1997), antioxidants (Iason and Hester, 1993; Hagerman et al., 1998; Close and McArthur, 2002), pathogen protection (Tomova et al., 2005), UV-filtration (Lois, 1994), frost hardiness and drought resistance (Samanta et al., 2011), chemical- (Mandal et al., 2010), visual- or aromatic signals (Samanta et al., 2011), and allelopathic substances (Inderjit, 1996). Phenols are also known to affect decomposition rates (Kraus et al., 2003). Prevailing hypotheses on plant defence and resource allocation predict a negative correlation between the synthesis of CBSCs and plant growth rates due to a presumption that factors limiting primary metabolism can free photosynthates that can be used for the subordinate secondary metabolism (Loomis, 1932; Bryant et al., 1983; Herms and Mattson, 1992). These hypotheses have been tested in several studies, but they have generally focused on the chemical response in a single plant structure (Koricheva et al., 1998), often leaves, partly because foliar responses are important for understanding herbivore dynamics. However, to better understand the regulation of plant secondary metabolism in relation to soil fertility and plant growth rates it is necessary to investigate chemical responses in specific plant parts (e.g. in roots, stems, leaves, and needles) (see Keski-Saari and Julkunen-Tiitto, 2003).

Today, it is estimated that 10–15 million hectares of boreal forests burn annually (Stocks et al., 2002) and considerable amounts of fire-derived charcoal are found in temperate- and boreal forest soils (Zackrisson et al., 1996; Ohlson et al., 2009; Santín et al., 2016). The projected climate change will increase the input of charcoal to future forests through lengthened fire seasons in the boreal zone (Soja et al., 2007) and by the end of this century, it is projected that the area burned will increase by 74–118% (Flannigan et al., 2005; Flannigan et al., 2009). A rapidly growing body of research indicates that charcoal has the potential to increase soil fertility and plant productivity by impacting a broad range of soil biological processes (Lehmann et al., 2011; Biedermann and Harpole, 2013). Newly produced charcoal may serve as an input of nutrients (Pluchon et al., 2014) and can increase microbial activity, decomposition (Zackrisson et al., 1996; Wardle et al., 2008), and nitrification (DeLuca et al., 2006). Further, charcoal in soils has the ability to adsorb allelopathic compounds (Nilsson, 1994; Zackrisson et al., 1996; Wardle et al., 1998; Keech et al., 2005; but see Lau et al., 2008), to increase water storage capacity, cation exchange capacity, and pH, and to decrease soil bulk density (Laird et al., 2010). Several studies have also shown that the effects of charcoal on soils and plants are dependent on feedstock species due to their differing nutritional contents and porosity. For example, Gundale and DeLuca (2007) and Pluchon et al. (2014) showed that angiosperm-derived charcoal possessed higher levels of phosphorous than did gymnosperm-derived. Angiosperm-derived charcoal also has greater quantities of macropores than charcoal from gymnosperms, which enhance the ability to adsorb toxic phenols in the soil (Keech et al., 2005). Given the strong effects of charcoal on soil properties, it is likely that its presence may modify the differences between soils from spruce and beech forests. Increased charcoal amounts are, as described above, expected to increase soil fertility both directly and indirectly. This may result in higher plant growth rates, which again could lower secondary metabolism, as predicted by the plant defence hypotheses.

To test if the establishment of beech in spruce forests is promoted or constrained by the spruce forest soil type, we set up a reciprocal experiment in which beech and spruce seedlings were grown in either beech- or spruce-forest soils. By including the addition of beech or spruce derived charcoal in the experiment, we simultaneously tested if a future increase in fire frequency is likely to have fertilization effects on tree seedling growth in these forest soils, and if the charcoal effect on tree seedlings will differ among soil types and charcoal feedstock. More specifically, we tested the following two hypotheses: (1) The most nutrient rich soil type will result in the highest tree seedling growth rates and shoot:root ratios, the lowest whole-plant concentrations of phenolics (in line with the prevailing hypotheses on resource allocation), as well as the highest phenolic content in shoots versus roots (see Randriamanana et al., 2014); (2) Addition of charcoal produced from nutrient rich wood will have a stronger positive effect on seedling growth and result in lower investments into secondary metabolites than that of nutrient poor wood, and the effects will be more pronounced in the soil with the greatest nutrient limitations.

2. Materials and methods

2.1. Sampling and preparations

Seeds of European beech (*Fagus sylvatica*) marketed for use in Götaland, S-Sweden were purchased from Svenska Skogsplantor AB (Albjershus, Sweden, about 57°N 18°E), and Norway spruce (*Picea abies*) seeds of provenance CØ1 (SE-Norway, 0–100 m a.s.l., about 59°N 10°E) were provided by The Norwegian Forest Seed Center (Hamar, Norway). On 4 April 2014 soil was sampled in a beech- (59°13′N 10°21′E; 41 m a.s.l.) and spruce forest (59°13′N 10°19′E; 74 m a.s.l.) 1.9 km apart in an area around Melsomvik, Vestfold, S-Norway. Sampling included the entire depth of the organic horizon from smaller excavation inside an approximately 30 m^2 area. The soil from each forest type was bulked to form one composite sample. The two forests had the same underlying bedrock (larvikite) and subsoil (marine beach deposits). Both soils had supported their respective forest types in excess of two forestry cycles (>140 years). The beech forest supported a low herb vegetation and showed an abundance of *Anemone nemorosa* and earthworms at the time of sampling. The soil was a brown soil with no signs of podsolisation, and the humus was about 15 cm thick. The spruce forest was of the *Vaccinium* type and the forest floor was sparsely vegetated. The soil had clear podsolisation and the humus layer was variable and therefore sampled to avoid the most shallow areas, as well as areas of peat formation. The soil was stored in plastic bags in a cool room (~10 °C) for three days before being sieved through a 1 cm mesh and homogenised by hand, and then stored in plastic containers until they were added to pots.

Fresh spruce and beech branches were sampled from a small number of individuals growing in Ås, S-Norway (59°39′N 10°47′E; 94–126 m a.s.l). The bark was stripped off and the wood dried for 48 h at 70 °C. Maximum diameter of the wood was 2 cm, and larger branches were split lengthwise. Charcoal was prepared in a muffle furnace (B170; Nabertherm GmbH, Lilienthal/Bremen, Germany). Sticks of wood *c.* 15 cm long were covered in sand and placed in a steel box with a lid and the box inserted into the muffle furnace which then gradually heated up to 450 °C within 40 min, and was left there for 30 min after which the oven was turned off and the wood was allowed to cool inside the oven. The maximum temperature is the same as used by Pluchon et al. (2014) and