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Vegetation dynamics of herb layer in managed submountain beech forest

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Abstract

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Dynamics of herb layer within two communities in managed submountain beech forest was studied. Sampling was done on three differently managed forest plots over the period of 16 years (1995–2011). The first plot was situated in an original 110-year-old beech stand (control), the second was covered by a thicket (in 2011 – aged ca 23 years) developed after clear-cut. At the third plot, several interventions were performed along with a gradual reduction of the original stand density, and finally the parent stand was completely felled. Results revealed conspicuous changes in community structure, especially in species richness and composition. Also, changes in population dynamics of two dominant herb species were observed, mainly on the managed plots. Using Shannon-Wiener's index we ranked the communities to the category with low-diversity, however increasing diversity was denoted on the area with complete removal of the tree layer. Bioindication using the Ellenberg's indicator values for selected ecological factors (temperature, light, soil moisture and nitrogen content) was used to find a reflection of the human-caused environmental changes on herb layer structure in a beech forest. Mean values for the both light and nitrogen content were changed significantly only on the managed plots, while no biologically significant changes in mean values for the both temperature and soil moisture were found.

Keywords

beech stand, bioindication, *Carici pilosae-Fagetum*, density, *Dentario bulbiferae-Fagetum*, species richness

Introduction

Plant communities of beech stands are considered rather poor in the diversity of their herb component. However, also species rich communities of beech forests are reported (Ujházyová and Ujházy, 2007). Hrivnák et al. (2013) described inversely unimodal species richness-altitude relationship in Central European beech forests. The diversity of herb layer depends on multiple factors and has not been explained sufficiently yet. Ground vegetation development depends on light supply (Davis et al., 1998; Härdtle et al., 2003; Diaci et al., 2012). Slowly degradable leaf litter represents barrier for plant germination and growth (Kooijman, 2010). Also water uptake in upper soil layers is another limiting factor which can be affected by strong suction of beech roots (Gálhidy et al., 2006). Typical example of negative interactions among beech and understorey vegetation are "nudal" beech dominated forests classified as *Fagetum pauper* group of forest types in Slovak typological system (Hančinský, 1972) or *Dentario bulbiferae-Fagetum* association (Jarolímek and Šibík, 2008), respectively. They are characterised by poorly developed herbal synusia with both low cover and low number of herb species. Partial or complete removal of the dominant trees from the forest ecosystem results in an increase of litter decomposition and topsoil nitrification rate (Purahong et al., 2014). Increased availability of multiple resources is associated with increasing species diversity and productivity of herb layer in general. As a consequence, seasonal dynamics of the communities are modified (Schieber, 1996, 2007; Graae and Heskjaer, 1997; Pykälä, 2004; Godefroid et al., 2005). Subsequently, restoration of the communities may require a relatively long time (Bossuyt and Hermy, 2000; Łaska, 2000).

The aim was to examine the response of herb understorey to the changed ecological conditions in managed beech forest and to identify the temporal changes in selected ecological factors through the bioindication.

Material and methods

The research was done at the Beech Ecological Experimental Site (BEES) localized in the SE part of the Kremnické vrchy Mts (48°38′N, 19°04′E, 450–520 m asl). Site is located on a west-southwest oriented slope with an inclination of 5–15°. The area belongs to a moderately warm region, moderately warm and humid, in a hilly sub-region (Lapin et al., 2002). The annual mean air temperature was increased from 6.8 $°C_{(1951–1980)}$ to 7.5 $°C_{(1994–2013)}$ and the mean annual rainfall is 780 mm. The mean January and July air temperatures are –3.5 °C and +18.0 °C, respectively for the period of 1994–2013 (unpublished). More than 55% of the annual rainfall occurs between April and September. The soils are skeletal cambisols with a moderate acidic reaction and skeletal cover ranging from 10 to 60% (Kukla et al., 1998).

Investigations were carried out in three different plots of the BEES area (Fig. 1):

- K – control plot representing a 115-year-old beech stand with stocking density of 1.0;
- H – formerly a clear-cut area until intervention in 1989. By 2011 this plot had a 23-year-old thicket.
- M – managed; original stocking degree of the parent stand was decreased from 0.9 to 0.7 in 1989. Subsequently stocking degree was reduced to 0.5 in spring 2004 and finally the rest of a parent stand was completely felled in spring 2009.

Dominant tree species in the plot K is *Fagus sylvatica*, and associated species include *Abies alba*, *Quercus dalechampii*, *Carpinus betulus* and *Tilia cordata*. In addition to these, naturally regenerated thicket on the plot H is supplemented with *Salix caprea, Populus tremula, Betula pendula, Acer pseudoplatanus, Cerasus avium* and *Picea abies* species. Plant communities of the study area are classified as *Carici pilosae-Fagetum* and *Dentario bulbiferae-Fagetum* associations (Kontriš et al., 1995). More detailed information concerning BEES is in Kontriš et al. (1993a, b), Križová (1993), Kodrík (1997), Kuklová et al. (2005), Kellerová and Janík (2006), Janík (2010), Barna and Schieber (2011) and Janík et al. (2011).

Two subplots of the 400 m^2 area were established on each of three plots. The first subplot represented the association of *Carici pilosae-Fagetum* (*CpF*), the second *Dentario bulbiferae-Fagetum* (*DbF*). Herb species in the understorey were sampled in 1995, and repeatedly in 2008 and 2011 in three pairs of subplots (within K, H, M plots and two associations).

Species richness was evaluated for herb layer excluding tree-species juveniles. Braun-Blanquet combined scale modified by Zlatník (1953) was used to determine the species cover within the herb layer. Shannon-Wiener's index was applied to evaluate the changes in species diversity. Floristic similarity of the communities was expressed by Sørensen's index. Communities were considered to be similar if the index was

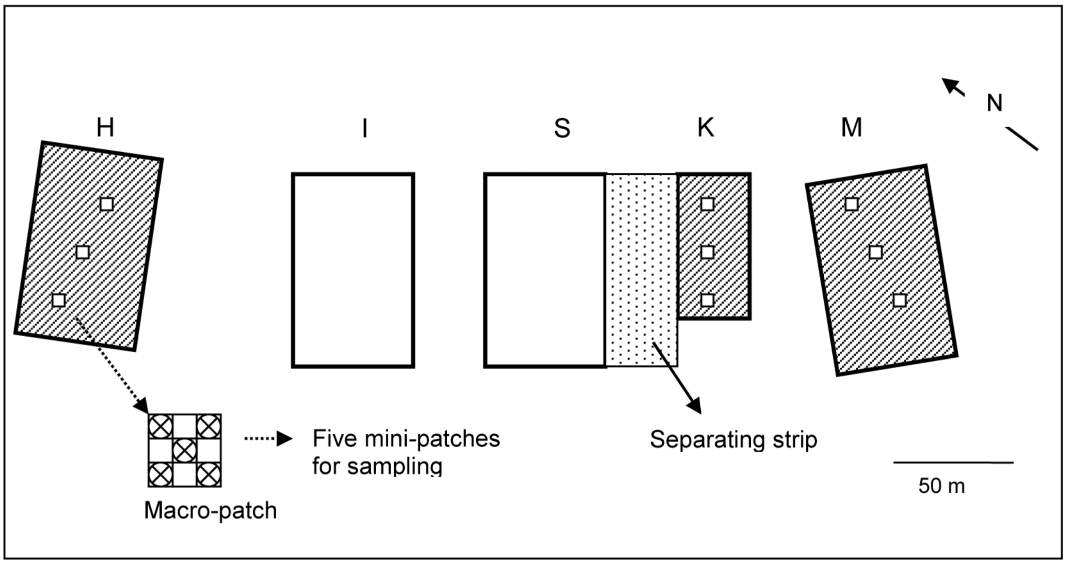

Fig.1. Scheme of sampling in the plots (H, I, S, K, M) of BEES.

equal or higher than 70% (Moravec, 2000). Temporal changes in selected ecological factors (light, temperature, soil humidity and nitrogen content) were analyzed by bioindication method based on eco-analysis using Ellenberg′s indicator values – EIVs (Ellenberg et al., 1992). Ecological analysis was processed manually and calculations were done in regard to percentage cover (dominance) of the species. The difference > 0.5 between two mean values was considered as an ecologically significant change of the factor (Križová and Nič, 2000). Considering that conditions at the whole space on each of study plots were relative homogeneous, the both communities within each plot were merged together as a whole for bioindication analysis. The presence of generative phenophases within all species was also observed to express the vitality of the species (Bottlíková, 1975). The dynamics of population density for two dominant species was analysed at the time of its optimal vegetative development – in May and in July for *Dentaria bulbifera* and *Carex pilosa*, respectively. Density of fertile and sterile shoots (ramets) was sampled on 15 mini-patches with a dimension of 1m^2, which were placed within three macro-patches (9 m^2). Macro-patches were localised along the line transect within each subplot (Fig. 1). Temporal changes in the density within the plots were tested by Fisher’s LSD test (Statistica® program). Measurements of light conditions were done by Luxmeter PU 150 (Metra Blansko) at 7 different points within each studied plot of BEES during anti-cyclonal, sunny conditions in June 1995 and the following measurements were performed repetitively in June 2008 and 2011. Nomenclature for plants and for plant communities followed Marhold and Hindák (1998) and Jarolímek and Šibík (2008), respectively.

Results

Changes in species richness and composition

Changes in species composition of the herb layer within three plots managed by different way during the period of 16 years are summarised in Tables 1–3. Species richness on control plot K with completely closed canopy was relative stable and varied from 12 to 17 taxa. The number of species with cover > 1% was 12 in 1995, but only three species were present in 2011. Conspicuous change on this plot was observed in *Ajuga reptans* and *Veronica officinalis*, within 16 years these taxa had disappeared. Also *Lathyrus vernus* suffered a considerable decrease in its cover. However, some species were absent in at least one association, such as *Fragaria vesca, Pulmonaria officinalis* and *Rubus hirtus*. In another plot H with dense young tree stand, 29 taxa were recorded in both associations in 1995, but a 55% decrease to 13 taxa was noted after 16 years. The number of taxa with dominance exceeding 1% on this plot was 16 in 1995, but only 3 in 2011. The largest changes were observed in the *Calamagrostis epigejos*, *Atropa belladona*, *Eupatorium cannabinum* and *Rubus idaeus* species. Their cover in 1995 reached of 5–50%, whereas in 2011 were not present. A considerable drop in dominance or absolute absence was also recorded in the *Ajuga reptans*, *Fragaria vesca*, *Chamerion angustifolium*, *Senecio fuchsii*, *Tussilago farfara*, *Veronica officinalis* and *Viola reichenbachiana* species. On the third plot M, influenced by three cutting operations in 1989, 2005 and in 2009 years, there was found out the opposite trend. The species diversity gradually increased in time. While a total number of taxa was 22 in 1995, increasing to 68 species was detected by 2011. The most remarkable increase in dominance was found in the *Cirsium arvense*, *Carduus nutans* and *Rubus hirtus* species. Spatio-temporal analysis of diversity, expressed by Shannon-Wiener index, showed increasing values on plot M, especially in *DbF*, but the opposite trend was observed on plot H with young thicket. There was found the decrease in values of the index for the both communities. Diversity on the control plot K was relative stable. The values of Shannon-Wiener index were less than 2.5 for all communities on the studied plots, so we can classify them as a low-diversity communities. Only *DbF* community on plot M was the exception with the index of 2.8, which may be ranked to category of medium-diversity (Fig. 2). Floristic similarity of studied communities is expressed by Sørensen’s index (Table 4). The highest values of the index were detected between the communities on control plot K (68.9–72.7%). On the other hand the lowest values were found within the plot M (32.8–41.5). Comparison between the plots showed, that the index of similarity reached the highest values of 77.8% and 63.6% (between K and M) within the both *CpF* and *DbF* communities, respectively. This similarity was found at the beginning of the study period in 1995. Also, high index of similarity (69.6%) was calculated between K and H at the end of the study period in 2011. Contrary to this, the lowest values of index were detected between K and M at the end of the study period (Table 4).

Population dynamics of the dominant species

The presence of generative phases within life cycle of a taxon reflects its good vitality and vice versa. Accordingly, generative phenophases were observed in 81% of the taxa in both associations on plot K in 1995. By 2011, this was noted in 53%, accounting for 9 species including two ferns. Decrease in number of taxa with generative phases from 29 recorded in 1995 to 4 species in 2011 on the second plot H was found. Compared to these plots, the opposite temporal trend in presence of generative phases was observed on the third plot M.

Table 1. Changes in species composition and dominance of herb layer in *Dentario bulbiferae-Fagetum* (*DbF*) and *Carici pilosae-Fagetum* (*CpF*) communities on control plot K; (a) – absence of generative phenophases

Years	1995		2008		2011	
Phytocoenoses	*DbF*	*CpF*	*DbF*	*CpF*	*DbF*	*CpF*
Herb layer						
Ajuga reptans	1 (a)	1 (a)	.	.	.	.
Athyrium filix-femina	.	+	.	r	+	+
Brachypodium sylvaticum	.	.	.	.	.	r
Carex digitata	.	.	.	.	+	.
Carex pilosa	.	4	.	3	.	-2
Cephalanthera longifolia	.	.	r (a)	.	r(a)	+(a)
Dentaria bulbifera	2	2	-2	-2	1	1
Dryopteris filix-mas	+	+	.	r	+	+
Fragaria vesca	1	1	.	+ (a)	r(a)	+(a)
Galium odoratum	2	1	+	1	1	1
Geranium robertianum	r (a)	.	.	.	.	.
Geum urbanum	.	r	.	.	.	.
Lathyrus vernus	.	2	.	r (a)	.	+
Melittis melissophyllum	.	.	.	.	.	r(a)
Oxalis acetosella	.	1	.	+	+	+
Pulmonaria officinalis	1	1	.	+ (a)	+(a)	.
Rubus hirtus	1	2 (a)	.	+(a)	+(a)	+(a)
Sanicula europaea	2	1	.	.	+(a)	.
Symphytum tuberosum	.	.	.	.	.	+(a)
Veronica officinalis	.	1	.	.	.	.
Viola reichenbachiana	1	2	.	+ (a)	+(a)	+(a)
Total number of species	16		12		17	

Table 2. Changes in species composition and dominance of herb layer in *Dentario bulbiferae-Fagetum* (*DbF*) and *Carici pilosae-Fagetum* (*CpF*) communities on plot H – thicket; (a) – absence of generative phenophases

Years	1995		2008		2011	
Phytocoenoses	*DbF*	*CpF*	*DbF*	*CpF*	*DbF*	*CpF*
Herb layer						
Ajuga reptans	1	+	.	.	.	.
Atropa belladona	2	+	.	.	.	.
Calamagrostis epigejos	3	.	.	.	.	.
Campanula persicifolia	.	+	.	.	.	.
Carduus acanthoides	.	+	.	.	.	.
Carex digitata	1	+	+	.	+	+
Carex pilosa	.	4	.	3 (a)	.	-2(a)
Carex sylvatica	+	.	+	.	+	+
Cephalanthera longifolia	.	.	r (a)	.	r(a)	.
Cirsium arvense	.	+	.	.	.	.
Coronilla varia	+	.	.	.	.	.
Dentaria bulbifera	2	2	-2	1	1	1
Epilobium montanum	+	.	.	.	.	.
Eupatorium cannabinum	2	.	.	.	.	.
Fragaria vesca	1	+	.	.	.	.
Galium odoratum	1	+	+	.	+	.
Geranium robertianum	.	.	r (a)	r (a)	r(a)	.
Glechoma hederacea	+	.	.	.	.	.
Hypericum hirsutum	+	+	.	.	.	.
Chamerion angustifolium	1	.	.	.	.	.
Juncus effusus	r	.	.	.	.	.

Table 2. Changes in species composition and dominance of herb layer in *Dentario bulbiferae-Fagetum* (*DbF*) and *Carici pilosae-Fagetum* (*CpF*) communities on plot H – thicket; (a) – absence of generative phenophases – continued

Years	1995		2008		2011	
Phytocoenoses	*DbF*	*CpF*	*DbF*	*CpF*	*DbF*	*CpF*
Herb layer						
Platanthera bifolia	.	.	.	.	.	+(a)
Pulmonaria officinalis	+	+	+ (a)	.	+(a)	.
Rubus hirtus	1	+	1 (a)	+ (a)	+(a)	1(a)
Rubus idaeus	2	.	.	.	.	.
Sanicula europaea	+	.	.	.	.	.
Scrophularia nodosa	+	.	.	.	.	.
Senecio fuchsii	.	1	.	.	.	.
Tithymalus amygdaloides	.	+	+ (a)	.	r(a)	.
Tussilago farfara	.	1	.	.	.	.
Veronica officinalis	1	1	+ (a)	.	r(a)	.
Viola reichenbachiana	1	1	+ (a)	.	+(a)	r(a)
Total number of species	29		12		13	

Table 3. Changes in species composition and dominance of herb layer in *Dentario bulbiferae-Fagetum* (*DbF*) and *Carici pilosae-Fagetum* (*CpF*) communities on plot M; (a) – absence of generative phenophases

Years	1995		2008		2011	
Phytocoenoses	*DbF*	*CpF*	*DbF*	*CpF*	*DbF*	*CpF*
Herb layer						
Ajuga reptans	1 (a)	1 (a)	+	.	.	+
Alliaria petiolata	.	.	.	.	+	.
Asarum europaeum	.	.	.	.	+	.
Astragalus glycyphyllos	.	.	.	.	+	1
Athyrium filix-femina	.	r	+	+	+	.
Atropa belladona	.	.	+	1	+	1
Brachypodium sylvaticum	.	+	.	r	1	.
Calamagrostis epigejos	.	.	.	.	+	.
Campanula trachelium	.	.	.	.	+	.
Cardamine pratensis	.	.	.	.	1	.
Carduus acanthoides	.	.	.	.	1	+
Carex digitata	.	.	+	.	+	.
Carex echinata	.	.	.	.	.	+
Carex pilosa	.	4	.	+4	.	4
Carex sylvatica	.	.	+	.	+	.
Cephalanthera longifolia	.	.	+	.	.	.
Cirsium arvense	.	.	.	r	3	1
Cirsium oleraceum	.	.	.	.	1	.
Cirsium vulgare	.	.	.	.	-2	.
Coronilla varia	.	.	.	.	+	.
Dentaria bulbifera	2	2	+2	2	2	2
Dryopteris filix-mas	.	+	.	+	+	.
Epilobium montanum	.	.	r	r	+	.
Eupatorium cannabinum	.	.	r	.	+	+
Fragaria vesca	1(a)	1(a)	1	.	2	r
Galium aparine	.	.	.	.	.	r
Galium odoratum	2	1	+2	-2	1	2
Geranium robertianum	+(a)	+(a)	1	+	1	1
Geum urbanum	.	r(a)	.	.	.	.

Table 3. Changes in species composition and dominance of herb layer in *Dentario bulbiferae-Fagetum* (*DbF*) and *Carici pilosae-Fagetum* (*CpF*) communities on plot M; (a) – absence of generative phenophases – continued

Years	1995		2008		2011	
Phytocoenoses	*DbF*	*CpF*	*DbF*	*CpF*	*DbF*	*CpF*
Herb layer						
Glechoma hederacea	.	r(a)	.	r	.	.
Hieracium sp.	.	.	.	.	r	.
Hypericum hirsutum	.	.	+	.	+	+
Hypericum perforatum	.	.	.	.	.	+
Chamerion angustifolium	.	.	r	.	.	.
Lactuca serriola	.	.	.	.	+	.
Lathyrus vernus	+	+	.	r	+	.
Leontodon sp.	.	.	.	.	+	r
Lysimachia vulgaris	.	.	.	.	+	.
Lysimachia nummularia	.	.	.	.	+	.
Melica nutans	.	.	.	.	+	.
Melica uniflora	.	.	.	.	+	.
Mycelis muralis	.	r	1	.	+	+
Myosotis sylvatica	+	.	.	.	1	+
Oxalis acetosella	.	+	.	.	.	.
Petasites albus	.	+	.	.	.	.
Plantago sp.	.	.	+	.	.	+
Platanthera bifolia	.	.	.	r	.	r
Prunella vulgaris	.	.	r	.	.	+
Pulmonaria mollis	.	.	.	.	.	+
Pulmonaria officinalis	.	+	.	+	.	+
Ranunculus lanuginosus	.	.	.	.	+	.
Rosa sp.	.	.	r	.	.	.
Rubus hirtus	+	+	+	1	+2	1
Rubus idaeus	.	.	+	+	1	+
Salvia glutinosa	.	.	.	.	.	+
Sanicula europaea	+	+	r	.	.	.
Scrophularia nodosa	.	.	+	+	+	+
Senecio fuchsii	.	.	.	.	+	.
Senecio viscosus	.	.	.	.	+	.
Senecio vulgaris	.	.	.	.	+	.
Stellaria nodosa	.	.	.	.	+	.
Symphytum officinale	.	.	.	.	r	+
Symphytum tuberosum	.	.	.	.	+	.
Stachys sylvatica	.	.	.	.	+	.
Stenactis annua	.	.	.	.	r	.
Taraxacum officinale	.	.	.	.	.	+
Tithymalus amygdaloides	+(a)	+(a)	+	+	+	.
Tithymalus cyparissias	.	.	.	.	1	.
Tragopogon sp.	.	.	.	.	r	.
Urtica dioica	.	.	.	.	+	.
Veronica chamaedrys	.	.	.	.	+	.
Veronica officinalis	1(a)	1(a)	+	.	+	.
Vicia cracca	.	.	+	.	1	+
Viola reichenbachiana	1	2	+	+	r	+
Vignea muricata	.	.	.	.	+	.
Verbascum thapsiforme	.	.	.	.	.	+
Total number of species	22		34		68	

While a relative rate of taxa with generative phases was 68% in 1995, increase to 100% species was detected by 2011.

Figure 3 illustrates variability and differences in density of fertile and sterile shoots in two dominant taxa within the herb layer of the communities during the period of 16 years. No statistically significant changes in density of sterile and fertile shoots of *Carex pilosa* were found on control plot K. On the other hand, significant changes in density were found on the other two plots M

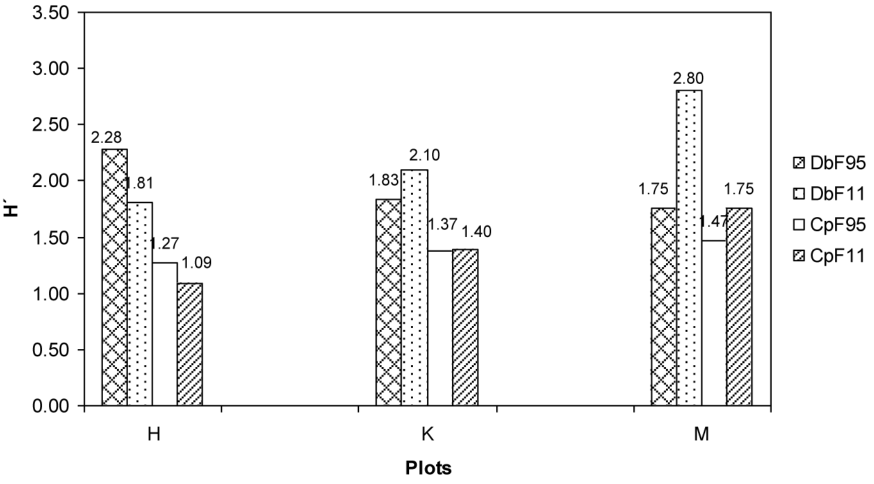

Fig. 2. Shannon-Wiener′s index of diversity within the herb layer of two communities on the studied plots.

Table 4. Sørensen's index of similarity of the communities calculated within the plots and between the pairs of relevés between 1995 and 2011 (values in bold italic denote high similarity > 70 %)

Plots Communities	Sørensen‘s index (%)
Plot H	
DbF_{95}–DbF_{11}	51.6
CpF_{95}–CpF_{11}	40.0
Plot K	
DbF_{95}–DbF_{11}	**72.7**
CpF_{95}–CpF_{11}	68.9
Plot M	
DbF_{95}–DbF_{11}	32.8
CpF_{95} –CpF_{11}	41.5
Plot K–H	
DbF_{95}–DbF_{95}	43.7
DbF_{11}–DbF_{11}	69.5
CpF_{95}–CpF_{95}	54.5
CpF_{11}–CpF_{11}	38.1
Plot K–M	
DbF_{95}–DbF_{95}	63.6
DbF_{11}–DbF_{11}	20.9
CpF_{95}–CpF_{95}	**77.8**
CpF_{11}–CpF_{11}	26.1
Plot M–H	
DbF_{95}–DbF_{95}	47.1
DbF_{11}– DbF_{11}	27.3
CpF_{95}–CpF_{95}	51.3
CpF_{11}–CpF_{11}	30.8

and H for the both sterile and fertile shoots. Similarly as was in the case of *Carex pilosa* species, the density of the both sterile and fertile shoots of *Dentaria bulbifera* species showed no statistically significant temporal changes on plot K. Significant changes in density of sterile shoots were detected on the plots M and H. The density of fertile shoots was changed significantly only on plot M during the study period.

Bioindication analysis

The spatio-temporal changes in selected ecological factors on the plots are shown in Fig. 4. Ellenberg′s indicator values (EIVs) analysis revealed that the both light and nitrogen content were changed significantly on two managed plots (plots H and M), the differences in average values were higher than 0.5. Mean EIVs for light on plot K at the end of the study period changed by 0.45, which was not ecologically significant. The value of 3.64 in 2011 enabled us to conclude that the understory vegetation (herb layer) of the analyzed communities was shade-tolerant or moderately shade-tolerant. Plot H, with the thicket, exhibited more pronounced changes in ecological conditions. In 1995, the communities on this plot were created by hemi-sciophytes and also hemi-heliophytes. However, sixteen years later, the relative presence and dominance of hemi-heliophytes rapidly decreased. Mean EIVs on plot H was reduced by 1.31, and this indicates an ecological change. The character of herb layer on this plot was hemi-sciophytic or hemi-heliophytic in 1995, but only sciophytes or hemi-sciophytes were recorded in 2011. On the other hand, light conditions were gradually improved on the third plot M. Mean EIVs on this plot increased by 1.38 between 1995 and 2011. In 1995 the communities on this plot were created by sciophytes or hemisciophytes, but hemi-sciophytes or hemi-heliophytes were observed in

2011. Nitrogen content was another factor which was changed in time, changes were not as high as it was in the case of light conditions. Nitrogen content mean value, indicated by phytocoenoses, had decreasing trend between 1995 and 2011 on plot H, but it was the opposite on plot M. Mean EIVs vary from 4.95–5.21 on plot K to 5.29–5.96 on plot M. The ecotopes characterised by a moderately rich soils were detected on plots as follows: on plot K during the whole study period, on plot M in 1995 and also on plot H in 2008–2011. Moderately rich soils or rich soils were indicated on plot H in 1995 and also on plot M in 2008–2011. Two other factors soil moisture and temperature were not changed among all studied plots in time, the differences in mean EIVs for these factors were lower than 0.5. Mean values for these two factors showed that the ecotopes of all studied plots can be characterised as a moderately warm and mesic.

Discussion and conclusion

Environmental conditions were changed after human impact. It led to changes in structure of the herb layer of plant communities on the studied plots. The species richness on plot K (control) was relatively stable during the study period. However, moderate changes in communities were also recorded on this plot caused by side-light penetrating through clear-cut strips separating the partial plots, thereby influencing part of the almost fully-shaded plot K (Fig. 1). By 2011, separating strip had grown by natural regeneration of trees and shrubs resulting in considerable decrease in side-light intensity. Evident increase in species richness was observed on managed plot M, where the number of taxa increased more than three times. Improved light conditions and increasing rate of decomposition and nitrification processes after removing of the parent stand on this plot in 2004 and 2009 accelerated the development of natural regeneration of trees. Herb layer was also synchronously supported. Statistically increasing density of sterile and fertile shoots of dominant *Carex pilosa* species was found on this plot. On the other hand, the density of sterile shoots of *Dentaria bulbifera* species decreased in time. It may be caused by increasing cover of fast-growing and high biomass-producing species in *DbF* on this plot, mainly in the representatives of nitratophiles and heliophytes (genus *Carduus*, *Cirsium*, *Rubus* and *Fragaria vesca*), which gradually occupied free niches. These conditions seem to be similar to those, which were reported from the forest gaps (Hull, 2002; Ritter et al., 2005). Similarly Križová (1993) reported, that the average value of the above-ground biomass of *CpF* association has increased several times after clear-cutting on BEES. Also Couwenberghe et al. (2011) found that distribution of 12 common herbal forest species was affected by stand structure (canopy openness) through the light gradient. McLachlan and Bazely (2001) reported that no significant differences were detected in the diversity of native forest understory species between restored and undisturbed sites, however significant among-site variation was found.

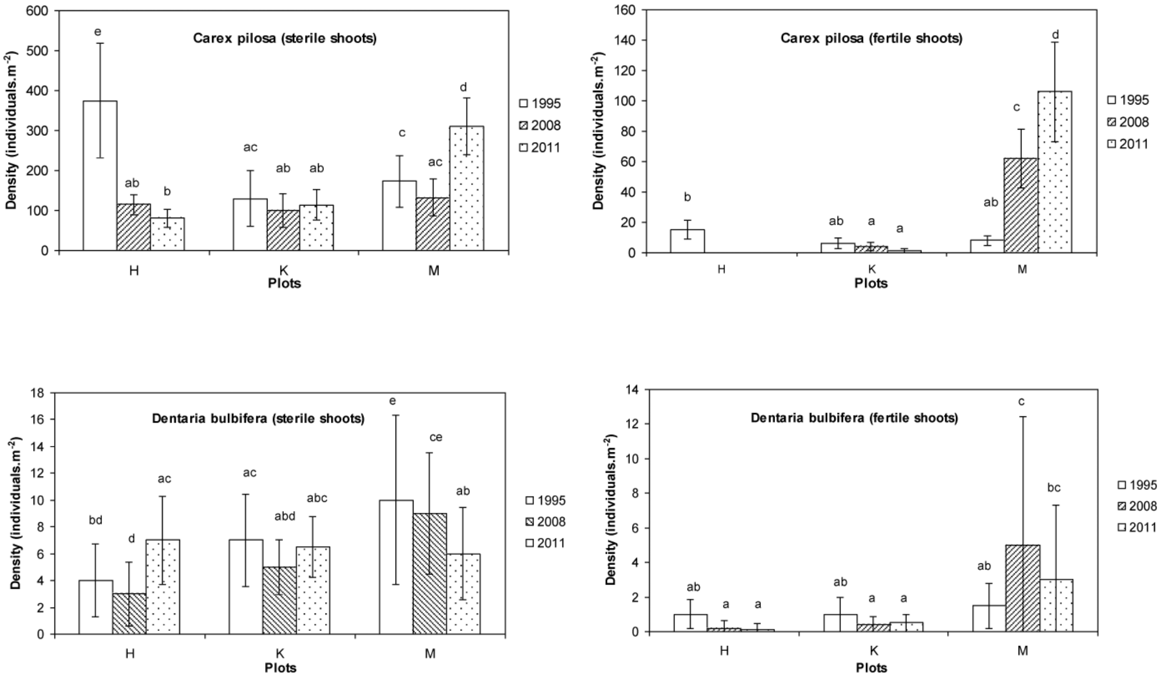

Fig. 3. Changes in density of sterile (ster) and fertile (fert) individuals within two dominant species on differently managed plots (means ± SD and results of Fisher´s LSD test; $n = 15$, $P \leq 0.05$).

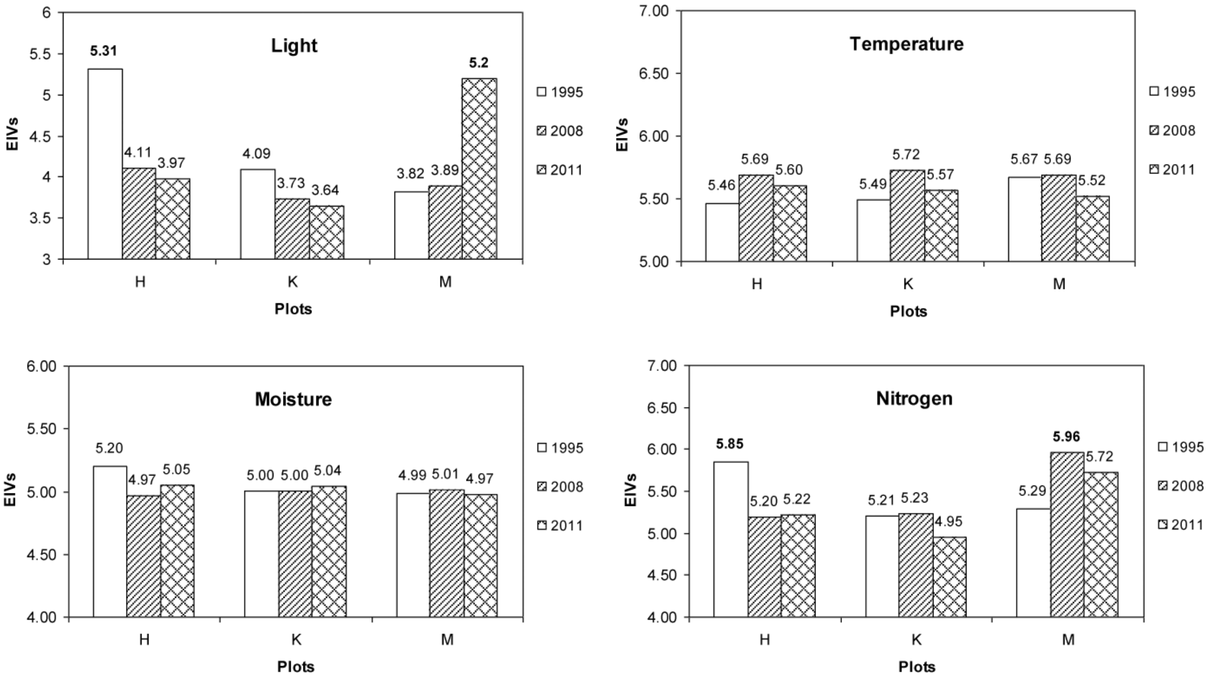

Fig. 4. Temporal changes in mean Ellenberg indicator values (EIVs) for selected ecological factors within the studied plots (values in bold denote significant difference).

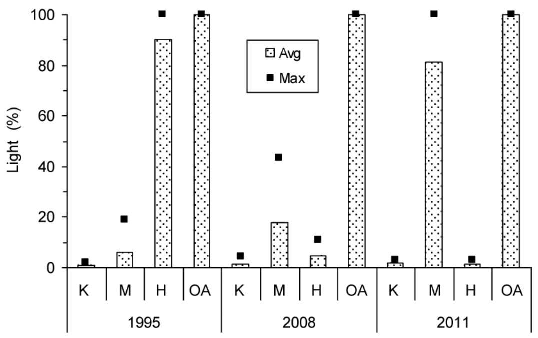

Fig. 5. Average (Avg) and maximum (Max) values of light on the studied plots K, M, and H compared to the open area (OA) measured by luxmeter.

The value of Shannon-Wiener′s index of diversity confirms increasing diversity on this plot for *DbF*, but not for *CpF* community. It seems to be that high density of *Carex pilosa* caused the weakening the competition ability of the other species. Sørensen’s index showed the low similarity between original communities in 1995 and those in 2011 on this plot. While the total number of taxa on the third plot H (thicket) at the beginning of the study period in 1995 was the highest, compared to the other plots K and M, subsequently the species diversity on this plot was rapidly decreased by 2011. The total removal of the tree layer in 1989 opened growth space for vigorously developing natural tree regeneration (Kodrík, 1997). This led to the 23-year old thicket fully covering plot H by 2011 and the light availability to the herb layer became more limited. The values of accessible light measured directly in a space of communities on the plots indicate a conspicuous reduction (Fig. 5). The competition capacity within this natural regeneration of woody plants is considerable, and its continual developing shade lowers vegetation layers. The vastly reduced light supply on plot H was responsible for considerable impoverishment of the species spectrum and a large decrease in species vitality, which was indicated by the absence of the generative phases. Species typical for clearings – *Chamaerion angustifolium*, *Eupatorium cannabinum, Atropa belladonna* and *Calamagrostis epigejos* were disappeared (Fajmonová, 1986). Significant decrease in density of sterile and fertile shoots of *Carex pilosa* species was observed. On the other hand, significant increase in density of sterile shoots was detected for *Dentaria bulbifera* species. This fact may be explained by contrasting requirements on light supply during vegetation period. *Carex pilosa* has relative higher demands on stable light conditions compared to *Dentaria bulbifera*, which utilizes more favourable light conditions before full leafing of tree layer. Also sufficiency of free niches supported the development of this species. Sørensen’s index of similarity confirmed, that succession processes on plot H led to development of the communities similar to those recorded on plot K. Bioindication analyses confirmed, that light mean value was changed significantly on managed plots (H and M) but not on control plot K. The light was reported as an important factor in the study presented by Ujházy et al. (2007). They state that disintegration of stand canopy improved the site conditions for some heliophytes, such as *Fragaria vesca, Rubus idaeus, Stellaria nemorum* etc. Our results are comparable to the results of Pykälä (2004), who summarised that the clear-cut areas are characterized by considerable increase in biomass volume and also species richness. However, subsequent succession processes result in a gradual decrease in species diversity, changes in biometric characteristics and changes in phenological traits of individual species, dependent on intensity of disturbance to the original status.

The herb layer in forest understory reflects changes in ecological conditions, especially in changing structure of tree stand. Different intensity of human impact leads to different subsequent changes in ecosystems, whereby destructive management forms (clear-cut) cause more expressive changes (Pilková, 2013) than less disturbed micro-sites which possess more favourable conditions for the survival of sensitive species (Brunet and Oheimb 1998). Also climatic variability may affect forest development, however, stand type-dependent sensitivity is reported by Kardol et al. (2010). Our data and results could be used in the near future for modelling the forest vegetation dynamics following natural or anthropogenic disturbances.

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