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The effect of elevated air humidity on young silver birch and hybrid aspen biomass allocation and accumulation – Acclimation mechanisms and capacity

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ABSTRACT

Climate change is predicted to bring about a rise in precipitation and atmospheric humidity at northern latitudes, which could have a considerable impact on forest ecology and management. This study investigates the effect of elevated relative air humidity (RH) on tree growth and biomass accumulation and allocation in six-year-old seedling-originated silver birch (*Betula pendula* Roth) and monoclonal hybrid aspen (*Populus tremula* L.×*P. tremuloides* Michx.) stands. The study was conducted in the unique Free Air Humidity Manipulation experimental facility in Estonia. Two understory vegetation types (forest and pasture) were used in the experimental plots. As a short-term response during the first manipulation years, a small rise (6–7%) in RH reduced the growth of both tree species. In the fifth humidification year, suppression of growth continued in aspen, but birch acclimated effectively to elevated RH – differences in biomass and stem diameter increments levelled out in humidified (H) and control (C) plots. The H birches ensured biomass accumulation by changing the biomass and morphology of the physiologically most active tree parts: increasing fine-root biomass, as well as specific areas of fine roots (SRA) and leaves (SLA). The effect of elevated RH on most leaf and fine root characteristics of aspens was in a similar direction as that of birches, but weaker, and the plasticity of the functional traits was also lower compared to birches, probably due to the lack of genetic variation in monoclonal aspens. The biomass of young aspens was 22% lower in H plots. The relative aboveground biomass allocation was not affected by elevated RH. The aboveground biomass of humidified birches was higher in plots with forest understory, where root competition was lower compared to the dense root systems of grasses in pasture understory plots. Aspen biomass was not affected by understory vegetation type. We conclude that young silver birches have sufficient phenotypic plasticity to acclimate to elevated RH and the forests retain biomass accumulation. However, the growth acclimation of planted forests of clonal plant material is more complicated and humidity-tolerance should be considered in the selection of new clones for areas where an increase in RH is anticipated.

1. Introduction

The higher rainfall and relative air humidity (RH) as well as the rise in temperature, as predicted for climate of Northern Europe (IPCC, 2007), may change biomass formation and partitioning of tree species and, hence, shape forest management practices in the region in the nearest future. Many studies about irrigation/drought and warming effects on tree biomass have been carried out (reviews of Poorter et al., 2012 and Way and Oren, 2010), but field manipulation experiments studying the effect of RH were absent until recent studies (Kupper et al., 2011; Sellin et al., 2013; Tullus et al., 2012a). The influence of RH on tree growth is globally important because carbon sequestration in tree biomass and soil may be affected correspondingly. Estimations show that about half of total forest carbon storage is sequestered in boreal forests (Dixon et al., 1994). Forests have a considerable capacity for carbon storage in the short- or mid-term in live biomass, detritus, and soil organic matter (Fahey et al., 2010; Uri et al., 2012). Tree biomass allocation pattern is one factor affecting the sequestrated carbon storage time, which is obviously longer in perennial tree parts like stems and stumps (especially in stems used for

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timber). However, short-living fine roots play a key role in forest ecosystem carbon accumulation and supply soils throughout the rooting depth with significant amounts of carbon – soil C is more of root than shoot origin (Finér et al., 2007; Rasse et al., 2005).

Plants invest more biomass into aboveground or belowground parts, depending on in which part the most limiting resource is located (Brouwer, 1963; Poorter et al., 2012; Shipley and Meziane, 2002). Hence, the biomass allocation pattern reflects the carbon capture and root nutrition capacity of trees and reflects the implementation of fine-root foraging strategies (Lõhmus et al., 2006; Ostonen et al., 2011). Nevertheless, the influence of increased atmospheric humidity on biomass partitioning and accumulation in different tree species is still poorly studied. Generally, high RH enhances stomatal opening of tree leaves, which allows higher diffusion of CO_2 to the leaf interior enhancing photosynthesis (Fordham et al., 2001). On the other hand, humid air decreases water fluxes through the canopy, as well as steady state transpiration of trees (Burgess and Dawson, 2004; Kupper et al., 2011; Reinhardt and Smith, 2008), which may lead to diminished nutrient supply to foliage and diminished photosynthetic capacity (Sellin et al., 2013). Knowledge of aboveground and belowground biomass allocation patterns, as well as nutrient status of leaves and fine roots is essential for understanding tree acclimation to elevated RH conditions in a forest ecosystem.

A unique free air humidity manipulation facility (FAHM) and experimental forest ecosystems were established for determining how the increase in RH – a formely unexplored factor of climate change – influences forest ecosystems. Since temperature increase is probably more favourable for deciduous pioneer trees, the overall ecological and economic importance of those species will increase at higher latitudes as a result of global warming (Kellomäki et al., 2008; Prentice, 1993). To assess the humidification effect on two fast-growing deciduous tree species, silver birch seedlings (*Betula pendula* Roth) and micropropagated clonal hybrid aspens (*Populus tremula* L.×*P. tremuloides* Michx.) were planted at the FAHM site on former agricultural land. Silver birch is the economically most significant deciduous species in the boreal zone (Hynynen et al., 2010) and it grows on mineral soils in Europe as well as in Asia and can have high production rates in fertile sites (Elowson, 1996; Ferm, 1993; Uri et al., 2007a,b). Hybrid aspen is grown to produce raw material for high-quality paper production as well as for bioenergy and has been proven to be a suitable species for short-rotation plantation in Northern Europe, owing to its very fast growth rate at a young age (Rytter, 2006; Tullus et al., 2012b; Weih, 2004).

The study aims (1) to reveal possible changes in biomass allocation in the above- and belowground parts of stands of silver birch and hybrid aspen as a response to more humid climate conditions and (2) to find out growth acclimation capacity and strategies of the studied tree species to elevated RH, reflected in biomass accumulation and leaf and fine-root functional traits.

2. Material and methods

2.1. Study site and humidification treatment

The study area lies at Rõka village, Järvselja Experimental Forest District, in South-East Estonia (58°14′N, 27°18′E), representing the boreo-nemoral vegetation zone. The long-term average annual precipitation of the region is 650 mm and the average temperature is 17.0 °C in July and −6.7 °C in January. The growing season usually lasts 175–180 days from mid-April to October. The study site lies on a former agricultural field, where soil is a fertile Endogleyic Planosol (IUSS Working Group, 2007). The FAHM experimental facility is a 2.7 ha fenced area with six circular (diameter = 14 m) experimental plots: three humidity manipulated plots (H) and three control plots (C). Half of each experimental plot was planted with micropropagated hybrid aspen (clone C05-99-34 according to the Finnish Plant Production Inspection Centre) and the other half with silver birch seedlings. One-year-old trees were planted in monocultures in the experimental area in spring (bare-rooted birches) and autumn (potted aspens) in 2006. The stand density in the buffer zone around the experimental plots is 2500 hybrid aspen per ha. The adding of water vapour began on 1. June 2008 and took place if the ambient RH was < 75% and wind speed < 4 ms^{-1}. In three humidity manipulated plots, the average daytime relative humidity of the air was raised 6–7% points during mist fumigation in growing seasons. Monthly mean RH values in C and H plots in 2008–2011 are presented in Parts et al. (2013) and monthly total precipitation and mean air temperature at FAHM site during the growing seasons 2008–2012 are presented in Godbold et al. (2014) and Kupper et al. (2011). A detailed description of the FAHM facility and technology is provided in our previous papers (Kupper et al., 2011; Tullus et al., 2012a).

Mean thickness of the surface horizon (Ap-horizon) is 27 cm and the subsoil consists of sandy loam. As soil is well-drained and automorphic, water availability for plants depends primarily on precipitation and soil water holding capacity, ranging from 150 to 160 mm in a 75 cm soil layer in Planosols (Tullus et al., 2010). The soil water potential was significantly higher in H plots compared to C plots during the summers 2009–2012, probably due to decreased transpiration (Hansen et al., 2013; unpublished data). Humidification increased soil pH under both species (Table 1). However, soil nitrogen content was significantly higher for birch compared to aspen plots (pairwise *t*-test, $p < 0.05$). Soil chemical properties did not differ between C and H plots before the beginning of the manipulation (pH_{KCl} was 4.51 ± 0.05, N% 0.121 ± 0.003, and OM% 2.98 ± 0.12).

Since ecosystem response to climate change may depend on plant community composition (Bengtsson et al., 2000), two different types of ground vegetation were established in the plots, representing either the vegetation of a recent clearcut or the early-successional vegetation of an abandoned arable field, with low diversity and the strong dominance of a few grass species (Kupper et al., 2011; Parts et al., 2013). As stand age was one year older for birch than aspen, the harvesting was carried out in 2011 and 2012, respectively, to compare biomass allocation of even-aged (7-yr-old) trees.

2.2. Aboveground biomass

The aboveground biomass allocation of 7-yr-old trees was estimated six years after stand establishment in August, when the process of biomass formation was largely completed. To evaluate biomass allocation, the method of model trees (Bormann and Gordon, 1984; Uri et al., 2007a,b) was used. Model trees were selected using a random procedure based on diameter distribution. A total of 24 model trees were felled for both species: 12 from humidification (H) and 12 from control (C) plots, four trees per plot. The stems of the model trees were divided into four sections: the living crown was divided into three equal layers and the fourth section consisted of the stem up to the living crown. The fresh mass of each section was determined. In the sections, the living branches were divided into the following fractions: the leaves, the current-year shoots, and the older branches. From every fraction, a subsample was taken for estimation of dry matter content as well as for chemical analysis. The samples were dried at 70 °C until constant weight and weighed to 0.01 g. The share of the wood and the bark of the stem were determined using cross section discs cut from the middle of each stem section. The stem (bark + wood) density was calculated as the weighted average of stem disc