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Increased air humidity and understory composition shape short root traits and the colonizing ectomycorrhizal fungal community in silver birch stands

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ABSTRACT

Climate change is predicted to bring about a rise in precipitation and air humidity at northern latitudes, which could have considerable impact on forest management. This paper investigates the effect of increased air humidity and understory composition on short root morphology and on the relative abundance of colonizing ectomycorrhizal (EcM) fungal associates in silver birch (*Betula pendula* Roth.) stands.

Short root morphological traits of silver birch were analyzed at increased humidity and ambient conditions for two different understories (early-successional grasses and diverse "forest" understory) in three consecutive years (2009–2011). The fungal community was determined in 2010 (after three seasons of misting) using molecular methods. The study was conducted on the Free Air Humidity Manipulation (FAHM) experimental facility established in Estonia.

Silver birches responded to the rise in air humidity by forming longer and thinner short roots, which can be interpreted as a morphological adaptation leading to an increase in the absorptive area. The response was stronger when humidification concurred with the species-poor understory of pioneer grasses. The inter- and intra-treatment variation in short root morphological parameters decreased by the third year. Using molecular methods, overall 64 EcM taxonomic units were distinguished. Hydrophilic fungal morphotypes dominated significantly in humidified plots, hydrophobic morphotypes in control plots.

Our results suggest that rising air humidity causes a morphological stress response in EcM short roots. Young trees show the ability to adapt to climate change with great plasticity by modifying short root length, diameter and specific root length (SRL). Humidification leads to a shift in the fungal colonizers towards the dominance of hydrophilic taxa, which may alter ecosystem functioning.

1. Introduction

Climate change scenarios for the year 2100 predict an increase in air temperature (by 2.3–4.5 °C) and precipitation (by 5–30%) in Northern Europe including the Baltic region (IPCC, 2007; Kont et al., 2003). Because the increase in precipitation is generally manifested through increased cloud cover and frequency of wet days, air humidity will rise too . A unique Free Air Humidity Manipulation (FAHM) facility was established in Estonia to investigate the effect of increased air humidity on the forest ecosystem (Kupper et al., 2011). The silver birch (*Betula pendula* Roth.) was chosen as the object of investigation in the FAHM experiment, as it is commercially the most important broadleaved species in Northern Europe, an excellent pioneer and improver of soil fertility on abandoned agricultural and mining areas or otherwise unproductive sites (Rosenvald et al., 2011a).

It has been shown that air humidification, both directly and through a decline in leaf temperature, decreases the humidity gradient between leaf and air, which reduces the average diurnal stem sap flux density per unit of projected leaf area (Kupper et al., 2011). This impedes the mass flow of soluble minerals in the soil and nutrient uptake of roots (Cramer et al., 2009), potentially leading to decreased growth and productivity in fast-growing tree species.

Abbreviations: D, short root diameter (mm); SRA, specific root area ($m^2\ kg^{-1}$); RTD, root tissue density ($kg\ m^{-3}$); SRL, specific root length ($m\ g^{-1}$); *L*, short root length (mm); *M*, short root mass (mg); RTFL, root tip frequency per unit of length (no mm^{-1}); TF, throughfall precipitation (mm); SWP, soil water potential at the depth of 15 cm (kPa); ST, soil temperature at the depth of 15 cm (°C); AT, air temperature (°C); RH, relative air humidity (%); SOM, soil organic matter (%); SoilN, soil nitrogen concentration (%); ESG, early-successional grasses; F, diverse "forest" understory; H, humidification, misting; C, control.

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Indeed, lower leaf nitrogen (N) and phosphorus (P) contents have initially been witnessed in silver birches growing in conditions of elevated air humidity (Sellin et al., 2013). Decreased transpiration also causes a rise in soil humidity (Hansen et al., 2013), which directly influences the growth environment of plant roots and soil microbes.

The forestś response to climate change depends highly on the acclimation ability of plant fine root systems and their microbial and fungal partners in the rhizosphere. Short roots (the distal roots with primary structure) constitute the most active part of the fine roots and are responsible for water and nutrient uptake. In boreal forests, short roots are predominantly colonized by EcM fungi, which increase the absorbing surface up to 60 times (Simard et al., 2002). For example, over 95% of the short roots of silver birch may form ectomycorrhizae (Uri et al., 2007).

Plants react to changes in environmental conditions (a rise in atmospheric [CO_2] and temperature, nutrient limitation, shifts in soil moisture, etc.) through alterations in short root morphology, biomass, and turnover or stimulation of microorganisms adjacent to roots – shifts in the mycorhizosphere (Lõhmus et al., 2006a; Phillips and Fahey, 2006). For example, it has been shown that CO_2 enrichment and long-term warming induce an increase in high biomass fungi with proteolytic capacity and a decrease in fungi that utilize labile N (Deslippe et al., 2011; Godbold et al., 1997). These alterations can significantly influence the nutrient uptake and vitality of plants (Fransson et al., 2005; Gorissen and Kuyper, 2000), thus the productivity of ecosystems, their potential in sequestering carbon, and consequently atmospheric [CO_2] and global climatic conditions. While the effects of CO_2 enrichment on fine roots and the EcM fungal community have been well documented (Cudlin et al., 2007; Lukac et al., 2009; Simard and Austin, 2010), the effects of increased air humidity remain poorly understood.

Short roots can be characterized by morphological parameters such as specific root length (SRL), specific root area (SRA) and root tissue density (RTD). Presuming that nutrient acquisition is proportional to the length or surface area, and the cost of forming and maintaining roots is proportional to mass (Eissenstat and Yanai, 1997; Ostonen et al., 2007), SRA and SRL are characteristics of root economy and foraging efficiency (Lõhmus et al., 1989; Ostonen et al., 2007). SRA and SRL depend on the diameter, length and RTD of the root (Ostonen et al., 2007), which may react to changes in the environment in opposite ways and must be taken into consideration when analyzing the functional morphological parameters.

High SRL suggests fast growth and intensive soil exploration and is important for sufficient uptake of P (Silberbush and Barber, 1983). In stress conditions, trees have been shown to apply an intensive foraging strategy, i.e. increasing the absorptive surface per unit of mass (SRA, SRL and branching frequency) (Rosenvald et al., 2011a,b; Ryser, 2006), along with an extensive foraging strategy of increasing the biomass of the fine root system (Lõhmus et al., 2006b; Ostonen et al., 2011). Fast-growing species in productive habitats, where rapid acquisition of nutrients is essential to withstand competition, also exhibit high SRL and SRA (Kupper et al., 2012; Ostonen et al., 1999).

In forest ecosystems, understory vegetation has considerable effects on the carbon cycle (Borja et al., 2008), nutrient availability to trees (Picon-Cochard et al., 2006), and thus, stand regeneration through resource competition. Previous studies have shown that grass vegetation shows higher water and NO_3^- capture capacity than tree seedlings (Picon-Cochard et al., 2006) and has greatest effect on early-successional tree species through competition for both resources and soil space (Messier et al., 2009). Early-successional tree seedlings responded to the fine root competition of grasses with higher fine root biomass and SRL in unoccupied soil space, indicating a strategy of root avoidance when possible (Messier et al., 2009). Understory plants have also been shown to influence the rhizosphere through differences in soil microbial community and the particular plant-soil effect may depend on plant species, functional group (e.g. grasses vs. forbs) and site-specific soil properties (Bezemer et al., 2006). So far, little is known about the possible morphological reaction of tree short roots to the varying growing conditions induced by different understory types.

Besides the above-mentioned environmental factors, morphological parameters of EcM short roots are highly dependent on the age of the plant and the colonizing fungi (Ostonen et al., 2009; Rosenvald et al., 2013; Ryser, 2006). Younger trees have higher SRL and SRA, due to lower root diameter, mass and RTD (Rosenvald et al., 2011a, 2013). The identity of the fungal colonizer is the main factor determining EcM short root diameter, length and mass. Thereby, it also significantly influences SRA and SRL (Makita et al., 2012; Ostonen et al., 2009; Sun et al., 2010). EcM fungal taxa with contrasting foraging strategies also differ in their capacities of enzymatic activities, nutrient uptake and translocation (Courty et al., 2010; Lilleskov et al., 2002, 2011; Tedersoo et al., 2012). Therefore, EcM partners have major impact on tree nutrition both directly and through changes in morphological traits.

The different ecological strategies of EcM fungi have been associated with exploration type and hydrophobicity (Lilleskov et al., 2011; Unestam and Sun, 1995). Hydrophilic morphotypes (prevalently concurring with contact-, short-distance and medium-distance smooth exploration types) have lower proteolytic capabilities and depend on the availability of labile nitrogen forms, thus representing the exploiting ruderal strategy (Hobbie and Agerer, 2010; Lilleskov et al., 2011; Tedersoo et al., 2012). These morphotypes prosper in humid environments and have been shown to tolerate waterlogging and oxygen deficiency better (Bakker et al., 2006; Stenström, 1991). Because of lower investment in proteolytic enzymes and extramatrical mycelium, these morphotypes are assumed to be less costly to the host in terms of carbon expenditure.

On the other hand, high extramatrical biomass and rhizomorph forming hydrophobic morphotypes characterize environments, where labile N is scarce and insoluble organic N-sources are widely dispersed and spatially concentrated. Hydrophobic rhizomorphs facilitate effective long-distance water transport, prevent leakage of solutes and represent stress tolerant species in cases of drought and consequent nutrient limitation (Hobbie and Agerer, 2010). In such conditions, the costly formation of high extramatrical biomass and exudation of extracellular enzymes, capable of decomposing complex organic substrates, is advantageous. Producing extensive hydrophobic hyphal mats may also drive out other microorganisms and thus render a competitive quality (Unestam and Sun, 1995). Undoubtedly the effectiveness of a morphotype, whether low biomass forming and hydrophilic or high extramatrical biomass forming and hydrophobic, depends on the specific conditions and limiting resources.

Our objective was to investigate the interactive effects of increased air humidity and understory composition on the morphology and colonizing fungal community of EcM short roots of silver birch. In order to comprehend the dynamics in root morphology, samples were taken before the treatment commenced and in three consecutive years starting after two seasons of misting. The colonizing EcM fungal community was identified after three years of humidification. This paper aims to contribute to understanding how much silver birches rely on the intensive strategy of modifying short root morphology as an alternative to the extensive strategy of expanding their root systems in response to environmental stress. On the basis of morphological plasticity we aim to assess short root acclimation ability of the silver birch in relation to the increase in air humidity, predicted to co-occur with climate change at higher latitudes. Knowledge about the effect of