Changes in Ground Vegetation of Arable Lands under Afforestation in Latvia

SOLVITA RŪSIŅA[1], BAIBA BAMBE[2] AND MUDRĪTE DAUGAVIETE[2]

[1]*University of Latvia, Faculty of Geography and Earth Sciences*

[2] *Latvian State Forestry Research Institute (LSFRI) Silava*

Corresponding author: Solvita Rūsiņa, e-mail: Solvita.Rusina@lu.lv; phone: + 371 6733627

Rūsiņa, S., Bambe, B. and Daugaviete, M. 2011. Changes in Ground Vegetation of Arable Lands under Afforestation in Latvia. *Baltic Forestry* 17(2): 243–255.

Abstract

Dynamics of herb and bryophyte layer following afforestation of arable land were analyzed on two research sites – Vestiena and Malta, Latvia. Vegetation data on a twelve year period were processed, and data were collected in 1996, 1999, 2003 and 2008. Environment and vegetation of both areas were quite similar at the beginning of the research – fallow land vegetation dominated by ruderal grasses and annual herbs. Changes in vegetation were negligible during the first years because young planted trees grew slowly and light conditions did not change substantially. At the end of the observation period, the herb layer became very scarce, ruderal species declined, and typical species of forests and forests edges appeared. Most of plant species had wide ecological amplitude of climatic and edaphic factors, which indicates that the ground vegetation composition on research sites remained very different from the vegetation of forests ecosystem. There were no differences among birch plantations with different density of planted trees, and only small differences among plantations with different tree species (spruce, pine, birch), which appeared only in the last observation year.

Key words: afforestation, succession, fallow land, *Pinus sylvestris, Picea abies, Betula pendula*, plantation

Introduction

Artificial and natural afforestation of agricultural land in Europe has been a very important process during the past decades, affecting both the biota and landscape (Mather and Thomson 1995, Dostalova 2009, Stoate et al. 2009). In Latvia, extensive afforestation of agricultural lands was carried out in the 20s, 60s and 70s of the XX century, and it has increased again since 2000, as Latvia started receiving EU funding as a part of SAPARD and EU structural funds. During the period from 2000 to 2009, the total area of artificially afforested agricultural land equaled 14,200 ha, including 3,747 ha of plantation forest (or 26.4% of all artificially afforested area) (Daugaviete and Daugavietis 2008, Liepiņš et al. 2008).

Essentially, the goal of forest planting is to accelerate succession or even entirely eliminate one of its stages (e.g., the pioneer species stage), in order to achieve a result as soon as possible. On the other hand, forest planting in Europe is not only a way to obtain wood by efficient usage of abandoned agricultural land, but also one of the methods of ecosystem restoration (Prach et al. 2001a). Therefore, it is essential to develop not only a productive tree stand but a diverse and forest-specific herb and bryophyte layer as well (Elemans 2004).

While a lot of studies have dealt with forest understory development after forest clear cutting (e.g. Selmants and Knight 2003, Moora et al. 2007, Aavik et al. 2009 etc.) and natural afforestation of agricultural lands (e.g. Prach et al. 2001b, Bartha et al. 2003, Flinn and Vellend 2005, Dostalova 2009, Kopecký, Vojta 2009 etc.), less attention has been paid to the establishment of ground vegetation in plantation forests (e.g. Hill 1979, Bråkenhielm 2000).

In contrast to naturally overgrowing agricultural lands, where development of the forest ecosystem is mainly determined by natural factors, in artificially afforested territories the development of both the tree layer and herb and bryophyte layer is significantly affected by the cultivation of plantations and the fact that timber stands usually develop quicker, which facilitates faster stabilization of the microclimate and light conditions typical of forest environment (Dostalova 2009, Gutko et al. 2001, Flinn and Vellend 2005, Daugaviete 2005a, 2005b). However, with the exception of the initial cultivation, the herb layer is usually under natural succession (Elemans 2004). Therefore, natural conditions determine the development of herb layer characteristic of forest. In the same place, due to site differences (e.g. soil moisture and fertility), succession can occur at various rates. For example, moist and fertile soil can facilitate appearance of shrubs in the territory, but on the other hand, it can also facilitate the spreading of competitive grasses, which can temporarily stop succession entirely (Alard et al. 2005).

Up until now, in Latvia, there have been no studies on the effect of afforestation of arable land on the dynamics of the herb and bryophyte layers. Existing studies are mainly focused on the landscape scale effects of natural overgrowth of agricultural land (Nikodemus et al. 2005, Penēze 2009), the effect on animal species (e.g., Keišs, 2006) the growth rate of tree species (Sacenieks and Gaross 1961, Maike 1953, Sarma 1949) depending on various aspects of soil cultivation (Daugaviete et al. 2001, Daugaviete 2005a, 2005b, Daugaviete and Daugavietis 2008 etc.).

Our study was focused on the ground vegetation development on afforested arable land at early stages of succession (first 12 years) with the following tasks: to assess the course of ground vegetation development towards a forest, to investigate if the differences in tree species cause different ground vegetation development at early stage of succession, and to clarify how the ground vegetation composition is affected by plantation density.

Material and methods

Site description

Research was done in two model territories – Madona District, Vestiena parish, "Birzes" (coordinates according to the LKS-92 system: (x) 703420 and (y) 6243820; 2.4 ha) (further referred as Vestiena site) and Rēzekne District, Malta parish, "Bitītes" (coordinates: (x) 618991 and (y) 6309637; 2.4 ha) (further referred as Malta site). Vestiena site was located in a forested landscape on the moraine hill (glacial sand deposits) and it bordered with grasslands on the North and East and with a *Vacciniosa* forest (mature 50-60 year-old stands) on the South and West. Malta site was located in a forested landscape on the moraine hill (glacial gravely sand deposits) and it bordered with *Vacciniosa* and *Hylocomiosa* forests (mature 60-70 year-old stands) on the North, East and South, but on the West – with grasslands. On both sites, the areas afforested were fallow lands on sandy and very dry sites with weak sod podzolic soils.

The following plantations have been established on both sites: pine (layout: 1×2 m, density: 5,000 trees·ha^{-1}), spruce (layout: 1.5×2 m, density: 3,000 trees·ha^{-1}) and birch with 5 different layouts (1×1 m, density: 10,000 trees·ha^{-1}; 1×2 m, density: 5,000 trees·ha^{-1}; 2×2 m, density: 2,500 trees·ha^{-1}; 2×3 m, density: 1,600 trees·ha^{-1}; 3×3 m, density: 1,100 trees·ha^{-1}). In Malta and Vestiena, the plantations were nursed only during the first years after planting – from 1996 to 2000, the grass between planted tree rows was mowed, and the grass was left to rot. The birch litter mass at the time was still insignificant (Daugaviete et al. 2001).

Both sites initially were almost identical in terms of ground vegetation structure and species richness. The herb layer was dominated by or had high frequency of typical fallow land species like *Elytrigia repens, Achillea millefolium* (dominating), *Omalotheca sylvatica, Rumex acetosella.* In Vestiena there was higher frequency of *Phleum pratense* and *Erigeron acris,* in Malta – *Jasione montana* and *Conyza canadensis.* There were no differences between the sample plots described in the territories afforested with birch (various densities), pine and spruce. Ellenberg's indicator values showed xero-mesophytic growing conditions (the humidity value of both sites was 4.3) with soil reaction value: 4.6 in Vestiena and 3.9 in Malta and nitrogen value 4.6 and 4.5, respectively.

Data collection

During the period from 1996 to 2009, observation of vegetation was taken four times – in 1996, 1999, 2003 and 2008. The first inventory of vegetation was taken in 1996, before the preparation of soil and afforestation. During this inventory, a total of 10 sample plots (1×1 m each) were described throughout the whole plantation territory (2.4 ha). In the inventories taken in 1999 and 2003, three 1×1 m sample plots were established in each tree species plantation. In birch plantations with five different densities, 3 such plots were established for each density. In total, in each model territory, 3 sample plots were established in the pine plantation, 3 plots in the spruce plantation, and 15 plots in the birch plantation. In 2008, the tree crowns had already closed, so vegetation was recorded in three 10×10 m sample plots instead of three former 1×1 m plots. The sample plots were semi-permanent: they were laid down along transect both ends of which were marked by wooden sticks. The location of plots was determined by the distance from the beginning of transect.

The tree growth were determined by measuring the diameter of tree at the breast height in cm and tree height in m. Measurements were done in 100 m² plots; at least 100 trees per plot were measured. Four plots were established in each tree species plantation.

Data analysis

The vegetation data have been stored in a database using TURBOVEG Software (Hennekens and Schaminée 2001). The data obtained in the vegetation inventory of 1996 have been taken into account only in descriptive analysis, as, due to fully homogenous vegetation, a smaller number of sample plots has been used than in the following inventories.

Only the data of the herb layer – including woody plant species whose height did not exceed the herb layer (~70 cm) – have been used in the analysis. Inventory of the shrub layer has been taken only in 2008, and its differences have been presented in the comparison of both observation areas (Malta and Vestiena) in 2008.

The similarity of the species composition was assessed using the Jaccard similarity coefficient (Kent and Coker 1994). A catalogue of synanthropic elements (Laiviņš and Zundāne 1989) was used for analysis of the species composition by classification in various types of vegetation (shrubs and forests, grasslands, ruderal areas). For each site and observation year, a functional signature of Grime's plant strategies (Grime 2001) was derived using the Excel spreadsheet-based tool developed by Hunt et al. (2004). Changes of the species composition (coverage and abundance) were tested by means of the Indicator Species Analysis (Dufrene and Legendre 1997), which is based on calculation of the proportion of coverage and abundance of each species in a single classification unit of vegetation (sample plots), in comparison to all other data set (the other classification units). The ideal indicator species of a group is a species that occurs only in this group (and all plots of the group), and not in any other groups. The significance of the indicator values obtained is calculated with a Monte Carlo test (McCune and Grace 2002).

The dynamics of vegetation have been analyzed with an indirect ordination method, Detrended Correspondence Analysis (DCA: Hill and Gausch 1980) with the use of computer software PC-ORD 5 (McCune and Mefford 1999). The DCA analysis used square root transformed data on herb species coverage to reduce the weight of rare species. This reduced the potential effect of the variable sample size. The explained variation of ordination axes has been assessed by using a determination coefficient between Euclidean distance in the ordination space and the relative Euclidean distance in the original multidimensional space (McCune and Grace 2002). To determine the differences of the process of vegetation changes in both observation areas, DCA was carried out simultaneously for the sample plots of both sites, but, in order to determine the vegetation differences between plantations of different tree species, ordination was carried out individually for the sample plots of each site. In both cases, all plots on same tree species and, in the birch plantation, all same density sample plots, were combined.

Ellenberg's indicator values for light, moisture, reaction and nitrogen (Ellenberg et al. 1992), as well as data on the vegetation layer coverage, were used to explain ordination. Ellenberg's indicator values were calculated by using the herb layer data in computer software JUICE (Tichy 2002), taking into consideration only the presence of a species, but not its coverage. Mean indicator values were calculated for each plot from all present vascular plant species for which an indicator value according to Ellenberg et al. (1992) was available. Kendall rank correlation between ordination axes and the above-mentioned parameters were calculated using computer software PC-ORD 5.

Nomenclature of vascular plants follows Gavrilova and Šulcs 1999; nomenclature of bryophytes follows Āboliņa 2001.

Results

Ground vegetation changes

During the first four years after the establishment of the plantation, there was little increase in trees height (Figure 1). So, significant changes in the herb vegetation did not occur yet. However, soon thereafter, the trees grew rapidly, and reached 8–9 m in eight years (Figure 1). After twelve years, the average coverage of the herb layer had declined considerably (Table 2). It had also become less homogenous: in 1999, in Vestiena there were one or two frequently dominating

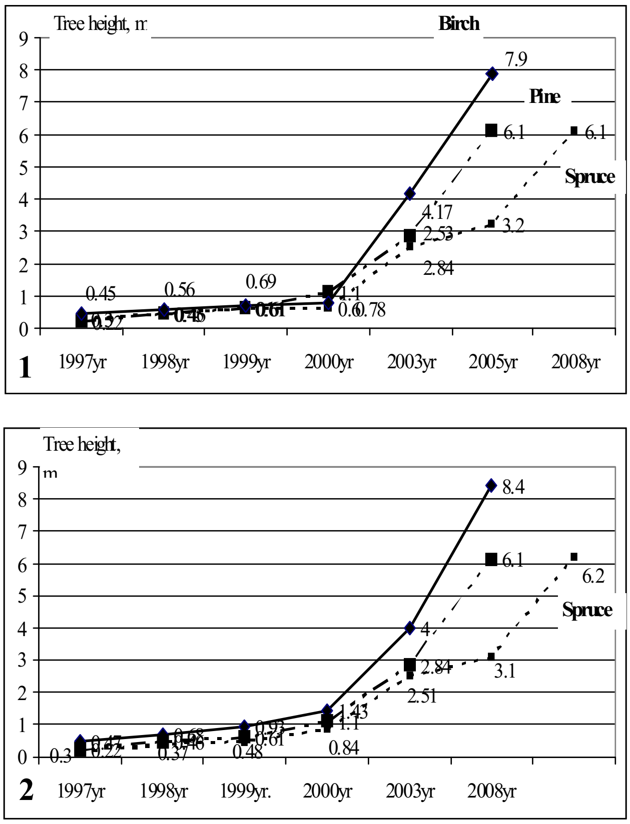

Figure 1. Growth of planted trees in Vestiena (1) and Malta (2) between 1997 and 2008

species (their coverage was above 25% in more than 20% of the sample plots), and four or five species dominating in up to 5% of the cases, but after nine years there were no more frequently dominating species, and six species dominating in up to 15% of the cases. In Malta, the herb layer had become very sparse and only *Elytrigia repens* and *Lupinus polyphyllus* had reached 3% coverage on average.

In Vestiena, the similarity of the species composition between 1999 and 2008, according to the Jaccard similarity coefficient, was 43%; in Malta – 33%. On both observation sites, there was a continuous decline in number, frequency, and coverage of ruderal species and increase of forest and shrubland species; the number of grassland species almost did not change (Table 1, App. 1 and 2). Ruderal species were mainly fallow land species, which were initially dominant in the vegetation (e.g. *Elytrigia repens,* and *Achillea millefolium*). Species increasing in number and frequency were mainly species of a wide ecological amplitude typical for shady forest edges (*Trifolium medium, Holcus mollis*) and forests (*Rubus idaeus, Picea abies, Solidago virgaurea, Sorbus aucuparia, Fragaria vesca*). However, several of them are not characteristic of forests, and their appearance was not indicative of stabilization of the environment characteristic to forests (e.g., *Carlina vulgaris, Pimpinella saxifraga, Festuca rubra, Agrostis tenuis, Campanula patula*) (App.1 and 2).

Table 1. Ecological species group spectra of study sites in 3 observation periods

Ecological group	Vestiena			Malta		
	1999	2003	2008	1999	2003	2008
Synanthropic elements (according to Laiviņš and Zundāne 1989)						
Grassland species	43.2	48.7	38.0	34.3	35.0	35.5
Ruderal/segetal species	40.6	28.2	22.8	54.3	48.6	34.2
Forest and shrubland species	16.2	23.1	39.2	11.4	22.5	30.3
C-S-R signatures (according to Hunt et al. 2004)						
C-component	0.51	0.35	0.48	0.45	0.53	0.55
S-component	0.20	0.38	0.34	0.24	0.264	0.21
R-component	0.29	0.27	0.18	0.31	0.20	0.24
Nearest type	CR/CSR	CSR	SC/CSR	CR/CSR	C/CSR	C/CSR
Cartesian distance:						
Vestiena 1999 and 2008	0.15					
Malta 1999 and 2008	0.11					
Vestiena and Malta 1999	0.06					
Vestiena and Malta 2008	0.13					

C-S-R signatures indicated a movement away from environmental disturbance (the R-component declined) on both sites. The dynamics of the C and S-component were not so clear (Table 1). Ellenberg's indicator value for light decreased by 0.8 units in Vestiena, and only by 0.6 units in Malta; the indicator value for humidity has increased by 0.7 units in Vestiena, and by 0.4 units in Malta; the indicator value for site fertility (nitrogen) has increased negligibly (Table 2).

It must be noted that the increase in the number of species on both observation sites (Table 2) cannot be unambiguously interpreted as an indicator of the rate and progression of succession, as the small changes in methodology must be taken into account (in 2008, 10 m^2 sample plots were used instead of 1 m^2 sample plots).

In 1996, the mean coverage of bryophyte layer 50–95% in Vestiena. The dominating species were *Ceratodon purpureus* and *Brachythecium albicans*, in some sample plots – also *Bryum caespiticium*. In Malta, the coverage of bryophyte layer was 85% of the area; the dominating species were *Ceratodon purpureus* and *Bryum caespiticium*, as well as *Pogonatum urnigerum*; lichens coverage – 20–40% (*Peltigera* sp.). In 1999, the mean coverage of bryophytes in Malta was 10%, exceeding 30% in individual plots; however, in many plots there was no bryophyte coverage left at all. The main dominating species was *Ceratodon purpureus*, in some areas – *Polytrichum juniperinum*, less pronouncedly – *Brachythecium albicans.* In Vestiena, the average bryophyte layer coverage was 20%; in some areas there was no bryophyte coverage at all, although there were also spots of congregation with coverage reaching 65%.

Table 2. Changes in the coverage of vegetation layers and Ellenberg's indicator values in Vestiena and Malta (standard deviations between brackets), and Kendall rank correlation coefficients with ordination axes 1 and 2

Parameter	Vestiena			Malta			r axis 1	r axis 2
Year	1999	2003	2008	1999	2003	2008	0.61	0.21
Number of species per plot	8.4 (2.3)	9.8 (1.8)	15.2 (6.8)	8.2 (2.2)	7.8 (3.5)	17 (6.8)	n*	n
Bryophyte layer coverage	20.3 (20.3)	23.3 (22.0)	20.8 (33.1)	10.7 (15.7)	26.1 (34.9)	7.5 (15.3)	-0.32	0.12
Herb layer coverage	55.5 (14.5)	49.8 (18.8)	36.7 (26.4)	51.9 (9.4)	33.2 (25.7)	13.3 (19.1)	-0.40	-0.39
Shrub layer coverage	0.0	0.0	59.2 (23.8)	0.0	0.0	65.2 (16.1)	0.63	0.19
Light	7.6 (0.3)	6.9 (0.4)	6.8 (0.4)	7.3 (0.3)	7.1 (0.3)	6.7 (0.3)	-0.47	-0.19
Humidity	4.4 (0.4)	4.7 (0.4)	5.1 (0.5)	4.3 (0.4)	4.4 (0.4)	4.7 (0.4)	0.31	0.42
Reaction	4.6 (0.9)	5.8 (0.8)	5.3 (0.7)	3.9 (0.9)	3.9 (1.7)	5.1 (0.6)	0.04	0.44
Nitrogen	4.6 (0.5)	4.6 (0.6)	4.9 (0.4)	4.5 (0.7)	4.5 (0.9)	4.7 (0.7)	0.17	0.21

*n – not calculated

The dominating species were *Ceratodon purpureus* and *Brachythecium albicans* (App. 1 and 2, Table 2 and 4). There was very little lichen remaining (*Peltigera* sp.), and *Plagiomnium affine* was registered in one area (pine). Overall, during a four year period no significant changes were observed in the bryophyte species composition. Dominating were acrocarpous species typical of open and dry places, which are also colonizers of open soils (e.g., *Ceratodon purpureus*). In 2008, in the bryophyte layer of Vestiena, 18 bryophyte species (11 pleurocarpous and 7 acrocarpous) and t2wo lichen species were found. Pleurocarpous forest species dominated, especially in plantations of coniferous trees: *Pleurozium schreberi, Hylocomium splendens, Brachythecium oedipodium*. In Malta, 14 species (8 pleurocarpous and 5 acrocarpous) have been found in the bryophyte layer; the most widespread ones were pleurocarpous forest species such as *Pleurozium schreberi, Brachythecium oedipodium*, as well as species characteristic of more open areas: *Brachythecium albicans* and *Polytrichum juniperinum* (App. 1 and 2).

Comparison of the sites at the end of the observation period

In the beginning of the study, both observation sites were rather similar in terms of the species composition and vegetation structure (App. 1 and 2). After twelve years, the similarity of the species composition (flora) between the two sites had increased – the Jaccard similarity coefficient for the herb layer was 42% (32% in 1999). The differences in vegetation structure had become greater (App. 3). The greatest differences were observed in the coverage and frequency of species found at both sites. In Vestiena, forest species were more frequent (e.g., *Chamaenerion angustifolium, Rubus idaeus, Equisetum pratense*), while in Malta prevalence was exhibited mainly by species characteristic of open areas, such as *Galium album, Veronica officinalis, Rumex acetosella, Elytrigia repens*. In Malta, the frequency of *Pinus sylvestris* was still larger than in Vestiena (it was a part of the herb layer in 1999, but had already reached the shrub layer in 2008) (App. 3).

The proportion of species characteristic of shrubs and forests was highest in Vestiena, but the part of ruderal species was highest in Malta, while the part of grassland species was almost the same at both sites (Table 2). C-S-R signatures revealed the same pattern – C and R-components were highest in Malta, while the S-component had the highest value in Vestiena. Cartesian distance between Vestiena and Malta increased between 1999 and 2008 indicating that the vegetation similarity between the two sites decreased (Table 1).

Thus, during the period from the beginning of the afforestation in 1996 to 2008, the composition of species in the herb and bryophyte layer had changed in the direction of a forest ecosystem at both sites. However there was a slightly higher proportion (species number, coverage and frequency) of forest species in Vestiena than in Malta. In some areas of Malta, there was still a vegetation characteristic of open fallow land.

This is also demonstrated by the results of DCA ordination. At both sites, the herb vegetation had changed in one direction (Figure 2). Ordination axis 1 (gradient length: 2.32 standard deviations) can be interpreted as a succession gradient from vegetation characteristic of open areas toward vegetation characteristic of forests. In the direction of the axis 1, the coverage of herbs has fallen, but the shrub coverage has increased, and Ellenberg's indicator value for light has decreased (increased shadiness) (Table 2). However, axis 2 (gradient length: 2.42 standard deviations)

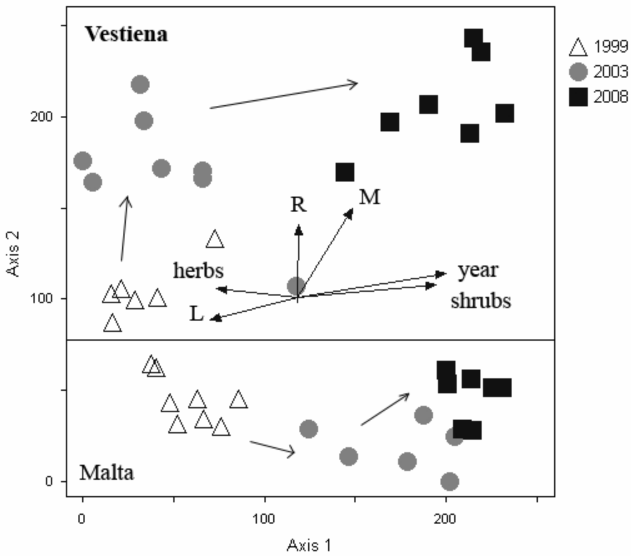

Figure 2. DCA ordination of the Vestiena and Malta sample plots (plots from the same tree species plantation and from the same density were merged). The cumulative determination coefficient of the original multidimensional space and the ordination space was 61% (axis 1 accounts for 31% of the variation, axis 2 – for 24%). Ellenberg indicator values R – reaction, M – moisture, L – light, shrubs – cover of shrub layer, herbs – cover of herb layer

accounts for variation almost as much as axis 1 (axis 3 was not interpreted, as it accounted for only 6% of the variation). Axis 2 can be interpreted as a gradient of site moisture and reaction, in which greater changes have occurred in Vestiena (in the direction of increasing reaction and moisture), while almost none have occurred in Malta (the sample plots of Vestiena have moved on this axis by almost two standard deviations; the sample plots of Malta – by only slightly more than 0.5 standard deviations).

Differences of vegetation among plantations of different tree species and densities

In the first inventories (1999–2003), differences in herb vegetation among plantations of different tree species (pine, spruce, birch) and birch plantations of various densities were not observed in either Vestiena or Malta. The first differences appeared in 2008, but there were still no significant herb vegetation differences among birch plantations of various densities. In Vestiena, Indicator Species Analysis revealed that no species appeared that could serve as indicators for any of the plantations. In 2003, significantly larger frequency and coverage was shown by only two species (*Festuca ovina* and *Veronica chamaedrys*) in the pine plantation. There were 4 such species in 2008 (Table 3).

In Malta, the differences of herb vegetation among plantations of different tree species were more expressed (Table 3). In 1999, birch plantations had a significantly larger coverage of *Achillea millefolium,* while the herb layer of the pine plantation had constant occurrence of *Betula pendula*. In 2003, 3 species had significantly larger frequency in the spruce plantation, while in 2008 there were 5 herb layer indicator species in the birch plantations; the pine plantation had 3 such species, while the spruce plantation was characterized by a significantly larger coverage and frequency of 3 bryophyte species (Table 3).

Table 3. Herb and bryophyte layer species with significant differences in frequency and coverage among plantations of birch, pine and spruce in Vestiena in 2008, and Malta in 1999, 2003, and 2008

Species	Frequency, %			IV*	p
	Birch	Pine	Spruce		
Vestiena (2008)					
Agrostis gigantea Roth	**100**	0	0	16.88	0.000
Equisetum pratense Ehrh.	**93**	7	0	13.43	0.045
Epilobium montanum L.	25	**75**	0	13.76	0.028
Achillea millefolium L.	20	**57**	23	11.21	0.060
Malta (1999)					
Achillea millefolium L.	**100**	100	67	53.5	0.008
Betula pendula Roth	20	**67**	0	64.2	0.027
Malta (2003)					
Artemisia vulgaris L.	27	0	**100**	84.2	0.010
Vicia angustifolia Reichard	0	0	**67**	66.7	0.028
Taraxacum officinale F.H. Wigg. s.l.	27	0	**67**	62.5	0.036
Malta (2008)					
Festuca rubra L.	**80**	0	0	39.1	0.002
Achillea millefolium L.	**60**	0	0	34.3	0.050
Rumex acetosella L.	**60**	0	0	34.1	0.051
Knautia arvensis (L.) Coult.	**60**	0	0	34.2	0.053
Epilobium montanum L.	**60**	0	0	34.1	0.054
Betula pendula Roth	0	**100**	0	100.0	0.002
Carex ovalis Gooden	7	**100**	0	93.7	0.006
Picea abies (L.) H. Karst.	40	**100**	0	71.4	0.035
Pleurzium schreberi (Brid.) Mitt.	67	100	**100**	94.8	0.003
Hylocomium splendens (Hedw.) B., S. et G.	0	0	**67**	66.7	0.027

*IV – the indicator value of the species

Thus, the differences in Vestiena were less expressed than in Malta. This is also demonstrated by the results of DCA. The ordination of the Vestiena sample plots showed that greater differences of vegetation can be noted between observations made in different years, while differences between plantations of different tree species were negligible – the sample plots of each year make up a compact group in the ordination diagram, with the sample plots of spruce, pine and birch being very close to one another (i.e., the vegetation in them is very similar) (Figure 3).

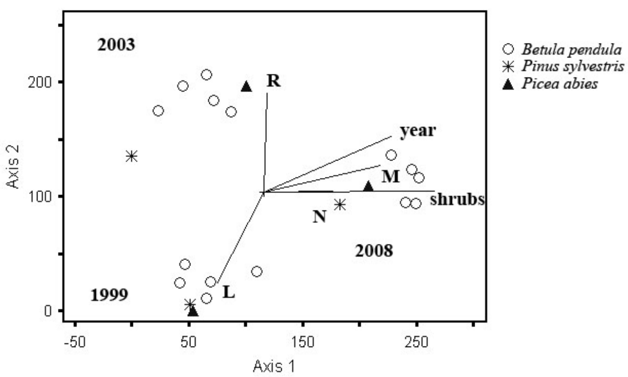

Figure 3. DCA ordination of the Vestiena sample plots (plots of the same tree species and of the same density were merged). The cumulative determination coefficient of the original multidimensional space and the ordination space is 66 % (axis 1 accounts for 49% of the variation, axis 2 – for 17%). Ellenberg indicator values R – reaction, M – moisture, L – light, N – nitrogen, shrubs – cover of shrub layer

In the plantations of Malta, the first ordination axis (gradient length: 2.58 standard deviations) can be explained as the succession gradient, and sample plots of plantations of different tree species were not separated on it. This axis is most correlated with the year and Ellenberg's indicator value for light (Figure 4). The pine, spruce and birch plantations were separated on the second ordination axis (gradient length: 1.99 standard deviations). The pine sample plots already differed from the others during the first year of observation, and this difference remained until the end of the observation.

A total of 19 bryophyte species were registered in 2008. The species composition was very similar at

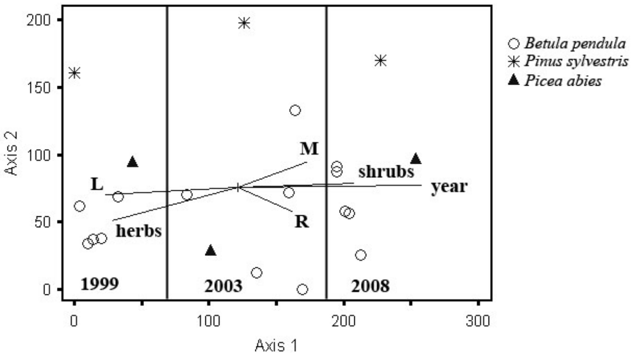

Figure 4. DCA ordination of the Malta sample plots (plots of the same tree species and of the same density were merged). The cumulative determination coefficient of the original multidimensional space and the ordination space is 60% (axis 1 accounts for 47% of the variation, axis 2 – for 13%). Vertical lines separate sample plots of different years. Ellenberg indicator values R – reaction, M – moisture, L – light, shrubs – cover of shrub layer, herbs – cover of herb layer

the Vestiena and Malta sites (Table 4). The coverage of the bryophyte layer was greatest in spruce plantations, where the herb layer coverage was low. Birch plantations, had a large herb coverage and small bryophyte coverage. Cover of vegetation layers was intermediate in pine plantations but it must be noted that they had been recently thinned. Among bryophyte species, in spruce plantations *Hylocomium splendens*, *Pleurozium schreberi* and *Brachythecium oedipodium* predominated. In pine plantations *Pleurozium schreberi* had a large coverage, whereas in birch plantations bryophytes rarely exceeded 1%. In the birch plantations of Malta, *Polytrichum juniperinum* was relatively frequent (in 48 % of plots).

Table 4. The coverage (%) of the bryophyte, herb and tree layers in Vestiena and Malta in 2008

Vegetation layer	Birch plantation		Pine plantation		Spruce plantation	
	Vestiena	Malta	Vestiena	Malta	Vestiena	Malta
Tree layer (E2)	70	60	20	70	70	70
Herb layer (E1)	50	20	30	1	10	1
Bryophyte layer (E0)	3	1	40	4	85	40

Discussion

Overall, succession at both observation sites had developed in one direction: over twelve years, the ground vegetation of fallow land had become thinner due to the shading created by the saplings, and transformation to forest vegetation had begun. Light-demanding species had disappeared or significantly declined, while species typical of forests edges and forests had appeared; however, those were mainly ecologically-flexible species, which in ancient forests are mainly found in disturbed areas (felling sites, glades, forest edges) (Elemans 2004, Aavik et al. 2009). The results of the bryophyte inventory show that ground vegetation characteristic of forest, with an expressed bryophyte layer, develops considerably quicker in coniferous tree plantations than in birch plantations. In birch plantations, ground vegetation characteristic of grasslands and fallow lands, with insignificant bryophyte coverage, persisted for a longer time.

When comparing with similar plantations on fertile, moderately moist soils elsewhere in Latvia, tree growth was slow in Malta and Vestiena. The average tree height in Malta in 2000 was only 78 cm; it was only slightly more in Vestiena (143 cm), whereas it can exceed 200 cm in fertile loamy and sandy clay soil rich in nutrients (Daugaviete et al. 2001). The slow tree growth is mainly explained by the soil characteristics – poor and very dry soil limiting development of saplings. Evidently, natural disturbances (dryness) in such extremely dry sites interfere with the appearance of new species, rather than facilitating it like at mesophytic, fertile sites (Davis et al. 2000).

The appearance of forest species in the herb layer can occur as early as during the first five years (Bartha et al. 2003), but those are mainly species with wide ecological amplitude. Recolonization of ancient-forest species occurs considerably later – after 25-100 and even more years (De Keersmaeker et al. 2004, Aavik et al. 2009). Dwarf shrubs have been referred to as species characteristic of ancient forests, which enter afforested areas very slowly (Palo et al. 2008). Dwarf shrubs had appeared in neither Malta nor Vestiena (although the biotope match those of dry boreal forests, where dwarf shrubs are the most important part of ground vegetation), with the exception of two species – *Calluna vulgaris* in one sample plot (at both observation sites) and *Orthilia secunda* in one sample plot of Vestiena. Both species were registered only in the final year of observation.

Low appearance of forest species may be explained by the fact that the herb layer vegetation initially consisted mainly of plant species characteristic of dry, nutrient poor areas. In such areas, formation of vegetation characteristic of forest takes longer than in mesic, fertile soils. Forest species appear more quickly on sites that are former meadows or pastures with a large number of nitrophylous species, and thus have fertile soil (Dupouey et al. 2002, Kopeckż and Vojta 2009). Another significant factor may be the fact that many forest species are clonal (mainly propagating vegetatively) or have weak migration abilities (e.g., species that spread under the effect of gravity or via ants), and thus colonize new sites very slowly (Dzwonko and Loster 1992, Brunet and Oheimb 1998, Grashof-Bokdam and Geertsema 1998, Flinn 2006, Aavik et al. 2009). In addition, it must be noted that the diversity of species in planted forests is usually lower than in naturally afforested territories, as planted trees shade the ground vegetation more evenly and reduce the heterogeneity of environmental conditions, which lies at the basis of ensuring diversity of species in naturally afforested areas (Gutko et al. 2001).

Due to mowing in the first four years development of forest vegetation in the herb layer was delayed, as the shading provided by saplings was initially slight. Afterwards the shadiness was rapidly increasing, which reduced the number of species characteristic of open areas, but at the same time also prevented the appearance of forest species, which was evidenced by a very pronounced decline in the total coverage of the herb layer. A significant role has also been played by preparation of the soil, which resulted in vegetation characteristic of arable land making up the herb layer of both Vestiena and Malta during the planting of trees, and in which there were no species characteristic of forest. It has been proven that, although there are no significant differences between arable land and grassland in terms of the rate of tree colonization (Alard et al. 2005), forest species enter the herb layer of forests created in grasslands more quickly, or some are even already present in the grassland vegetation, as light-tolerant forest species may appear during agricultural use of pastures or meadows, while forest species can only appear in arable land only after the land is abandoned (Kopecký and Vojta 2009).

However, it is difficult to compare previous studies with this one, as the rate and level of forest ecosystem development is affected by many factors. The quality and dimensions of the planting stock can affect the rate of settling of plantations and development of young stands. The cultivation of plantations can be another significant factor; for instance, in a study on oak and ash-tree plantations in a cultivated plantation, sprayed with herbicides, the saplings were on average 2.5 times taller, than in an uncultivated plantation, and their survival was 1.8 times higher (Daugaviete 2005a).

At both sites, vegetation has generally developed in a similar way as both the initial vegetation, and the planting stock and cultivation were similar. However, it must be noted that birch trees of an older stage (2-year-old bare-root trees) were planted in Vestiena, although their dimensions were the same at both sites. This could also explain the differences in the succession rate between the two sites Random events can also have an impact on succession. Cold and frost can affect plantations, and rodents and forest animals can cause damage (Daugaviete et al. 2001, Daugaviete 2005b). Depending on the previous vegetation and the presence of competitive herb species, succession may develop in very different directions and at different rates. It has been observed that some aggressive, competitive herb species may temporarily stop succession entirely. Such species are, for instance, *Calamagrostis epigeios* (Prach et al. 2001b) and *Dactylis glomerata* (Myster and Pickett 1992). Grasses in general may act as inhibitors of succession, even if their part in total coverage on the territory is negligible (Myster and Pickett 1992).

In Malta, *Calamagrostis epigeios* only appeared in 2008 as a rare species, but *Lupinus polyphyllos,* another aggressive species, already was observed during the first inventory, and continuously increase. In some places, where even rather large patches d were dominated by this species, saplings had died. The species initially dominating at both sites, *Elytrigia repens*, declined faster in Vestiena than in Malta, where its abundance and, in some areas, also coverage, were still high in the final year of observation. The differences between the two sites with similar environmental conditions may also be explained by initial differences in vegetation, which are determined by the local species bank (Kopecký and Vojta 2009). It is likely that appearance of forest species, from the viewpoint of their migration ability, could have been equally successful at both sites, as both territories are surrounded by forests, although it must be noted that forest species generally are weak colonizers of new areas (Aavik et al. 2009).

Although the herb layer in Vestiena had shifted towards a forest vegetation more than in Malta, there were larger differences in the herb layer among plantations of different tree species in Malta than in Vestiena. Local differences in the species bank and the edaphic conditions could be explanatory, as indicated ,by the fact that the herb layer vegetation of the pine plantations in Malta already differed from the other plantations during the first year of observation. In Malta, the growth of both pine and spruce was excellent: the trees developed large crowns, which relatively quickly changed the intensity of light on the ground vegetation. This could explain the relatively quick change of ground vegetation species in plantations of both tree species as compared to the birch plantations. *Achillea millefolium*, a light-demanding species, was an indicator of the birch plantation in Malta in 2008, but in previous years it was found in all plantations.

No differences between the birch plantations of various densities were found during this study. This may be explained by the fact that the shadiness in various densities remained similar. Trees are shorter in areas of larger density and taller in areas of lower density, they branch off faster in areas of higher density and slower in areas of lower density, suppressing sunlight equally well (Daugaviete 2005b).

The obtained results on changes of site reaction according to Ellenberg indicator values are in contrast to the generally known progression of succession under the effect of afforestation. Instead of the decrease of Ellenberg indicator value , which is what normally happens in boreonemoral forests (Holmberg et al. 2000, Flinn and Marks 2007, Aavik et al. 2009), it increased. The use of Ellenberg scales is justified in studies such as this, as it has been proven, in Latvia as well, that Ellenberg scale indicators correlate with the data of chemical analysis of the soil (Laiviņš and Jermacāne 2002). However, it must be admitted that the number of sample plots involved in this research was relatively low, so it was impossible to ascertain the level of reliability of the data, as well as to calculate Ellenberg reaction values individually for plantations of different tree species – and changes of soil pH directly depend on the tree species composition (Persson et al. 1987).

It is possible that the site reaction could increase in the birch plantation as birch litter does not cause soil acidification. It has been found that, in deciduous tree forests on agricultural lands, soil reaction does not change under the effect of afforestation during the first decades (Kopecký and Vojta 2009).

Conclusions

After twelve years of afforestation of arable land, the average coverage of the herb layer declined considerably and became less homogenous due to the shading created by the saplings, and transformation to forest vegetation had begun. However, species appearing were mainly ecologically-flexible species, which in ancient forests are mainly found in disturbed areas. Specific forest species (e.g. dwarf shrubs) had not appeared in neither Malta nor Vestiena.

The composition of species in the herb and bryophyte layer had changed in the direction of a forest ecosystem comparatively slowly which can be explained by slow growth of trees due to very dry and infertile soils and by management history of these sites.

The first differences in herb vegetation among plantations of different tree species (pine, spruce, birch) appeared 12 year after afforestation, but there were still no significant herb vegetation differences among birch plantations of various densities.

Ground vegetation, typical of forest with a well-developed bryophyte layer, established quicker in coniferous tree plantations than in birch plantations. In birch plantations, ground vegetation characteristic of fallow lands, with insignificant bryophyte coverage, persisted for a longer time.

Acknowledgements

The authors wish to express their gratitude to Austra Āboliņa , head researcher of LFRI Silava, for her contribution to determination of bryophytes at the sites in 1996, and to Egita Grolle for taking inventory of vegetation at the sites in 2003. The authors are grateful to two anonymous referees for their helpful comments on an earlier version of this manuscript.

References

Aavik, T., Pussa, K., Roosaluste, E. and Moora, M. 2009. Vegetation change in boreonemoral forests during succession – trends in species composition, richness and differentiation diversity. *Annales Botanici Fennici* 46: 326–335.

Alard, D., Chabrerie, O., Dutoit, T., Roche, P. and Langlois, E. 2005. Patterns of secondary succession in calcareous grasslands: can we distinguish the influence of former land uses from present vegetation data? *Basic and Applied Ecology* 6: 161–173.

Āboliņa, A. 2001. Latvijas sūnu saraksts [List of Latvian bryophyte species]. *Latvijas Veģetācija* 3, 47–87. (In Latvian with English summary).

Bartha, S., Meiners, S.J., Pickett, S.T.A. and Cadenasso, M.L. 2003. Plant colonization windows in a mesic old field succession. *Applied Vegetation Science* 6: 205–212.

Bråkenhielm, S. 2000. Plant succession on afforested farmland. *Proceedings IAVS Symposium*, IAVS, Opulus Press Uppsala, 63-66.

Brunet, J., and Oheimb, G. 1998. Migration of vascular plants to secondary woodlands in southern Sweden. *Journal of Ecology* 86: 429–38.

Daugaviete, M. 2005a. Ošu un ozolu stādījumu attīstība lauksaimniecības platību apmežojumos [Development of ash-tree and oak plantations in afforested agricultural areas]. *Mežzinātne* 14 (47): 3–27 (In Latvian with English summary).

Daugaviete, M. 2005b. Stādījumu biezības ietekme uz bērza (*Betula pendula* Roth.) augšanas gaitu un masas pieaugumu lauksaimniecības zemju apmežojumos [The effect of stand density on the growth rate and mass increase of birch in afforested agricultural areas]. *Mežzinātne* 15 (48): 14–25 (In Latvian with English summary).

Daugaviete, M., Krūmiņa, M., Kāposts, V. and Lazdiņš, A. 2001. Bērza (*Betula pendula* Roth.) augšanas gaita dažādās lauksaimniecības augsnēs [The growth rate of birch in various agricultural soils]. *Mežzinātne* 11(44)'2002: 13–51 (In Latvian with English summary)

Daugaviete, M. and Daugavietis, M. 2008. The choice of tree species for afforestation of abandoned agricultural lands in Latvia. Proceedings of International Symposium "Interactions of Wood with Various Forms of Energy", September, 9-10, 2008, Slovakia: 14–21.

Davis, M.A., Grime, J.P. and Thompson, K. 2000. Fluctuating resources in plant communities: a general theory of invasibility. *Journal of Ecology* 88: 528–534.

De Keersmaeker, L., Martens, L., Verheyen, K., Hermy, M., Schrijver, A. and 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.

Dostalova, A. 2009. Tree seedlings: how do they establish in spontaneously developed forests? A study from mountainous area in the Czech Republic. *Biodiversity and Conservation* 18: 1671–1684.

Dufrene, M. and Legendre, P. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs* 67: 345–366.

Dupouey, J.L., Dambrine, E., Laffite, J.D. and Moares, C. 2002. Irreversible impact of past land use on forest soils and biodiversity. *Ecology* 83 (11): 2978–2984.

Dzwonko, Z. and Loster, S. 1992. Species richness and seed dispersal to secondary woods in southern Poland. *Journal of Biogeography* 19: 195–204.

Elemans, M. 2004. Light, nutrients and the growth of herbaceous forest species. *Acta Oecologica* 26: 197–202.

Ellenberg, H., Weber, H.E., Düll, R., Wirth, V., Werner, W. and Paulißen, D. 1992. Zeigerwerte von Pflanzen in Mitteleuropa. Verlag Erich Goltze KG, Göttingen, p. 258. (In German with English summary).

Flinn, K. 2006. Reproductive biology of three fern species may contribute to differential colonization success in post-agricultural forests. *American Journal of Botany* 93: 1289–1294.

Flinn, K. and Marks, P.L. 2007. Agricultural legacies in forest environments: tree communities, soil properties and light availability. *Ecological Applications* 17 (2): 452–463.

Flinn, K. and Vellend, M. 2005. Recovery of forest plant communities in post-agricultural landscapes. *Frontiers of Ecology and Environment* 3(5): 243–250.

Gavrilova, Ģ. and Šulcs, V. 1999. Latvijas vaskulāro augu flora. Taksonu saraksts [Latvian flora of vascular plants. Listing of taxa]. Latvian Academic Library, Riga, 136 pp. (In Latvian with English summary)

Grashof-Bokdam, C. J., and Geertsema, W. 1998. The effect of isolation and history on colonization patterns of plant species in secondary woodland. *Journal of Biogeography* 25: 837–846.

Grime, J.P. 2001. Plant strategies, vegetation processes, and ecosystem properties. Wiley, Chichester, UK, 417 pp.

Gutko, Ž., Brūmelis, G., Liepiņš, I. and Nikodemus, O. 2001. Plant species richness, and Shannon diversity and evenness during secondary succession on abandoned agricultural land in Latvia. *Proceedings of the Latvian Academy of Sciences,* Section B, vol. 55, 1 (612): 36–42.

Hennekens, S.M., and Schaminée, J.H.J. 2001. Turboveg, a comprehensive database management system for vegetation data. *Journal of Vegetation Science* 12: 589–591.

Hill, M.O. 1979. The development of a flora in even-aged plantations. In: Ford, E.D., Malcolm, D.C., Atterson, J. (Eds.) *The ecology of even-aged forest plantations.* Cambridge, Institute of Terrestrial Ecology p. 175-192.

Hill, M.O. and Gausch, H.G. 1980. Detrended correspondence analysis: an improved ordination technique. *Vegetatio* 42: 47–58.

Holmberg, M., Rankinen, K., Johansson, M., Forsius, M., Kleemola, S., Ahonen, J. and Syri, S. 2000. Sensitivity of soil acidification model to deposition and forest growth. *Ecological Modelling* 135: 311–325.

Hunt, R., Hodgson, J.G., Thompson, K., Bungener, P., Dunnett, N.P., Askew, A.P. 2004. A new practical tool for deriving a functional signature for herbaceous vegetation. *Applied Vegetation Science* 7: 163–170.

Keišs, O. 2006. Lauksaimniecības pārmaiņu ietekme uz griezes *Crex crex* L. populāciju Latvijā: skaita dinamika, biotopu izvēle un populācijas struktūra [The effect of agricultural changes on the corncrake population in Latvia: dynamics of numbers, selection of biotopes and structure of population]. Summary of dissertation for the degree of Doctor of Biology. Riga, 23 pp. (In Latvian with English summary).

Kent, M. and Coker, P. 1994. Vegetation Description and Analysis. A Practical Approach. John Wiley & Sons, England, 363 pp.

Kopecký, M. and Vojta, J. 2009. Land use legacies in post-agricultural forests in the Doupovské Mountains, Czech Republic. *Applied Vegetation Science* 12: 251–260.

Laiviņš, M. and Jermacāne, S. 2002. Ellenberga ekoloģisko skalu izmantošana veģetācijas pētījumos Latvijā [The use of Ellenberg's ecological scales in studies of vegetation in Latvia]. Theses of the 60th scientific conference of the University of Latvia. Geography. Geology. Environmental science. Riga, p. 83–85. (In Latvian).

Laiviņš, M. and Zundāne, A. 1989. Latvijas ziedaugu un paparžaugu datu katalogs. Sinantropie elementi [Data catalogue of Latvian flowering plants and pteridophytes. The synanthropic elements]. ZRA "Silava", Salaspils, 40 pp. (In Latvian).

Liepins, K., Lazdins, A., Lazdina, D., Daugaviete, M. and Miezite, O. 2008 Naturally Afforested Agricultural Lands in Latvia – Assessment of Available Timber Resources and Potential Productivity. The 7th International Conference "Environmental Engineering" Selected Papers. Vol. I: 194–200.

Maike, P. 1953. Bērza kultūru augšanas gaita tīrumu augsnēs [Growth rates of birch plantations on field soil]. *Mežsaimniecības.problēmu institūta raksti, IV sēj.* [Articles of the Latvian Scientific Research Institute for Forestry Problems, vol. IV]. Riga, p. 24–36 (In Latvian).

Mather, A.S. and Thomson, K.J. 1995. The effects of afforestation on agriculture in Scotland. *Journal of Rural Studies* 11, 2: 187-202.

McCune, B. and Grace, J.B. 2002. Analysis of ecological communities. MjM Software Design, Gleneden Beach, Oregon, US, 299 pp.

McCune, B. and Mefford, M.J. 1999. PC-ORD. Multivariate analysis of ecological data, version 4. MjM Software Design, Gleneden Beach, OR, US, 237 pp.

Moora, M., Daniell, T.J., Kalle, H., Liira, J., Pussa, K., Roosaluste, E., Opik, M., Wheatley, R. and Zobel, M. 2007. Spatial pattern and species richness of boreonemoral forest understorey and its determinants – a comparison of differently managed forests. *Forest Ecology and Management* 250: 64-70.

Myster, R.W. and Pickett, S.T.A. 1992. Dynamics of associations between plants in ten old fields during 31 years of succession. *Journal of Ecology* 80: 291–302.

Nikodemus, O., Bell S., Grīne, I. and Liepiņš, I. 2005. The impact of economic, social and political factors on the landscape structure of the Vidzeme Uplands in Latvia. *Landscape and Urban Planning* 70: 57–67.

Palo, A., Linder, M., Truu, J. and Mander, U. 2008. The influence of biophysical factors and former land use on forest floristic variability on Saaremaa and Muhu islands, Estonia. *Journal for Nature Conservation* 16: 123–134.

Penēze, Z. 2009. Latvijas lauku ainavas izmaiņas 20. un 21. gadsimtā: cēloņi, procesi un tendences [Changes of the rural landscape of Latvia in the 20th and 21st century:

causes, processes and trends]. Dissertation. University of Latvia, Riga, 255 p. (In Latvian with English summary).
Persson, S., Malmer, N. and Wallén, B. 1987. Leaf litter fall and soil acidity during half a century of secondary succession in a temperate deciduous forest. *Vegetatio* 73: 31–45.
Prach, K., Bartha, S., Joyce, C.B., Pyšek, P., Diggelen, R. and Wiegleb, G. 2001a. The role of spontaneous succession in ecosystem restoration: A perspective. *Applied Vegetation Science* 4: 111–114.
Prach, K. Pyšek, P. and Bastl, M. 2001b. Spontaneous vegetation succession in human-disturbed habitats: a pattern across seres. *Applied Vegetation Science* 4: 83–88.
Sacenieks, R. and Gaross, V. 1961. Tīrumu augsnēs augošo egļu audžu ekonomiski izdevīgākais apsaimniekošanas veids [The most economically-beneficial methods of cultivation of spruce stands naturally growing on field soil]. Latvian State Institute of Wood Chemistry of Latvian Academy of Sciences, report on 1961, 54 pp. (In Latvian).
Sarma, P. 1949. Pētījumi par priežu un egļu augšanas gaitu tīrumu augsnēs [Research on pine and spruce growth rates on field soil]. *ZA Vēstis* 7: 7–20. (In Latvian).
Selmants, P.C. and Knight, D.H. 2003. Understory plant species composition 30-50 years after clearcutting in southeastern Wyoming coniferous forests. *Forest Ecology and Management* 185 (3): 275-289.
Stoate, C., Baldi, A., Beja, P., Boatman, N.D., Herzon, I., van Doorn, A., de Snoo, G.R., Rakosy, L. and Ramwell, C. 2009. Ecological impacts of early 21st century agricultural change in Europe – A review. *Journal of Environmental Management* 91: 22–46.
Tichy, L. 2002. JUICE, software for vegetation classification. *Journal of Vegetation Science* 13: 451–453.

Received 03 August 2010
Accepted 16 November 2011

ИЗМЕНЕНИЯ В ТРАВЯНИСТОЙ И МОХОВОЙ РАСТИТЕЛЬНОСТИ НА ОБЛЕСЕННЫХ СЕЛЬСКОХОЗЯЙСТВЕННЫХ ЗЕМЛЯХ

С. Русиня, Б. Бамбе и М. Даугавиете

Резюме

Исследована динамика травяного и мохового яруса под воздействием облесения сельскохозяйственных земель в двух модельных территориях – Вестиена и Малта. Анализированы данные учётов растительности травяного и мохового яруса в двенадцатилетнем периоде, в котором учёты проведены четыре раза – в 1996, 1999, 2003 и 2008 году. Перед закладкой насаждений условия среды и растительность в обоих местах была очень сходная – в ней доминировали виды молодых залежей. В первых годах изменения в растительности были незначительны, что можно обяснить медленным ростом молодых деревьев и малым отенением, которое они создавали. В конце периода наблюдений растительность травяного яруса становилась всё более разрежённой, в ней уменьшилось число видов залежей и появились виды лесов и опушек. Однако большинство этих видов эврибионты, что свидетельствует о большой разнице травяного яруса по сравнении с растительностью стабильных лесных экосистем. Между посадками разных древесных пород (сосна, ель, берёза) выявлены только небольшие различия, и они проявились только в данных последнего учёта, кроме Малты, где травяная растительность сосновых насаждений отличалась от других ужй в первом году учета. В растительности берёзовых насаждений разной густоты различий не было.

Ключевые слова: облесение, сукцессия, *Pinus sylvestris, Picea abies, Betula pendula,* насаждение

Acknowledgment: publication of this article is provided by European Regional Develeopment Fund project No 2DP/2.1.1.2.0/10/APIA/VIAA/021

ERAF
EIROPAS REĢIONĀLĀS ATTĪSTĪBAS FONDS

IEGULDĪJUMS TAVĀ NĀKOTNĒ

EIROPAS SAVIENĪBA

Appendix 1. Changes in the frequency and coverage of herb layer species in the Vestiena site over three inventory periods

Species	Average coverage, %			Frequency, %			Group*	IV**	p
	1999	2003	2008	1999	2003	2008			
1	2	3	4	5	6	7	8	9	10
Species with significant prevalence (p<0.05) in one of the inventory years									
Elytrigia repens (L.) Nevski	**18**	3	1	**90**	48	29	1	74	0.000
Omalotheca sylvatica (L.) Sch.Bip. et F.W. Schultz	**3**	0	0.1	**86**	0	14	1	84	0.000
Rumex acetosella L.	**2**	0	0	**76**	5	5	1	74	0.000
Achillea millefolium L.	**13**	8	0.5	**95**	100	62	1	58	0.001
Trifolium hybridum L.	**4**	0.1	0	**29**	14	5	1	28	0.020
Rumex acetosa L.	0.1	**0.2**	0	5	**29**	0	2	25	0.013
Equisetum sylvaticum L.	0	**0.5**	0	0	**19**	0	2	19	0.029
Phleum pratense L.	1	**3**	0.2	48	**62**	29	2	41	0.040
Erigeron acris L.	0.4	**1**	0	43	**43**	5	2	32	0.047
Equisetum pratense Ehrh.	0.3	0	**2**	19	5	**57**	3	47	0.000
Rubus idaeus L.	0	0	**7**	0	0	**57**	3	57	0.000
Epilobium montanum L.	0.1	0	**0.2**	5	0	**38**	3	30	0.001
Holcus mollis L.	0	0	**5**	0	0	**33**	3	33	0.001
Picea abies (L.) H. Karst.	0	0	**0.2**	0	0	**33**	3	33	0.001
Chamaenerion angustifolium (L.) Scop.	0.1	2	**5**	5	29	**71**	3	50	0.001
Agrostis tenuis Sibth.	0	0	**0.2**	0	0	**29**	3	28	0.002
Anthriscus sylvestris (L.) Hoffm.	0	0	**0.1**	0	0	**24**	3	23	0.010
Sorbus aucuparia L.	0	0	**0.1**	0	0	**24**	3	23	0.010
Trifolium arvense L.	0	0	**0.1**	0	0	**24**	3	23	0.011
Agrostis gigantea Roth.	2	0	**2**	19	0	**71**	3	36	0.027
Trifolium medium L.	0	0	**0.1**	0	0	**19**	3	19	0.030
Other species									
Acer platanoides L.	0	0	0.1	0	0	5	3	4.8	1.000
Anchusa officinalis L.	0.2	0.1	0.1	14	29	24	2	8	1.000
Arenaria serpyllifolia L.	0.1	0.1	0	10	10	0	1	4.8	1.000
Artemisia campestris L.	0.1	0.4	0.1	5	14	14	2	10	0.406
Artemisia vulgaris L.	1	0.3	0.3	24	29	43	1	12	0.962
Betula pendula Roth	0.3	0.5	0.1	14	10	5	2	5	0.773
Betula pubescens Ehrh.	0	0	0.1	0	0	14	3	14.3	0.096
Calluna vulgaris (L.) Hull	0	0	0.1	0	0	5	3	4.8	1.000
Campanula patula L.	0	0.1	0.1	0	19	29	3	15	0.179
Campanula persicifolia L.	0	0	0.1	0	0	5	3	4.8	1.000
Carex pallescens L.	0	0	0.1	0	0	5	3	4.8	1.000
Carlina vulgaris L.	0	0	0.1	0	0	14	3	14.3	0.108
Cerastium holosteoides Fr.	0.1	0	0.1	5	0	14	3	8.6	0.302
Clinopodium vulgare L.	0	0	0.1	0	0	5	3	4.8	1.000
Carex ovalis Gooden.	0	0	0.1	0	0	5	3	4.8	1.000
Dactylis glomerata L.	0.1	0	0.2	5	0	19	3	15.9	0.092
Deschampsia cespitosa (L.) P. Beauv.	0.6	0	0	10	0	0	1	9.5	0.324
Dryopteris carthusiana (Vill.) H.P. Fuchs	0	0	0.1	0	0	5	3	4.8	1.000
Equisetum arvense L.	0.1	0	0	5	0	0	1	4.8	1.000
Conyza canadensis (.L) Cronquist	0.1	0.1	0	5	5	0	1	2.4	1.000
Festuca ovina L.	0	2	0	0	14	0	2	14.3	0.104
Festuca rubra L.	0	3	1	0	19	38	2	15	0.320
Fragaria vesca L.	0	2	3	0	10	33	3	19.8	0.077
Galeopsis tetrahit L.	0	0	0.1	0	0	5	3	4.8	1.000
Galium album Mill.	0.1	0	0.1	5	0	10	3	6.3	0.773
Geum urbanum L.	0	0	0.6	0	0	10	3	9.5	0.322
Helictotrichon pubescens (Huds.)Pilg.	0	0	0.1	0	0	5	3	4.8	1.000
Hieracium umbellatum L.	0	0	0.1	0	0	5	3	4.8	1.000
Hypericum perforatum L.	2	2	0.1	24	43	29	2	16	0.606
Hypochoeris radicata L.	0	0	0.1	0	0	10	3	9.5	0.316
Jasione montana L.	0.2	0	0.1	10	0	14	1	6.9	0.652
Juncus effusus L.	0	0	0.1	0	0	5	3	4.8	1.000
Knautia arvensis (L.) Coult.	0	0	0.1	0	0	5	3	4.8	1.000
Lathyrus pratensis L.	0.1	0.1	0.1	5	5	14	3	7	0.612
Leontodon autumnalis L.	0	0	0.1	0	0	5	3	4.8	1.000
Leucanthemum vulgare Lam.	0.1	0.2	0.1	5	19	29	2	10	0.714
Luzula campestris (L.) DC.	0	0.1	0	0	5	0	2	4.8	1.000
Luzula multiflora (Ehrh.) Lej.	0	0	0.1	0	0	5	3	4.8	1.000
Malus domestica Borkh.	0	0	0.1	0	0	5	3	4.8	1.000
Melampyrum polonicum (Beauverd.) Soó	0	0	0.1	0	0	10	3	9.5	0.327
Melampyrum pratense L.	0	0.1	0	0	5	0	2	4.8	1.000
Melilotus albus Medik.	0	0.1	0	0	10	0	2	9.5	0.327
Myosotis arvensis (L.) Hill	0.1	0	0.1	5	0	10	3	6.3	0.770
Origanum vulgare L.	0	0	0.1	0	0	10	3	9.5	0.332

Appendix 1. (Continuation)

1	2	3	4	5	6	7	8	9	10
Orthilia secunda (L.) House	0	0	0.1	0	0	5	3	4.8	1.000
Pilosella officinarum F.W. Schultz et Sch.Bip.	0.1	0	0.1	5	0	5	1	2.4	1.000
Pimpinella saxifraga L.	0	0.1	0	0	5	0	2	4.8	1.000
Poa pratensis L.	0	1	0	0	10	0	2	9.5	0.327
Potentilla argentea L.	2	3	0.1	62	71	29	2	10.1	0.451
Prunella vulgaris L.	0	0.1	0.1	0	5	14	3	10.7	0.303
Quercus robur L.	0	0	0.1	0	0	10	3	9.5	0.331
Scrophullaria nodosa L.	0	0	0.1	0	0	5	3	4.8	1.000
Silene vulgaris (Moench) Garcke	0.1	0	0.1	5	0	10	1	3.6	1.000
Solidago virgaurea L.	2	6	5	14	52	81	3	30	0.233
Stellaria graminea L.	0	0.1	0	0	5	0	2	4.8	1.000
Taraxacum officinale F.H. Wigg. s.l.	0.1	0.1	0.1	14	14	10	2	7	0.865
Tragopogon pratensis L.	0	0	0.1	0	0	5	3	4.8	1.000
Trifolium aureum Pollich	2	3	0.1	19	38	5	2	23	0.102
Trifolium pratense L.	0	0.1	0	0	10	0	2	9.5	0.331
Trifolium repens L.	0.1	0	0.1	14	0	19	3	9.5	0.487
Tripleurospermum perforatum (Mérat) M. Laínz	0.1	0	0	5	0	0	1	4.8	1.000
Urtica dioica L.	0	0	0.1	0	0	5	3	4.8	1.000
Valeriana officinalis L.	0	0	0.1	0	0	5	3	4.8	1.000
Verbascum nigrum L.	0	0	0.1	0	0	10	3	9.5	0.319
Veronica chamaedrys L.	0	0.1	0.1	0	10	5	2	6.3	0.760
Veronica officinalis L.	0	0	0.1	0	0	10	3	9.5	0.329
Veronica serpyllifolia L.	0	0	0.1	0	0	5	3	4.8	1.000
Vicia cracca L.	1	1	0.3	33	52	52	2	27	0.333
Vicia sepium L.	0.1	0.4	0.1	5	19	24	2	13	0.351
Viola arvensis Murray	0	0	0.1	0	0	10	3	9.5	0.318

*Group – the year in which the respective species had significant prevalence. 1 – 1999, 2 – 2003, 3 – 2008

**IV – the indicator value of the species

Appendix 2. Changes in the frequency and coverage of herb layer species in the Malta site over three inventory periods

Species	Average coverage, %			Frequency, %			Group*	IV**	p
	1999	2003	2008	1999	2003	2008			
1	2	3	4	5	6	7	8	9	10
Species with significant prevalence (p<0.05) in one of the inventory years									
Achillea millefolium L.	**30**	3	0.2	**95**	86	43	1	85	0.000
Omalotheca sylvatica (L.) Sch.Bip. et F.W. Schultz	**1.0**	0.1	0	**57**	5	0	1	56	0.000
Pinus sylvestris L.	**2**	0	0.1	**48**	0	14	1	45	0.000
Jasione montana L.	**1.0**	0.2	0.1	**67**	24	29	1	47	0.001
Conyza canadensis (.L) Cronquist	**0.2**	0.1	0	**38**	5	0	1	34	0.001
Rumex acetosella L.	**1**	0.5	0.2	**81**	52	43	1	48	0.007
Vicia hirsuta (L.) Gray	0.1	**0.3**	0.1	14	**43**	14	2	29	0.019
Carlina vulgaris L.	0	0	**0.2**	0	0	**43**	3	43	0.000
Epilobium montanum L.	0	0	**0.2**	0	0	**43**	3	43	0.000
Senecio jacobaea L.	0	0	**0.5**	0	0	**67**	3	67	0.000
Veronica officinalis L.	0	0	**0.3**	0	0	**52**	3	52	0.000
Knautia arvensis (L.) Coult.	0	0.1	**0.2**	0	5	**43**	3	35	0.000
Acer platanoides L.	0	0	**0.1**	0	0	**29**	3	29	0.002
Picea abies (L.) H. Karst.	0	0.1	**0.2**	0	5	**43**	3	30	0.004
Equisetum pratense Ehrh.	0	0	**0.1**	0	0	**24**	3	24	0.010
Solidago virgaurea L.	0	0.5	**0.4**	0	19	**71**	3	32	0.024
Rumex acetosa L.	0	0	**0.1**	0	0	**19**	3	19	0.028
Anthriscus sylvestris (L.) Hoffm.	0	0	**0.1**	0	0	**19**	3	19	0.029
Hypericum perforatum L.	0	0	**0.1**	0	0	**19**	3	19	0.029
Clinopodium vulgare L.	0	0	**0.1**	0	0	**19**	3	19	0.031
Myosotis micrantha Pall. ex Lehm.	0.1	0	**0.1**	5	0	**24**	3	20	0.039
Other species									
Agrimonia eupatoria L.	0	0	0.1	0	0	5	3	4	1.000
Agrostis gigantea Roth	1	0	1	24	0	33	3	17	0.219
Agrostis tenuis Sibth.	0.2	0.1	0.1	14	10	19	1	8	0.615
Anchusa officinalis L.	0	0	0.1	0	0	5	3	4	1.000
Anthemis arvensis L.	0	0	0.1	0	0	10	3	9	0.319
Anthemis tinctoria L.	0.1	0.5	0.1	10	24	10	2	20	0.068
Artemisia campestris L.	0.1	0.0	0.2	5	5	33	3	19	0.067
Artemisia vulgaris L.	1	1	0.3	24	33	57	2	15	0.897

Appendix 2. (Continuation)

1	2	3	4	5	6	7	8	9	10
Betula pendula Roth	1	0.3	0.1	24	24	14	1	16	0.315
Calamagrostis epigeios (L.) Roth	0	0	1	0	0	14	3	14	0.102
Calluna vulgaris (L.) Hull	0	0	0.1	0	0	5	3	4	1.000
Carex ovalis Gooden.	0.1	0	0.1	5	0	19	3	7	0.397
Centaurea cyanus L.	0.1	0.1	0	5	5	0	1	2	1.000
Centaurea scabiosa L.	0	0	0.1	0	0	10	3	9	0.318
Cerastium holosteoides Fr.	0.1	0.4	0.1	10	10	29	3	6	0.891
Cerastium semidecandrum L.	0	0	0.1	0	0	5	3	4	1.000
Chaerophyllum aromaticum L.	0.1	0	0.1	5	0	5	1	2	1.000
Chamaenerion angustifolium (L.) Scop.	0	0	0.1	0	0	14	3	14	0.099
Cirsium arvense (L.) Scop.	0	0	0.1	0	0	10	3	9	0.316
Dactylis glomerata L.	0	0	0.1	0	0	5	3	4	1.000
Deschampsia cespitosa (L.) P. Beauv.	0	0	0.1	0	0	14	3	14	0.104
Elytrigia repens (L.) Nevski	6	2	3	71	38	67	1	38	0.131
Equisetum arvense L.	1	0.4	0.1	29	33	24	1	15	0.671
Erigeron acris L.	1	0.1	0	19	5	0	1	18	0.074
Euphrasia micrantha Rchb.	0	0.1	0	0	5	0	2	4	1.000
Fallopia dumetorum (L.) Holub	0	0	0.1	0	0	14	3	14	0.095
Festuca rubra L.	1	5	2	19	43	57	2	24	0.252
Fragaria vesca L.	0	5	2	0	29	67	3	20	0.471
Galeopsis tetrahit L.	0	0.1	0.1	0	10	14	3	8	0.615
Galium album Mill.	0.1	1	1.0	10	33	76	3	34	0.085
Geum urbanum L.	0	0	0.1	0	0	5	3	4	1.000
Hypochoeris radicata L.	0.2	0.1	0	10	5	0	1	8	0.545
Leontodon autumnalis L.	0	0	0.1	0	0	10	3	9	0.323
Lupinus polyphyllus Lindl.	3	9	3	5	43	76	2	26	0.285
Luzula pilosa (L.) Willd.	0.1	0	0.2	5	0	10	3	6	0.537
Melampyrum polonicum Beauverd.) Soó	0	0	0.1	0	0	10	3	9	0.318
Melampyrum pratense L.	0	0	0.1	0	0	5	3	4	1.000
Melandrium album (Mill.) Garcke	0	0	0.1	0	0	5	3	4	1.000
Melilotus albus Medik.	0	0.1	0	0	10	0	2	9	0.315
Mentha arvensis L.	0.1	0	0	5	0	0	1	4	1.000
Myosotis arvensis (L.) Hill	0.1	0.2	0	14	24	0	2	18	0.092
Phleum pratense L.	3	0	0.1	19	0	14	1	18	0.162
Pilosella officinarum F.W. Schultz et Sch.Bip.	0	2	0.1	0	5	19	2	4	0.946
Pimpinella saxifraga L.	0	0.2	0.2	0	14	38	3	18	0.178
Poa pratensis L.	0.1	0.1	0.1	5	5	5	1	1	1.000
Potentilla argentea L.	0	0	0.1	0	0	5	3	4	1.000
Ranunculus repens L.	0	0	0.1	0	0	5	3	4	1.000
Rubus idaeus L.	0	0.2	0.3	0	5	19	3	11	0.276
Rubus saxatilis L.	0	0.2	0	0	10	0	2	9	0.323
Salix myrsinifolia Salisb.	0	0	0.1	0	0	5	3	4	1.000
Scleranthus perennis L.	0.0	0	0.1	5	0	10	3	6	0.768
Selinum carvifolia (L.) L.	0	0	0.1	0	0	5	3	4	1.000
Seseli libanotis (L.) W.D.J.Koch	0	0	0.1	0	0	10	3	9	0.314
Silene nutans L.	0	0.1	0	0	5	0	2	4	1.000
Silene vulgaris (Moench) Garcke	0	0	0.1	0	0	10	3	9	0.325
Sonchus arvensis L.	0.1	0.1	0	5	19	0	2	13	0.124
Sorbus aucuparia L.	0	0	0.1	0	0	14	3	14	0.100
Stellaria graminea L.	0	0.1	0.1	0	10	14	3	8	0.604
Tanacetum vulgare L.	0	0	0.1	0	0	5	3	4	1.000
Taraxacum officinale F.H. Wigg. s.l.	0.2	0.4	0.1	24	29	19	2	15	0.485
Trifolium arvense L.	0.1	0	0.1	14	0	14	1	7	0.871
Urtica dioica L.	0	0	0.1	0	0	5	3	4	1.000
Veronica arvensis L.	0	0	0.1	0	0	5	3	4	1.000
Veronica chamaedrys L.	0	0.1	0.1	0	10	19	3	8	0.510
Vicia angustifolia Reichard	0.1	0.1	0.1	29	10	5	1	17	0.089
Vicia cracca L.	0.1	0.2	0.1	10	10	24	3	7	0.905
Vicia sepium L.	0	0	0.1	0	0	10	3	9	0.332
Viola arvensis Murray	0	0	0.1	0	0	14	3	14	0.106

*Group – the year in which the respective species had significant prevalence. 1 – 1999, 2 – 2003, 3 – 2008

**IV – the indicator value of the species

Appendix 3. Differences in vegetation composition in Vestiena and Malta in 2008 (only the frequent species unique to each site, and species with significant differences in frequency of coverage between the two sites)

Species	Average coverage, %		Frequency, %		Group**	IV***	p
	V*	M	V	M			
Species unique to each site							
Holcus mollis L.	**4.9**	0.0	**33**	0	V	15	0.007
Campanula patula L.	**0.1**	0.0	**29**	0	V	12.2	0.018
Leucanthemum vulgare Lam.	**0.1**	0.0	**29**	0	V	12.3	0.019
Amblystegium serpens (Hedw.) B., S. et G.E0	**0.1**	0.0	**24**	0	V	11.3	0.044
Trifolium medium L.	**0.1**	0.0	**19**	0	V	9.1	0.100
Pilosella x floribunda (Wimm. et Grab.) Fr.	**0.1**	0.0	**19**	0	V	9.2	0.105
Trifolium repens L.	**0.1**	0.0	**19**	0	V	9.3	0.113
Lupinus polyphyllus Lindl.	0.0	**2.8**	0	**76**	M	30.1	0.000
Senecio jacobaea L.	0.0	**0.5**	0	**67**	M	23.7	0.000
Pimpinella saxifraga L.	0.0	**0.2**	0	**38**	M	15.3	0.004
Polytrichum commune Hedw. E0	0.0	**0.4**	0	**33**	M	14.3	0.009
Myosotis micrantha Pall. ex Lehm.	0.0	**0.1**	0	**24**	M	11.3	0.049
Equisetum arvense L.	0.0	**0.1**	0	**24**	M	11.2	0.045
Rumex acetosa L.	0.0	**0.1**	0	**19**	M	9.4	0.114
Species with significant prevalence (p<0.05) in one of the sites							
Chamaenerion angustifolium (L.) Scop.	**4.9**	0.1	**71**	14	V	33.7	0.000
Rubus idaeus L.	**6.9**	0.3	**57**	19	V	28.4	0.003
Equisetum pratense Ehrh.	**1.7**	0.1	**57**	24	V	28.2	0.003
Hylocomium splendens (Hedw.) B., S. et G. E0	**2.4**	0.1	**43**	10	V	21.9	0.011
Brachythecium oedipodium (Mitt.) Jaeg. E0	**5.3**	0.1	**62**	24	V	38.7	0.013
Agrostis gigantea Roth	**2.3**	0.5	**71**	33	V	40.5	0.025
Solidago virgaurea L.	**5.0**	0.4	**81**	71	V	53.4	0.039
Galium album Mill.	0.1	**0.9**	10	**76**	M	33.5	0.000
Pinus sylvestris L.E2	2.0	**11.1**	14	**67**	M	30.3	0.005
Veronica officinalis L.	0.1	**0.3**	10	**52**	M	22.3	0.008
Rumex acetosella L.	0.1	**0.2**	5	**43**	M	17.9	0.010
Knautia arvensis (L.) Coult.	0.1	**0.2**	5	**43**	M	17.7	0.011
Elytrigia repens (L.) Nevski	0.9	**3.2**	29	**67**	M	36.3	0.044
Species dominating and frequent at both sites							
Betula pendula Roth E2	48.5	43.4	81	100	M	50.4	0.748
Picea abies (L.) H. Karst.E2	8.6	10.5	19	67	M	30.4	0.180
Festuca rubra L.	0.8	2.3	38	57	M	31.6	0.068
Fragaria vesca L.	2.8	2.4	33	67	M	35.3	0.673
Achillea millefolium L.	0.4	0.2	62	43	V	33.2	0.162
Artemisia campestris L.	0.1	0.2	14	33	M	18	0.287
Artemisia vulgaris L.	0.3	0.3	43	57	M	32.3	0.598
Picea abies L.) H. Karst.	0.2	0.2	33	43	M	25.6	0.748
Epilobium montanum L.	0.2	0.2	38	43	M	27.1	1.000
Pleurozium schreberi (Brid.) Mitt.E0	7.7	5.3	52	76	V	42.6	0.999
Polytrichum juniperinum Hedw. E0	0.5	0.7	14	48	M	24	0.291

* – Observation site: V – Vestiena, M - Malta

**Group – the place where the species is an indicator species

***IV – the indicator value of the species

E0 – bryophyte layer, E2 – shrub/tree layer; other species in the herb layer