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Response of bryophytes to afforestation, increase of air humidity, and enrichment of soil diaspore bank

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ABSTRACT

The abandonment of agricultural areas is usually accompanied by the stochastic encroachment of shrubs and trees or deliberate afforestation, but this leads as a rule to the decline of grassland plant diversity. Future climate change may increase precipitation and air humidity in temperate and boreal forest zones, and thus change vegetation dynamics.

We conducted a five-year experiment on the Free Air Humidity Manipulation experimental facility (FAHM) with planted deciduous trees to examine how both the grassland afforestation with deciduous trees and the increase of air humidity in interaction with forest soil supplementation and cover of herbaceous layer affect the species richness, composition and cover of bryophyte layer. The effects of the same factors on the cover of herbaceous layer were also analysed. The species of bryophytes and cover of herbaceous and bryophyte layer were surveyed in September of 2007–2011.

During these early years of forest succession, herbaceous layer cover decreased and bryophyte cover increased, although the direct suppressing effect of tree canopy was observed on both layers. The input of forest soil as diaspore deposit of bryophytes had some positive effect on the cover of bryophytes, while the increased air humidity had quite limited effect. The density of tree canopy (defined in our study through Leaf Area Index) first promoted the species richness of bryophytes, particularly of species with grassland preference. However, together with the herbaceous layer it became suppressing in the last year.

The species richness of bryophytes declined during the first years and then stabilised. The decline relied mainly on the disappearance of grassland species. The richness of bryophytes was supported by forest soil supplementation only in the initial year.

The bryophyte species composition changed rapidly in first two years mainly due to decline of short-lived grassland species and perennial species started to dominate.

Our results show that bryophyte succession during the afforestation is largely driven by natural loss of grassland specialists after tree canopy closure, while diaspore supplementation from forest and improved air moisture level had small effects.

1. Introduction

The importance of bryophytes in ecosystems has been recognized increasingly in recent years. Bryophytes are among the earliest land plants and have a long evolution history (Laenen et al., 2014) that has enabled them to get efficiently adapted to different environments and plant communities. Bryophytes hold a key position in several ecosystems, which is especially conspicuous in temperate and arctic regions. For instance, they prevail in many tundra and forest communities and inhibit soil temperature and moisture fluctuations, thereby regulate vascular plant growth (Soudzilovskaia et al., 2011; 2013). They also constitute the main carbon stores in peatlands throughout the world (Rydin and Jeglum, 2013), and serve as nitrogen fixing mediators in boreal forests (Bay et al., 2013; Lindo et al., 2013). Bryophytes can also direct the herbaceous layer succession (Zobel et al., 2000; Otsus and Zobel, 2004; Aude and Ejrnaes, 2005).

The accelerating rate of climate change is influencing plant communities. Numerous scenarios for climate change in Northern Europe suggest an increase in precipitation (Räisänen et al., 2004; Christensen and Christensen, 2007) which usually leads to rise in air humidity.

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Climate change analysis (Jaagus, 2006) shows that precipitation has already risen in winter and spring months in Estonia during the second half of the 20th century.

Bryophyte species can emerge and get extinct in communities due to changes in environmental conditions (Fenton et al., 2003). Lack of roots and efficient water conducting tissues makes bryophytes sensitive to changes in air humidity, and therefore, changes in the compositions and functional properties of bryophyte assemblages can be early indicators of plant community response to climatic change (Gignac, 2011). The sensitivity of bryophyte community has been shown also by a long-term study in French forests, where the rise in temperature together with nitrogen deposition shifted the bryophyte composition much more than that of vascular plants (Scarpitta et al., 2017). On Norwegian alpine meadows (Vanneste et al., 2018) temperature rise caused increase in bryophyte richness during 15 years while richness of vascular plants remained stable.

Both vascular plants and bryophytes form rather persistent soil diaspore bank. The forest soil diaspore bank is important to maintain species composition of particular community and to regenerate after disturbance (Rydgren and Hestmark, 1997; Ross-Davis and Frego, 2004; Caners et al., 2009; Plue et al., 2017). Formation of diaspore bank is influenced by species-specific as well as environmental factors (During, 1997). The dispersal capacity (appearing as spore rain) of bryophytes exceeds that of vascular plants since bryophytes can produce small spores in large quantities that can be carried in great distances by wind, but also by migrating birds (Lewis et al., 2014). However, trees inhibit spread of diaspores of forest species. But plants can also emerge from diaspore banks. Although the diaspore banks include more diaspores of pioneer and colonist species, also several long-lived forest species are found to be present (Jonsson, 1993; Caners et al., 2009). It is generally recognized that disturbance can enhance species richness by preventing natural communities from reaching an equilibrium (Sousa, 1984; Petraitis et al., 1989). Revegetation of disturbance gaps may occur by germination of buried spores or other propagules, dispersal of propagules into the disturbed areas, or clonal spread (During et al., 1987; Rydgren et al., 1998; Heinken and Zippel, 2004). The first colonizers after disturbance are typically colonists, but over a longer period the colonists will be overgrown by more competitive perennials (During et al., 1987; van Tooren and During, 1988; Jonsson, 1993; Jonsson and Esseen, 1998; Heinken and Zippel, 2004).

Afforestation is favoured by the policy of landscape greening and habitat restoration on set-aside areas (Buscardo et al., 2008; Jõgiste et al., 2016) and by the increase in precipitation in some regions (Yang et al., 2006). Afforestation changes the vegetation composition and has usually detrimental effect on plant diversity of grassland communities, reflected by the decline in species richness and their cover (Bråkenhielm, 1977; Bonet and Pausas, 2004), although these changes may take a long time (Tullus, T. et al., 2012; Jagodziński et al., 2018). It has been shown, that the main factors affecting bryophyte species composition during afforestation are light conditions and the vicinity to mature forest area (Randlane et al., 2017; Jagodziński et al., 2018). On the other hand, greater precipitation favours bryophytes (Möls et al., 2013; Sun et al., 2013). Earlier studies have concentrated on either climatic (Frahm and Klaus, 2001; Ingerpuu and Kupper, 2007; Alatalo et al., 2014), tree canopy (Vellak et al., 2003; Bartels and Chen, 2013; Oakes et al., 2014) or herbaceous layer cover effects on bryophytes (Aude and Ejrnaes, 2005; Ingerpuu et al., 2005), but we are not aware of studies that include all aspects concurrently and experimentally.

The aim of our study is to examine how the cover of bryophyte layer, bryophyte species richness and composition is related to (i) concurrent afforestation by deciduous tree species and the experimental increase of air humidity in interaction with herbaceous layer succession, and (ii) supplementation of soil diaspore bank. We hypothesize that greater humidity and experimental enrichment with propagules via forest soil will promote bryophyte growth during the forest formation.

2. Material and methods

We conducted our study at Järvselja Experimental Forest District in South-East Estonia (58°14′N; 27°18′E) between 2007 and 2011. We used the Free Air Humidity Manipulation experimental facility (FAHM), which was built to study the effects of changes in air humidity on young forest ecosystem (Kupper et al., 2011; Tullus, A. et al., 2012). The FAHM site is a 2.7 ha fenced area in an abandoned agricultural land. The soil is classified as Endogleyic Planosol (Hansen et al., 2013). The area contains nine permanent 14 × 14 m experimental plots arranged in two rows and surrounded by a buffer zone, six of these were included in our study (see also Fig. 2 in Tullus, A. et al., 2012). The distance between plots was at least 30 m. The build-up of the experimental area started in autumn 2005 when the vegetation was removed with herbicide, and after that, the area was ploughed. In each plot, vegetation combinations of tree and herbaceous layer in a factorial design were planted, forming four combinations as quarters (Supplementary material: Fig. 1). In 2006 the plots were planted with one-year old trees with 1 × 1 m spacing. One half of each experimental plot was planted with silver birch (*Betula pendula* Roth) and the other half with hybrid aspen (*Populus tremula* × *tremuloides*). The herbaceous layer was also manipulated equally under aspen and birch trees (cross-positioning of treatments). *Phleum pratense* L. was sown in two quarters of the experimental plot in spring 2006. In the other two quarters, 50 × 50 cm patches of forest vascular plants with soil of 20 cm depth (without bryophytes), collected from the nearby moist boreo-nemoral mixed forest, were planted.

In three experimental plots, air humidity was increased artificially in daylight hours during the vegetation period (May-October) using a misting technique and FACE-like technology to mix humidified air inside the plots (for more detailed technical description see Kupper et al., 2011; Tullus, A. et al., 2012). Three other experimental plots stayed without air humidity treatment. The humidity was manipulated since May 2008. Humidification treatment was activated when the ambient relative humidity was < 75%, air temperature was > 10 °C and wind speed was < 4 m/s. The humidification treatment raised relative humidity inside the plot by approximately 7% over ambient level.

During the experiment, the first four (2007–2010) growing seasons (from May to October) had average precipitation (355–465 mm/season) and average temperature (12.4–13.7 °C). However, the most recent year (2011) was characterised by lower average precipitation and higher temperature (199 mm; 14.2 °C) (Tullus, A. et al., 2012; Sellin et al., 2017).

In each growing season, tree leaf litter was collected using 0.21 m^2 litter traps (38 × 54 cm). In each experimental plot, one trap was installed in each quarter (Supplementary material: Fig. 1). After drying to constant weight at 70 °C, the litter dry weight (g m^{-2}) was registered. The obtained weight estimate was multiplied by the specific leaf area of tree species (m^2 g^{-1}) to determine leaf area index (LAI, m^2 m^{-2}) for each quarter of the experimental plot, indicating the tree cover density. During 2007–2011, LAI of aspen increased from 0.07 in 2007, to 1.7 in 2011, and LAI of birch from 0.8 to 4.7. As the result of faster growth of birches than aspens, tree species created a long gradient of crown cover conditions within and between years. Because of collinearity between LAI and tree species identity, in analyses the categorical factor 'Tree species' cannot be used in parallel to the continuous variable 'LAI' as both tend to reflect the same gradient of canopy closure. Therefore, in analyses we use only LAI since it is more universal indicator of forest growth, and also the direct driver of herbaceous and bryophyte layer. Tree species effect on herbaceous layer has been shown to appear only after many years of the succession and even then mainly as contrast between deciduous and evergreen conifers (Rūsiņa et al., 2011).

Bryophyte sampling started in 2007, was repeated in 2009, 2010, and finally in 2011. All fieldworks were carried out in mid-September. The 1 × 1 m size squares were set as the groups of four into each quarter of the six experimental plots, totalling in 96 permanent squares.