

HERB LAYER RESPONSE TO ECOLOGICAL CONDITIONS DURING SUCCESSION PROCESSES IN A BEECH ECOSYSTEM

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Abstract

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Changes within the *Dentario bulbiferae-Fagetum* and *Carici pilosae-Fagetum* phytocoenoses were studied during secondary succession in a submountainous beech forest. Investigations were carried out on two different forest plots over a period of 13 years (1995–2008): the first was situated in an original beech stand (in 2008-ca 110-year-old as the control), the second was covered by a thicket (in 2008- aged ca 20 years) developed in a successional process following the clear-cut. Temporal and spatial comparison of phytocoenoses structure on the two plots revealed that more conspicuous changes occurred on the plot with a thicket. The 60% decrease in species composition detected at the end of the study period highlighted evident impoverishment. Moreover, a significant decrease in species vitality was demonstrated by the absence of the generative phase, and also by a distinct reduction in the density of the two dominant species. We suggest, that this phenomenon was most likely due to the considerably reduced light supply to the herb layer on this plot.

Key words: *Dentario bulbiferae-Fagetum*, *Carici pilosae-Fagetum*, species composition, light availability, Ellenberg indicator values

Introduction

Apart from the exceptions reported in Jurko, Kontriš (1982) and Ujházyová, Ujházy (2007), beech stand phytocoenoses are considered to be rather poor in the diversity of their herb component. The development of ground vegetation in these conditions is restricted because of limited light supply (Střepec, 1992; Janík, 2010) and due to the quality of leaf litter. This litter is difficult to degrade, thus presenting a considerable barrier for plant germination and growth (Kooijman, 2010). Another limiting factor is the lack of water content in the upper soil layers (Gálhidy et al., 2006) which can be considerably affected by strong suction of beech roots. The upper soil layers form a substantial part of the active root zone of herb

vegetation. This is very evident in the *Fagetum pauper* forest-type group, which comprises dominant beech with a very low synusia cover in the understorey (Slavíková, 1986). Both natural and artificial disturbances (silvicultural intervention) initiate changes in the stand microclimate (Petřík, 1988). The rate of decomposition and nitrification processes increase, which provides better conditions for development of both the understorey level and the herb layer (Křižová, 1995). These processes are associated with increasing species diversity and productivity of herb phytocoenoses. The cover and abundance of several taxa is enhanced, phenology and seasonal rhythms in individual species are modified (Kontriš et al., 1993; Kontrišová et al., 1993; Křižová, 1993; Zobel et al., 1993; Kováčová et al., 1996; Schieber, 1996, 2007; Graae, Heskjaer, 1997; Janík, 1998; Łaska, 2001; Pykälä, 2004; Godefroid et al., 2005). The original phytocoenosis is regenerated step by step dependent on disturbance level and the occurrence of repeated disturbances which hamper the regeneration process. Therefore, it may require a relatively long time to return to its original state (Bossuyt, Hermy, 2000; Łaska, 2000).

The aim of this work is to analyze the response of herb understorey to changing ecological conditions in a sub-mountainous beech forest stand during secondary succession following the anthropogenic intervention of tree-felling. The species composition and vitality of individual plant species in two phytocoenoses, with succession on a former clear-cut and herb layer in a closed adult forest stand, are compared in relation to light availability at the beginning and end of a 13-year-period.

Material and methods

The study was carried out at the Beech Ecological Experimental Site (BEES) in the SE part of the Kremnické vrchy Mts (48°38' N, 19°04' E, 450–520 m a.s.l.), located on a west-southwest oriented slope with an inclination of 5–15°. The area is a moderately warm region, moderately warm and humid, in a hilly sub-region (Lapin et al., 2002). The annual mean air temperature is 6.8 °C, and the annual rainfall is 780 mm. The mean air temperature values in the January coldest and July warmest periods are -4,0 °C and +17,0 °C, respectively. Approximately 55% of the annual rainfall occurs between April and September. The soil cover ranges from 10 to 60% skeletal Cambisols with a moderate acidic reaction (Kukla et al., 1998). Investigations were carried out on two different plots of BEES. The first was the “K” control plot representing a 110-year-old beech stand with stocking density of 1.0, while the second was the investigated “H” plot, which was formerly a clear-cut area until intervention in 1989. By 2008 this plot had a 20-year old thicket. The dominant tree on the K plot is *Fagus sylvatica*, and associated species include *Abies alba*, *Quercus dalechampii*, *Carpinus betulus* and *Tilia cordata*. In addition to these, the naturally regenerated thicket on the H plot is supplemented with *Salix caprea*, *Populus tremula*, *Betula verrucosa*, *Acer pseudoplatanus*, *Prunus avium* and *Picea abies* species. The vegetation cover consists mainly of patches of the following associations: *Carici pilosae-Fagetum* and *Dentario bulbiferae-Fagetum* with the permanent presence of *Carex pilosa*, *C. digitata*, *C. sylvatica*, *Dentaria bulbifera*, *Galium odoratum*, *Athyrium filix-femina* and *Dryopteris filix-mas* (Kontriš et al., 1993). More detailed information concerning BEES is in Gregor (1991), Kodrík (1997), Barna (2004), Kuklová et al. (2005) and Kellerová, Janík (2006).

Two mini-plots with the 400 m² dimension of a standard phytocoenological relevé were established on each of the two plots, to enable precise analysis. The first miniplot represented the association of *Carici pilosae-Fagetum* and the second *Dentario bulbiferae-Fagetum*. Both of these were in fully developed and successional phases. The understorey herbs in these two associations were surveyed in 1995, and repeatedly in 2008. Species composition and vitality were analyzed in relation to light availability. Vitality is expressed through the presence or absence of

species' vegetative and generative stages within the associations. The number of fertile and sterile shoots in the two dominant species delivers a mean value of five patches chosen for detailed counting. Illumination measurements were performed by the Luxmeter PU 150 (Metra Blansko) at 7 points in the studied plots during anti-cyclonal conditions on the 21st of June 2005. Ellenberg indicator values for light were used in this analysis, and the species' nomenclature followed Marhold, Hindák (1998).

Results

Table 1 shows the species composition of the two studied associations: *Dentario bulbiferae-Fagetum* and *Carici pilosae-Fagetum*. The species spectrum on plot K with completely closed adult forest stand comprised 16 taxa in 1995, but this was reduced by 25% to 12 taxa in 2008. The number of species with dominance of > 1% was 12 in 1995, and this decreased to only 3 species after the 13 years. The most conspicuous change on this plot was observed in the two *Ajuga reptans* and *Veronica officinalis* taxa, with a dominance of 1–5%. In 1995, both were present in both associations, but within 13 years all had disappeared. Also some other species including *Lathyrus vernus* which were recorded on plot K suffered a considerable decrease in their dominance. However, some exhibited complete absence in at least one association, such as *Fragaria vesca*, *Pulmonaria officinalis* and *Rubus hirtus*. On the second study plot H containing the thicket, 29 taxa were recorded in both associations in 1995, but a 59% decrease to 12 taxa was noted after 13 years. The number of taxa with dominance exceeding 1% on this plot was 16 in 1995, but only 3 in 2008. The most marked changes were observed in the *Calamagrostis epigejos*, *Atropa belladonna*, *Eupatorium cannabinum* and *Rubus idaeus* species. While their dominance in 1995 had relative values of 5–50%, their presence was not detected in 2008. A considerable drop in dominance or absolute absence was also recorded in the *Ajuga reptans*, *Fragaria vesca*, *Chamerion angustifolium*, *Senecio fuchsii*, *Veronica officinalis* and *Viola reichenbachiana* species. The presence of a generative cycle in a taxon reflects its vitality. Accordingly, a generative cycle was observed in 87.5% of the taxa in both associations on plot K in 1995, with the only exceptions being *Ajuga reptans* and *Rubus hirtus*. However by 2008, this was noted in only 41.6%, accounting for 5 species, these included two fern taxa. There was an even a more pronounced decrease in the number of taxa with generative cycle on the second plot during this 13-year study period. While a generative cycle was recorded in all 29 taxa in both associations in 1995, this occurred in only 4 taxa by 2008. This amounted to less than 14% of the number recorded in 1995, and 33% of that recorded in both associations in 2008 (Table 1). Fig. 1 illustrates changes in density in fertile and sterile shoots in two dominant taxa studied in the association in the 13-year-succession period. *Carex pilosa* on plot K recorded a decrease of 33% in fertile shoots and 58% sterile shoots per unit area. The corresponding values on plot H were 78% and 100%, respectively. Similarly, the decrease in density in fertile and sterile shoots of *Dentaria bulbifera* species was most pronounced on plot H.

Considering that light conditions throughout the study plots were relatively homogeneous, we attempted to express changes in the light spectrum in both associations

Table 1. Changes in species composition in *Dentario bulbiferae-Fagetum* (Db-F) and *Carici pilosae-Fagetum* (Cp-F) associations on the studied plots (r, +, 1,2,3,4 – dominance of the species; (a) – absence of the generative stage).

Plots	K – parent stand				H – thicket			
	1995		2008		1995		2008	
Associations	Db-F	Cp-F	Db-F	Cp-F	Db-F	Cp-F	Db-F	Cp-F
Understorey herb species								
<i>Ajuga reptans</i>	1 (a)	1 (a)	.	.	1	+	.	.
<i>Athyrium filix-femina</i>	.	+	.	r
<i>Atropa belladonna</i>	2	+	.	.
<i>Calamagrostis epigejos</i>	3	.	.	.
<i>Campanula persicifolia</i>	+	.	.
<i>Carduus acanthoides</i>	+	.	.
<i>Carex digitata</i>	1	+	+	.
<i>Carex pilosa</i>	.	4	.	3	.	4	.	3 (a)
<i>Carex sylvatica</i>	+	.	+	.
<i>Cephalanthera longifolia</i>	.	.	r (a)	.	.	.	r (a)	.
<i>Cirsium arvense</i>	+	.	.
<i>Coronilla varia</i>	+	.	.	.
<i>Dentaria bulbifera</i>	2	2	-2	-2	2	2	-2	1
<i>Dryopteris filix-mas</i>	+	+	.	r
<i>Epilobium montanum</i>	+	.	.	.
<i>Eupatorium cannabinum</i>	2	.	.	.
<i>Fragaria vesca</i>	1	1	.	+	1	+	.	.
<i>Galium odoratum</i>	2	1	+	1	1	+	+	.
<i>Geranium robertianum</i>	r	r (a)	r (a)
<i>Geum urbanum</i>	.	r
<i>Glechoma hederacea</i>	+	.	.	.
<i>Hypericum hirsutum</i>	+	+	.	.
<i>Chamerion angustifolium</i>	1	.	.	.
<i>Juncus effusus</i>	r	.	.	.
<i>Lathyrus vernus</i>	.	2	.	r (a)
<i>Oxalis acetosella</i>	1	1	.	+
<i>Pulmonaria officinalis</i>	1	1	.	+	+	+	+	.
<i>Rubus hirtus</i>	2 (a)	2 (a)	.	+	1	+	-1 (a)	+
<i>Rubus idaeus</i>	2	.	.	.
<i>Sanicula europaea</i>	.	1	.	.	+	.	.	.
<i>Scrophularia nodosa</i>	+	.	.	.
<i>Senecio fuchsii</i>	1	.	.
<i>Tithymalus amygdaloides</i>	+	+	.
<i>Tussilago farfara</i>	1	.	.
<i>Veronica officinalis</i>	1	1	.	.	1	1	+	.
<i>Viola reichenbachiana</i>	1	2	.	+	1	1	+	.
Total number of species	16		12		29		12	

on the whole. Figure 2 illustrates no substantial changes in the relative presence of species corresponding to individual Ellenberg indicator light values on plot K, so the light spectrum of phytocoenoses there remained relatively narrow. The prevalence of sciophytes or hemisciophytes was noted, (Ellenberg value 4), with the relative presence of 62% in 1995 and 74% in 2008. The presence of species which corresponded

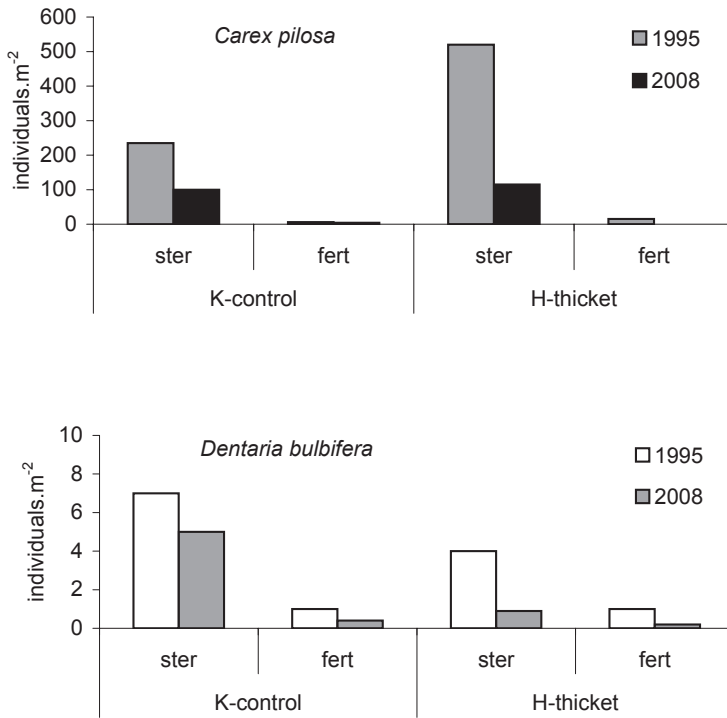


Fig. 1. Changes in density of sterile (ster) and fertile (fert) individuals within two dominant species.

to the remaining Ellenberg values was low, with a moderate increase observed only in the sciophyte species, which recorded an Ellenberg value of 3. The average Ellenberg indicator value on plot K at the end of the study period changed by 0.39, and this value was relatively insignificant. The value of 3.77 in 2008 enabled us to conclude that the ecotope of the analyzed phytocoenoses is shade-tolerant or moderately shade-tolerant (Fig. 3). Plot H, with the thicket, exhibited more pronounced changes in phytocoenoses associated with modified light supply. In 1995, the light spectrum on this plot was created by hemi-sciophytes (Ellenberg value 4) and also hemi-heliophytes (Ellenberg value 7), with a relative presence of 39 and 40%, respectively (Fig. 2). However, thirteen years later, the relative presence of hemisciophytes increased to 76% and a moderate increase was also observed in the sciophytes, similar to that in plot K. The average Ellenberg indicator value on plot H was reduced by 1.37, and this indicates a significant change. The ecotope on this plot was hemi-sciophyte or hemi-heliophyte in 1995, but only sciophyte or hemi-sciophyte was recorded in 2008 (Fig. 3).

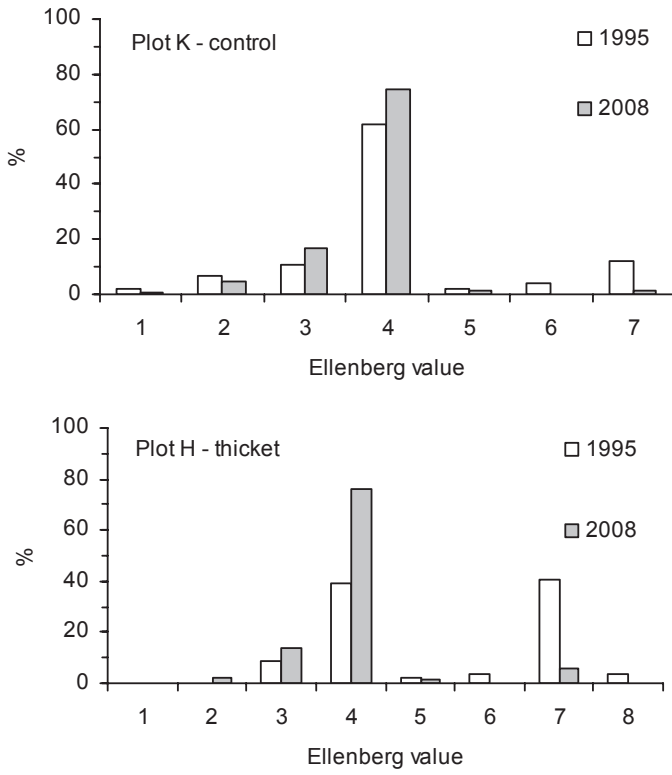


Fig. 2. Relative rate of Ellenberg indicator values for light on the plots.

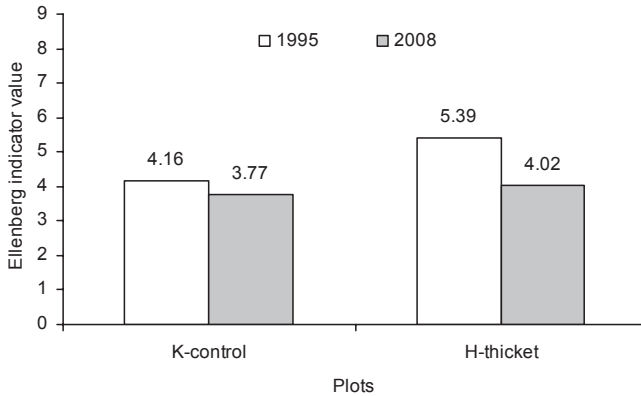


Fig. 3. Average Ellenberg indicator values for light.

Discussion and conclusion

Changes in ecological conditions during the secondary succession process were reflected on the structure of the studied plant associations. While the total number of taxa on plot H in 1995 was approximately 2.5-times higher compared to control plot K, 13 years later the ratio was equal, at 1:1. Half of the 12 taxa identified on the two plots occurred on both. These were *Carex pilosa*, *Dentaria bulbifera*, *Galium odoratum*, *Pulmonaria officinalis*, *Rubus hirtus*, and *Viola reichenbachiana*. The vastly reduced light supply was responsible for considerable impoverishment of the species spectrum and a large decrease in species vitality. This was indicated by the absence of a generative phase, and also by the decrease in density values in the two most dominant species on plot H. The total removal of the tree layer in 1989 opened growth space for vigorously developing natural regeneration. Kodrik (1997) reported the height of natural regeneration on plot H in 1994 to be from 60 to 110 cm. In the following years, this trend accelerated, enabling natural regeneration heights from 200 cm in *Fagus sylvatica* to 400 cm in *Salix caprea*, by 1998. This led to the 20-year old thicket fully covering plot H by 2008. Since the density of the natural regeneration was considerably high, the light availability to the herb layer became more limited. While the average shade value on this plot was less than 10% in 1995, this increased to more than 90% in 2008 (Fig. 4). In addition, the illumination values measured directly in phytocoenoses on both plots indicated a conspicuous reduction in accessible light to plot H (Fig. 5). The competition capacity within this natural regeneration of woody plants on plot H is considerable, and the developing woody plants partly shade the lower vegetation layers (Davis et al., 1998). However, certain changes in phytocoenoses were also recorded on plot K. These differences were most likely caused by side-light penetrating through clear-cut strips separating the partial plots, thereby influencing part of the almost fully-shaded plot K. By 2008,

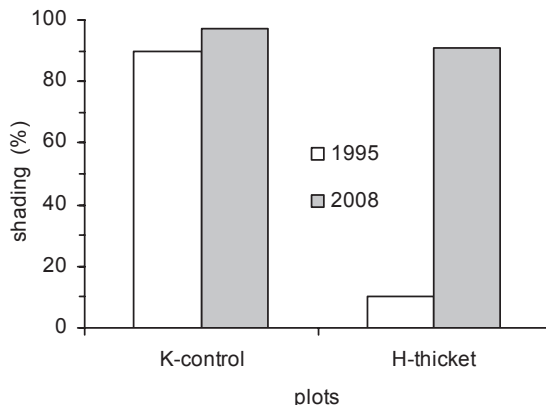


Fig. 4. Degree of shade on the studied plots.

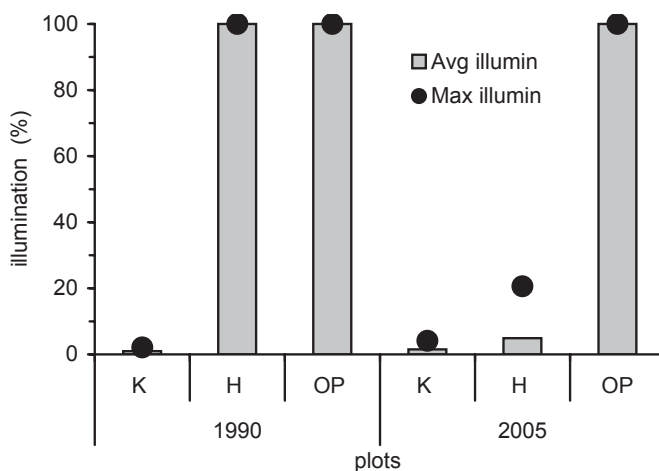


Fig. 5. Average (Avg illumin) and maximum (Max illumin) values of illumination measured in 1990 (Střelec, 1992) and our 2005 measurements on plots K and H, compared to the open plot (OP).

this separating strip had increased with natural regeneration, resulting in a considerable decrease in side-light intensity. Falińska (1975) reported that the structure of the phytocoenoses affected the species' behaviour. A significantly lower species' ratio was noted in the *Pino-Quercetum* association vegetative stage than in the *Tilio-Carpinetum stachyetosum* association. Also, Härdtle et al. (2003) concluded that light had an essential influence on species richness in acidophytic beech and mixed beech-oak forests.

The response of the understorey herb layer reflects the different ecological conditions in this studied forest ecosystem. Brunet, Oheimb (1998) consider that forest management methods effect subsequent changes in ecosystems, whereby destructive management forms cause more expressive changes than less disturbed micro-sites which possess more favourable conditions for the survival of sensitive species. The clear-cut areas are characterized by considerable increase in biomass volume and also species spectrum richness (Pykälä, 2004). 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 results of this work are consistent with this fact. Research of this type, focussed on analysis of succession processes *in situ* is time-consuming, because the data can be comprehensively evaluated only several years or even several decades later. However, the data contained in our research results can now be used for modelling succession processes following the natural and artificial disturbances which are continuously occurring.

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