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ARTICLE

Vascular plant and bryophyte flora in midterm hybrid aspen plantations on abandoned agricultural land[1]

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Abstract: Short-rotation forest plantations with hybrid aspen on abandoned agricultural land are a novel use of land in eastern and northern Europe; however, to date, their impact on floristic diversity has not been thoroughly studied. Our aim is to determine the kind of vascular plant and bryophyte (including epiphytes) species that benefit from such plantations. Data on understorey and soil humus layer properties were collected as part of the repeated monitoring of 204 permanent vegetation plots in twenty-four 13- to 14-year old commercial hybrid aspen plantations in boreonemoral Estonia. Data analysis indicated that the understorey of midterm hybrid aspen plantations is formed of species with different ecological requirements, ranging from typical fallow species to shade-tolerant forest species. Midterm plantations were dominated by common grassland species; however, occasionally less frequent and protected grassland species were also found. No rare species of epigeic or epiphytic bryophytes were recorded. Overall, a slow succession towards a shade-tolerant understorey was observed when comparing midterm and young plantations, with the occurrence of forest species in negative correlation with the amount of canopy-transmitted total solar radiation. The number of species characteristic of forests growing on similar soil types was low. Further studies will clarify how close the habitat in such intensively managed plantations on abandoned agricultural lands can approach that of natural forests in hemiboreal conditions.

Key words: hybrid aspen, forest plantations, vascular plants, bryophytes, repeated vegetation survey.

Résumé : Les plantations forestières de peuplier hybride à courte rotation sur des terres agricoles abandonnées constituent une nouvelle utilisation des terres dans l'est et le nord de l'Europe, mais leur impact sur la diversité floristique n'a pas été étudié à fond jusqu'à maintenant. Notre but est de déterminer le type d'espèces de plante vasculaire et de bryophyte (incluant les épiphytes) qui tirent profit de telles plantations. Des données sur la végétation de sous-bois et les propriétés de la couche d'humus du sol ont été récoltées dans le cadre d'un inventaire répété de 204 parcelles permanentes de végétation établies dans 24 plantations commerciales de peuplier hybride âgées de 13 à 14 ans dans la zone boréo-némorale de l'Estonie. L'analyse des données a indiqué que le sous-étage des plantations de peuplier hybride à mi-rotation est constitué d'espèces ayant des exigences écologiques différentes, allant d'espèces typiques de jachère aux espèces forestières tolérantes à l'ombre. Les plantations à mi-rotation étaient dominées par des espèces de prairie communes, bien qu'on ait occasionnellement trouvé des espèces de prairie moins fréquentes et protégées. Aucune espèce rare de bryophyte épigée ou épiphytique n'a été signalée. Globalement, une lente succession vers un sous-étage tolérant à l'ombre a été observée en comparant des plantations jeunes et à mi-rotation, avec une corrélation négative entre la présence d'espèces forestières et le rayonnement solaire total transmis par le couvert. Le nombre d'espèces caractéristiques des forêts se développant sur des types de sol similaires était faible. D'autres études permettront de clarifier jusqu'à quel point l'habitat de telles plantations aménagées intensivement sur des terres agricoles abandonnées peut approcher celui des forêts naturelles dans des conditions hémiboréales. [Traduit par la Rédaction]

Mots-clés : peuplier hybride, plantations forestières, plantes vasculaires, bryophytes, inventaire répété de la végétation.

1. Introduction

Fast-growing hybrid aspen (*Populus tremula* L. × *P. tremuloides* Michx.) is a suitable tree species for intensive production of biomass and pulpwood in northern Europe (Rytter and Stener 2005; Tullus et al. 2012*a*). It is apparently the most cold-resistant commercially used *Populus* hybrid in the region. The area covered by hybrid aspen plantations managed according to the principles of short-rotation forestry (SRF) was estimated to be over 4500 ha in Nordic and Baltic countries by the end of the first decade of the 21st century (Tullus et al. 2012*a*). Since then, this number has doubled due to extensive plantation establishment in Lithuania (M. Šilininkas, personal communication, 2014) and Sweden (L. Rytter, personal communication, 2014). The majority of hybrid aspen plantations are located on former agricultural land.

Although the main aim of SRF plantations is the production of industrial wood, plantation forests can be designed for multiple purposes (Paquette and Messier 2010). In addition to the generally acknowledged virtues of plantations such as carbon accumulation in the soil (Kahle et al. 2007) and offering an alternative wood resource to natural forests (Paquette and Messier 2010), it has recently been demonstrated that plantations with fast-growing tree species may contribute to the conservation of biodiversity by providing a suitable habitat for reintroduced forest herbs (Boothroyd-Roberts et al. 2013). As the area covered by hybrid

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aspen plantations is increasing in the Baltic Sea region, it raises a question: what kinds of species benefit from the expansion of hybrid aspen plantations? Understorey vegetation in hybrid aspen plantations has been studied in Estonia (Soo et al. 2009*a*, 2009*b*; Tullus et al. 2012*b*), as well as in Germany (Heilmann et al. 1995) and Sweden (Weih et al. 2003); however, these studies were all conducted in plantations not older than 10 years. The recommended rotation period for hybrid aspen is 20–30 years in the Nordic and Baltic countries (Tullus et al. 2012*a*), and therefore the understorey vegetation in older plantations also needs to be studied. In addition, no study has hitherto focused on epiphytic bryophyte flora in hybrid aspen plantations. European aspen (*Populus tremula* L.) and quaking aspen (*Populus tremuloides* Michx.) are both known for their unique and rich epiphytic flora of bryophytes (Kuusinen 1996; Boudreault et al. 2000), but their hybrid has not been studied from this perspective.

In general, successional patterns can be observed in the development of understorey vegetation in SRF plantations, as changes in the understorey are governed by changes in the overstorey. The older the trees become and the closer together they are planted, the more shaded is the understorey, leading to the replacement of light-demanding and short-lived species with shade-tolerant perennials (Baum et al. 2009). In addition to competition for light with the tree layer, belowground competition also impacts understorey development (Harrington et al. 2003). Understorey species richness is generally lower in mature plantations than in young ones (Baum et al. 2009; Archaux et al. 2010); however, the number of forest species increases throughout succession together with the increasing age of the tree layer (Archaux et al. 2010; Baum et al. 2012*a*). In addition to plantation age, the formation of a forest-like understorey is also dependent on other factors. In the case of plantations that are located on former agricultural land, the formation of a forest understorey requires colonization from nearby forests, as the soil seed bank of former agricultural soils does not usually contain the seeds of forest species (Baum et al. 2013). Due to the low migration rates of many forest species (Brunet and von Oheimb 1998; Dzwonko 2001), differences can be found in the species composition of the understorey vegetation of recent forests bordering on ancient forests and that of isolated recent forests (Dzwonko 1993), although forest specialists and generalist species are affected differently by isolation (Brunet et al. 2011). In addition to dispersal limitations (Brunet et al. 2000; Jaquemyn et al. 2001), the recruitment of forest species may be hampered by site quality variables (e.g., soil properties) or exclusion due to competitive species (Honnay et al. 1999; De Keersmaeker et al. 2004) in new stands on former agricultural land. In the long run, the development of a forest understorey in SRF plantations is also affected by silvicultural management practices such as thinnings and final harvests that are repeated in a fairly short period of time. As many forest species are not adapted to frequent disturbances, it has been suggested that repeated harvests in SRF systems may reduce their populations (Halpern and Spies 1995; Weih et al. 2003).

The understorey vegetation of SRF plantations is usually dominated by common species (Gustafsson 1987; Weih et al. 2003; Baum et al. 2012*b*), and rare species are only occasionally found. For instance, no rare species were recorded in Swedish poplar plantations (Weih et al. 2003), and although several red list species were found in hybrid poplar plantations in Switzerland, their number declined as the plantations grew older and light conditions deteriorated (Delarze and Ciardo 2002). On the other hand, the mass occurrence of orchids (*Epipactis helleborine*, *Platanthera bifolia*, and *Dactylorhiza incarnata*) was observed in 20-year-old hybrid poplar plantations in Poland, indicating that poplar plantations may offer suitable habitat for orchids (Adamowski and Conti 1991).

An important aspect in the understanding of SRF systems is whether they improve or deplete soil nutrient pools and affect other physicochemical soil properties (Kahle et al. 2007; Baum et al. 2009). As SRF plantations are usually established on abandoned agricultural lands, it is economically essential that they do not have a negative impact on the soil if there is a possibility that agricultural land use will be resumed in the future. The changes in soil properties caused by trees are also likely to affect understorey vegetation (Barbier et al. 2008).

The aim of the current study is to investigate the vascular plant and bryophyte flora of midterm hybrid aspen plantations and answer the following questions.

1. Which site- and stand-related factors affect understorey vegetation characteristics (species composition, species richness)?
2. Do midterm hybrid aspen plantations offer habitat for rare species?
3. How do fast-growing hybrid aspen plantations affect the chemical properties of the soil humus layer?
4. How much does understorey species composition in midterm hybrid aspen plantations on abandoned agricultural lands resemble the understorey of forests growing on similar soil types?
5. How has the understorey of plantations changed between young and midterm age regarding the occurrence of forest species and species' light tolerance?

2. Materials and methods

2.1. Study area

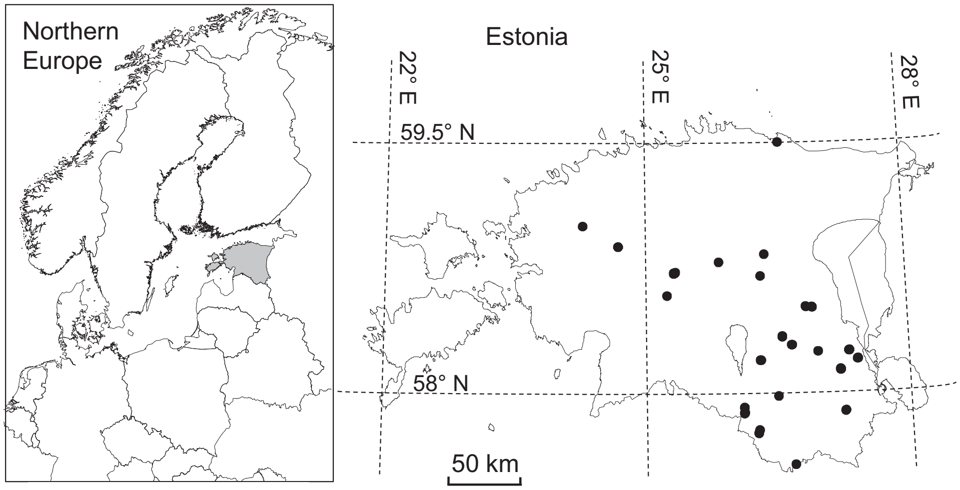
The study comprised 24 commercial hybrid aspen plantations situated on former agricultural land in the continental part of Estonia (57°33′N–59°29′N, 24°16′E–27°24′E) (Fig. 1). The plantations were established in 1999 and 2000 with 1-year-old clonal plants. Previous agricultural land use for plantations was either crop field or grassland, and mechanical site preparation (either whole-area ploughing or strip tillage) was carried out before planting trees. Data were collected from midterm (13- to 14-year-old) plantations in the middle of the growing season, using the previously established network of 51 permanent experimental plots (each 0.1 ha) in which the growth of the trees is monitored (Tullus et al. 2007). As the sizes of hybrid aspen plantations varied from 0.7 to 32 ha and 14 larger plantations consisted of smaller scattered parts with different soil types and land use history, the number of experimental plots in one plantation varied from one to five. Results concerning the understorey vascular plant and bryophyte vegetation in young (7- to 8-year-old) plantations have been published elsewhere (Soo et al. 2009*a*; Tullus et al. 2012*b*). In the current study, data from young stands were used to characterise the initial status when analysing the main successional changes.

2.2. Data collection

Vascular plant and bryophyte data were collected from permanent vegetation plots (four in every experimental plot, each 2 × 2 m in size). In every vegetation plot, a list of vascular plant and bryophyte species was compiled and the cover of each species was estimated visually using a scale of 1%–100%. Total cover of the field layer and total cover of the bryophyte layer were also estimated. In addition, a list of bryophyte species growing on the trunks of four trees situated near the vegetation plot corners was compiled. Bryophytes that could not be identified in field conditions were collected for further investigation under a microscope. The occurrence of rare species was recorded for every experimental plot. The nomenclature follows the key books of Estonian vascular plants (Leht 2010) and bryophytes (Ingerpuu and Vellak 1998).

Hemispherical photos were taken from the centre of each vegetation plot from the height of the field layer (approximately 50 cm) using a Sigma 8 mm 1:3:5 EX DG FISHEYE lens attached to a Canon EOS 5D digital camera. The photographs were analysed using Gap Light Analyzer 2.0 (Frazer et al. 1999) to estimate canopy openness and the amount of canopy-transmitted direct, diffuse,

Fig. 1. Locations of the studied hybrid aspen plantations in Estonia.



and total solar radiation incident on a horizontal receiving surface.

Leaf and branch litter was collected from the ground of two subplots (each 20 × 20 cm) located at opposite sides of a vegetation plot. Composite litter samples were dried at +70 °C to constant mass and weighed to the nearest 0.001 g. Arithmetic mean litter estimates (tonnes (t)·ha^{-1}) were then calculated for each vegetation plot. Soil samples were taken from the middle of the humus horizon using the same subplots as for litter collection. Concentrations of total nitrogen (N) and extractable phosphorus (P) and potassium (K) and $\mathrm{pH_{KCl}}$ were determined from composite soil samples for each vegetation plot. Analyses were performed by the Laboratory of Agrochemistry of the Agricultural Research Centre in Saku using methods ISO 10390 for pH, ISO 11261 (Kjeldahl) for total N, and Mehlich 3 extractant for available P and K. The experimental plots were grouped according to soil moisture conditions based on earlier studies (Tullus et al. 2007). Following the correspondence matrix on Estonian forest site types and soil types (Lõhmus 1984), potential forest site type was determined for every experimental plot. The occurrence of characteristic vascular plant and bryophyte species for the potential forest site type (Lõhmus 1984) was checked. The system of Estonian forest site types consists of over 20 site types that are distinguished by soil water regime and the texture and calcareousness of parent material and are named after the genera of characteristic understorey species (e.g., *Oxalis*, *Aegopodium*, etc.).

In every 0.1 ha experimental plot, tree height (H) and stem diameter at breast height (DBH) of every tree were measured and the number of trees (n, trees·ha^{-1}) was counted. Stand basal area (BA) per hectare was estimated, and to express the average distance between the trees, the stand sparsity index (L) was calculated according to Nilson (2006) as follows: $L = 100n^{-0.5}$.

Using recent aerial photos superimposed on a base map of Estonia, the distance from experimental plot to the nearest forest was estimated with the distance measuring tool of the online GIS application of the Estonian Land Board (http://xgis.maaamet.ee/xGIS/XGis).

2.3. Data analysis

Species richness (S) and Simpson's diversity index (D') for vascular plants and bryophytes that grow on the ground were estimated for vegetation plots using PC-ORD Version 6 (McCune and Mefford 2011). Following the Estonian key book of vascular plants (Leht 2010), vascular plants were classified by habitat preference into the following categories: forest species, forest and grassland species, grassland species, and fallow species. Habitat preference of bryophytes was determined based on Ingerpuu et al. (1994), and the following categories were formed: forest species, forest and grassland species, and open-habitat species. Ellenberg and Düll indicator values for light (Ellenberg et al. 1991) were assigned to vascular plant and bryophyte species, and weighted average light values were calculated for vegetation plots.

The significance of the changes in the vegetation characteristics and soil humus layer properties (estimated at vegetation plot level) between young and midterm plantations were evaluated. We estimated the change in the given variable (Δvar) between the two monitoring periods (m1 and m2) as follows: $\Delta\mathrm{var} = \mathrm{var}_{\mathrm{m2}} - \mathrm{var}_{\mathrm{m1}}$ and then tested H0: $\Delta\mathrm{var} = 0$ with intercept-only linear mixed model, accounting for the random effect of experimental plot using Proc Mixed in SAS for Windows 9.1.3 (SAS Institute Inc., Cary, North Carolina). The significance of the changes in the main tree-layer characteristics (estimated at experimental plot level) were tested with a Student's t test for dependent samples.

A generalised linear mixed model (SAS Proc Glimmix), with experimental plot as a random effect, was used to evaluate the effects of soil- and overstorey-related characteristics on richness and coverage estimates of the understorey vegetation. Species richness estimates were treated as response variables with Poisson distribution, and Gaussian distribution was used for coverage estimates and diversity indices. If necessary, logarithmic transformation of variables was used to meet the assumption of normality. Extremely high soil N values in two experimental plots were excluded from the analysis. The multicollinearity of the continuous explanatory variables was checked via Spearman rank correlations (using function “varclus” in R package Hmisc for illustration; R Foundation for Statistical Computing, Vienna, Austria, available from http://www.r-project.org). The outcome indicated that canopy openness and the amount of canopy-transmitted direct, diffuse, and total solar radiation were strongly ($\rho^2 > 0.5$) intercorrelated, and therefore, only total solar radiation was included in the model. Strong intercorrelation also existed between DBH, H, and BA, and of these, DBH was included. Further, to detect possible multicollinearities, we looked at the variance inflation factor (VIF) of each predictor (in each model) but did not find any VIFs larger than 5.

Variation in species composition was investigated with nonmetric multidimensional scaling (NMDS) with the community ecology package Vegan in R (Oksanen et al. 2013). NMDS was run with the “metaMDS” function and Bray–Curtis dissimilarities.

Table 1. Comparison of soil humus horizon properties and tree layer characteristics in young and midterm plantations.

Variable	Young plantations	Midterm plantations	p value
Estimated for each vegetation plot			
pH$_{\mathrm{KCl}}$	5.8±0.1^a	5.5±0.1	**<0.001**
Available P (mg·kg^{-1})	81.0±4.0^a	81.1±4.2	0.977
Available K (mg·kg^{-1})	127.8±5.6^a	122.8±5.3	0.252
Total N (%)	0.18±0.01^a	0.17±0.01	0.065
Estimated for each experimental plot			
Trees (·ha^{-1})	1043.1±26.8^a	1016.7±26.8	**0.003**
Sparsity index	3.14±0.04	3.18±0.04	**0.014**
Height (m)	4.3±0.2	11.8±0.4	**<0.001**
Diameter at breast height (cm)	3.5±0.2	10.2±0.4	**<0.001**
Basal area (m^2·ha^{-1})	1.4±0.2^a	9.4±0.6	**<0.001**

Note: The significance (p values) of the differences between the two plantation ages was tested with the intercept-only mixed model (vegetation plot data) or t test for dependent samples (experimental plot data). Values in bold are significantly different ($p < 0.05$).

[a] Data from Tullus et al. 2012*b*.

Prior to ordination, square root transformation and Wisconsin double standardisation of the data were applied. The analysis was run until two convergent solutions were found. The solution was centred, rotated on the principal component axes, and scaled to half-change units following the default settings with "metaMDS". To interpret the ordination, environmental variables were fitted onto the ordination using the function "envfit". To find species characteristic of young and midterm plantations, an indicator species analysis (ISA) was performed with PC-ORD Version 6 (MjM Software, Gleneden Beach, Oregon, U.S.A.). NMDS and ISA were run with experimental plot-level understorey data (the averaged cover values of vascular plants and ground-inhabiting bryophytes from four vegetation plots were used). One experimental plot, dominated by invasive species *Galega orientalis*, which allowed the growth of only a few other vascular plant species, was left out of ordination and ISA due to the radically different understorey species composition.

To illustrate the changes in species composition between the two monitoring periods, a Venn diagram was composed using package vennDiagram in R.

A level of significance $a = 0.05$ was used for rejecting null hypotheses in all statistical tests.

3. Results

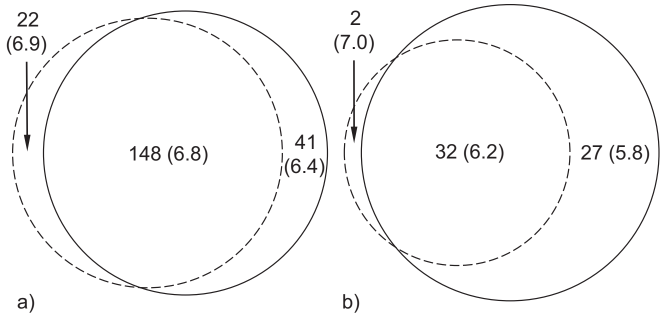
3.1. Differences in vegetation characteristics and environmental variables between young and midterm hybrid aspen plantations

3.1.1. Soil properties and overstorey characteristics

In comparison with the results from young stands, all variables related to tree growth (*H*, DBH, BA, *L*) were significantly higher in midterm plantations, but the density of trees had decreased considerably. Concentrations of macronutrients (N, P, and K) in the soil humus horizon remained on the same level as in young plantations, whereas soil pH had decreased significantly (Table 1).

3.1.2. Species richness and species composition

Fig. 2. Venn diagrams for the number of (*a*) vascular plant and (*b*) bryophyte species found from young (dashed line) and midterm (solid line) hybrid aspen plantations. The intersection of the two circles indicates the species that had persisted in the community. The number in parentheses shows the average light demand value of the species that had disappeared from, had persisted in, or had colonised midterm plantations.



Altogether, 189 vascular plant and 59 bryophyte species were found in midterm hybrid aspen plantations. There were also a few specimens that were identified at the genus level. The numbers of vascular plant and bryophyte species had both increased when compared with the overall species richness in young plantations, as the numbers of vascular plant and bryophyte species found from young hybrid aspen plantations were 170 and 34 (Tullus et al. 2012*b*), respectively. Although 22 vascular plants that were present in young plantations could not be found in midterm plantations, 41 new vascular plant species had colonised the midterm plantations (Fig. 2). Only two bryophyte species had disappeared from the midterm plantations, and 27 new bryophyte species had been added. The majority of new species were found in only one experimental plot (e.g., forest species and forest–grassland species *Athyrium filix-femina*, *Dryoptheris filix-mas*, *Pyrola minor*, *Anemone nemorosa*, *Campanula persicifolia*, *Cirsium oleraceum*, *Hypochaeris maculata*, *Dicranum scoparium*, and *Ptilium crista-castrensis*). New species recorded more than once were *Agrimonia eupatoria*, *Arenaria serpyllifolia*, *Campanula rapunculoides*, *Carduus crispus*, *Lapsana communis*, *Padus avium*, *Sorbus aucuparia*, *Campylium sommerfeltii*, *Chiloscyphus polyanthos*, *Conocephalum conicum*, *Eurhynchium angustirete*, *Hylocomnium splendens*, *Leptobryum pyriforme*, *Plagiomnium affine*, *Plagiomnium undulatum*, *Sanionia uncinata*, *Orthotrichum affine*, *Orthotrichum speciosum*, and *Pylaisia polyantha*. The comparison of average light demand values for the species that had disappeared from, were present in, or had colonised midterm plantations revealed a slow succession towards a more shade-tolerant understorey (Fig. 2). The same tendency was revealed when comparing the weighted average Ellenberg and Düll light value indices per vegetation plot in young and midterm stands (Table 2).

The majority of the vascular plant species recorded in hybrid aspen plantations were common species, with the exception of *D. incarnata* found in one experimental plot and *Platanthera* sp. found in two experimental plots in young plantations. In midterm plantations, orchids (*Dactylorhiza fuchsii*, *D. incarnata*, and *P. bifolia* and vegetative specimens from the same genera) grew in 10 experimental plots, and a protected species *Thalictrum lucidum* grew in one experimental plot. All bryophytes recorded in hybrid aspen stands were common species. No bryophyte species were found on tree trunks in young plantations, but in midterm plantations, 28 species were recorded growing on tree bases and (or) tree trunks. Among these, 19 species were also growing on the ground and 9 species were found only on trunks. The most frequent trunk-inhabiting bryophyte species were *P. polyantha*, *C. sommerfeltii*, and *O. speciosum*.

The mean numbers of vascular plant and bryophyte species per experimental plot (based on four vegetation plots), as well as vegetation plot level estimates for species richness and diversity, were significantly higher in midterm plantations (Table 2), similar to the increase in the overall species richness of vascular plant and bryophyte species. Opposite trends were observed in the cover of the field layer and the cover of the bryophyte layer, as the cover of field layer had dropped and the cover of bryophyte layer had increased significantly in midterm plantations (Table 2). The number and cover of vascular plant and bryophyte forest and forest–grassland species had increased. Although the cover of both grassland and fallow vascular plant species had decreased, the

Table 2. Experimental and vegetation plot mean values of vascular plant (VP) and bryophyte (B) characteristics from young and midterm plantations.

Characteristic	Young plantations	Midterm plantations	*p* value
Experimental plot mean (based on four vegetation plots) values			
S_{VP}	28.6±1.1[a]	33.5±1.2	**<0.001**
$S_{\text{B\_ground}}$	4.0±0.3[b]	7.4±0.4	**<0.001**
$S_{\text{B\_trunk}}$	0	5.2±0.3	**<0.001**
Vegetation plot mean values			
S_{VP}	16.7±0.4[a]	19.5±0.4	**<0.001**
D'_{VP}	0.77±0.01	0.82±0.01	**0.006**
$S_{\text{VP\_forest}}$	0.4±0.1	0.9±0.1	**<0.001**
$S_{\text{VP\_forest, grassland}}$	0.2±0.03	0.5±0.05	**<0.001**
$S_{\text{VP\_grassland}}$	10.3±0.3	12.1±0.3	**<0.001**
$S_{\text{VP\_fallow}}$	5.4±0,2	5.2±0.2	0.401
C_{VP}	70.1±0.8[a]	61.5±1.1	**<0.001**
$C_{\text{VP\_forest}}$	0.8±0.1	3.6±0.7	**0.001**
$C_{\text{VP\_forest, grassland}}$	1.1±0.3	4.6±0.8	**0.002**
$C_{\text{VP\_grassland}}$	50.4±1.5	40.1±1.3	**<0.001**
$C_{\text{VP\_fallow}}$	24.1±1,4	19.3±1.1	**0.005**
Ellenberg's value for light	7.0±0.02[a]	6.8±0.03	**<0.001**
$S_{\text{B\_ground}}$	1.8±0.1[b]	3.7±0.2	**<0.001**
$S_{\text{B\_trunk}}$	0	2.3±0.1	**<0.001**
$D'_{\text{B\_ground}}$	0.3±0.02	0.5±0.02	**<0.001**
$S_{\text{B\_forest}}$	0.8±0.1	2.3±0.1	**<0.001**
$S_{\text{B\_forest, grassland}}$	0.9±0.05	1.3±0.1	**<0.001**
$S_{\text{B\_open habitats}}$	0.2±0.03	0.2±0.03	0.928
C_{B}	11.7±1.5[b]	22.8±1.7	**<0.001**
$C_{\text{B\_forest}}$	4.3±0.7	12.1±1.1	**<0.001**
$C_{\text{B\_forest, grassland}}$	6.7±1.0	10.3±1.1	**0.045**
$C_{\text{B\_open habitats}}$	0.4±0.1	0.4±0.1	**0.812**
Düll's value for light	6.2±0.1	5.6±0.1	**<0.001**

Note: *S*, species richness; *C*, cover; *D*′, diversity. The significance (*p* values) of the differences between the two plantation ages was tested with the intercept-only mixed model (vegetation plot data) or *t* test for dependent samples (experimental plot data). Values in bold are significantly different ($p < 0.05$).

[a]Data from Soo et al. 2009*a*.

[b]Data from Tullus et al. 2012*b*.

number of fallow species had remained at the same level as in young plantations and the number of grassland vascular plant species had even increased.

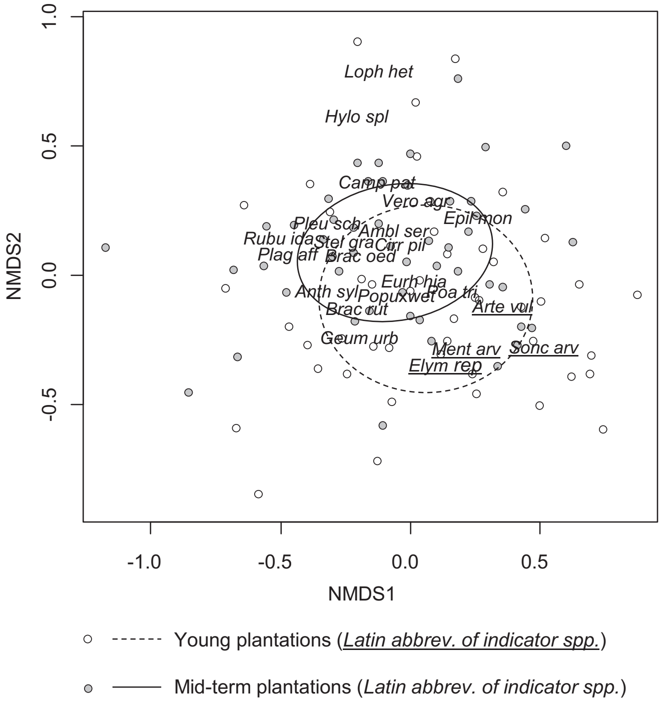
Plantation age significantly affected the position of experimental plots in the NMDS ordination space (Fig. 3). Species that were characteristic of young plantations (*Artemisia vulgaris*, *Elymus repens*, *Mentha arvensis*, *Sonchus arvensis*), according to indicator species analysis, were all species typical on abandoned agricultural sites. The species characteristics of midterm plantations involved more variable habitat preferences, with forest species (e.g., *Rubus idaeus*, *Lophocolea heterophylla*, *Pleurozium schreberi*, *H. splendens*), grassland species (e.g., *Stellaria graminea*), and fallow species (*Veronica agrestis*) represented.

3.2. The effect of environmental variables on vegetation characteristics in midterm plantations

Variation in species composition in the understorey of midterm hybrid aspen plantations was affected by several environmental variables such as previous land use, the method of site preparation, soil pH, concentrations of P and N in the soil humus horizon, distance to the nearest forest, transmitted total solar radiation, and DBH of trees (Fig. 4; Table 3). Although some of these effects were highly significant ($p < 0.01$), the respective r^2 values did not indicate very strong correlations between understorey and environmental variables (Table 3).

The occurrence of forest species (both vascular plants and bryophytes) was negatively influenced by the amount of canopy-transmitted total solar radiation (Table 4). Light conditions also affected the cover of the field and bryophyte layers, but in the opposite directions: in more shaded stands the cover of the field layer decreased, while the cover of the bryophyte layer, as well as the number of bryophytes, showed an increase. Both the field layer and the bryophyte layer showed a similar (negative) response to the amount of leaf litter. The species richness of vascular plants (in particular the number of grassland species) was negatively affected by higher concentrations of N in soil humus layer. The number of vascular plant fallow species was in positive correlation with soil pH.

Fig. 3. NMDS ordination of experimental plots from young and midterm plantations. Ellipses indicate standard deviation. Species that, according to indicator species analysis, were characteristic of young or midterm plantations are shown on the plot. Species abbreviations: Arte vul, *Artemisia vulgaris*; Elym rep, *Elymus repens*; Ment arv, *Mentha arvensis*; Sonc arv, *Sonchus arvensis*; Anth syl, *Anthriscus sylvestris*; Camp pat, *Campanula patula*; Epil mon, *Epilobium montanum*; Geum urb, *Geum urbanum*; Poa tri, *Poa trivialis*; Popuxwet, *Populus tremula* × *P. tremuloides*; Rubu ida, *Rubus idaeus*; Stel gra, *Stellaria graminea*; Vero agr, *Veronica agrestis*; Ambl ser, *Amblystegium serpens*; Brac oed, *Brachythecium oedipodium*; Brac rut, *B. rutabulum*; Cirr pil, *Cirriphyllum piliferum*; Eurh hia, *Eurhynchium hians*; Hylo spl, *Hylocomnium splendens*; Loph het, *Lophocolea heterophylla*; Plag aff, *Plagiomnium affine*; Plag cus, *P. cuspidatum*; Pleu sch, *Pleurozium schreberi*. Goodness of fit: $r^2 = 0.05$, $p = 0.007$ (*p* value is based on 999 permutations).



Based on the soil types, experimental plots were divided into 10 potential forest site types, with *Oxalis*, *Oxalis–Myrtillus*, *Hepatica*, *Aegopodium*, and *Dryopteris* being the most frequent site types (Table 5). Only a few species characteristic of potential forest site types were found in the understorey of hybrid aspen stands (Table 5).

4. Discussion

The main aims of the current study were (*i*) to evaluate what kind of species benefit from the expansion of novel land use (short-rotation forestry on abandoned agricultural lands) in the

Fig. 4. NMDS ordination of experimental plots (stress 0.22) in midterm plantations. The arrows indicate environmental vectors that were significantly ($p < 0.05$) related to the ordination (see also Table 3). Ellipses indicate standard deviation.

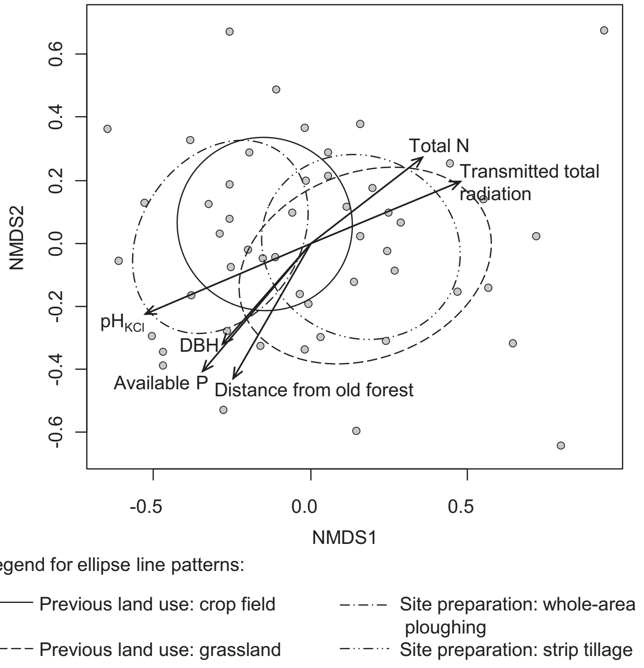


Table 3. Relationships between understorey vascular plant and bryophyte species composition (NMDS ordination; Figure 4) and environmental variables in midterm plantations.

Environmental factor	r^2	p value
Previous land use	0.13	**0.002**
Site preparation method	0.21	**0.001**
Soil pH$_{KCl}$	0.21	**0.005**
Soil available P	0.18	**0.014**
Soil available K	0.07	0.163
Soil total N	0.13	**0.043**
Soil humidity	0.10	0.071
Distance from old forest	0.16	**0.017**
Transmitted total radiance	0.17	**0.016**
Stand sparsity	0.01	0.708
Quantity of grounded leaf litter	0.09	0.112
Quantity of grounded branch litter	0.05	0.332
Overstorey trees mean DBH	0.12	**0.048**

Note: The r^2 values show the squared correlation coefficient for the environmental vectors fit onto the NMDS ordination, and p values are based on random permutations of the data. Values in bold are significantly different ($p < 0.05$). DBH, diameter at breast height (cm).

region and (*ii*) to determine which environmental variables influence variation in understorey species composition and richness in midterm hybrid aspen plantations. As understorey species composition and species richness change throughout the development of plantations, data from young stands were included in the current study to highlight the main successional patterns. Studies following understorey succession on permanent vegetation plots in SRF plantations of different age groups have been quite rare, and more studies have used the space-for-time substitution (chronosequence) technique to analyse the effect of plantation age on the understorey (Weih et al. 2003; Archaux et al. 2010; Baum et al. 2012*a*, 2012*b*). Although chronosequence is widely used to study vegetation dynamics, this method has some disadvantages when compared with long-term studies of permanent plots, as biotic and abiotic conditions are likely to vary over the time span of any successional sequence (Johnson and Miyanishi 2008).

As expected, a slow development towards shade-tolerant forest understorey was observed in midterm plantations. The occurrence of forest species was affected by the amount of total solar radiation. In poorer light conditions, the cover of the field layer dropped and the number of forest species increased, obviously benefitting from lower competition. Surprisingly, the number of forest species showed no correlation with distance to nearby forests as propagule sources, although the position of experimental plots in NMDS ordination was affected by this distance. One possible explanation might be that we estimated only the distance between the experimental plot and the nearest forest but did not evaluate these forests as source populations of the observed forest species. Besides that, hedgerows (Wehling and Diekmann 2009) can also serve as habitats for forest plants but were not monitored in the current study.

According to NMDS ordination, species composition was also affected by pre-establishment disturbances (site preparation and previous land use) and soil properties (pH, concentrations of N and P), similar to what was observed at the young stand age (Soo et al. 2009*a*). No impact of the overstorey on the understorey at a young age was detected (Soo et al. 2009*a*); however, in midterm plantations, it was evident by the effect of DBH and canopy-transmitted total radiation on the understorey. The availability of nutrients and light also influenced understorey species composition in Swedish and German SRF plantations with poplars and willows (Baum et al. 2012*b*).

The successional changes were not accompanied by a decrease in overall species richness as observed in several other studies (Delarze and Ciardo 2002; Archaux et al. 2010). This can be explained by the persistence of grassland species in midterm plantations. Although the cover of grassland species had decreased, following the same trend as the overall cover of the field layer, the number of grassland species had increased, indicating that midterm hybrid aspen stands (especially on soils with lower nitrogen content and in stands with slower tree growth; Table 4) are a suitable habitat for many grassland species as well. Common grassland species such as *Achillea millefolium*, *Alchemilla vulgaris* (coll.), *Hypericum perforatum*, *Lathyrus pratensis*, *S. graminea*, and *Trifolium repens* were frequently recorded; however, grassland species that are less frequent in Estonia were also occasionally found (e.g., *Trollius europaeus*, *Polemonium caeruleum*, and *Crepis praemorsa*). Between 1950 to 2005, the total area of Estonian grasslands decreased by about 90% (Sammul et al. 2008), posing a serious threat to grassland flora. It is therefore positive that midterm hybrid aspen plantations can offer an alternative habitat for a number of grassland species. Protected species found in hybrid aspen stands were also either grassland species (*D. incarnata*, *T. lucidum*) or species that grow in grasslands as well as in forests (*D. fuchsii*, *P. bifolia*). The monitoring of epiphytic bryophyte flora on hybrid aspen trees showed that species that are common on *P. tremula* such as *P. polyantha* and *O. speciosum* (Hazell et al. 1998) were already quite common on the trunks of 13- to 14-year-old hybrid aspens. No rare species were recorded among bryophytes; however, this is not surprising, as aspen-associated rare bryophytes such as *Neckera pennata* are usually found on large trees in old-growth stands (Kuusinen and Penttinen 1999).

To evaluate the resemblance between understorey species composition in midterm hybrid–aspen plantations and native forests, the occurrence of species characteristic to native forest site types was recorded in hybrid aspen stands (Table 5). As the number of characteristic species in hybrid aspen stands was low, it may be concluded that, in the current age, hybrid aspen plantations do not help to preserve flora typical to native forests. This is not surprising, as the colonization of forest species to the former agricultural stands that hybrid aspen plantations represent is known to be a slow process (Bossuyt and Hermy 2000) and the

Table 4. Significance (p values based on type III ANOVA of fixed effects) of the factors contributing to species richness (S), diversity (D'), and coverage (C) estimates of vascular plants (VP) and bryophytes (B) in midterm plantations according to the GLIMMIX model.

Vascular plants							
Factor	C_{VP}	S_{VP}	D'_{VP}	$S_{\mathrm{VP\_forest}}$	$S_{\mathrm{VP\_forest,\ grassland}}$	$S_{\mathrm{VP\_grassland}}$	$S_{\mathrm{VP\_fallow}}$
Site preparation[b]	**0.002**[a]	0.599	0.272	0.496	0.430[a]	0.485[a]	0.110
Previous land usec	0.816	0.926[a]	0.480	0.369	0.789[a]	0.491[a]	0.072
Soil humidity	0.642[a]	0.505	0.490	0.652[a]	0.290	0.416	0.797
Soil pH	0.533[a]	0.528	0.312	0.173	0.189	0.515[a]	**0.004**
Soil N	0.877	**0.027**[a]	0.775[a]	0.444[a]	0.051[a]	**0.048**[a]	0.448a
Soil P	0.465[a]	0.442[a]	0.630[a]	0.362[a]	0.912[a]	0.656[a]	0.688
Soil K	0.699	0.730	0.681	0.617[a]	0.711	0.803[a]	0.064
Distance	0.222	0.378	0.962[a]	0.235	0.227[a]	0.788	0.139
Transmitted total radiation	**<0.001**	0.833[a]	0.559[a]	**0.018**[a]	0.343[a]	0.711	0.827
Leaf litter	**<0.001**[a]	0.831[a]	0.618[a]	0.810	0.328	0.478[a]	0.708a
Branch litter	0.229[a]	0.909[a]	0.474	0.542	0.731	0.412[a]	0.633
Stand sparsity	0.375[a]	0.575[a]	0.907	0.393[a]	0.494[a]	0.599[a]	0.829a
DBH	0.619	0.086[a]	0.140[a]	0.779[a]	0.314[a]	**0.026**[a]	0.241
Bryophytes							
Factor	$C_{\mathrm{B\_ground}}$	$S_{\mathrm{B\_ground}}$	$D'_{\mathrm{B\_ground}}$	$S_{\mathrm{B\_forest}}$	$S_{\mathrm{B\_forest,\ grassland}}$	$S_{\mathrm{B\_open\ habitats}}$	$S_{\mathrm{B\_trunk}}$
Site preparation[b]	0.748	0.998	0.500	0.785	0.865[a]	0.245	0.507
Previous land use[c]	0.087	0.399	0.879[a]	0.989[a]	0.339	0.854	0.959
Soil humidity	0.147	0.731	0.983[a]	0.843[a]	0.842	0.487[a]	0.761a
Soil pH	0.089	0.504	0.408[a]	0.959	0.654	0.335[a]	0.782a
Soil N	0.792	0.512[a]	0.749[a]	0.947[a]	0.521[a]	0.921[a]	0.455
Soil P	0.096[a]	0.758[a]	0.670	0.287[a]	0.818	0.377[a]	0.343a
Soil K	0.141	0.432	0.268[a]	0.138	0.260[a]	0.267	0.776a
Distance	0.094	0.713	0.875[a]	0.118[a]	0.206	0.136[a]	0.766a
Transmitted total radiation	**0.030**[a]	**0.027**[a]	0.151[a]	**0.013**[a]	0.871[a]	0.632	0.347a
Leaf litter	**0.024**[a]	0.153[a]	0.908[a]	0.527[a]	0.175[a]	0.539	0.376a
Branch litter	0.290	0.422[a]	0.090[a]	0.596	0.396[a]	0.875	0.953
Stand sparsity	0.604[a]	0.822	0.500	0.206	0.499[a]	0.601	0.634
DBH	0.999	0.225[a]	0.186[a]	0.889	0.749	0.235[a]	0.208

Note: Values in bold are significantly different ($p < 0.05$). DBH, diameter at breast height.

[a] Negative effect.

[b] Whole-area ploughing vs. strip tillage.

[c] Crop field vs. grassland.

Table 5. The occurrence of characteristic understorey species of potential forest site types in experimental plots.

			Mean no. of characteristic species per experimental plot		No. of characteristic species to forest site type[a]	
Potential forest type group	Forest site type according to Estonian classification[a]	N[b]	Vascular plants	Bryophytes	Vascular plants	Bryophytes
Alvar forests	*Calamagrostis*-alvar	2	2.5±0.5	1.5±0.5	42	5
Dry boreal forests	*Oxalis–Rhodococcum*	1	1	0	22	5
Fresh boreal forests	*Oxalis–Myrtillus*	11	0.9±0.3	0.5±0.3	22	8
	Oxalis	11	3.3±0.5	0.9±0.3	47	8
	Hepatica	9	2.1±0.6	1.0±0.2	59	7
Fresh boreonemoral forests	*Aegopodium*	8	4.8±1.0	3.0±0.6	64	12
	Dryopteris	6	2.3±0.6	2.3±0.4	67	12
Paludified and drained peatland forests	*Filipendula*	1	3	1	78	14
	Polytrichum	1	4	1	31	9
	Oxalis drained swamp	1	5	1	66	18

[a] Derived from Lõhmus (1984).

[b] Number of experimental plots.

number of forest species is likely to increase in time. In the case of successful dispersal, the recruitment of forest species in new stands may be further hampered by site quality variables such as high soil nutrient status (especially high phosphorus content), which promotes the vigorous growth of competitive species, leading to the exclusion of forest species (Honnay et al. 1999; De Keersmaeker et al. 2004). The possible impact of the relatively high nutrient status of former agricultural soils to the recruitment of forest species needs to be considered during future monitoring of these plantations; however, the results of the current study revealed no effect of soil properties on the number of forest species.

Another issue that impacts understorey succession in hybrid aspen plantations is silvicultural practices. Thinning practices usually need to be carried out in midterm hybrid aspen plantations to ensure a better quality of stems at final harvest (Rytter and Stener 2005; Tullus et al. 2012*a*). According to literature (Ares et al. 2010; Hedwall et al. 2013), management practices such as thinning support the spread of early-successional understorey species. It is therefore quite likely that during the next 10–15 years preceding the clear-cut, a forest understorey typical to native forests may not be fully developed. Clear-cutting also favours the spread of shade-intolerant early-successional species (Yorks et al. 2000) and may have long-term negative effects on late-successional forest species (Moola and Vasseur 2004; Godefroid et al. 2005). On the other hand, De Keersmaeker et al. (2011) recently showed that clear-cutting may promote the colonization of shade-tolerant herbs into forests on former agricultural land, as several shade-tolerant herbs that were absent before clear-cutting from 45-year-old Belgian poplar plantations were established at high frequencies after clear-cutting. New aspen trees are expected to grow in hybrid aspen plantations from root and stump suckers after clear-cut, which may result in a very dense stand in which initially over 100 000 suckers·ha^{-1} may arise (Rytter 2006; Lutter et al. 2013). Naturally regenerated hybrid aspen stands can be managed either with repeated very short rotations for the production of energy wood or with 20- to 30-year rotations with the aim of producing larger assortments, similarly to the first generation (Tullus et al. 2012*a*). In a study of the effect of two silvicultural systems with different disturbance frequencies on the understorey of forest stands in France, Decocq et al. (2004) concluded that short cutting intervals repeated after every 4 years maintained communities dominated by early successional species and impacted true forest species negatively when compared with longer cutting intervals. Understorey development in second-generation hybrid aspen stands is therefore likely to be determined by the choice of management scheme. In the long term, after several consecutive harvest cycles, it is possible that hybrid aspen plantations may offer a habitat comparable with traditional coppice woods, which are known to contain a rich flora of both forest and open-land plants, as the cyclic changes between light and shade phases enable the growth of species with different ecological requirements (Peterken 1993).

Differences observed in the tree-layer characteristics between young and midterm plantations were caused by rapid tree growth and the exclusion of stems via competition and mechanical damage. Despite the high productivity of trees (stand BA increased 6.7 times on average; Table 1), concentrations of macronutrients did not decrease, which agrees with the general experience that hybrid aspen plantations do not require fertilization in northern Europe (Tullus et al 2012*a*). In some studies, the depletion of nutrients has been observed in fast-growing willow and poplar stands (Kahle et al. 2007), and thus fertilization is essential to maintaining productivity. This could hinder the inclusion of generally less competitive forest species. At the same time, soil pH decreased significantly, which is consistent with other studies of changes in soil chemistry after afforestation (Jug et al. 1999; Ritter et al. 2003). Interestingly, the number of fallow vascular plant species, which had decreased in midterm plantations, showed a positive correlation with soil pH (Table 4). The impact of the overstorey on their persistence might thus be governed indirectly through changes in soil acidity.

The effect of overstorey trees on understorey vegetation was usually manifested through transmitted radiance and sometimes also through the quantity of litterfall and DBH of trees. Stand sparsity, which could indicate competition (crowding) effect from the overstorey, was not a significant factor. This is probably because sparsity (average distance between the trees, derived from stand density) varied in a relatively small range (3.18 ± 0.04 m) (Table 1) and was not related to the average growth rate of the trees.

To conclude, the understorey of midterm hybrid aspen plantations is formed of species with different ecological requirements, ranging from typical fallow species to shade-tolerant forest species. It has previously been observed that a mixture of species from different successional phases is established in SRF plantations, including shade-tolerant and light-tolerant species (Gustafsson 1988). Although the number of forest species was low in midterm hybrid aspen stands, the significantly higher number of forest species compared with the young stands reflects the fact that forest species are able to colonize and grow in hybrid aspen stands. To evaluate hybrid aspen stands as a habitat for native forest flora, these stands should be resurveyed in the future.

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