Bryophyte Vegetation in Young Deciduous Forest Plantations

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Abstract

We studied species richness, composition and coverage of the bryophyte layer in young deciduous forest plantations on abandoned agricultural lands in relation to overstory tree species (hybrid aspen or silver birch), land use history (crop field or grassland), site preparation method (whole-area ploughing or strip tillage), and soil properties (moisture, pH, concentrations of N, P and K). The aim of these plantations is to produce pulpwood and energy-wood under the principles of short-rotation forestry. The area under forest plantations is increasing in the region; however their impact on biodiversity is still scantily studied. Previous studies on understory vegetation have focused more often on vascular plants and less frequently on bryophytes. For this experiment, a total of 248 vegetation plots (2 m × 2 m) were established within 62 long-term experimental plots (size 0.1 ha). Thirty eight bryophyte species were found in total, with an average of 1.86 ± 0.11 species per vegetation plot and 4.02 ± 0.26 per experimental plot. The mean coverage of the bryophyte layer was 11.54 ± 2.14%. As expected, typical bryophytes were light-demanding perennials. According to substrate preference the majority of species were either epigeic or generalist. Positive correlation was observed between soil pH and coverage of the bryophyte layer. The impact of land use history and site preparation method on species composition was still evident, since the number of short-living bryophytes was higher in former fields and whole-area ploughed sites. Bryophyte species richness was not affected by overstory tree species in young plantations. Obviously during the further management of plantations the emergence of new substrata e.g. stem bark of bigger trees, leaning stems, branch litter and cutting residues should add diversity to the bryophyte vegetation.

Key words: abandoned agricultural lands, bryophytes, floristic diversity, hybrid aspen, plantation forestry, silver birch

Introduction

The establishment of forest plantations is considered to be an alternative land-use for abandoned agricultural areas in Central and Northern Europe (Makeschin 1999, Weih 2004, Tullus et al. 2012). In commercial forest plantations the production of timber and bioenergy is of primary concern, nevertheless the implications for biodiversity (including floristic diversity) can not be neglected (Carnus et al. 2006, Stephens and Wagner 2007, Brockerhoff et al. 2008, Baum et al. 2009, Bremer and Farley 2010). Studies analysing the understory vegetation of forest plantations on former agricultural land have concentrated mainly on vascular plant species diversity (e.g. Heilmann et al. 1995, Weih et al. 2003). Bryophytes have received less attention; usually they have been analysed together with vascular plants (e.g. Gustafsson 1988 for deciduous plantations and Bråkenhielm 1977, Hill and Jones 1978, Newmaster et al. 2006, Buscardo et al. 2008 for coniferous plantations and French et al. 2008 for deciduous as well as coniferous plantations).

This means that more attention should be paid to bryophytes, since in northern forests bryophytes are dominating constituents of the forest floor vegetation (Newmaster et al. 2006). Moreover, earlier studies (e.g. Herben 1987, Ingerpuu et al. 1998, 2001, 2003, Hokkanen 2006) have indicated that bryophytes and vascular plants may respond differently to environmental factors.

As a rule, bryophyte species richness and diversity increase with the availability of substrata where bryophytes can occur, e.g. ground, bark of living trees, decaying wood and stones (Ingerpuu 2002, Pharo and Beattie 2002, Zechmeister et al. 2003). Most of these structures, except the ground, are represented in very small quantities or are absent on abandoned agricultural lands where forest plantations have recently been established and where big stones have been removed from the topsoil during previous land use. The bryophyte layer is also affected by soil moisture conditions (Proctor 2008). Although bryophytes receive nutrients mainly from precipitation (including leachates from tree canopies and plant leaves), the nutritional properties and pH of the substratum can also be important (Bates 2008). In a study conducted in Pyrenean *Pinus sylvestris* forests, Pausas (1994) found that moss species richness was the highest at intermediate moisture levels and was positively related to soil pH. Correspondence between high soil pH and bryophyte species richness has been observed in several studies in boreal areas (Virtanen et al. 2000, Löbel et al. 2006).

Our previous study on vascular plants in young hybrid aspen plantations on former agricultural land in Estonia (Soo et al. 2009a) showed that soil-related variables (soil moisture properties, pH and nutrient stocks of the soil humus layer) significantly affected understory vegetation of vascular plants, and that species composition was related to previous land use and site preparation method. Short-living ruderals were typical species on former fields and in the case of the more intensive site preparation method (whole-area ploughed sites). At the same time, species richness of vascular plants was higher in plantations where the less intensive site preparation method (strip tillage) had been used. Although we provided a short overview of bryophyte species in this study, we did not analyse the bryophyte layer and its associations with environmental characteristics.

The species richness of vascular plants in the understory of young hybrid aspen and silver birch plantations on former agricultural land was similar (Soo et al 2009b). In the case of bryophytes, several studies have demonstrated the connection between bryophyte species richness and canopy species, which is explained mainly by the differences in throughfall and litter quality (Weibull 2001, Weibull and Rydin 2005). In terms of crown architecture, young hybrid aspen and silver birch trees have some differences. Birch has sympodial branching type (Hynynen et al. 2010) and a tendency to produce sylleptic shoots, resulting in a uniformly dense crown. Aspen has monopodial branching and strong apical control (Remphery and Pearn 2003), which means that leader shoots grow much faster and the emergence and growth of lateral shoots is suppressed. As a result, crowns of young aspen trees are sparser and their light transmittance is higher. Some differences have also been observed regarding litter decomposition rate and chemistry between *Betula* and *Populus* spp. (Moore et al. 2006, Parsons et al. 2008).

The aim of the current study was to describe the formation of the bryophyte layer in young deciduous forest plantations, to provide ecological characterization of bryophyte species common to such sites, and to investigate which environmental factors have influenced the bryophyte layer. Soil-related variables (moisture, pH and nutrient concentrations of the humus layer), previous land use, site preparation method and overstory characteristics (tree species and stand basal area) were included as possible factors explaining variation in bryophyte species richness and coverage.

The following hypotheses were formulated:

i) Among typical bryophytes in the understory of young unclosed forest plantations the proportion of light-demanding open community species is high and the proportion of shade-tolerant forest species is low;

ii) The proportion of bryophytes that prefer deadwood and logs as substrata is low in young forest plantations;

iii) The number of short-living bryophyte species is higher in sites with more intensive cultivation history (former fields and in whole-area ploughed areas) than in sites with less intensive cultivation history (former grasslands and in strip tilled sites).

Material and methods

Study area

The study was carried out in 7- to 9-yr-old silver birch (*Betula pendula* Roth) and hybrid aspen (*Populus tremula* L. × *P. tremuloides* Michx) plantations that had been established in 1999 and 2000 on abandoned agricultural land in the continental part of Estonia, with an exception of one silver birch plantation situated on Hiiumaa island (Fig. 1). These stands are aimed at the production of pulp- and energy-wood. The predicted rotation period is 20-30 years for hybrid aspen and 30-40 years for silver birch; during the rotation period one to three thinnings are planned. In the studied young plantations no thinnings had yet been carried out. The mean annual temperature near the studied plantations during a decade before the study was 6.1 ± 0.86 °C; mean annual precipitation was 630 ± 30.5 mm and the mean precipitation during the growing season (April-October) was 409 ± 31.1 mm (Tullus et al. 2010).

Altogether 24 hybrid aspen and 11 silver birch plantations were included in the study (Fig. 1). One plantation refers here to one real estate property. In these plantations a network of 62 long-term experimental plots (each 0.1 ha) for studying and monitoring the growth dynamics of birch and aspen at various site conditions had previously been created (Jõgiste et al. 2003, Tullus et al. 2007). All silver birch plantations

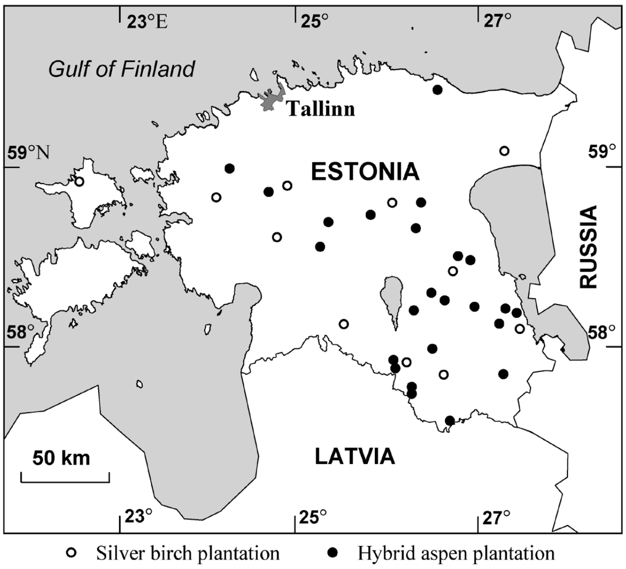

Figure 1. Locations of the studied plantations

were one ha in size and in each of them one experimental plot had been created. The size of hybrid aspen plantations varied from 0.7 to 32 ha. One experimental plot had been established in ten hybrid aspen plantations with uniform site properties. 14 larger hybrid aspen plantations consisted of smaller stands or parts with different soil type and land use history; in those plantations two to five experimental plots had been established. Each plot was located in homogeneous part (based on microrelief and soil type) of the respective plantation or part of the plantation.

Data collection

In total 248 permanent vegetation plots (each 2 × 2 m in size, 4 in each experimental plot) were established for the characterization of vascular plant and bryophyte species cover. Four vegetation plots were distributed systematically across each 0.1 ha experimental plot with two vegetation plots in both sides from the experimental plot centre. The results from vascular plant diversity analyses have been published elsewhere (Soo et al. 2009a, 2009b). As the part of the current study, the list of bryophyte species was compiled and species richness and total percentage cover of the bryophyte layer in each vegetation plot was estimated. Bryophytes were not found on the stems of young trees. Bryophytes not identified in the field were taken to the laboratory for further investigation under a microscope. In a few cases the specimen were juvenile and not fully developed and were identified on a genera level. The nomenclature follows the keybook of Estonian bryophytes (Ingerpuu and Vellak 1998).

The relations between bryophyte diversity and several site characteristics were studied. The plantations were grouped according to tree species, previous agricultural land use and site preparation method used before planting (Table 1). Stand basal area (BA, $m^2\ ha^{-1}$) was estimated in each 0.1 ha experimental plot as the cross-sectional area (over the bark) at breast height in order to characterize the impact of the tree layer (Table 2).

Species richness (S_{vasc}) and coverage (C_{vasc}) of the understory vascular plant layer, estimated in earlier studies (Soo et al. 2009a, 2009b), were used to investigate relations between vascular plant and bryophyte layers.

In order to determine pH_{KCl}, total N, available P and available K in the soil humus horizon (Table 2), soil samples were taken from the centre of each vegetation plot (n = 248). The total N in soil samples was determined by the Kjeldahl procedure. To analyse available P and K in the soil, Mehlich 3 extracant was

Table 1. The distribution of the studied deciduous forest plantations according to overstory tree species, previous agricultural land use and mechanical site preparation method

Planted tree species	Previous land use	Site preparation method	Experimental plots (size 0.1 ha)	Vegetation plots (2 x 2 m)
Hybrid aspen	Crop field	Whole-area ploughing	13	52
		Strip tillage	15	60
	Grassland	Whole-area ploughing	5	20
		Strip tillage	18	72
Silver birch	Crop field	Whole-area ploughing	6	24
	Grassland	Whole-area ploughing	5	20
		Total	62	248

Table 2. Stand characteristics and properties of the soil humus horizon (mean ± standard error, range in brackets) in the studied experimental plots (n = 62) and significance of the differences between two plantation types according to t-test

Variable	All plantations	Hybrid aspen plantations	Silver birch plantations	t-stat	p-value (two-tailed)
Stand density, trees ha^{-1}	1227 ± 62 (640–3070)	1043 ± 27 (640–1540)	2078 ± 164 (1340–3070)	-11.011	**< 0.001**
Stand basal area, $m^2\ ha^{-1}$	1.88 ± 0.23 (0.02–7.29)	1.40 ± 0.17 (0.02–5.33)	4.09 ± 0.73 (0.49–7.29)	-5.385	**< 0.001**
pH_{KCl}	5.7 ± 0.10 (4.0–7.3)	5.8 ± 0.11 (4.1–7.3)	5.6 ± 0.30 (4.0–7.3)	0.524	0.602
Total N, %	0.18 ± 0.02 (0.07–1.36)	0.18 ± 0.03 (0.07–1.36)	0.16 ± 0.02 (0.10–0.29)	0.366	0.716
Extractable P, mg kg^{-1}	84 ± 8.6 (8–403)	81 ± 7.7 (8–291)	100 ± 33.7 (19–403)	-0.843	0.403
Extractable K, mg kg^{-1}	133 ± 9.9 (29–495)	128 ± 10.5 (43–459)	155 ± 27 (29–331)	-1.072	0.288
Moisture[a]	1.6 ± 0.11 (0–3)	1.6 ± 0.11 (0–3)	1.5 ± 0.31 (0–3)	0.603	0.549

[a]soil moisture classes: 0 – excessively well-drained automorphic, 1 – automorphic, 2 – semi-hydromorphic, 3 – hydromorphic

used. The soil pH in 1M KCl suspensions was measured in the ratio 10 g : 25 ml. Analyses were performed by the Laboratory of Agrochemistry of the Agricultural Research Centre in Saku [/http://pmk.agri.ee]. The experimental areas were grouped according to soil moisture conditions, based on earlier studies (Vares et al. 2003, Tullus et al. 2007, 2010).

Data analysis

Light value index was assigned to bryophyte species according to Düll (1991). Based on the system of bryophyte life strategies (During 1992), the studied species were classified into the following categories: species with a life span of a few years (pioneer colonists, colonists, short-lived shuttle) and species with a life span of many years (competitive perennials, perennials, stress tolerant perennials, long-lived shuttle) according to Dierßen (2001). Habitat and substrate preference of bryophyte species was determined based on Ingerpuu et al. (1994) and Ulvinen et al. (2002). Arithmetic mean species richness (S_{bryo}) and coverage (C_{bryo}) of the bryophyte layer were estimated for all experimental plots on the basis of vegetation plot level measures of these variables. In addition, total species richness (ST_{bryo}) of the experimental plot, number of species with a life span of a few years (ST_{short}) and number of species with a life span of many years (ST_{long}) were estimated on the basis of all species found within 4 vegetation plots. Experimental plot-level measures of the analysed traits were used in further statistical processing of the data.

Pearson correlation coefficients were computed between experimental plot-level measures of bryophyte and habitat variables with STATISTICA 7 (StatSoft, Inc. 2004). The effect of tree layer species, land use history, and site preparation method on bryophyte traits was analysed with Student's *t*-test. Both one-tailed and two-tailed results are reported. One-way ANOVA was used to test the significance of differences in means of S_{bryo} , $ST_{bryo,}$ and C_{bryo} between soil moisture groups. Fisher LSD multiple comparison test was applied to determine the significant differences after one-way ANOVA. Normality of the analysed variables was checked with the Shapiro-Wilk's and Kolmogorov-Smirnov test; if necessary, log- or square root-transformation of the variables was used. The mean values are followed by ± standard error in the text. Level of significance $\alpha = 0.05$ was applied in all cases.

Results

Species composition

Altogether 38 bryophyte species (Appendix) and eight taxa identified on the genera level (*Bryum* spp, *Brachythecium* sp, *Riccia* sp, *Dicranella* sp) were found in 221 vegetation plots; in 27 vegetation plots the bryophyte layer was absent. 34 species and eight taxa were found in hybrid aspen plantations and 17 species in silver birch plantations. All observed bryophyte species were common; no rare species were found. The majority of the species were light-demanding species (the most frequent values of light index varied between 6 and 8) (Fig. 2).

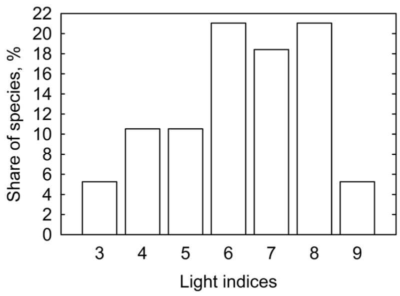

Figure 2. Distribution of bryophyte species according to light index

On the basis of typical habitats, 16 species were species that usually grow in forests, 17 species were species that in addition to forests also grow in grasslands and/or fields, and five species were typical open community species. On the basis of substrate preference the majority of the species were either epigeic or generalists, growing on a variety of different substrata, including usually the ground (Appendix). An epixylic species *Lophocolea heterophylla* can be singled out as an exception.

As hypothesized, ST_{short} was significantly higher in plantations established on former fields and in the case of whole-area ploughed sites (one-tailed *p*-values in Table 3). The species with a life span of a few years (e.g. colonists: *Bryum caespiticum* and *Ceratodon purpureus* and pioneer colonists: *Eurhynchium hians* and *Brachythecium salebrosum*), which appeared more frequently in former fields than in former grasslands were also more frequent in plantations where whole-area ploughing had been applied. ST_{long} did not differ between sites with different land use history and site preparation method.

Species richness and coverage and factors affecting them

S_{bryo} (vegetation plot mean bryophyte species richness) varied from 0 to 6 (arithmetic mean = 1.86 ± 0.11, the most frequent value = 2, Fig. 3a) and ST_{bryo} (total bryophyte species richness within experimental plot) from 0 to 8 per experimental plot (arithmetic mean = 4.02 ± 0.26, the most frequent value = 3). ST_{bryo} was generally two times higher than S_{bryo}, following the linear relationship: $ST_{bryo} = 0.39 + 1.95S_b$ ($r = 0.87$, $p < 0.001$). The experimental plot mean C_{bryo} (coverage of the bryophyte layer) was 11.54 ± 2.14% (range: 0-75%). On 75% of the vegetation plots with an existing bryophyte layer, C_{bryo} was below 10 % (Fig. 3b). On 12 % of the plots, C_{bryo} exceeded 30%.

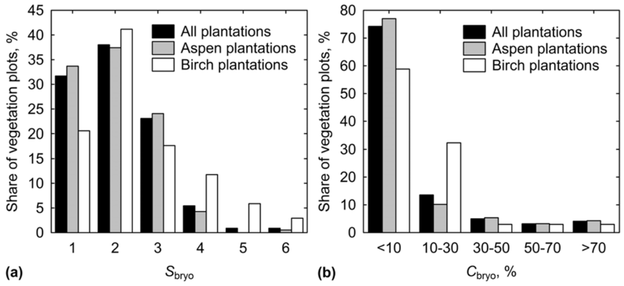

Figure 3. Distribution of vegetation plots with existing bryophyte layer according to a) species richness (S_{bryo}) and b) coverage (C_{bryo}) of the bryophyte layer

Based on two-tailed results of the t-test, there were no significant differences in S_{bryo} , ST_{bryo} and C_{bryo} between plantation groups according to overstory tree species, previous land use or site preparation method (Table 3). C_{bryo} was higher in excessively well-drained soils (Fig. 4). Excessively well-drained soils in the studied plantations were usually stony soils on calcareous parent material (*Leptosols* and *Calcaric Cambisols*) (Vares et al. 2003, Tullus et al. 2007, 2010). S_{bryo} and ST_{bryo} did not differ between soil moisture groups.

Pair-wise correlations between bryophyte and habitat variables indicated the significance of soil pH for C_{bryo}; both measures of bryophyte species richness were positively correlated with C_{bryo} (Table 4).

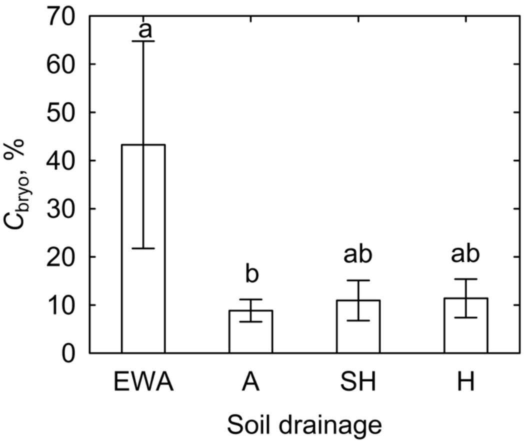

Figure 4. Comparison of C_{bryo} in different soil moisture groups, EWA – excessively well-drained automorphic soils, A – automorphic soils, SH – semi-hydromorphic soils, H – hydromorphic soils. Letters denote significant differences in group means of ln(C_{bryo}) according to Fisher LSD test, whiskers denote standard error

Table 3. Experimental plot mean and total species richness (S_{bryo} and ST_{bryo}), number of long-living (ST_{long}) and short-living (ST_{short}) species and coverage (C_{bryo}) of bryophytes in the studied plantation groups according to overstory tree species, previous land use and site preparation method

Tree layer species:	Hybrid aspen	Silver birch	*t*-stat	*p*-value one-tailed	*p*-value two-tailed
S_{bryo}	1.84 ± 0.11	1.93 ± 0.41	-0.294	0.385	0.769
ST_{bryo}	3.98 ± 0.26	4.18 ± 0.84	-0.298	0.384	0.767
ST_{long}	2.65 ± 0.23	3.09 ± 0.74	-0.774	0.233	0.466
ST_{short}	1.29 ± 0.18	1.09 ± 0.21	0.518	0.303	0.606
C_{bryo} (%)	11.71 ± 2.43	10.73 ± 4.56	0.174	0.431	0.862
Previous land use:	Crop field	Grassland	*t*-stat	*p*-value one-tailed	*p*-value two-tailed
S_{bryo}	2.05 ± 0.16	1.62 ± 0.16	1.898	**0.032**	0.063
ST_{bryo}	4.26 ± 0.34	3.71 ± 0.39	1.068	0.145	0.289
ST_{long}	2.71 ± 0.32	2.75 ± 0.35	-0.095	0.463	0.925
ST_{short}	1.53 ± 0.22	0.93 ± 0.18	2.061	**0.022**	**0.044**
C_{bryo} (%)	11.65 ± 2.64	11.40 ± 3.54	0.057	0.478	0.955
Site preparation method:	Whole-area ploughing	Strip tillage	*t*-stat	*p*-value one-tailed	*p*-value two-tailed
S_{bryo}	1.86 ± 0.19	1.86 ± 0.14	0.026	0.490	0.979
ST_{bryo}	3.97 ± 0.41	4.06 ± 0.32	-0.183	0.428	0.855
ST_{long}	2.41 ± 0.38	3.00 ± 0.28	-1.277	0.103	0.206
ST_{short}	1.55 ± 0.25	1.00 ± 0.16	1.887	**0.032**	0.064
C_{bryo} (%)	11.00 ± 2.76	12.00 ± 3.25	-0.233	0.409	0.817

Table 4. Simple correlations between experimental plot (n = 62) level measures of bryophyte-, vascular plant layer-, overstory- and soil characteristics

	S_{bryo}		ST_{bryo}		ln(C_{bryo})	
	r	*p*	*r*	*p*	*r*	*p*
S_{bryo}	1.00	-	**0.87**	**<0.001**	**0.65**	**<0.001**
ST_{bryo}	**0.87**	**<0.001**	1.00	-	**0.53**	**<0.001**
S_{vasc}	0.19	0.142	0.21	0.100	0.13	0.299
sqrt(C_{vasc})	0.03	0.817	0.08	0.539	0.08	0.545
ln(Tree density)	0.09	0.547	0.08	0.535	-0.01	0.984
sqrt(Plantation basal area)	-0.07	0.577	-0.12	0.339	-0.07	0.604
Soil pH	0.23	0.075	0.13	0.305	**0.33**	**0.008**
ln(Soil N)	-0.01	0.991	-0.01	0.965	0.12	0.347
ln(Soil P)	0.15	0.238	0.12	0.355	0.09	0.494
ln(Soil K)	0.18	0.168	0.13	0.303	0.23	0.076

Discussion and conclusions

In the studied plantations the formation of the bryophyte layer was still in the preliminary phase, with low percentage coverage and no bryophyte layer on

11% of the vegetation plots. One of the factors inhibiting the formation of the bryophyte layer was probably a thick litter layer (formed mainly by field layer species). Low cover values of the bryophyte layer were also observed in hybrid poplar plantations in NE Germany (Zerbe 2003).

As we hypothesized, the proportion of light-demanding species typical of open communities was high (the most frequent values of light indices 6-8, Fig. 2). In Estonian forests growing in *Aegopodium* and *Oxalis* forest site types, species associated with half-shade habitats dominated (value of light indices 4-5) (Vellak and Paal, 1999). We may predict the likely colonization of new shade-tolerant bryophyte species during the next 10-20 years preceding the planned clearcut. As the majority of the plantations are situated near mature forests, the availability of propagules of forest species should be good.

The average S_{bryo} and C_{bryo} did not differ between plantation groups according to former land use or site preparation method (Table 3). Thus the bryophyte vegetation of the studied young deciduous stands did not show similar response to site preparation as did vascular plant cover of young hybrid aspen plantations, where higher species richness was observed in less disturbed (strip tilled) sites (Soo et al. 2009a). Overstory tree species had no significant effect on the average S_{bryo} and C_{bryo}. However, the distribution of vegetation plots according to C_{bryo} indicated the slightly higher share of plots with C_{bryo} ranging from 10 to 30% in silver birch plantations, although C_{bryo} was below 10% in the majority of plots in both plantation types (Fig. 3b). This could be partly due to the almost two times higher number of trees ha^{-1} and consequently larger stand basal area (BA) in silver birch plantations (Table 2). At the same time there existed no significant relations between stand density or BA and S_{bryo} or C_{bryo} (Table 4). Nevertheless, a higher number of trees could provide more favourable conditions for the bryophyte layer by suppressing competition with the vascular plant layer. In young plantations such developments were in the preliminary phase and were thus difficult to validate with statistical methods.

Soil pH was positively correlated with C_{bryo}, being significantly higher in the soils that have developed on calcareous parent material. S_{bryo} showed a positive trend (p = 0.08) with pH. Soils with high pH level are represented in the northern and north-western parts of Estonia, where soils have developed on stony calcareous till on Ordovician and Silurian limestone. These soils are usually dry and had higher C_{bryo} compared to more humid sites (Fig. 4). Soil pH has been found to be a significant variable affecting the distribution of bryophytes on grassland also in other studies in the temperate zone (Virtanen et al. 2000, Löbel et al. 2006). The relation between bryophyte richness and soil pH in the mentioned studies was linear or curvilinear depending on the pH range. In our study, the soil pH range (4.0–7.3, Table 2) did not include extremely acid or alkaline soils. Calcareous soils have been less favourable for the fast growth of trees in the studied plantations due to their high stoniness and small water holding capacity (Tullus et al. 2010). Except the above-mentioned higher C_{bryo} in excessively well-drained soils, there were no other differences in bryophyte traits between soil moisture groups (Fig. 4). A possible explanation is that the moisture regime of wet soils had been improved with drainage during previous agricultural land use and thus the differences in actual moisture conditions between these groups could be smaller than expected from their hydromorphological classification.

The strong cover-richness relation (Table 4) has been observed also in previous studies with bryophytes (Økland 1994, Aude and Ejrnæs 2005). Bryophyte cover of abandoned agricultural lands may thus be used to predict bryophyte richness and site quality for bryophytes.

S_{bryo} was relatively low: on average two species per vegetation plot and four species per experimental plot (based on four vegetation plots). Bryophyte richness is associated with the diversity of available substrata (Ingerpuu 2002, Pharo and Beattie 2002). In our study the majority of the bryophyte species were generalists growing on a variety of substrata, or epigeics growing on soil (Appendix). Substrata such as the bark of large tree trunks, decaying wood and bare rocks were missing in young forest plantations on abandoned agricultural land. In a study conducted in Estonian broad-leaved forests, plot (size 1 m^2) mean S_{bryo} was six, whereas only 42% of all bryophyte species were found on the soil (Ingerpuu et al. 2003). The importance of deadwood and logs as substrata for enhancing bryophyte diversity is emphasized in several studies conducted in boreal forests (Gustafsson and Hallingbäck 1988, Ferris et al. 2000). During the management of plantations, the increasing diameter of tree stems and the emergence of stumps after harvest will offer new habitats for bryophytes. As small-dimensional timber is nowadays valued as energy wood (e.g. Di Fulvio et al. 2011), the share of felling residues left on site after thinnings and final harvests could be rather low. Leaving less-valuable residues on site or keeping some retention trees after harvest would probably be beneficial for bryophyte diversity in plantation forestry systems, providing habitats for epixylic and epiphytic species.

The impact of land use history and site preparation method was still visible in the species composition, as ST_{short} was higher in former fields and in whole area ploughed sites, as we had hypothesized based on the results from the study with vascular plants (Table 3). Further succession should result in a higher impact of the tree layer on the understory, which was insignificant in 7-9-year-old plantations. Further monitoring is needed to clarify whether differences in the bryophyte layer under different overstory tree species will occur. Differences in litter decomposition rate and quality between birch and aspen (Moore et al. 2006, Parsons et al. 2008) could be one factor causing changes in the understory vegetation layer. Probably in the studied young plantations the litter quantities were too small to have a detectable effect on bryophytes. We can expect an increase in richness and abundance of epiphytic bryophytes when plantations are older. According to the study performed in Finnish old-growth forests (Kuusinen 1996), the epiphyte flora on *Betula pendula* was rather poor while the epiphyte flora on *Populus tremula* was unique and characterized by the occurrence of rather specialized species. At the same time it is not known whether hybrid aspen can provide similar habitats for bryophytes as native aspen. The predicted felling age of hybrid aspen is less than 30 years (Tullus et al. 2012), whereas the high diversity of organisms living in association with aspens is observed in old trees.

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МОХОВОЙ ПОКРОВ В МОЛОДЫХ ЛИСТВЕННЫХ ПЛАНТАЦИЯХ

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Резюме

Изучалось видовое разнообразие, видовой состав и проективное покрытие мохового покрова в молодых плантациях лиственных пород из березы повислой (*Betula pendula* Roth) и тополя гибридного (*Populus tremula* L. × *P. tremuloides* Michx) на прежних сельскохозяйственных землях в связи с историей использования земли (бывшее поле или луг), методом подготовки земли (пахотная земля или насаждение в борозды) и с параметрами почвы (влажность, pH, содержание элементов N, P и K). Целью создания таких плантаций является потребность большого количества древесины для бумажной и энергетическтой промышленности за короткий промежуток времени. Площадь таких насаждений увеличивается во всем регионе, но их влияние на биологическое разнообразие до сих пор слабо изучено. Прежние исследования в основном были направлены на изучение видового состава сосудистых растений и в меньшей мере касались мхов. Изучен моховой ярус на 248 пробных площадках (2 м × 2 м), размещенных на 62 постоянных участках (площадью 0,1 га). На пробных площадках найдено 38 видов мхов, средное их число составило 1.86 ± 0.11 на отдельных площадках и 4.02 ± 0.26 на постоянных участках. Среднее проектное покрытие мохового яруса – 11.54 ± 2.14%. Типичными мхами являются многолетние светолюбивые виды. Большинство видов были эпифитные или генералисты, неимеющие предпочтения субстрата. Незначительная позитивная корреляция определена между реакцией почвы и проективным покрытием мохового яруса. Выявлено заметное влияние истории использования земли и ее подготовки на видовой состав мхов так как число кратковозрастых мхов оказалось выше на бывших полях и пахотных землях. Влияние древесного яруса на число мхов было незначительным. По всей вероятности, в течение дальнейшего ухода за плантациями возрастет количество различных субстратов для мхов, из-за чего увеличивается и разнообразие их видов.

Ключевые слова: прежние сельскохозяйственные земли, мхи, флористическое разнообразие, тополь гибридный, лесная плантация, береза повислая.

Appendix. The list of bryophyte species in the analysed vegetation plots, share of plots where the given species was present from all analysed vegetation plots, habitat and substrate preferences and life strategy categories (epigeic – species growing on the ground, generalist – species growing on various substrata, including usually the ground, epixylic – species growing on decaying wood, *c* – colonists, *cp* – pioneer colonists, *s* – short-lived shuttle, *p* – perennials, *pc* – competitive perennials, *ps* – stress tolerant perennials, *l* – long-lived shuttle)

Bryophyte species	Share of plots, %	Habitat	Substrate preference	Life strategy
Eurhynchium hians	39.9	forest, (grassland, field)	generalist	cp
Brachythecium rutabulum	18.1	forest	generalist	pc
B. salebrosum	16.5	forest	generalist	cp
Eurhynchium praelongum	14.1	forest, abandoned field	generalist	p
Plagomnium cuspidatum	10.5	forest	generalist	pc
Brachythecium albicans	10.1	forest, grassland	generalist	p
B. rivulare	7.7	forest	generalist	pc
B. velutinum	7.7	forest	generalist	p
B. mildeanum	7.3	forest, grassland	epigeic	p
B. oedipodium	6.0	forest	generalist	pc
Calliergonella cuspidata	6.0	forest, grassland	epigeic	pc
Rhytidiadelphus squarrosus	4.4	grassland	epigeic	pc
Brachythecium erythrorrhizon	3.6	forest	generalist	p
Cirriphyllum piliferum	3.6	forest, grassland	generalist	pc
Ceratodon purpureus	3.2	grassland, field	generalist	c
Amblystegium riparium	2.8	forest, grassland, banks of water bodies	generalist	p
Atrichum undulatum	2.4	forest, grassland, field	epigeic	s
Plagiomnium ellipticum	2.4	forest, grassland	epigeic	pc
Bryum caespiticum	2.0	grassland	generalist	c
Lophocolea heterophylla	1.6	forest	epixylic	cp
Amblystegium serpens	1.2	forest	generalist	p
Campylium chrysophyllum	1.2	forest, grassland	generalist	p
Barbula convoluta	0.8	forest, grassland, abandoned field	epigeic	c
Brachythecium reflexum	0.8	forest	generalist	ps
Plagiomnium medium	0.8	forest	epigeic	pc
Thuidium delicatulum	0.8	forest, grassland	generalist	p
Atrichum tenellum	0.4	forest, fallow	epigeic	s
B. starkei	0.4	forest	generalist	ps
Calliergon cordifolium	0.4	forest, banks of water bodies	epigeic	pc
Campylium stellatum	0.4	grassland, swamp, mire	epigeic	pc
Climacium dendroides	0.4	forest	epigeic	pc
Eurhynchium pulchellum	0.4	forest	generalist	ps
Hylocomium splendens	0.4	forest, (alvar grassland)	epigeic	pc
Plagiothecium laetum	0.4	forest	generalist	ps
Pleurozium schreberi	0.4	forest, (alvar grassland)	epigeic	pc
Polytrichum juniperinum	0.4	forest, grassland	generalist	ps, pc
Preissia quadrata	0.4	grassland	epigeic	l
Rhytidiadelphus triquetrus	0.4	forest	epigeic	pc