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Floristic diversity responses in young hybrid aspen plantations to land-use history and site preparation treatments

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ABSTRACT

Floristic diversity was studied in 7- to 8-year-old commercial hybrid aspen (*Populus tremula* L. × *Populus tremuloides* Michx.) plantations on abandoned agricultural sites with a different land use (grassland or crop field) and site preparation (whole-area ploughing or strip tillage) history. The aim of the study was to investigate how the understorey vegetation had developed in such repeatedly disturbed communities and which environmental variables had significantly affected this. A total of 204 vegetation plots (2 m × 2 m) were established within 51 experimental areas; vegetation descriptions were compiled, concentrations of total N, extractable P and K, and pH of the soil humus layer were determined, and canopy cover of the trees was estimated. Weighted average Ellenberg values for light, moisture, pH, and nitrogen, as well as several life-history characteristics, were calculated for the vegetation plots. Altogether 191 vascular plant species were described: on average 16.7 ± 0.4 species per plot and 28.6 ± 1.1 species per experimental area. Former land use and site preparation method had a significant impact on the position of vegetation plots in detrended correspondence analysis (DCA) ordination, confirmed also by the multiresponse permutation procedure (MRPP). Soil characteristics were significantly correlated with DCA axes. Former land use and site preparation method also affected the species composition. All sites were dominated by competitor species; ruderals were represented in a higher proportion in former fields and whole-area ploughed sites. Species richness and Simpson's diversity index were higher in plantations where strip tillage had been used for site preparation and lower on sites with higher nutrients concentrations in the humus layer. Generally, overstorey vegetation, characterized in the current study using canopy cover, had not started to affect understorey vegetation in young plantations. Application of less intensive site preparation methods is recommended in order to support higher species richness and lower share of ruderal species.

1. Introduction

As a result of the rising demand for timber, pulpwood, bioenergy and several other products from woody plants, the area under forest plantations is continuously increasing in the world (Evans, 2004; FAO, 2005). Further advantages of plantations include the reduction of timber harvested from natural forests and the accumulation of atmospheric carbon in order to slow down global warming. Meanwhile, more attention is paid to the biodiversity of forest plantations, including floral diversity (Moore and Allen, 1999; Hartley, 2002).

Hybrid aspen (*Populus tremula* L. × *Populus tremuloides* Michx.) has received attention in the Baltic Sea region due to its fast growth, cold-hardiness and suitability for the production of pulpwood and bioenergy. It has been recommended as an alternative species for the afforestation of abandoned agricultural lands (Liesebach et al., 1999; Karacic et al., 2003). Recent studies have mainly focused on biomass production, clonal tests, and site-growth relations of hybrid aspen (Yu and Pulkkinen, 2003; Karacic et al., 2003; Rytter and Stener, 2003; Rytter, 2006; Tullus et al., 2007). Studies of floristic diversity have been rare in commercial hybrid aspen plantations in the Baltic Sea region. The floristic diversity of hybrid aspen plantations has been briefly analysed together with other fast-growing poplar plantations on former arable land in Germany (Heilmann et al., 1995) and Sweden (Weih et al., 2003) and in exhausted oil shale quarries in Estonia (Tullus et al., 2008).

Typical secondary successional processes cause changes in the understorey vegetation of forest plantations with additional influences coming from the tree canopy and root-related factors

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(Brockerhoff et al., 2003; Newmaster et al., 2006). Thus, plantation age is associated with plant species composition, richness, and diversity. Young plantations have shown higher species diversity and richness compared to older plantations. This is due primarily to colonization by light-demanding ruderal species, which are suppressed as soon as light availability in the ground layer decreases (Nagaike et al., 2003). Forest species tend to increase in abundance during succession, depending on distance from colonization sources (Dzwonko, 2001; Verheyen et al., 2003). In the current study, we investigated whether the overstorey impact on the understorey vegetation characteristics is significant in young sparsely spaced hybrid aspen plantations on abandoned agricultural land.

Silvicultural treatments used for plantation management also play a significant role in vegetation development (Lindgren and Sullivan, 2001; Nagaike, 2002; Ito et al., 2006; Nagai and Yoshida, 2006), and may even set a plant community back to an earlier successional stage. Site preparation is common practice in the establishment of plantations. Depending on the nature and intensity of the site preparation method, some or the majority of the existing vegetation could be removed, consequently affecting the species richness and diversity of the plant cover (Haeussler et al., 2002; Newmaster et al., 2007). We compared the understorey responses to two site preparation methods with different intensities (strip tillage and whole-area ploughing) in young plantations.

Land use history is another important factor affecting the vegetation of forest plantations (e.g. Ito et al., 2004; Wulf, 2004; Gachet et al., 2007). Former land use impacts soil structure and chemistry, consequently influencing the succession of the understorey, and this effect may remain visible for long periods of time, varying from decades to centuries (Honnay et al., 1999; Graae et al., 2003; De Keersmaker et al., 2004; Falkengren-Grerup et al., 2006). The significant relations between physicochemical soil properties (e.g. moisture conditions, pH, concentrations of the major mineral nutrients) and vegetation traits in plantations have been described in several studies (Ferris et al., 2000; Lu et al., 2006; Prach and Řehounková, 2006). We included the physicochemical soil properties and former land use (crop field or grassland) as potential site factors when explaining the variation in the understorey vegetation characteristics.

The aim of the current study was to investigate how understorey vegetation characteristics in young commercial hybrid aspen plantations are related to previous agricultural land use, site preparation method used for the establishment of these plantations, physicochemical soil properties and overstorey canopy cover. The following hypotheses were formulated:

(i) a less intensive mechanical site preparation method (strip tillage) will support higher vascular plant species richness (S) and diversity (D') compared to full-area ploughing;
(ii) differences in the concentrations of the major mineral nutrients, the acidity of the humus horizon and the moisture condition of the previous field soils will affect vegetation patterns;
(iii) former agricultural land use (crop field or grassland) and site preparation method will affect the species composition;
(iv) the overstorey will influence the understorey vegetation characteristics.

2. Materials and methods

2.1. Study area

The study uses 7- to 8-year-old commercial hybrid aspen plantations established in 1999 and 2000 on former agricultural land mostly in the southeastern and central part of continental Estonia (Fig. 1, Table 1). The land had previously been used as crop fields (number of experimental plots $n = 28$) or grassland ($n = 23$). Before planting 1-year-old micro-propagated hybrid aspens belonging to 27 clones (Tullus et al., 2007), site preparation was carried out. The plantation areas were either ploughed completely ($n = 18$, referred

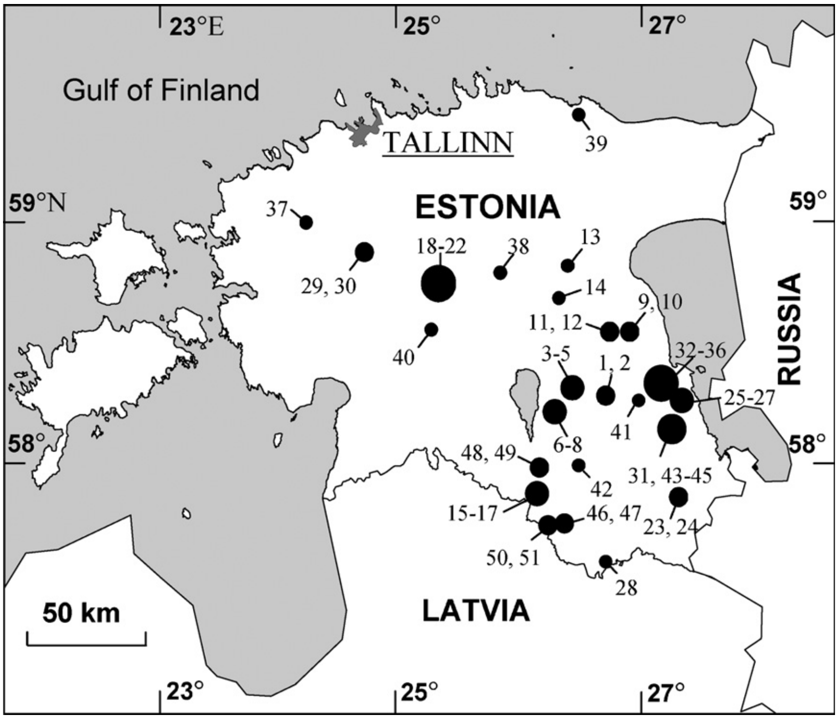

Fig. 1. Locations of the studied hybrid aspen plantations (marked with black dots) and experimental areas (size of the dots is related to the number of experimental areas within the plantations). Numbers of the experimental areas are explained in Table 1.

Table 1
General characteristics of the experimental areas, for the locations on the map please see Fig. 1.

No.	Noltfox ID/exp. no.[a]	Geographic coordinates	Previous land use	Site preparation	Soil moisture condition	Canopy cover of trees (%)
1	101/HHB1	58°16′N; 26°39′E	F[b]	ST[c]	1[d]	19
2	101/HHB2	58°16′N; 26°39′E	F	ST	2	7
3	102/HHB3	58°19′N; 26°33′E	F	WAP	1	63
4	102/HHB4	58°19′N; 26°33′E	F	WAP	1	16
5	102/HHB5	58°19′N; 26°33′E	F	WAP	1	59
6	103/HHB6	58°11′N; 26°18′E	F	WAP	1	33
7	103/HHB7	58°11′N; 26°18′E	G	WAP	2	33
8	103/HHB8	58°11′N; 26°18′E	G	WAP	3	31
9	104/HHB9	58°29′N; 26°54′E	G	WAP	H	35
10	104/HHB10	58°30′N; 26°54′E	G	WAP	1	59
11	105/HHB11	58°30′N; 26°50′E	F	WAP	3	28
12	105/HHB12	58°30′N; 26°50′E	F	WAP	2	18
13	106/HHB13	58°49′N; 26°22′E	G	ST	3	12
14	107/HHB14	58°41′N; 26°19′E	G	WAP	3	41
15	108/HHB15	57°52′N; 26°06′E	G	ST	2	17
16	108/HHB16	57°52′N; 26°06′E	G	ST	2	20
17	108/HHB17	57°52′N; 26°06′E	F	ST	1	29
18	109/HHB18	58°43′N; 25°20′E	F	ST	1	47
19	110/HHB19	58°43′N; 25°20′E	F	ST	2	42
20	110/HHB20	58°43′N; 25°19′E	F	ST	2	13
21	110/HHB21	58°43′N; 25°19′E	F	ST	2	18
22	110/HHB22	58°43′N; 25°20′E	G	ST	1	11
23	111/HHB23	57°52′N; 27°14′E	F	WAP	1	26
24	111/HHB24	57°52′N; 27°14′E	F	WAP	1	11
25	112/HHB25	58°10′N; 27°24′E	G	ST	1	32
26	112/HHB26	58°10′N; 27°24′E	G	ST	2	63
27	112/HHB27	58°10′N; 27°24′E	G	ST	2	30
28	113/HHB28	57°33′N; 26°39′E	G	ST	3	15
29	114/HHB29	58°53′N; 24°41′E	F	WAP	1	31
30	114/HHB30	58°53′N; 24°41′E	F	WAP	1	9
31	115/HHB31	58°07′N; 27°12′E	F	WAP	1	27
32	116/HHB32	58°13′N; 27°18′E	G	ST	1	24
33	116/HHB33	58°13′N; 27°18′E	G	ST	1	7
34	116/HHB34	58°13′N; 27°18′E	G	ST	1	20
35	116/HHB35	58°13′N; 27°19′E	G	ST	3	16
36	116/HHB36	58°13′N; 27°18′E	F	ST	2	5
37	117/HHB37	59°00′N; 24°16′E	G	ST	3	5
38	118/HHB38	58°47′N; 25°51′E	G	ST	1	4
39	119/HHB39	59°29′N; 26°34′E	G	ST	1	6
40	120/HHB40	58°35′N; 25°14′E	G	ST	2	59
41	121/HHB41	58°13′N; 26°57′E	F	ST	1	24
42	122/HHB42	57°58′N; 26°29′E	G	ST	2	38
43	123/HHB43	58°07′N; 27°12′E	F	ST	2	42
44	123/HHB44	58°07′N; 27°12′E	F	ST	3	17
45	123/HHB45	58°07′N; 27°12′E	F	ST	1	21
46	124/HHB46	57°46′N; 26°16′E	F	ST	1	3
47	124/HHB47	57°46′N; 26°15′E	F	ST	1	45
48	125/HHB48	57°54′N; 26°06′E	F	WAP	2	72
49	125/HHB49	57°54′N; 26°06′E	F	WAP	1	25
50	126/HHB50	57°45′N; 26°15′E	G	ST	2	30
51	126/HHB51	57°45′N; 25°15′E	F	ST	1	1

[a] Experimental area identification number according to Noltfox online database (http://noltfox.metla.fi);
[b] F: crop field, G: grassland.
[c] ST: strip tillage, WAP: whole-area ploughing.
[d] Soil moisture regime: 1: automorphic, 2: semi-hydromorphic, 3: hydromorphic, H: histosol.

as whole-area ploughing in the current study), or only furrows marking the tree lines were ploughed ($n = 33$, referred as strip tillage). No chemical vegetation treatment was applied; however, in areas with exceptionally intensive grass growth, the grass was flattened around the trees by foot one or two times during the first season after planting. The former field soils in the study area were mainly auto-, semihydro- or hydromorphic soils with sandy loam and loamy sand dominant profile texture. The soils have been described in detail in a previous study (Tullus et al., 2007).

The average spacing of hybrid aspen plantations was quite even, varying between 1200 and 1600 trees ha^{-1}. In order to study relations between the ground vegetation layer and trees, percentage canopy cover was used, indicating both the light conditions in the ground layer and the growth speed of trees. In the studied young monocultural and evenly structured plantations the overstorey canopy cover was significantly related to the plantation basal area ($R = 0.92$; $p < 0.001$) and the mean height of the trees ($R = 0.91$; $p < 0.001$), confirming the reliability of using canopy cover as a surrogate for plantation productivity. Canopy cover can also be seen as an indirect measure of the root competition intensity with the trees. Due to sparse spacing and considerably variable growth of the trees, it was decided to use canopy cover both as a continuous and categorical effect. The plantations were divided into two groups, with canopy cover above and below 45%, respectively.

2.2. Experimental plots

In the studied hybrid aspen plantations, a long-term network of 51 experimental circle plots (each 0.1 ha) had been previously created for the study and monitoring of growth traits and biomass production of hybrid aspens and tree–soil interactions (Tullus et al., 2007). The centre of each circle plot is marked and, in addition, GPS coordinates have been recorded (Table 1). As part of the current study, four vegetation plots (each 2 m × 2 m) were established within each circle plot and the canopy diameter of all the trees within the circle plots was measured and percentage canopy cover computed. In every vegetation plot a list of vascular plant and moss species was compiled. The total percentage cover of the field and moss layers and the percentage cover of individual species were recorded. The nomenclature follows the atlases of Estonian vascular plants (Kukk and Kull, 2005) and bryophytes (Ingerpuu and Vellak, 1998).

2.3. Soil analysis

In the centre of each vegetation plot, four subsamples were taken from the middle part of the soil humus layer and mixed to form a 0.5-kg composite sample in which $\mathrm{pH_{KCl}}$ and concentrations of total nitrogen (N) and extractable phosphorus (P) and potassium (K) were determined. Analyses were performed by the Laboratory of Agrochemistry of the Agricultural Research Centre in Saku [http://pmk.agri.ee], using methods: pH: ISO 10390; total N: ISO 11261; P, K: Mehlich III. The experimental areas were grouped according to soil moisture conditions (Table 1) based on an earlier study (Tullus et al., 2007).

2.4. Data analysis

Several floristic traits were used to characterize the vascular plants growing in the ground vegetation layer of hybrid aspen plantations. Ellenberg values for light, moisture, pH and nitrogen were assigned to vascular plant species according to Lindacher (1995) and weighted average Ellenberg values were calculated for each plot. Based on the BIOFLOR database (Klotz et al., 2002) covering the biological and ecological traits of the flora of Germany, which includes all the vascular plant species from our study, species were classified by habitat preference into the following categories: forest species, grassland species, forest and grassland species, fallow species, grassland and fallow species. Ecological strategy types (competitors, competitors/ruderals, competitors/stress-tolerators, competitors/stress-tolerators/ruderals and ruderals) were assigned to the studied species according to Grime (2001). Life-span categories (annuals, biennials and perennials) were assigned according to Leht (1999).

The general characteristics were calculated using the data matrix of 204 vegetation plots × 191 vascular plant species. Experimental area 121/HHB41 (four plots) was excluded from further analysis due to the radically different vegetation structure and composition—the area was dominated by *Galega orientalis*, which had been grown there for fodder during the previous land use and which is known as an invasive alien species in Estonia (Kull, 2005). Experimental area 104/HHB9 was excluded from the plant–soil analysis due to the extreme soil conditions (Histosol). Descriptive statistics and Spearman rank correlations between the floristic and environmental variables were calculated with Statistica 7 (StatSoft, Inc., 2004).

Species richness (S) and Simpson's diversity index (D') were estimated for all plots with PCORD-4 (McCune and Mefford, 1999) as follows:

$$\text{Species richness} = n \tag{1}$$

$$\text{Simpson's}\, D' = 1 - \sum (p_i^2) \tag{2}$$

where n is the number of species present in the vegetation sample plot and p_i is the proportion of the sample belonging to the ith species.

The studied variables contained both experimental area and vegetation plot level data. Therefore, a two-level hierarchical model was built in order to evaluate the effect of environmental variables on the vegetation plot level species richness and diversity using PROC MIXED with SAS for Windows 9.1.3 (SAS Institute 2002/2004; Littell et al., 2002) and MLwiN (Goldstein et al., 1998). The normality of S and D' was checked with Kolmogorov–Smirnov and Shapiro–Wilk's tests. The distribution of S did not differ from normal distribution at $p < 0.05$ according to both tests; D' was square-transformed, after which its normality was confirmed using the Kolmogorov–Smirnov test. The concentrations of N, P and K and pH of the soil humus layer were treated as plot-level fixed effects, and soil moisture condition (M), plantation canopy cover (C), previous land use (PLU) and site preparation method (SP) as experimental area level fixed effects. PLU and SP were used as dummy variables. Effect of experimental area was treated as a random variable with normal distribution. As a result, the following model was constructed:

$$\begin{aligned} Y_{ij} &= \beta_0 + \beta_1 \cdot \mathrm{SP}_j + \beta_2 \cdot \mathrm{PLU}_j + \beta_3 \cdot M_j + \beta_4 \cdot C_j + \beta_5 \cdot \mathrm{pH}_{ij} \\ &\quad + \beta_6 \cdot \log N_{ij} + \beta_7 \cdot \log P_{ij} + \beta_8 \cdot \log K_{ij} + u_{0j} + e_{0ij} \end{aligned} \tag{3}$$

where Y_{ij} is the plot level species richness or diversity index, β_0 is the intercept, $\beta_1 \ldots \beta_8$ are the coefficients for the fixed effects at experimental area (j) and plot (ij) level, u_{0j} is the random error at experimental area level: $u_{0j} \sim \mathrm{N}(0,\mathrm{var}(u))$, and e_{0ij} is the random error at plot level: $e_{0ij} \sim \mathrm{N}(0;\mathrm{var}(e))$.

In order to analyse the positioning of vegetation plots along the ordination axes, Detrended Correspondence Analysis (DCA, Hill, 1979) was applied with default options. To interpret the ordination axes, Spearman rank correlations between plot scores and soil variables were calculated. The Kruskall–Wallis test was used to test the significance between group means of DCA axis1 and axis2 scores followed by the Mann–Whitney U-test.

Differences in vascular plant community composition between groups formed on the basis of land use history, site preparation method and canopy cover were also tested with Multiresponse Permutation Procedures (MRPP) using the Euclidean distance measure. Both DCA and MRPP were performed with PCORD-4; species with less than two occurrences were excluded.

The significance of differences in the frequency of occurrence of common vascular plant species between former crop fields vs. grasslands and ploughed vs. furrowed sites was tested using SAS's PROC GENMOD, followed by ESTIMATE statement (chi-square test). The species that were present in at least 10% of all studied vegetation plots (i.e. on >20 plots out of 200) were included.

We applied only statistical methods that did not assume equality of the groups since we had to make some compromises in the experimental design of the study area and relied on earlier site selection as explained in the description of the study area and experimental plots. The mean values are followed by ±standard error in the text. Level of significance $\alpha = 0.05$ was applied in all cases.

3. Results

3.1. General characterization

Altogether 191 vascular plant species were found in 204 sample plots; the mean number of species was 16.7 ± 0.4 per plot, varying between 4 and 30 (Fig. 2). The mean number of species in an experimental area (based on four vegetation plots) was 28.6 ± 1.1 species, varying between 8 and 42. Among all vascular plant species, 59% were typical grassland species, 23% fallow species, 8% forest species, 6% grassland and fallow species, 4% forest and grassland species. As shown in Fig. 3, the majority of the species were half-light species (most frequent Ellenberg value for light was 7), preferring

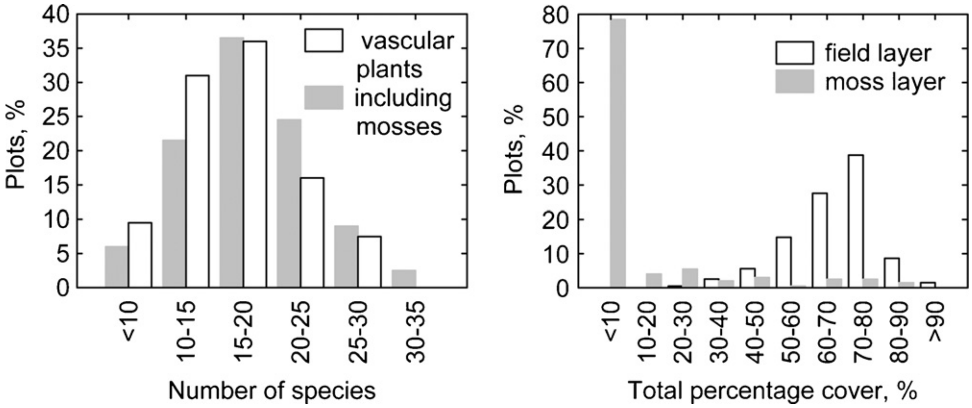

Fig. 2. Distribution of the vegetation plots by number of species and total percentage cover of the field and moss layers.

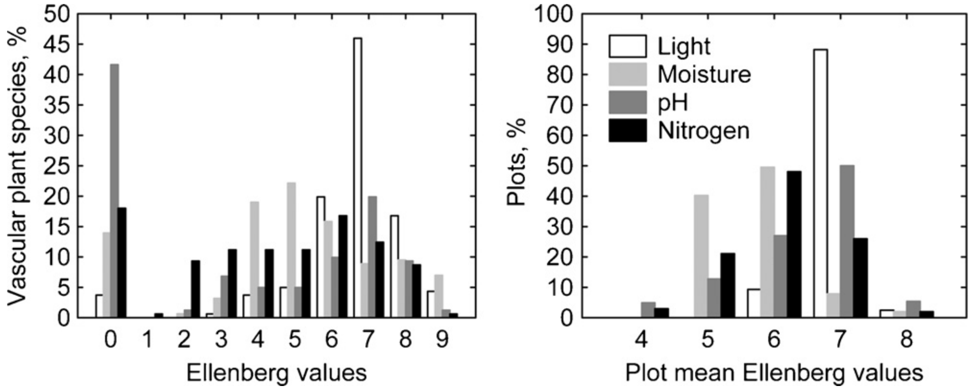

Fig. 3. Distribution of vascular plant species' and plot mean Ellenberg values.

sites with average moisture conditions (most frequent Ellenberg value for moisture was 5). Ellenberg values (except the value for light) showed weak but significant correlations with corresponding environmental variables (Table 2).

The total percentage cover of the field layer varied between 30 and 92%, with an average value of 70.1 ± 0.8% (Fig. 2). It was in significant, although weak correlation with the plantation canopy cover, both when the canopy cover was treated as a continuous variable (Spearman $R = -0.23$, $p > 0.001$) or as a grouping variable ($F_{1,194} = 3.8184$, $p = 0.05$). The mean percentage cover of the field layer in more shaded plantations (canopy cover >45%) was 67.2 ± 1.5% compared to 71.0 ± 1.0% in less shaded ones.

Forty-four bryophyte species were found in the vegetation plots. Moss layer was totally absent in 17 plots and one experimental area. The percentage cover of the moss layer was below 10% in most (79%) of the plots (Fig. 2). In plots with existing moss layer, the mean number of moss species was 2.0 ± 0.1, varying between 1 and 6. The most frequent species (present in >10% of plots) were: *Eurhynchium hians* (35.3% of plots), *Eurhynchium praelongum* (17.2%), *Brachythecium rutabulum* (17.2%), *B. salebrosum* (16.2%), *Brachythecium albicans* (12.3%) and *Plagiomnium cuspidatum* (11.8%). Since the percentage cover and species number of the moss layer were small, it was decided to exclude mosses from further analyses in the current study.

Table 2
Spearman rank order correlations between vegetation plot mean Ellenberg values and corresponding environmental variables.

Ellenberg value	Environmental variable	Spearman *R*	*p*
N	Humus horizon total *N*	0.24	0.001
Light	Canopy cover	0.06	0.406
Moisture	Soil moisture condition	0.21	0.003
pH	Humus horizon pH	0.24	0.001

3.2. Species richness and Simpson's diversity index

According to the model (Table 3), species richness and Simpson's diversity index were influenced by site preparation method. Fewer species appeared in the areas where whole-area ploughing had been applied. 17.9 ± 0.5 species on average were found in strip-tilled sites and 15.3 ± 0.5 species in whole-area ploughed sites; the difference was also confirmed by ANOVA ($F_{1,198} = 11.853$, $p < 0.001$). Higher concentrations of major mineral nutrients in the humus horizon significantly reduced the species richness.

3.3. Vegetation patterns and environmental factors

3.3.1. DCA ordination and MRPP analysis

The position of the vegetation plots in the ordination plot of the first two DCA axes was related to the previous land use and site preparation method and did not differ between the plantations with high (>45%) and low canopy cover (Fig. 4). The ordination axes were correlated with soil moisture, pH$_{\mathrm{KCl}}$, and concentrations of NPK in the humus horizon. The interpretation of DCA was confirmed by MRPP analysis (Table 4).

3.3.2. Species composition

We investigated the frequency of occurrence of 47 typical vascular plant species that were present in at least 10% of all studied vegetation plots (i.e. on >20 plots out of 200) in different site groups according to previous land use and site preparation method (Table 5).

Table 3

Solution for the two-level hierarchical model (SAS's PROC MIXED) describing the effect of environmental variables on vascular plant species richness and Simpson's diversity index, similar results were obtained with MLwiN (data not shown).

Variable	Species richness		Simpson's diversity index	
	F-value	*Pr* > *F*	*F*-value	*Pr* > *F*
Type 3 tests of fixed effects				
Site preparation	4.33	0.039	5.12	0.025
Previous land use	0.26	0.613	0.24	0.625
Soil moisture regime	0.57	0.452	0.28	0.600
Canopy cover	0.09	0.770	0.33	0.565
pH_{KCl}	0.82	0.368	0.74	0.391
Log N	6.36	0.013	5.18	0.024
Log P	4.79	0.030	0.09	0.763
Log K	6.65	0.011	1.14	0.288

Variable	Species richness			Simpson's diversity index		
	Estimate	*t* Value	*Pr* > |*t*|	Estimate	*t*-Value	*Pr* > |*t*|
Solution for fixed effects						
Intercept	34.763	6.58	<0.0001	0.875	3.89	<0.0001
Site preparation effect						
Whole-area ploughing	−2.736	−2.08	0.039	−0.117	−2.26	0.025
Strip tillage	0	–	–	0	–	–
Previous land use effect						
Crop field	−0.646	−0.51	0.613	−0.025	−0.49	0.625
Grassland	0	–	–	0	–	–
Canopy cover	−0.001	−0.29	0.770	−0.001	−0.58	0.565
Humus horizon properties						
Soil moisture regime	−0.685	−0.75	0.452	0.019	0.53	0.600
pH_{KCl}	0.549	0.90	0.368	0.022	0.86	0.391
Log N	−48.965	−2.52	0.013	−1.847	−2.28	0.024
Log P	−3.754	−2.19	0.030	−0.022	−0.30	0.763
Log K	−4.420	−2.58	0.011	−0.082	−1.07	0.288

Covariance parameters	Estimate	*Z*-value	*Pr Z*	Estimate	*Z*-value	*Pr Z*
Experimental area, var(*u*)	13.275	4.14	<0.0001	0.018	3.83	<0.0001
Vegetation plot, var(*e*)	7.657	8.46	<0.0001	0.019	8.51	<0.0001
Observations	196			196		

Life expectancy and Grime strategies were used for species characterization (Fig. 5). On the whole, 85% of these species were perennials (including one tree species) and 15% were annuals or biennials. According to Grime strategies, 47% were competitors, 23% were competitors/stress-tolerators/ruderals, 13% were competitors/stress-tolerators, 11% were competitors/ruderals and 6% were ruderals.

The share of annual or biennial plants was higher among the species occurring more frequently in previous crop fields and whole-area ploughed sites. A similar trend occurred for ruderals. In

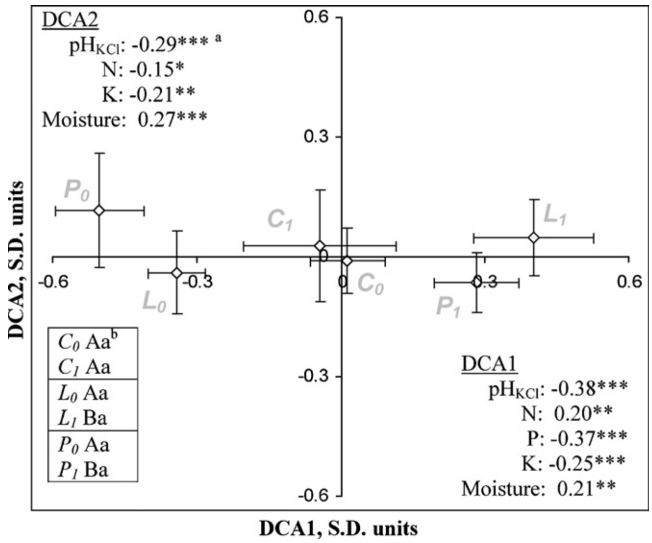

Fig. 4. Group centroids of DCA axis1 (Eigenvalue = 0.63) and axis2 (Eigenvalue = 0.48) scores, whiskers denote standard error of estimate. Group codes: canopy cover of trees: C_0: small, C_1: big; previous land use: L_0: crop field, L_1: grassland; site preparation: P_0: whole area ploughing, P_1: strip tillage. [a]Spearman rank correlations between DCA axis scores and environmental variables, $0.01 < p < 0.05^{*}$; $0.001 < p < 0.01^{**}$; $p < 0.001^{***}$. [b]Capital letters denote significant differences between group mean DCA1 scores and small letters between group mean DCA2 scores as a result of Kruskall–Wallis ANOVA followed by Mann–Whitney *U*-test.

Table 4
Results from MRPP analysis (*T*: test statistic; *A*: chance-corrected within-group agreement).

Factor	*T*	*A*	*p*
Site preparation method	−16.56	0.02	<0.001
Previous land use	−9.97	0.01	<0.001
Plantation canopy cover	−1.63	0.002	0.07

the case of former grasslands and strip-tilled sites, the typical species were perennials with the exception of *Anthriscus sylvestris*. The majority of these species were competitors with no ruderals included.

4. Discussion

4.1. Species richness and diversity

The most important contributors to vascular plant species richness and Simpson's diversity index of the understorey vegetation in young hybrid aspen plantations were site preparation method and concentrations of major mineral nutrients in the humus horizon (Table 3). Species richness was significantly higher in plantations where strip-tillage had been practiced. Obviously, vascular plant cover that had developed after intensive agricultural land-use was left quite undisturbed in the 3–4-m gaps between the furrows, whereas the ploughed strips allowed the colonization of new species. The relation between the intensity of site preparation and its impact on vegetation development has been observed also in other studies (Haeussler et al., 2002; Newmaster et al., 2007). Species richness and diversity were significantly reduced by higher nutrient concentrations in the humus horizon (Table 3). This is in accordance with several fertilization experiments showing that species richness decreases with nutrient addition (e.g. Wilson and Tilman, 2002; Hejcman et al., 2007).

4.2. Species composition and environmental factors

The vascular plant cover of young hybrid aspen plantations was dominated by grassland species and the share of forest plants was small. In general, the scanty occurrence of forest species in the vegetation of fast-growing poplar plantations has been observed both at a young age in Sweden (Weih et al., 2003) as well as in older sparsely spaced plantations in North-East Germany (Zerbe, 2003). The development of vegetation cover is still in a preliminary phase and the observable trends are mostly driven by the disturbances that took place before the establishment of the plantations, including previous agricultural land use and site preparation. An analysis of the occurrence of common vascular plant species (Table 5) suggested that the species composition was related to previous land use and site preparation method. However, it should be pointed out that 78% of the former grassland sites were prepared by strip tillage. This helps to explain why some species occurring mostly in former grasslands were more frequently found in strip-tilled areas. In the case of former fields, both site preparation methods had been applied almost equally. Typical field species (e.g. *Matricaria perforata* and *Myosotis arvensis*) occurred more often in the vegetation cover of plantations established in former fields where whole-area ploughing had been applied for site preparation. Typical grassland species (e.g. *Dactylis glomerata*, *Deschampsia cespitosa* and *Lathyrus pratensis*) dominated in former grasslands and strip-tilled areas (Table 5). All sites were dominated by competitors—common species in productive habitats (Fig. 5). Ruderal species were represented in a higher proportion in former fields and whole-area ploughed sites. These areas can be described as fertile sites, repeatedly disturbed by cultivation activities. In such conditions, the persistence of ruderals was probably supported by their high seed production and the ability of the seeds to remain dormant in the soil for long periods of time (Grime, 2001).

The detrended correspondence analysis (Fig. 4) confirmed the significant impact of previous land use and site preparation method on vascular plant cover in young plantations on abandoned agricultural land. At the same time, it indicated the heterogeneity of the vegetation since the significant differences in group centroids appeared only in the first ordination axes and they were concentrated in a rather small area comprising ±0.5 standard deviation units of the whole variation. Former fields and whole-area ploughed sites stood closer to each other in the negative side of DCA1, as did former grasslands and strip-tilled sites in the positive side. This position could be partly explained by the more frequently used site preparation method for former grasslands, as discussed earlier. Both DCA axes were positively correlated with soil moisture value. In general, moist sites are more often used as grasslands rather than crop fields and grassland sites also appeared in the positive side of DCA1.

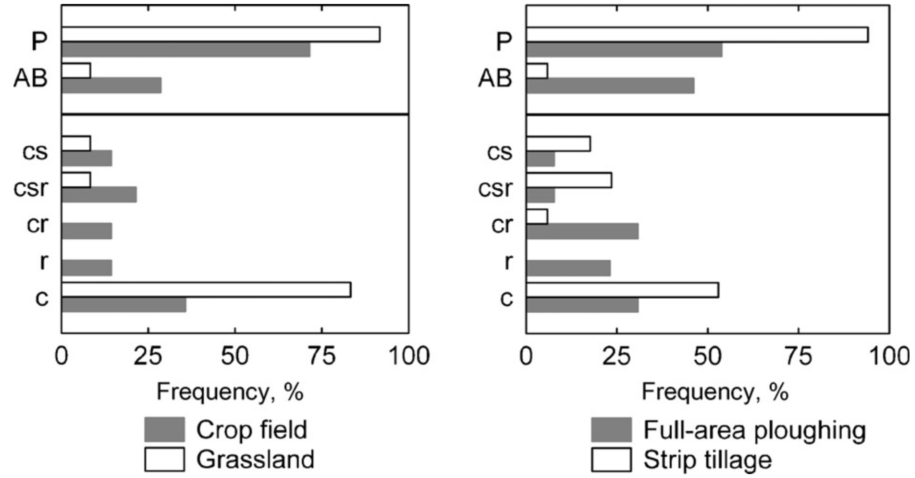

Fig. 5. Life expectancy (AB: annuals and biennials, P: perennials) and Grime strategies (cs: competitors/stress-tolerators, csr: competitors/stress-tolerators/ruderals, cr: competitors/ruderals, r: ruderals, c: competitors) of vascular plant species appearing significantly more frequently at sites with different former land use and site preparation history.

Table 5
The frequency of occurrence of common vascular plant species at sites with different former land use and site preparation history and the significance of differences according to chi-square test. The species that were present in at least 10% of all studied vegetation plots were included.

Vascular plant species	Former land use			Site preparation method		
	Crop field (%)	Grassland (%)	*p*	Whole-area ploughing (%)	Strip tillage (%)	*p*
Achillea millefolium	51	59	0.272	46	59	0.066
Agrostis capillaris	36	36	0.972	21	45	0.001
Agrostis gigantea	38	28	0.149	43	28	0.033
Alchemilla vulgaris (coll.)	11	18	0.144	8	18	0.070
Alopecurus pratensis	3	33	<0.001	13	19	0.256
Anthriscus sylvestris	25	52	<0.001	7	55	<0.001
Artemisia vulgaris	69	34	<0.001	74	41	<0.001
Betula pendula	19	3	0.002	25	5	<0.001
Campanula patula	16	5	0.026	10	12	0.665
Cerastium fontanum	50	35	0.031	60	34	<0.001
Cirsium arvense	81	79	0.704	88	77	0.065
Dactylis glomerata	30	50	0.004	10	55	<0.001
Deschampsia cespitosa	5	28	<0.001	6	21	0.007
Elymus repens	82	75	0.202	88	74	0.030
Epilobium montanum	21	1	0.002	17	9	0.132
Epilobium parviflorum	25	1	0.001	33	3	<0.001
Equisetum arvense	49	48	0.860	38	55	0.020
Fallopia convolvulus	18	10	0.117	22	9	0.014
Festuca pratensis	11	16	0.287	4	19	0.008
Festuca rubra	27	39	0.066	10	45	<0.001
Galium album	23	40	0.010	7	45	<0.001
Gnaphalium uliginosum	34	7	<0.001	33	15	0.003
Hypericum maculatum	15	10	0.287	10	14	0.376
Hypericum perforatum	22	14	0.145	22	16	0.311
Lathyrus pratensis	19	47	<0.001	6	47	<0.001
Leucanthemum vulgare	36	20	0.011	22	32	0.142
Lysimachia vulgaris	11	10	0.760	7	13	0.225
Matricaria perforata	20	7	0.007	22	9	0.014
Mentha arvensis	19	30	0.050	22	25	0.659
Myosotis arvensis	33	14	0.002	50	10	<0.001
Phalaris arundinacea	0	23	0.001	11	10	0.833
Phleum pratense	79	64	0.023	61	78	0.011
Plantago major	12	11	0.797	19	7	0.011
Poa angustifolia	15	36	0.001	15	30	0.025
Poa palustris	16	13	0.590	7	19	0.029
Poa trivialis	22	7	0.003	13	16	0.459
Potentilla anserina	10	20	0.064	6	20	0.012
Ranunculus repens	16	18	0.608	6	23	0.003
Sonchus arvensis	39	30	0.212	47	28	0.007
Stachys palustris	2	22	<0.001	6	14	0.075
Stellaria graminea	21	17	0.488	6	27	0.001
Taraxacum officinale (coll.)	91	78	0.016	89	83	0.252
Trifolium hybridum	26	11	0.009	24	16	0.215
Tussilago farfara	23	28	0.409	26	25	0.829
Veronica chamaedrys	19	32	0.035	7	34	<0.001
Vicia cracca	37	58	0.004	25	59	<0.001
Vicia hirsuta	31	23	0.221	42	19	<0.001

The strongest relations with DCA1 were found for pH_{KCl} and the concentration of phosphorus; DCA2 was more strongly related to soil moisture. The impact of soil moisture and pH on the vegetation are considered to be among the strongest for ecological factors (Hokkanen, 2006; Lu et al., 2006). In our study, the importance of soil moisture, pH, and concentrations of nutrients for the vegetation of young plantations was also confirmed by significant relations between Ellenberg values and the corresponding soil variables (Table 2).

MRPP analysis showed differences between the studied site groups similar to those found with DCA. Nevertheless, the *A* values were very small (Table 4), also indicating a strong within-group heterogeneity.

4.3. Overstorey influence

The typical vascular plant species in young hybrid aspen plantations can be characterized as light-demanding competitive species, which is in accordance with results from other studies in young forests, e.g. Bossuyt and Hermy (2000). We can predict a gradual decrease in their share during the latter successional stages when the understorey light conditions worsen due to increasing canopy cover of the trees. In the vegetation of abandoned agricultural areas, plant species with lower Ellenberg values for light (3–6) are more likely to persist during the succession (Harmer et al., 2001).

In the current study, no significant relation between canopy cover and Ellenberg value for light was found (Table 2), although there was a weak correlation between canopy cover and percentage cover of the field layer. The latter can be explained by the fact that the plantations are young and quite sparsely spaced, so even in plantations with the highest canopy cover (in our study 45–72%), canopy closure had only just started to occur during the last 1–3 years, and it is obvious that the understorey is likely to respond to changes in light availability with some delay, as also pointed out by Brockerhoff et al. (2003).

4.4. Management implications

4.4.1. Plantation forests on abandoned agricultural land: productivity vs. biodiversity

The studied plantations were established on former agricultural land, representing therefore communities repeatedly disturbed by human activities. Anthropogenic disturbances will also continue in the future in the form of short-rotation forestry practices. On the one hand, economic profitability is considered more important than the issue of biodiversity under these circumstances. On the other hand, thorough knowledge of the ecological processes taking place in these conditions is needed to avoid negative impacts on the environment, particularly if the area under short-rotation forestry continues to grow. Ideally, a landowner establishing a forest plantation should also pay attention to the factors influencing biodiversity, and apply appropriate methods (site preparation, tree species selection, silvicultural practices, rotation length) depending on soil properties, land use history, surrounding communities and landscape.

The results of our study supported the commonly known contradiction between the simultaneous achievement of a fast growth rate of the trees together with high species richness and diversity. More fertile sites favour the productivity of the trees but not the species richness of the ground vegetation layer. Poplars and aspens are known as species that prefer fertile sites, especially in short-rotation plantations (Stanturf et al., 2001). Already at an early age, the growth rate of hybrid aspen showed a positive correlation with the concentration of extractable P in the previous field soils (Tullus et al., 2007). We can predict that a high concentration of nutrients in the soil humus layer of fast-growing deciduous plantations will persist during the whole rotation. Affected initially by the fertilization practices during the previous agricultural land use, it will later be influenced by the nutritious aspen leaf litter and N-fixing mycorrhiza.

Although nutrient-rich soil does not support high species richness of the understorey vegetation, site requirements of fast-growing tree species should be met first when establishing forest plantations. High biodiversity of aspen forests is usually related to old economically over-mature stands. Old aspen forests and aspen trees are associated with a great number of bird, mammal, lichen, moss and vascular plant species, including several red-list species (Harestad and Keisker, 1989; Kuusinen, 1994; Hanski, 1998; Degteva, 2005; Hedenas et al., 2006). Thus, putting the biomass production pressure on short-rotation aspen plantations would help to preserve old aspen forests and the related environmental values. At the same time, forest plantations on former agricultural land have been found to increase the floristic diversity of areas dominated by agriculture, indicating the importance of landscape context for the evaluation of short-rotation forestry plantation effects on biodiversity (Weih et al., 2003).

The possible negative environmental impact of large monocultural stands can also be avoided by setting size limits and/or mixing aspen with other tree species, e.g. shade-tolerant *Picea abies* (L.) H. Karst., which creates more versatile conditions for ground vegetation development.

4.4.2. Site preparation impact on early vegetation and stand development

According to the results of our study, species richness was higher in the sites where strip tillage had been applied (Table 3) and there were no ruderals among the species typical of strip-tilled sites (Fig. 5). Less intensive site preparation treatments tend to favour the existing species, whereas more intensive treatments, which destroy or remove the existing vegetation and vegetative reproductive structures, tend to favour ruderal and invasive species (Haeussler et al., 2002). Ruderal species are able to grow in a large variety of sites including areas degraded by human activities. If the goal of the landowner is to support the compositional quality of the understorey vegetation, the spread of ruderals should not be favoured and less intensive site preparation method should be used for establishing forest plantations.

At the same time, the canopy cover of young hybrid aspen plantations, indicating the survival and growth rate, but also the dimensions of the root system of the trees, was significantly higher ($F_{1,49} = 5.6677$, $p = 0.02$) in plantations where whole-area ploughing had been applied (34.2 ± 4.3%), compared to strip-tilled plantations (22.5 ± 2.8%). However, in the long run, strip tillage could also have other advantages, e.g. strip tillage is recommended in order to keep microbiological activity as low as possible and to harmonize N mineralization in the soil and N uptake by trees (Jug et al., 1999).

New descriptions of the study area are planned in order to clarify how the impact of site preparation on the under- and overstorey of hybrid aspen plantations changes in time and to discover when a clearer distinction between plant community types, depending on the effects of stand development and soil conditions, will emerge.

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