

Change from agriculture to forestry: floristic diversity in young fast-growing deciduous plantations on former agricultural land in Estonia

Tea Soo^{1,*}, Arvo Tullus¹, Hardi Tullus¹, Elle Roosalu² & Aivo Vares³

¹ *Department of Silviculture, Institute of Forestry and Rural Engineering, Estonian University of Life Sciences, 5 Kreutzwaldi St., Tartu 51014, Estonia (*corresponding author's e-mail: tea.soo@emu.ee)*

² *Department of Botany, Institute of Ecology and Earth Sciences, University of Tartu, 40 Lai St, Tartu 51005, Estonia*

³ *Seed and Plant Management Department, State Forest Management Centre, 2 Rõõmu tee St., Tartu 51013, Estonia*

Received 27 Aug. 2008, revised version received 14 Jan. 2009, accepted 23 Jan. 2009

Soo, T., Tullus, A., Tullus, H., Roosalu, E. & Vares, A. 2009: Change from agriculture to forestry: floristic diversity in young fast-growing deciduous plantations on former agricultural land in Estonia. — *Ann. Bot. Fennici* 46: 353–364.

The understorey vascular plant cover and its relations with the overstorey tree species and site properties in young silver birch and hybrid aspen plantations were studied. Understorey vegetation was similar in both plantation types in terms of species richness, diversity, sensitivity to human impact, life-span and habitat preference. Nevertheless, in denser silver birch plantations some signs indicated a faster vegetation development overall, e.g., a higher share of shade tolerant plant species. The concentration of total N was higher in the humus layer of silver birch plantations consequently affecting the nutritional status of the understorey vegetation. The significant impact of the plantation type on the understorey vegetation was confirmed by the NMDS analysis. The hypothesis that semi-exotic hybrid aspen plantations may support the spread of alien species or may show a tendency towards smaller indigenous species richness was not confirmed. Irrespective of the overstorey tree species, a strong previous land use impact, i.e. disturbance history, on the ground vegetation was eminent.

Key words: abandoned agricultural land, biodiversity, hybrid aspen, plantation forestry, silver birch, understorey vegetation

Introduction

Forest plantations with fast-growing deciduous trees have been established in hemiboreal Estonia during the last two decades similarly to the other Baltic Sea region countries. At an early

age, deciduous trees tend to exceed conifers in biomass productivity in this region (Weih 2004). Traditionally deciduous trees have been disfavoured when managing the conifer dominated forests, however, according to the Centre of Forest Protection and Silviculture (2008),

the share of deciduous trees in the growing stock of Estonian forests has risen during the last half-century. On one hand, typical hardwood species (birches, alders and aspens) have become economically more valuable as pulpwood, timber and bioenergy resources since the late 20th century. On the other hand, the share of deciduous tree species has increased as a consequence of natural afforestation of abandonment of agricultural land, since several of them e.g. birches, grey alder and willows are pioneer species at such sites. Agricultural land use has fallen drastically in Estonia during the last decades. Due to political, economical and social changes, one third of the arable land was abandoned at the beginning of the 1990s (Peterson & Aunap 1998). However, natural afforestation is usually a slow and spatially uneven process. Therefore, the establishment of forest plantations with fast growing deciduous trees is recommended as an alternative land use for such areas. At the same time all long-term nature manipulations including management of forests and forest plantations should nowadays be analysed in the light of the predicted climate change. The impact of climatic factors on biodiversity of temperate European ecosystems has been found to be highly significant whereas in the case of vascular plant species richness land use intensity also plays an important role (Dormann *et al.* 2008). Modeling of the impact of climate change on boreal forests has suggested that the biomass productivity of both conifer and deciduous tree species should rise in general (Briceno-Elizondo *et al.* 2006, Garcia-Gonzalo *et al.* 2007). A vegetation shift in a northerly direction is probably going to affect the species composition (Kullman 2008, Morin *et al.* 2008). For hemiboreal forests it means an increasing share of deciduous tree species.

Several hundred hectares of hybrid aspen (*Populus tremula* × *P. tremuloides*) and silver birch (*Betula pendula*) plantations have recently been established in Estonia (Jögiste *et al.* 2003, Tullus *et al.* 2007). Hybrid aspen has proved to be one of the fastest growing deciduous trees in the Nordic countries, being also sufficiently cold resistant (Yu *et al.* 2001, Weih 2004, Rytter 2006). The recommended rotation period for hybrid aspen is 20–30 years, because up to this age the growth speed of hybrid aspen consider-

ably exceeds its parent species (Heräjärvi & Junkkonen 2006). Silver birch reaches bulk maturity in plantations in 30–40 years.

The increasing area under short-rotation forest plantations also means that their ecological impact is growing. The current study focuses on the vascular plant cover in young hybrid aspen and silver birch plantations on former agricultural land. The understorey vegetation of deciduous plantations on abandoned agricultural land in the boreal vegetation zone is a quite scantily researched topic (Gustafsson 1988, Heilmann *et al.* 1995, Weih *et al.* 2003, Soo *et al.* 2009). Forest plantations on abandoned agricultural land represent associations that have been repeatedly disturbed by human activities during the course of time. Species composition of understorey vegetation is affected by the previous land use (Ito *et al.* 2004, Gachet *et al.* 2007) and the intensity of site preparation and weed control before plantation establishment (Haeussler *et al.* 2004, Miller & Chamberlain 2008). Soil seed bank may influence understorey species composition as well (Zobel *et al.* 2007), although its role in old field forest succession is hardly studied. The anthropogenic impact continues via plantation management activities accompanied by the environmental impact from climate change. During the course of understorey vegetation development in forest plantations, the impact from overstorey trees will gradually rise in the form of intensifying light and root competition, formation of litter layer and consequent changes in physicochemical and biological properties of the humus layer, which in turn may depend on the tree species (Sydes & Grime 1981a, 1981b, Prescott 2002, Janišová *et al.* 2007). The impact of tree species on understorey vegetation is generally acknowledged (Légaré *et al.* 2001, Augusto *et al.* 2003, Qian *et al.* 2003, van Oijen *et al.* 2005). Overstorey composition and structure influence understorey vegetation by changing resource availability (light, water and soil nutrients) and through the physical effects of the litter layer (for detailed literature review see Barbier *et al.* 2008). According to some studies deciduous trees support higher understorey diversity than conifers in the boreal zone (e.g. Wallrup *et al.* 2006). There are fewer comparative studies about differences in ground

vegetation under different deciduous or different coniferous tree species.

As an important feature of the current study, besides investigating and comparing the understorey vegetation under two economically important deciduous tree species in young plantations we are also comparing vegetation characteristics under silver birch as an indigenous tree species and under hybrid aspen as a semi-exotic species (*P. tremula* is indigenous, *P. tremuloides* originates from North America). Although *P. tremula* and *P. tremuloides* are biologically similar species, some ecological differences have been observed between *P. tremula* and hybrid aspen in Scandinavia and the Nordic countries, which are partly associated with the North-American parent of the hybrid. These differences are related to the phenology and growth speed during the first 15–20 years (Yu *et al.* 2001, Heräjärvi & Junkkonen 2006), different susceptibility to some pests and diseases including those previously not recorded on *P. tremula* but common to *P. tremuloides* (Kasanen *et al.* 2002), differences in the viability of seeds from inter- and intraspecific crosses (Suvanto & Pulkkinen 2004). Thus, from environmental point of view it is important to find out whether hybrid aspen plantations could provide somewhat different site for understorey vegetation as compared with indigenous tree species. In regions, where a great number of various exotic tree species are cultivated, differences between understorey vegetation in indigenous and exotic tree species plantations have also been observed. Sometimes the ground vegetation of exotic plantations incorporates a higher share of exotic plant species (Brockerhoff *et al.* 2003, Mascaro *et al.* 2008, Paritsis & Aizen 2008).

The main research questions of the study were: (i) Are there any significant differences in vascular plant species richness, diversity, composition and ecological characteristics in the ground vegetation layer between young silver birch and hybrid aspen plantations growing on abandoned agricultural land? (ii) Which site and stand related factors have affected the vegetation characteristics? (iii) Does semi-exotic hybrid aspen offers suitable habitat for indigenous vascular plant species, comparable with domestic silver birch?

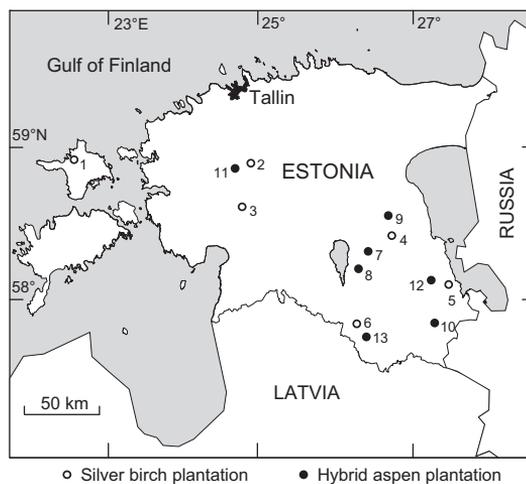


Fig. 1. Locations of the experimental areas. Experimental area numeration is explained in Table 1.

Material and methods

Study area

The study was carried out in 7- to 9-year-old silver birch and hybrid aspen plantations that had been established in 1999 and 2000 on abandoned agricultural land in Estonia. One-year-old silver birch seedlings and micropropagated 1-year-old hybrid aspen plants belonging to 27 different clones had been used as planting material. In order to reduce the heterogeneity of the study area we selected from the network of long-term experimental areas in hybrid aspen and silver birch plantations (Jõgiste *et al.* 2003, Tullus *et al.* 2007) only plantations established on former crop fields, where whole-area ploughing had been used for site preparation. As a result six silver birch and seven hybrid aspen plantations were included in the study (Fig. 1 and Table 1).

Four vegetation plots (each 2 × 2 m) were established within each experimental area. In every vegetation plot a list of vascular plant species was compiled. The total percentage cover of the field layer and percentage cover of individual species were recorded. The nomenclature follows the atlas of the Estonian flora (Kukk & Kull 2005). In order to characterize the impact of trees on the understorey vegetation, diameter of the stem at breast height (DBH) of all the trees within the experimental areas was measured and

plantation basal area (BA) per hectare was estimated (Table 1).

Soil analysis

In the centre of each vegetation plot, a soil sample was taken from the middle part of the humus horizon, from which 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, using methods: ISO 10390 for pH, ISO 11261 for total N, and Mehlich III for P and K. The experimental areas were grouped according to soil moisture conditions (Table 1) according to earlier studies (Jögiste *et al.* 2003, Tullus *et al.* 2007).

Data analysis

Ellenberg indicator 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), species were classified by habitat preference into the following categories:

forest species, grassland species, fallow species and intermediate types. Life-span categories were assigned to the studied species according to Leht (1999). The status of the species in Estonian flora (native *vs.* alien) was determined based on Kukku and Kull (2005). According to their sensitivity to human impact the studied plant species were divided into the following groups: apophytes, hemeradiaphores and anthropophytes. Apophytes prefer moderate to strong human impact and communities changed by human activities. Hemeradiaphores are indifferent to a certain degree of human activities; such plants are often found in communities with little human influence. Anthropophytes are very rare in natural communities surviving only in communities significantly changed by human activities, e.g. arable weeds (Kukku 1999).

Species richness (S) and Simpson's diversity index (D') were estimated for all plots with PCORD-4 (McCune & Mefford 1999). In order to investigate how environmental variables (overstorey tree species, stand basal area, soil moisture conditions, N, P, K and pH of the soil humus layer) corresponded to the understorey vegetation, non-metric multidimensional scaling (NMDS) with the community ecology package Vegan 1.15–1 for R (Oksanen *et al.* 2008) was performed. The analysis was run with three data sets: all observations together and both plantation types

Table 1. Main characteristics of the experimental areas (DBH = diameter of the stem at breast height, BA = basal area), for the locations on a map *see* Fig. 1. Letters denote significant differences of means determined by Tukey HSD test ($p < 0.05$) after one-way ANOVA.

No.	Experimental area ID	Geographic coordinates	Tree species	Soil	Density (trees ha ⁻¹)	DBH (cm)	BA (m ² ha ⁻¹)
1	Reigi	58°59' N, 22°32' E	Silver birch	Automorphic	1570	2.0 ± 0.2 ^a	0.7
2	Nadalama	58°54' N, 24°54' E	Silver birch	Automorphic	3070	5.5 ± 0.2 ^{cd}	7.7
3	Viluvete	58°39' N, 24°51' E	Silver birch	Hydromorphic	2950	4.1 ± 0.1 ^b	4.1
4	Kõrveküla	58°26' N, 26°45' E	Silver birch	Automorphic	1340	3.7 ± 0.2 ^b	1.6
5	Sillapää	58°05' N, 27°26' E	Silver birch	Automorphic	1960	4.5 ± 0.2 ^b	3.5
6	Rampe	57°52' N, 26°12' E	Silver birch	Automorphic	1790	3.6 ± 0.3 ^{ab}	2.0
7	102/HHB5*	58°19' N, 26°33' E	Hybrid aspen	Automorphic	1280	5.5 ± 0.2 ^d	3.5
8	103/HHB6*	58°11' N, 26°18' E	Hybrid aspen	Automorphic	1180	4.7 ± 0.1 ^{bc}	2.1
9	105/HHB11*	58°30' N, 26°50' E	Hybrid aspen	Hydromorphic	1130	4.4 ± 0.1 ^b	1.8
10	111/HHB23*	57°52' N, 27°14' E	Hybrid aspen	Automorphic	940	4.1 ± 0.1 ^b	1.4
11	114/HHB30*	58°53' N, 24°41' E	Hybrid aspen	Automorphic	1170	1.7 ± 0.1 ^a	0.4
12	115/HHB31*	58°07' N, 27°12' E	Hybrid aspen	Automorphic	880	4.2 ± 0.2 ^b	1.4
13	125/HHB48*	57°54' N, 26°06' E	Hybrid aspen	Semi-hydromorphic	1190	5.9 ± 0.2 ^d	3.7

* Experimental area identification number according to Noltfox online database (<http://noltfox.metla.fi>).

separately. In order to explain the ordination, the environmental vectors and a factor (plantation type) were fitted onto the NMDS plots, using the function ‘envfit’ (Oksanen *et al.* 2008).

The *t*-test was used to test the differences in the group means of experimental area level variables between silver birch and hybrid aspen plantations. The normality of these variables was checked with Shapiro-Wilk’s test. In order to compare variables estimated at the vegetation plot level, a MIXED model was applied, with experimental area treated as a random effect using SAS 9.1.3 (SAS Institute Inc., Cary, NC, USA). The significance of differences in the distribution of vascular plant species into ecological groups between hybrid aspen and silver birch plantations was tested using the chi-square test (SAS’s PROC GENMOD followed by ESTIMATE statement). In the text, the mean values are followed by \pm standard error. Differences are considered significant at $\alpha = 0.05$.

Results

Altogether 84 vascular plant species were found in the studied vegetation plots in hybrid aspen

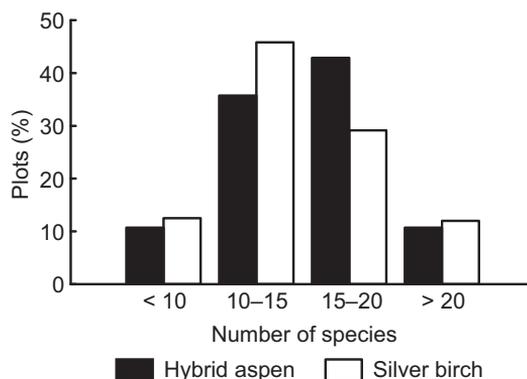


Fig. 2. Distribution of the vegetation plots by number of vascular plant species in silver birch and hybrid aspen plantations.

plantations and 83 species in silver birch plantations, the total number of species was 114. The mean species richness on a sample plot was 15.8 ± 0.7 species, varying between 8 and 32 species. In an experimental area (each comprising four plots) 26.9 ± 1.9 species were found on average, varying between 20 and 42 species. Both vegetation sample plot and experimental area level species richness and diversity were similar in silver birch and hybrid aspen plantations (Fig. 2 and Table 2). Neither did the plot mean Ellen-

Table 2. Comparison of ecological characteristics in silver birch and hybrid aspen plantations.

Variable	Hybrid aspen	Silver birch	<i>t</i>	Pr > <i>t</i>
Estimated for each experimental area (<i>t</i>-test)				
Trees (ha ⁻¹)	1110 \pm 55	2113 \pm 296	-3.60	0.004
BA (m ² ha ⁻¹)	2.04 \pm 0.45	3.25 \pm 1.02	-1.14	0.278
DBH (cm)	4.35 \pm 0.51	3.90 \pm 0.47	0.63	0.544
Total species richness	27.14 \pm 2.08	26.67 \pm 3.45	0.12	0.905
Estimated for each vegetation plot (MIXED model)				
Soil humus layer properties				
pH	6.01 \pm 0.15	6.00 \pm 0.18	0.03	0.973
Total N (%)	0.12 \pm 0.01	0.18 \pm 0.01	-1.99	0.050
Extractable P (mg g ⁻¹)	93.32 \pm 9.53	126.79 \pm 27.53	-0.63	0.535
Extractable K (mg g ⁻¹)	122.00 \pm 10.01	173.58 \pm 18.86	-1.40	0.170
Vegetation traits				
Total cover	64.57 \pm 3.02	68.58 \pm 3.44	-0.54	0.594
Species richness	15.50 \pm 0.72	16.21 \pm 1.22	-0.32	0.749
Simpson’s diversity index	0.69 \pm 0.03	0.76 \pm 0.02	-1.01	0.317
Ellenberg values				
Light	7.10 \pm 0.06	6.96 \pm 0.08	0.97	0.339
Light (3–6), percentage of plants	16.92 \pm 1.42	24.74 \pm 1.68	-2.55	0.015
Light (7–9), percentage of plants	76.18 \pm 1.80	68.97 \pm 1.80	2.17	0.036
Moisture	5.71 \pm 0.15	5.73 \pm 0.09	-0.06	0.950
pH	6.63 \pm 0.21	6.20 \pm 0.19	0.83	0.412
Nitrogen	6.08 \pm 0.15	6.31 \pm 0.13	-0.66	0.513

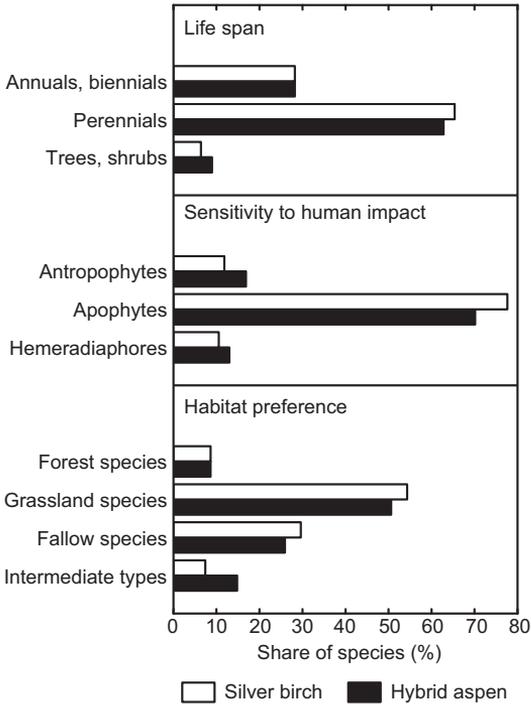


Fig. 3. Distribution of vascular plant species into ecological groups in silver birch and hybrid aspen plantations.

berg values for light, moisture, pH and nitrogen depend on the overstorey species. However, a significantly higher share of shade tolerant species (Ellenberg value 3–6) was found in silver birch plantations and a higher share of half-light and light species (Ellenberg value 7–9) in hybrid aspen plantations (Table 2). The species list of most frequent vascular plant species (present in > 10% of plots), their frequency and mean percentage cover in all plots, and separately in both studied plantation types, is presented in the Appendix.

Among the studied experimental area level characteristics, only plantation density was significantly related to the overstorey tree species, being higher in silver birch plantations. The concentration of total N in the soil humus layer of the vegetation plots was significantly higher in silver birch plantations; other observed soil properties were similar under both species (Table 2).

According to the chi-square test no significant differences were found in the distribution of vascular plant species into habitat preference,

sensitivity to human impact, and life span groups between hybrid aspen and silver birch plantations. All experimental areas were dominated by species belonging to similar ecological groups (perennials, grassland species, apophytes) (Fig. 3).

The NMDS ordination did not reveal any considerable groupings of the data. Approximately half of the vegetation plots from both plantation types were situated in the same area in the ordination diagram (Fig. 4A). However, the impact of the overstorey species was statistically significant (Table 3). The soil related variables had significantly affected the positioning of the vegetation plots in the ordination diagram of the whole study area (Fig. 4A) as well as in both plantation types (Fig. 4B and C). As the main difference between the two plantation types, stand basal area was significantly related to the understorey vegetation in silver birch plantations (Fig. 4B) but not in hybrid aspen plantations (Fig. 4C).

Discussion

The understorey vegetation of the studied young silver birch and hybrid aspen plantations was dominated by perennial grassland species irrespective of the overstorey tree species (Fig. 3). This is in accordance with other studies stating that during the transition from agricultural to forest land the ground vegetation will remain different from typical forest vegetation for a long period (Gachet *et al.* 2007). Vascular plant species typical to open-sites will persist. The addition of forest species may be hindered and may be a very long term process governed by dispersal limitations and habitat quality (e.g soil properties) in new forests (Honnay *et al.* 1999, Graae *et al.* 2003, De Keersmaker *et al.* 2004, Flinn & Vellend 2005). The high share of grassland species shows their high inertness and durability in the changing light conditions. However, further studies are needed in order to clarify the share of generative and vegetative individuals among grassland and forest species in relation to plantation density and basal area.

As expected no hemeraphobs (species severely disturbed by human activities) were found from plantations representing communi-

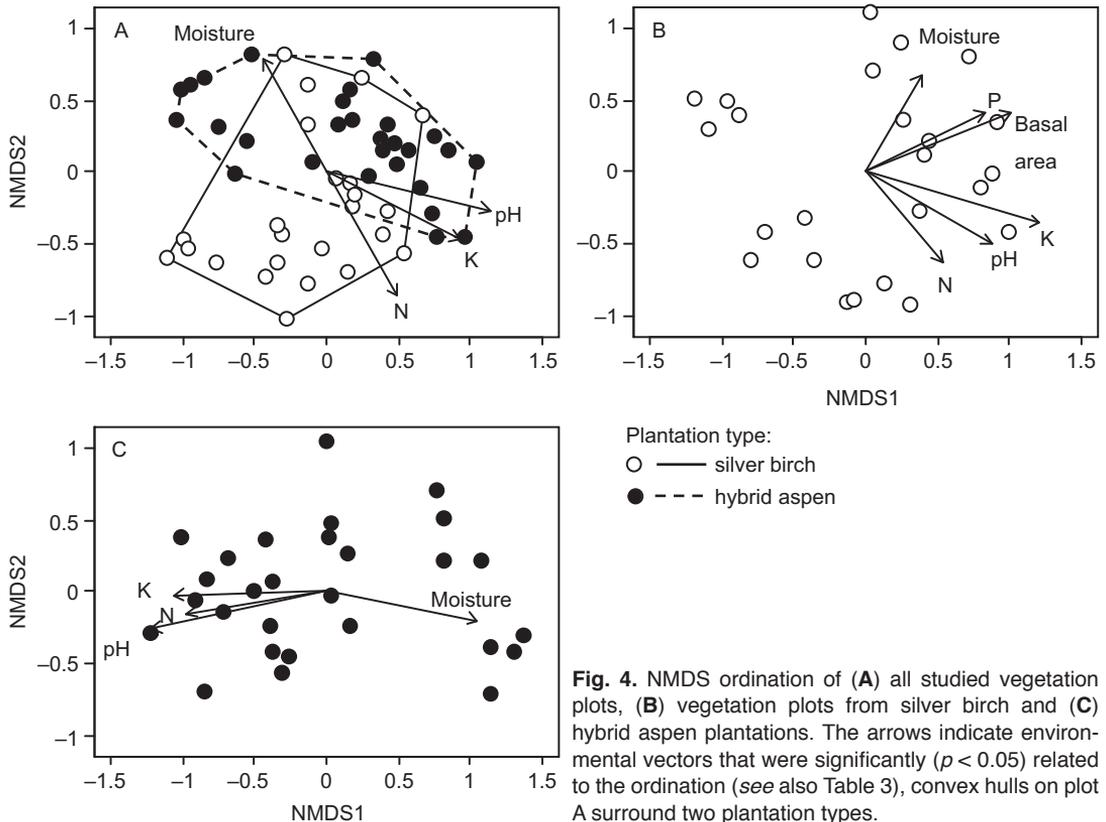


Fig. 4. NMDS ordination of (A) all studied vegetation plots, (B) vegetation plots from silver birch and (C) hybrid aspen plantations. The arrows indicate environmental vectors that were significantly ($p < 0.05$) related to the ordination (see also Table 3), convex hulls on plot A surround two plantation types.

ties repeatedly disturbed by human activities (Fig. 3). The studied vegetation was dominated by apophytes which are common to semi-natural communities. The share of hemeradiaphores and anthropophytes was roughly equal. It can be expected that during the following succession, as the impact of previous disturbances decreases, the share of hemeradiaphores is going to rise and the share of anthropophytes will diminish.

As one of the main objectives, the influence of overstorey tree species on the understorey vegetation was studied. Based on the results (Fig. 4, Tables 2 and 3), the overstorey impact has been weaker than that of soil properties. Similar findings have been reported in other studies, showing that the identity of canopy species may be less important than other factors like stand age and site properties (Geldenhuys 1997, Brockerhoff

Table 3. Significance of environmental variables fitted onto NMDS ordination

Environmental variable	Both plantation types		Silver birch plantations		Hybrid aspen plantations	
	r^2	Pr ($> r$)	r^2	Pr ($> r$)	r^2	Pr ($> r$)
Overstorey species	0.14	0.001	–	–	–	–
Basal area	0.05	0.339	0.51	0.001	0.02	0.789
Moisture	0.29	< 0.001	0.26	0.037	0.58	< 0.001
pH	0.48	< 0.001	0.44	0.005	0.78	< 0.001
N	0.35	0.001	0.29	0.038	0.49	< 0.001
P	0.10	0.072	0.37	0.004	0.03	0.672
K	0.38	< 0.001	0.69	< 0.001	0.57	< 0.001

et al. 2003). Légaré *et al.* (2001) showed that species richness, evenness and diversity did not vary significantly with forest overstorey composition, although it had influenced understorey composition. Also in the current study species richness and diversity were similar in both plantation types and a significant but weak relationship between overstorey species and understorey vegetation composition was observed (Fig. 4A and Table 3). It must be pointed out that the studied plantations were rather young and much stronger impact from overstorey tree species can be expected at higher age. The main differences observed in the vegetation characteristics between 7- to 9-year-old silver birch and hybrid aspen plantations could rather be attributed to the differences in stand densities (Table 1), which are associated with different planting densities recommended for establishing hybrid aspen and silver birch plantations in the region. For example the share of shade tolerant vascular plant species (Ellenberg value for light 3–6) was higher under silver birches and the share of half light and light species (Ellenberg value for light 7–9) was higher under hybrid aspens (Table 2). Denser stand means faster canopy closure in young plantations and consequently diminishing light conditions for the understorey layer. A significant relation between stand basal area and ground vegetation existed in silver birch plantations but not in two times sparser hybrid aspen plantations (Fig. 4B and C, Table 3). Light conditions in the ground vegetation layer depend on stand basal area and the canopy light transmittance, which in turn may differ among tree species (Messier *et al.* 1998, Comeau *et al.* 2006). Birches and aspens are both light-demanding fast-growing deciduous trees and although their crown architecture is somewhat different, it can be assumed that understorey light conditions in plantations with similar density and basal area are rather similar.

Another significant tree-species-related difference in the current study was the higher concentration of total N in the soil humus layer under silver birch plantations (Table 2). The concentrations of extractable P and K also tended to be higher in the humus layer of silver birch plantations, although these differences were not statistically significant. In the ordination diagram (Fig. 4A), the total N vector pointed to

the direction where only vegetation plots from silver birch plantations were presented. Two times denser silver birch plantations produce probably more leaf and root litter than the studied hybrid aspen plantations in a young age. This in turn affects nutrient concentrations in the humus layer. According to several studies the soil microbial activity and the annual rate of net nitrogen mineralization have been found to be high in birch stands compared to conifers or abandoned grassland (Smolander *et al.* 2005, Kanerva & Smolander 2007, Uri *et al.* 2008). However the concentration of total N in the humus layer of the studied former field soils could also have been affected by different fertilization practices during the previous agricultural land use. The vegetation plot mean Ellenberg value for N tended to be higher in silver birch plantations, but this difference was not significant at $p < 0.05$. It can be concluded that denser silver birch plantations start to affect nutrient concentrations in the soil humus layer, and consequently the nutritional status of the ground vegetation, sooner than sparser hybrid aspen plantations. Such a difference is likely to become less pronounced over the course of time, as faster growing hybrid aspen catches up with birch in terms of litter quantity.

As part of the study, the ground vegetation in silver birch and hybrid aspen plantations was analysed from the indigenous *vs.* semi-exotic tree species comparison point of view. No alien vascular plant species were found in the ground vegetation of hybrid aspen plantations. According to previous experience, forest plantations can be established in Estonian conditions without considerable risks of creating favourable habitat for new or previously introduced plant species, contrarily to the situation in some other world regions, e.g. New Zealand and Hawaii (Brockerhoff *et al.* 2003, Mascaro *et al.* 2008). In Estonia the extensive dispersal of introduced plant species is hindered by the lack of large-scale open communities and the temperate climate, which means rather slow plant growth (Kukk 1999). At the same time, final conclusions should be drawn cautiously, because the studied plantations were young, and the following vegetation development must show if and when typical forest species will start to appear and if the

semi-exotic tree species plantation can sustainably provide habitat similar to indigenous tree species. In the long run, however, the most serious environmental hazard will probably be that the exotic tree species itself turns invasive and spreads out from plantations, and/or crosses with endemic representative from the same genus (Suvanto & Pulkkinen 2004). Also possible mass propagation of new or so far less important pests and diseases could occur (Kasanen *et al.* 2002).

The significantly higher density of silver birch plantations did not result in significantly higher mean BA, although it was approximately 1 m² (1.6 times) higher in silver birch plantations. The mean DBH of hybrid aspens was 10% higher as that of silver birches, however the difference was statistically not significant (Table 2). At the same time hybrid aspens had shown individually faster growth while the mean DBH exceeded 4 cm at six out of seven study sites in hybrid aspen plantations and only at three out of six study sites in silver birch plantations (Table 1). The higher planting density for silver birch is recommended for several reasons. It promotes natural pruning ensuring better stemwood quality at final harvest. Silver-birch saplings are less expensive than micropropagated hybrid aspens. Finally, it also helps to compensate the possible loss of trees due to browsing and other damages, which could become a more serious problem in sparse hybrid aspen plantations. On the other hand it results in the need for thinning already at the end of the first decade, otherwise natural competition-driven self-thinning can be expected. Silvicultural practices often impose a disturbance for understorey vegetation development. In the light of the findings from the current study, it brings about a controversy: denser fast-growing silver birch plantations provide conditions for quicker ground vegetation development but also mean additional disturbance in the form of thinning, which as a rule is not planned in the first generation hybrid aspen plantations.

Conclusions

The understorey vascular plant cover in young silver birch and hybrid aspen plantations on abandoned agricultural land was similar in terms

of species richness, diversity and ecological characteristics. The anthropogenic disturbances from the previous agricultural land use were recognizable in the floristic traits of the ground vegetation 7–9 years after the plantations were established.

Soil variables as well as overstorey species had significantly affected the understorey vegetation in young deciduous plantations. However, the overstorey impact could mainly be explained by differences in stand densities rather than tree species. In denser silver birch plantations some signs indicated the overall faster development of the ground vegetation, for example, the share of shade tolerant species was higher and the share of half-light and light species was smaller. Also the concentration of total N in the soil humus layer was higher in silver birch plantations, indicating larger litter quantities and higher annual N mineralisation rate. At the same time, the higher density of silver birch plantations brings about the need for thinning, consequently disturbing the ground vegetation, which is something that is not planned during the first rotation in hybrid aspen plantations.

The fact that hybrid aspen is a semi-exotic species did not result in any environmentally unfavourable developments in the understorey vegetation characteristics. No alien species were found and both plantation types had provided similar habitat for indigenous vascular plant species during the first decade after establishment.

Monitoring of the following successional development is planned in the studied vegetation plots in order to provide data on how and when the impact from previous land use, overstorey tree species, physicochemical soil properties and plantation management activities will influence the understorey vegetation in fast growing forest plantations.

Acknowledgements

The study was supported by the Estonian Science Foundation (grant no. 7298) and the Centre of Renewable Energy of the Estonian University of Life Sciences. The authors would like to thank professor Martin Zobel and two anonymous reviewers for valuable comments on the earlier version of the manuscript and Mr. Ilmar Part for linguistic revision of the manuscript.

References

- Augusto, L., Dupouey, J.-L. & Ranger, J. 2003: Effects of tree species on understory vegetation and environmental conditions in temperate forests. — *Annals of Forest Science* 60: 823–831.
- Barbier, S., Gosselin, F. & Balandier, P. 2008: Influence of tree species on understory vegetation diversity and mechanisms involved — a critical review for temperate and boreal forests. — *Forest Ecology and Management* 254: 1–15.
- Briceno-Elizondo, E., Garcia-Gonzalo, J., Peltola, H., Matala, J. & Kellomäki, S. 2006: Sensitivity of growth of Scots pine, Norway spruce and silver birch to climate change and forest management in boreal conditions. — *Forest Ecology and Management* 232: 152–167.
- Brockerhoff, E. G., Ecroyd, C. E., Leckie, A. C. & Kimberley, M. O. 2003: Diversity and succession of adventive and indigenous vascular understory plants in *Pinus radiata* plantation forests in New Zealand. — *Forest Ecology and Management* 185: 307–326.
- Centre of Forest Protection and Silviculture. 2008: *Aastaraamat Mets 2007 [Yearbook Forest 2007]*. — Tartu. [In Estonian with English summary].
- Comeau, P., Heineman, J. & Newsome, T. 2006: Evaluation of relationships between understory light and aspen basal area in the British Columbia central interior. — *Forest Ecology and Management* 226: 80–87.
- De Keersmaker, L., Martens, L., Verheyen, K., Hermy, M., De Schrijver, A. & Lust, N. 2004: Impact of soil fertility and insolation on diversity of herbaceous woodland species colonizing afforestations in Muizen forest (Belgium). — *Forest Ecology and Management* 188: 291–304.
- Dormann, C. F., Schweiger, O., Arens, P., Augenstein, I., Aviron, S., Bailey, D., Baudry, J., Billeter, R., Bugter, R., Bukáček, R., Burel, F., Cerny, M., De Cock, R., De Blust, G., DeFilippi, R., Diekötter, T., Dirksen, J., Durka, W., Edwards, P. J., Frenzel, M., Hamersky, R., Hendrickx, F., Herzog, F., Klotz, S., Koolstra, B., Lausch, A., Le Coeur, D., Liira, J., Maelfait, J. P., Opdam, P., Roubalova, M., Schermann-Legionnet, A., Schermann, N., Schmidt, T., Smulders, M. J. M., Speelmans, M., Simova, P., Verboom, J., van Wingerden, W. & Zobel, M. 2008: Prediction uncertainty of environmental change effects on temperate European biodiversity. — *Ecology Letters* 11: 235–244.
- Flinn, K. M. & Vellend, M. 2005: Recovery of forest plant communities in post-agricultural landscapes. — *Frontiers in Ecology and the Environment* 3: 243–250.
- Gachet, S., Leduc, A., Bergeron, Y., Nguyen-Xuan, T. & Tremblay, F. 2007: Understory vegetation of boreal tree plantations: differences in relation to previous land use and natural forests. — *Forest Ecology and Management* 242: 49–57.
- Garcia-Gonzalo, J., Peltola, H., Briceno-Elizondo, E. & Kellomäki, S. 2007: Effects of climate change and management on timber yield in boreal forests with economic implications: a case study. — *Ecological Modelling* 209: 220–234.
- Geldenhuis, C. J. 1997: Native forest regeneration in pine and eucalypt plantations in Northern Province, South Africa. — *Forest Ecology and Management* 99: 101–115.
- Graae, B. J., Sunde, P. B. & Fritzboøger, B. 2003: Vegetation and soil differences in ancient opposed to new forests. — *Forest Ecology and Management* 177: 179–190.
- Gustafsson, L. 1988: Vegetation dynamics during the establishment phase of an energy forest on a riverside in south-eastern Sweden. — *Studia Forestalia Suecica* 178: 1–16.
- Haeussler, S., Bartemucci, P. & Bedford, L. 2004: Succession and resilience in boreal mixedwood plant communities 15–16 years after silvicultural site preparation. — *Forest Ecology and Management* 199: 349–370.
- Heilmann, B., Makeschin, F. & Rehfuess, K. E. 1995: Vegetationskundliche Untersuchungen auf einer Schnellwuchsplantage mit Pappeln und Weiden nach Ackerntzung [Phytosociological investigations in a fast growing plantation of poplars and willows on former arable land]. — *Forstwissenschaftliches Centralblatt* 114: 16–29. [In German with English summary].
- Heräjärvi, H. & Junkkonen, R. 2006: Wood density and growth rate of European and hybrid aspen in southern Finland. — *Baltic Forestry* 22: 2–8.
- Honnay, O., Hermy, M. & Coppin, P. 1999: Impact of habitat quality on forest plant species colonization. — *Forest Ecology and Management* 115: 157–170.
- Ito, S., Nakayama, R. & Buckley, G. P. 2004: Effects of previous land-use on plant species diversity in semi-natural and plantation forests in a warm-temperate region in southeastern Kyushu, Japan. — *Forest Ecology and Management* 196: 213–225.
- Janišová, M., Hrivnák, R., Gömöry, D., Ujházy, K., Valachovič, M., Gömöryová, E., Hegedúšová, K. & Škodová, I. 2007: Changes in understory vegetation after Norway spruce colonization of an abandoned grassland. — *Annales Botanici Fennici* 44: 256–266.
- Jõgiste, K., Vares, A. & Sendró, M. 2003: Restoration of former agricultural fields in Estonia: comparative growth of planted and naturally regenerated birch. — *Forestry* 76: 209–219.
- Kanerva, S. & Smolander, A. 2007: Microbial activities in forest floor layers under silver birch, Norway spruce and Scots pine. — *Soil Biology & Biochemistry* 39: 1459–1467.
- Kasanen, R., Hantula, J. & Kurkela, T. 2002: *Neofabraea populi* in hybrid aspen stands in southern Finland. — *Scandinavian Journal of Forest Research* 17: 391–397.
- Klotz, S., Kühn, I. & Durka, W. 2002: *BIOFLOR. Eine Datenbank mit Biologischökologischen Merkmalen zur Flora von Deutschland*. — Bundesamt für Naturschutz, Bonn.
- Kukk, T. 1999: *Eesti taimestik [Vascular plant flora of Estonia]*. — Teaduste Akadeemia Kirjastus, Tartu-Tallinn. [In Estonian with English summary].
- Kukk, T. & Kull, T. 2005: *Eesti taimede levikuatlas [Atlas of the Estonian flora]*. — Eesti Maaülikool, Põllumajandus- ja Keskonnainstituut, Tartu. [In Estonian with

English summary].

- Kullman, L. 2008: Thermophilic tree species reinvade supalpine Sweden — early responses to anomalous late holocene climate warming. — *Arctic, Antarctic, and Alpine Research* 40: 104–110.
- Légaré, S., Bergeron, Y., Leduc, A. & Paré, D. 2001: Comparison of understory vegetation in boreal forest types of southwest Quebec. — *Canadian Journal of Botany* 79: 1019–1027.
- Leht, M. (ed.) 1999: *Eesti taimede määraja*. — Eesti Loodusfoto, Tartu.
- Lindacher, R. 1995: *PHANART. Datenbank der Gefäßpflanzen Mitteleuropas. Erklärung der Kennzahlen, Aufbau und Inhalt*. — Veröffentl. des Geobot. Inst. der ETH, Stiftung Rübel, 125, Zürich.
- Mascaro, J., Becklund, K. K., Hughes, R. F. & Schnitzer, S. A. 2008: Limited native plant regeneration in novel, exotic-dominated forests on Hawai'i. — *Forest Ecology and Management* 256: 593–606.
- McCune, B. & Mefford, M. J. 1999: *Multivariate analysis of ecological data*, ver. 4. — MjM software, Glenden Beach, Oregon.
- Messier, C., Parent, S. & Bergeron, Y. 1998: Key issues in disturbance dynamics in boreal forests. — *Journal of Vegetation Science* 9: 511–520.
- Miller, D. A. & Chamberlain, M. J. 2008: Plant community response to burning and herbicide site preparation in eastern Louisiana, USA. — *Forest Ecology and Management* 255: 774–780.
- Morin, X., Viner, D. & Chuine, I. 2008: Tree species range shifts at a continental scale: new predictive insights from a process-based model. — *Journal of Ecology* 96: 784–794.
- Oksanen, J., Kindt, R., Legendre, P., O'Hara, B., Simpson, G. L., Solymos, P., Stevens, H. H. & Wagner, H. 2008: *The vegan Package*. — available at cran.r-project.org, and vegan.r-forge.r-project.org.
- Paritsis, J. & Aizen, M. A. 2008: Effects of exotic conifer plantations on the biodiversity of understory plants, epigeal beetles and birds in *Nothofagus dombeyi* forests. — *Forest Ecology and Management* 255: 1575–1583.
- Peterson, U. & Aunap, R. 1998: Changes in agricultural land use in Estonia in the 1990s detected with multitemporal Landsat MSS imagery. — *Landscape and Urban Planning* 41: 193–201.
- Prescott, C. E. 2002: The influence of the forest canopy on nutrient cycling. — *Tree Physiology* 22: 1193–1200.
- Qian, H., Klinka, K., Okland, R. H., Krestov, P. & Kayahara, G. J. 2003: Understorey vegetation in boreal *Picea mariana* and *Populus tremuloides* stands in British Columbia. — *Journal of Vegetation Science* 14: 173–184.
- Rytter, L. 2006: A management regime for hybrid aspen stands combining conventional forestry techniques with early biomass harvests to exploit their rapid early growth. — *Forest Ecology and Management* 236: 422–426.
- Smolander, A., Loponen, J., Suominen, K. & Kitunen, V. 2005: Organic matter characteristics and C and N transformations in the humus layer under two tree species, *Betula pendula* and *Picea abies*. — *Soil Biology & Biochemistry* 37: 1309–1318.
- Soo, T., Tullus, A., Tullus, H. & Roosaluuste, E. 2009: Floristic diversity responses in young hybrid aspen plantations to land-use history and site preparation treatments. — *Forest Ecology and Management* 257: 858–867.
- Suvanto, L. & Pulkkinen, P. 2004: Gene flow between European (*Populus tremula*) and hybrid aspen (*P. tremula* × *P. tremuloides*). — In: Li, B. & McKeand, S. (eds.), *Forest genetics and tree breeding in the age of genomics: progress and future*. IUFRO Joint Conference of Division 2, Conference Proceedings: 171–173. North Carolina State University.
- Sydes, C. & Grime, J. P. 1981a: Effects of tree leaf litter on herbaceous vegetation in deciduous woodland: I. Field investigations. — *The Journal of Ecology* 69: 237–248.
- Sydes, C. & Grime, J. P. 1981b: Effects of tree leaf litter on herbaceous vegetation in deciduous woodland: II. An experimental investigation. — *The Journal of Ecology* 69: 249–262.
- Zobel, M., Kalamees, R., Püssa, K., Roosaluuste, E. & Moora, M. 2007: Soil seed bank and vegetation in mixed coniferous forest stands with different disturbance regimes. — *Forest Ecology and Management* 250: 71–76.
- Tullus, A., Tullus, H., Vares, A. & Kanal, A. 2007: Early growth of hybrid aspen (*Populus* × *wettsteinii* Hämet-Ahti) plantations on former agricultural lands in Estonia. — *Forest Ecology and Management* 245: 118–129.
- Uri, V., Lõhmus, K., Kund, M. & Tullus, H. 2008: The effect of land use type on net nitrogen mineralization on abandoned agricultural land: silver birch stand versus grassland. — *Forest Ecology and Management* 255: 226–233.
- van Oijen, D., Feijen, M., Hommel, P., den Ouden, J. & de Waal, R. 2005: Effects of tree species composition on within-forest distribution of understory species. — *Applied Vegetation Science* 8: 155–166.
- Wallrup, E., Saetre, P. & Rydin, H. 2006: Deciduous trees affect small-scale floristic diversity and tree regeneration in conifer forests. — *Scandinavian Journal of Forest Research* 21: 399–404.
- Weih, M. 2004: Intensive short rotation forestry in boreal climates: present and future perspectives. — *Canadian Journal of Forest Research* 34: 1369–1378.
- Weih, M., Karacic, A., Munkert, H., Verwijst, T. & Diekmann, M. 2003: Influence of young poplar stands on floristic diversity in agricultural landscapes (Sweden). — *Basic and Applied Ecology* 4: 149–156.
- Yu, Q., Tigerstedt, P. M. A. & Haapanen, M. 2001: Growth and phenology of hybrid aspen clones (*Populus tremula* L. × *Populus tremuloides* Michx.). — *Silva Fennica* 35: 15–25.

Appendix. The list of most frequent vascular plant species (found in > 10% of the plots), their frequency (*F*, %) and mean coverage in plots where present (*C*, %).

Vascular plant species	Both plantation types		Hybrid aspen plantations		Silver birch plantations	
	<i>F</i>	<i>C</i>	<i>F</i>	<i>C</i>	<i>F</i>	<i>C</i>
<i>Achillea millefolium</i>	50	4.3	46	5.1	54	3.5
<i>Aegopodium podagraria</i>	12	17.0	7	11.5	17	19.8
<i>Agrostis capillaris</i>	42	5.2	21	7.5	67	4.3
<i>A. gigantea</i>	37	7.3	32	10.7	42	4.2
<i>Alchemilla vulgaris</i> (coll.)	17	1.1	4	1.0	33	1.1
<i>Alopecurus pratensis</i>	12	5.7	0	0.0	25	5.7
<i>Artemisia vulgaris</i>	62	2.9	79	3.5	42	1.6
<i>Betula pendula</i>	23	2.8	36	3.0	8	1.5
<i>Campanula patula</i>	15	1.1	18	1.0	13	1.3
<i>Cerastium fontanum</i>	48	1.4	64	1.5	29	1.3
<i>Cirsium arvense</i>	85	6.0	75	3.5	96	8.2
<i>Dactylis glomerata</i>	17	4.2	11	2.0	25	5.3
<i>Elymus repens</i>	85	10.3	79	10.3	92	10.2
<i>Epilobium montanum</i>	25	1.2	18	1.0	33	1.3
<i>E. parviflorum</i>	21	1.0	39	1.0	0	0.0
<i>Equisetum arvense</i>	23	1.8	29	1.1	17	3.0
<i>Fallopia convolvulus</i>	25	1.0	25	1.0	25	1.0
<i>Festuca rubra</i>	17	15.0	4	2.0	33	16.6
<i>Gnaphalium uliginosum</i>	13	1.3	25	1.3	0	0.0
<i>Hypericum perforatum</i>	17	1.4	32	1.4	0	0.0
<i>Leucanthemum vulgare</i>	27	1.4	32	1.1	21	2.0
<i>Luzula campestris</i>	15	2.0	29	2.0	0	0.0
<i>Lysimachia vulgaris</i>	13	4.1	14	5.3	13	2.7
<i>Matricaria perforata</i>	15	1.1	25	1.1	4	1.0
<i>Medicago lupulina</i>	17	1.9	14	2.3	21	1.6
<i>Mentha arvensis</i>	19	1.0	18	1.0	21	1.0
<i>Myosotis arvensis</i>	50	1.3	43	1.0	58	1.6
<i>Phleum pratense</i>	54	4.3	82	5.0	21	1.4
<i>Pinus sylvestris</i>	12	2.0	7	1.0	17	2.5
<i>Poa angustifolia</i>	25	4.2	14	1.5	38	5.4
<i>P. palustris</i>	19	1.6	14	2.0	25	1.3
<i>P. trivialis</i>	25	2.2	14	1.3	38	2.6
<i>Potentilla anserina</i>	13	1.1	0	0.0	29	1.1
<i>Ranunculus acris</i>	12	1.0	0	0.0	25	1.0
<i>Salix caprea</i>	12	2.0	21	2.0	0	0.0
<i>Sonchus arvensis</i>	42	3.0	54	3.9	29	1.1
<i>Taraxacum officinale</i> (coll.)	83	7.3	79	4.9	88	9.8
<i>Tussilago farfara</i>	37	10.8	39	11.5	33	10.0
<i>Urtica dioica</i>	12	1.5	7	1.0	17	1.8
<i>Veronica agrestis</i>	23	1.2	11	1.7	38	1.0
<i>Vicia cracca</i>	44	1.7	32	1.8	58	1.7
<i>V. hirsuta</i>	40	1.6	46	1.7	33	1.4