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CHANGES OF THE MOUNTAIN GRASSLAND VEGETATION AFTER ABANDONMENT AND COLONIZATION BY NORWAY SPRUCE

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Abstract

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Changes of herb and moss vegetation during the colonization of abandoned meadows by Norway spruce on the Poľana Mts were studied within a 20 x 170 m belt transect. It includes transition from the opened grassland with scarcely scattered young spruces and junipers to a 40 to 50-years-old spruce stand adjoined to a planted spruce forest edge.

Vegetation changes started after the cessation of mowing, establishing of irregular grazing and subsequent spruce colonisation. We identified and differentiated 9 types of vegetation in the transect [characterised by specific species combination and species dominance; *Trifolium medium-Brachypodium pinnatum* type of vegetation (A), *Antennaria dioica-Nardus stricta* (B), *Phyteuma spicatum-Agrostis capillaris* (C), *Knautia arvensis-Avenula* sp. (D), *Prunella vulgaris-Ajuga reptans* (E), *Platanthera bifolia-Avenella flexuosa* (F), *Vaccinium myrtillus* (G), *Hylocomium splendens* (H) and *Jungermannia leiantha-Plagiomnium affine* agg. (I)] using the Twinspan and DCA methods.

The first two DCA axes can be interpreted as a light and temporal gradient (axis 1) and a trophic gradient (axis 2). We differentiated two parallel successive paths (variants of the same succession series) – a mesotrophic (*Agrostis capillaris* comm. > C > E > I) and an oligotrophic (*Anthoxantho-Agrostietum tenuis nardetosum* > B > F > G > H > I) variant. Common are the initial type of vegetation of mowed meadows and the final phase of a pure spruce stand with poor moss vegetation (type I), but a course within both variants is different. In addition to this basic divergence several modifications mostly determined by strong competitive grass species were observed within both variants.

There is only limited species turnover during this short period of successional development. Cover and number of herb species decline gradually. Moss layer reaches the highest cover within the E, F and G types, where the herb layer cover is reduced and the shrub and tree layer is not closed yet. In these types of field layer vegetation, there is the highest diversity of seedlings and juvenile woody species.

Key words: secondary succession, abandoned meadows, *Arrhenatheretalia*, *Picea abies*, Central Slovakia, Western Carpathians

Introduction

Meadows and pastures belong to secondary plant communities depending on permanent agricultural use. The beginning of secondary succession is associated with the absence of the agricultural use and is characterised by changes of species composition, structure of stands and gradual colonization of the site by shrubs and trees. A mosaic structure of several types of vegetation is formed in the areas with more or less homogeneous grassland communities (and with more or less homogeneous ecological conditions) in the course of few decades. The formation and development of types of vegetation are related to many environmental factors: light, temperature, moisture, nutrients (and their changes), trees and shrubs expansion, competitive relationships, species´ strategy etc. (e.g. Grime, 1979; Glenn-Lewin, van der Maarel, 1992; van der Valk, 1992; van Andel et al., 1993; Lett, Knapp, 2003).

In Slovakia, significant changes in the management of meadows and pastures occurred in the 1950s due to changes of land ownership. They affected mainly mountain meadows and pastures, where use to spruce spread intensively. Meadows and pastures of the volcanic Poľana Mts represent a typical example of this process, with local specific features (for instance rich nutrients soils, a vigorous spread of clonal grasses like *Avenula* sp., *Brachypodium pinnatum*).

The research of the secondary succession on meadows and pastures of the mountain belt in the Western Carpathians is not satisfactorily resolved. Succession series with "spruce and juniper" were documented by Kuchnicka (1998) and Bodziarczyk et al. (1999) in the Pieniny Mts, Míchal (1992) in the Veľká Fatra Mts, Svoboda (1939) and Šmarda (1961) in the High Tatra Mts and Dražil et al. (1998) in the Slovenský Raj Mts. More attention to this problem was given in the Poľana Mts (Križová, 1995; Križová, Ujházy, 1997; Ujházy, 1995, 1998, 2001, 2003), where our model-area Príslopy is situated as well. Just at this locality, Ujházy (2003) described a "spruce-beech" succession series (further only succession series) of mountain meadows and pastures using the method of parallel sample plots in different stages of secondary succession (from grass stands used for agriculture to mixed fir-beech climax forest stands).

The aims of our study are:

- to characterize types of vegetation occurring within non-forest stages of the "spruce-beech" succession series
- to outline a scheme of field layer development (series of the types of vegetation)
- to detect changes of both species composition and richness during the colonisation of abandoned grasslands by spruce.

Material and methods

Study site

The study site was located in Central Slovakia, ENE from the town Zvolen in the central part of volcanic Poľana Mts. The locality Príslopy is situated between the hills Drábovka and Želobudská skala (Fig. 1). This grassland

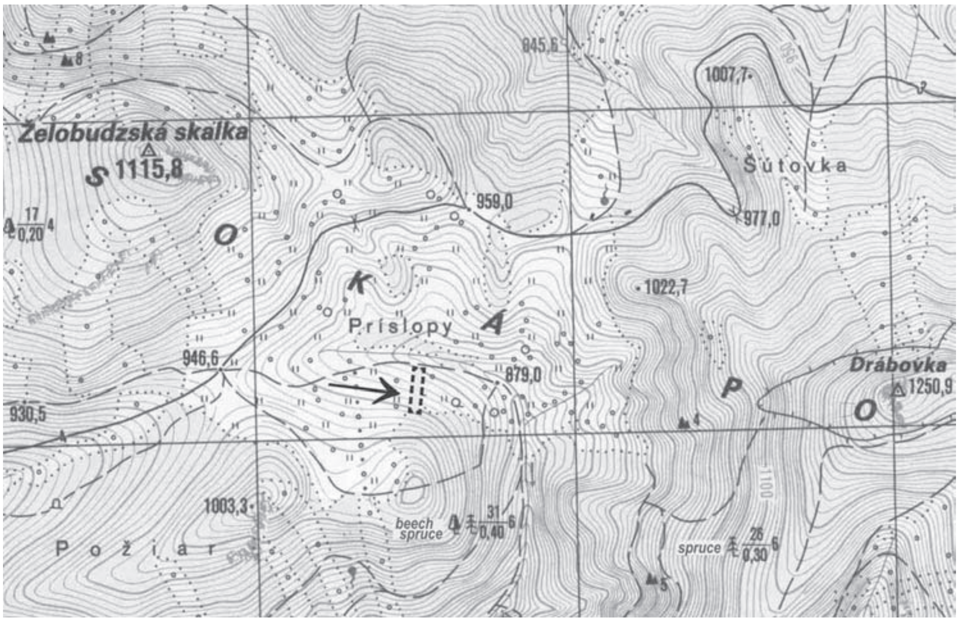


Fig. 1. Location of the transect within the Príslopy grassland area in the Poľana Mts (according to military map 1:25 000 with a 1 km square network).

area of about 100 ha is surrounded by a large forest complex. It was deforested around 1800 and since then it has been utilized as hay meadows until the collectivization of agriculture in 1951, when it was changed to pastures (cf. Ujházy, 2003). Norway spruce (*Picea abies*) was planted in the surroundings of the study site in 1890s. This plantations formed the seed source for the colonisation of grasslands (Ujházy, 2003).

A research transect was established on the northern slope of southern part of the Príslopy locality (48°38’10" N, 19°25’11" E, about 915 m a.s.l.) (Fig. 1). Spruce was planted along a previous forest margin here (it forms the upper margin of the transect now). Meadow stands were overgrown gradually from the forest margin. At the same time, in the parts colonized by spruce, cattle grazing has become more and more limited. The influence of grazing on the herbal and woody vegetation in the last 20 years was negligible. These processes can well be observed on a set of historical aerial photographs (1949–1999) we dispose of.

According to geomorphological classification of Slovakia (Mazúr, Lukniš, 1980), Poľana belongs to the Slovenské stredohorie region of the Inner Western Carpathians subprovince. The area has a cold and rainy climate with the mean July temperature of 11.5–13.5 °C and 1000–1400 mm annual precipitations (Tarábek, 1980). The bedrock of the transect, formed of andesite lava flows (Dublan, Jánošová, 1991), is covered by deep cambisols.

From the phytogeographical point of view, the study site belongs to the *Carpaticum occidentale* district, *Praecarpaticum* subdistrict (Futák, 1966). At Príslopy, 351 vascular plants were detected (more than 9% belong to endangered species of the Slovak flora). The recent non-forest vegetation is formed by pastures and meadows (*Polygalo-Cynosurenion*, *Polygono-Trisetion*), locally also fens and wet meadows (*Caricion fuscae*, *Calthion* and *Deschampsion cespitosae* alliances). *Fagus sylvatica*, *Abies alba* and species of the genera *Acer*, *Fraxinus* and *Ulmus* are typical for natural forest vegetation (*Eu-Fagenion* alliance).

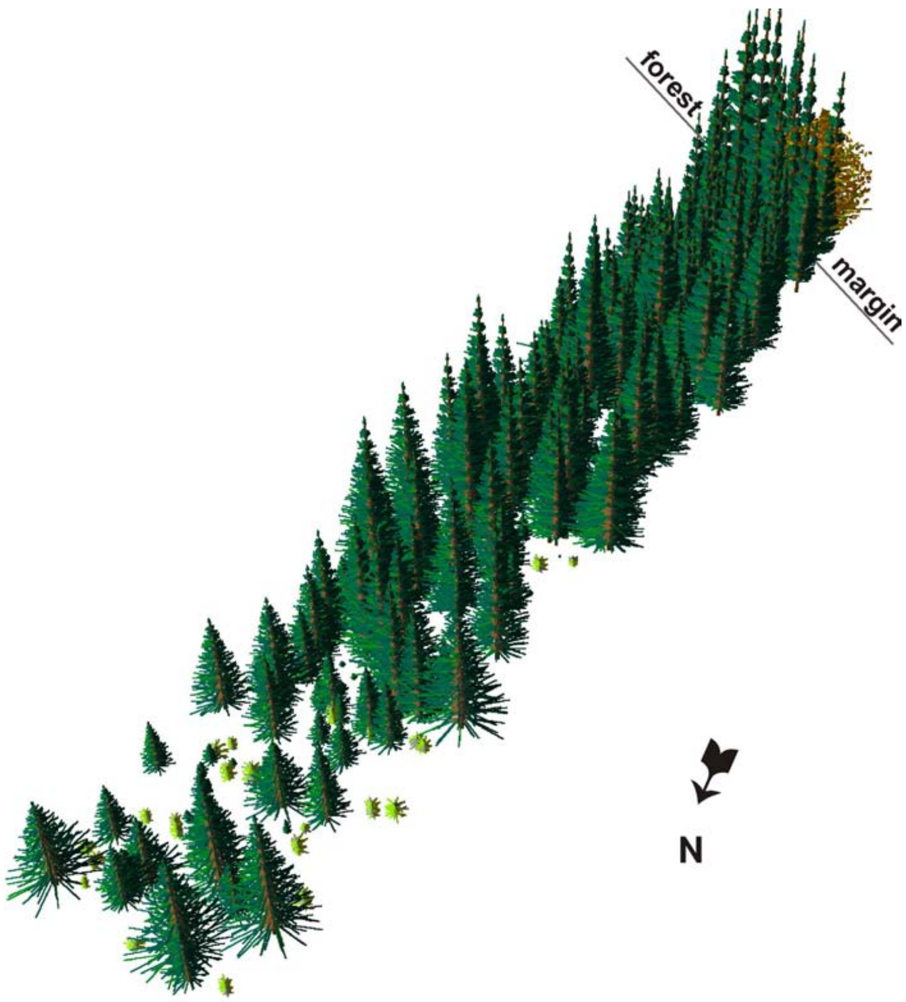


Fig. 2. Perspective view of the transect area created by SVS programme.

Vegetation sampling

The field work was carried out in August 2003. The vegetation was analysed on a 170 m long and 20 m wide transect perpendicular to contour line, crossing all succession stages from the old planted spruce forest margin to a relatively open non-forest grassland area (Fig. 2). The bottom part of the transect is formed of grassland communities with scattered individuals of *Picea abies* a *Juniperus communis*, the upper part of closed 40 to 50-years-old spruce stands almost without herbal vegetation.

Site conditions on regular northern slope with inclination of approx. 10^{o} are homogeneous on the whole area of the transect (relief morphology, bedrock, soil, moisture; some differences in microrelief and thus also in microclimatic and micropedological characteristics exist, of course). However, top part was overshaded by more than 30 m high spruce forest and less utilised in the past and thus spruce colonisation was faster there.

Types of vegetation of the transect were documented by phytosociological relevés according to Zürich-Montpellier approach (Braun-Blanquet, 1964) using the Braun-Blanquet scale modified by Barkman et al. (1964). Only homogeneous stands were sampled. The relevé area was 6–10 m^2. Relevé area was limited by small scale mosaic structure of field layer vegetation (see Fig. 3) and by the aim of recording vegetation changes on the lowest spatial level. Only plant individuals of E_1 and E_0 layer (field layer) rooting within the relevé area were recorded. Woody species of those layers were recorded, but higher individuals of E_2 and E_3 layers were not included to the subjectively placed plots. Cover of shrub and tree crowns extending over the plot was not recorded either. Field layer development is affected not only by vertical shading, but also by horizontal structure of surrounding tree stand and by a length of lateral shading period cf. Ujházy (2003), which was not possible to record by the used methods. To explain the relationships between the present state of the vegetation on the transect affected by succession processes and previous vegetation of mowed meadows and grazed pastures, we used relevés of an area 16–20 m^2 sampled before at adjacent localities within the complex of Prislopy (1995–1996; Ujházy, 2003; O1 a O2 in Table 2, 3 and relevé from 2001 in the text).

The nomenclature of plants and vegetation units followed Marhold, Hindák (1998) and Mucina, Maglocký (1985), respectively. For individuals of the genus *Avenula* (*A. planiculmis*, *A. preusta*, *A. adsurgens* sensu Janišová et al., 2004), we use the designation *Avenula* species (the recent status of these taxa is not satisfactorily known). The names of types of vegetation are presented according to differential/dominant and dominant species (two types are differentiated only according to dominant species, *Brachypodium pinnatum* and *Avenula* sp.), respectively.

Data analysis

The abundance/dominance scale was transformed to the ordinal scale according to van der Maarel (1979) for analyses and so it was used in Table 1 as well. Each potential vegetation unit was documented by more than (4)5 relevés. Species with cover higher than 25% were considered as dominant.

Phytosociological relevés were stored and processed by TURBOVEG and MEGATAB program packages (Hennekens, 1996a,b). Divisive polythetic classification (TWINSPAN; Hill, 1979), detrended correspodence anylysis (DCA; CANOCO program; ter Braak, Šmilauer, 1998) and the fidelity – Phi coefficient (cf. Bruelheide, 2000; JUICE program, Tichý, 2002) were used for vegetation data analysis. Tabular synthesis (cf. Moravec, 1994) were used to find the relationship between the vegetation development on the transect area (sampled on smaller plots) and the previous grassland vegetation. To assess the correlation between the first DCA axis scores and selected vegetation parameters, we used the STATISTICA package (StatSoft, 2001). Average indicator values were calculated following Ellenberg et al. (1992).

Results

Types of vegetation

We detected 9 types of vegetation on the transect – *Trifolium medium-Brachypodium pinnatum* type of vegetation (Table 1, relevés 1–5, type A), *Antennaria dioica-Nardus stricta* (6–10, B), *Phyteuma spicatum-Agrostis capillaris* (11–19, C), *Knautia arvensis-Avenula* sp. (20–23, D), *Prunella vulgaris-Ajuga reptans* (24–29, E), *Platanthera bifolia-Avenella flexuosa* (30–33, F), *Vaccinium myrtillus* (34–38, G), *Hylocomium splendens* (39–

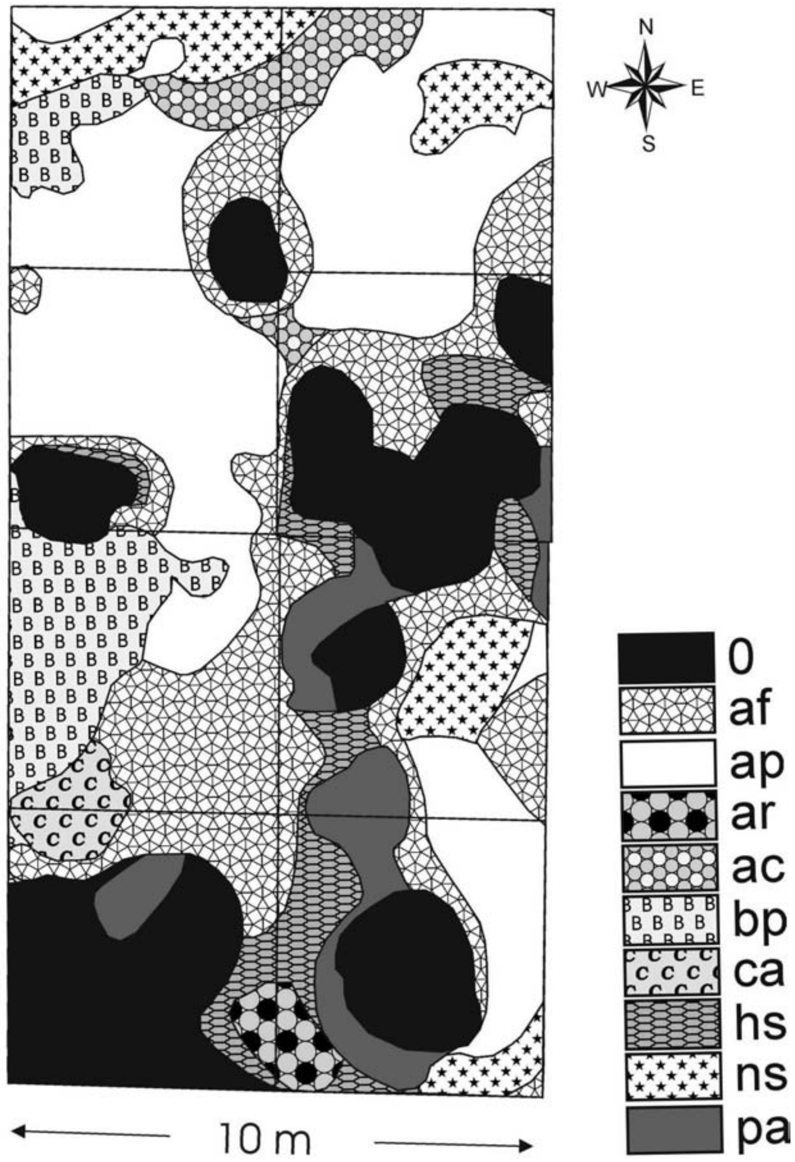


Fig. 3. An example of mosaic field layer vegetation structure in selected part of the transect (20–40 m). Abbreviations of the type names (mapping units): 0 – pure spruce litter; af – *Platanthera bifolia-Avenella flexuosa*; ap – *Knautia arvensis-Avenula* sp.; ar – *Prunella vulgaris-Ajuga reptans*; ac – *Phyteuma spicatum-Agrostis capillaris*; bp – *Trifolium medium-Brachypodium pinnatum*; ca – *Calamagrostis arundinacea* stand (not sampled as a type due to too small patch area within a transect); hs – *Hylocomium splendens*; ns – *Antennaria dioica-Nardus stricta*; pa – *Jungermannia leiantha-Plagiomnium affine* agg.

Table 1. Types of vegetation

Vegetation type	A	B	C	D	E	F	G	H	I
	Tf-Bp	Ad-Ns	Ps-At	Ka-Ap	Pv-Ar	Pb-Af	Vm	Hs	Jl-Pa
Variant:		oligotr.	mesotr.		mesotr.	oligotr.	oligotr.	oligotr.	
Average of phidelity	20.7	28.1	25.0	16.6	25.0	17.3	13.3	16.0	22.0
Average number of species	19.4	24.0	30.9	23.5	30.8	23.5	17.4	13.4	7.8
No. of species with phi more than 25	8.0	17.0	30.0	4.0	22.0	5.0	2.0	3.0	4.0
No. of species with constancy more than 50%	12.0	13.0	12.0	17.0	15.0	17.0	16.0	12.0	4.0
No. of dominant species (cover more than 25%)	2.0	3.0	7.0	3.0	4.0	3.0	4.0	1.0	1.0
Brachypodium pinnatum	**9 9 8 9 9**	. . . . .	2	. . . .	 2	2 . . .	. . . . .	1	. 2 . 2 . .
Trifolium medium subsp. *flexuosum*	. 2 2 2 .	. . . . .	2	. . . .	2 . . 2 . .	. . . .	. . . . .	. . . . .	. . . . . .
Viola canina	. . . 2 .	2 . 2 2 .	. . . .	. . . .	. . . . . .	. . . .	. . . . .	. . . . .	. . . . . .
Briza media	. . . . .	2 2 . . .	. . . . . . 1 . .	. . . .	. . . . . .	. . . .	. . . . .	. . . . .	. . . . . .
Luzula campestris agg.	. . . . .	2 . 2 . .	. . . .	2 . . .	. . . . . .	. . . .	. . . . .	. . . . .	. . . . . .
Anthoxanthum odoratum	. . . . .	2 **3** 2 . .	. . . .	2 . . .	. . . . . .	. . . .	. . . . .	. . . . .	. . . . . .
Antennaria dioica	. . . . .	2 2 . 2 .	. . . .	. . . .	. . . . . .	. . . .	. . . . .	. . . . .	. . . . . .
Plagiomnium cuspidatum	. . . . .	. . 2 . 2	. . . .	2 . . .	. . . . . .	. . . .	. . . . .	. . . . .	. . . . . .
Phyteuma spicatum	2 1 . . .	. . . . .	2 1 2 2 1 . 1 2 1	2 . . .	 2	. . . .	 2	. . . . .	. . . . . .
Ranunculus polyanthemos	 1	. . . . .	**2** . 1 1 . **2** 1 . .	. . . .	. . . . 1 1	. . . .	. . 1 . .	. . . . .	. . . . . .
Carex hirta	 2	. . . . .	**5** 2 . 1 . 2 2 . .	. . . .	. . . . . .	. . . .	 2	. . . . .	. . . . . .
Plantago media	. . . . .	. . . . .	. 2 . . 2	. . . .	. . . . . .	. . . .	. . . . .	. . . . .	. . . . . .
Deschampsia cespitosa	2	. . . . .	2 . . 2 2 **3** . . .	2 . . .	. . . . . .	1 . . .	. . . . .	. . . . .	. . . . . .
Campanula patula	. . . . .	. . . . .	. . . . . 2 1 . .	. . . .	. . . . . .	. . . .	. . . . .	. . . . .	. . . . . .
Lotus corniculatus	. . . 2 .	. . . . .	2 2 2 2	**3** . **3** **3**	. . 1 . 2 .	. . . .	. 2 . . .	. . . . .	. . . . . .
Knautia arvensis	. . . . .	. . . . .	. . . .	1 2 . .	. . . . . .	. . . .	. . . . .	. . . . .	. . . . . .
Hieracium murorum	. . . . .	1 . . . 2	 2	. . 2 .	**3** 1 1 **3** **3** .	. . . .	 2	. 2 . . .	. . . . **3** .
Prunella vulgaris	. . . . .	. . . . .	. . . . . . 1 . .	. . . .	2 2 . 2 **3** 2	. . . .	. . . . .	. . . . .	. . . . . .
Fagus sylvatica	. . . . .	. . . 1 1	. . . .	. . . .	**2** **2** 1 . . .	. . . 1	. . . . .	. . . . .	. . . . 1 .
Sorbus aucuparia	. . . . .	. . . . .	. . . . 1 . **3** . .	. . . .	1 . . 1 1 .	. . . .	. . . . .	. . . . .	. . . 1 . .
Fraxinus excelsior	. . . . .	. . . . .	. . . . . 1 . . .	. . . .	1 . 1 . . .	. . . .	. . . . .	. . . . .	. . . . . .
Ranunculus acris	. . . . .	. . . . .	. 2 . 2	. . . .	. . . 1 1 2	. . . .	. . . . .	. . . . .	. . . . . .
Abies alba	. . . . .	. . . . .	. . . .	. . . .	. . 1 1 . .	. . . 1	. . . . .	. . . . .	. . . . . .
Platanthera bifolia ssp. *latifolia*	1	. . . . .	. . . 1 . 1 . **2** 1	. . . .	. . . . . .	**2** . 1 **2**	 1	. . . . **2**	. . . . . .
Vaccinium myrtillus	. . . . .	. . . 2 .	. . . .	2 . . .	. . . . . .	. . 3 2	**8** **9** **7** **8** **7**	. . . . .	 2
Plagiothecium denticulatum	. . . . .	. . . . .	. . . .	. . . .	. . . . 2 .	. . . .	. . 2 . **3**	. . . . .	. 2 . **5** . .
Lophocolea heterophylla	. . . . .	. . . . .	. . . .	. . . .	. . . . . .	. 2 . .	. . **3** . .	. . . 2 .	. . . 2 **5** **3**
Jungermannia leiantha	. . . . .	. . . . .	. . . .	. . . .	. . . . . .	. . . .	. . . . .	. . . . .	. . 2 2 . .
Aulacomnium palustre	. . 2 . .	**3** **3** **6** . .	. . **3** **3** . . . 2 .	. . 2 .	. . . . . .	. **3** . .	 2	. . . . .	. . . . . .
Achillea millefolium	. . 1 2 2	2 2 2 . .	2 2 2 1 2 2 1 2 2	**3** 2 2 .	. . . 1 2 .	. 2 . .	. . . . .	. . . . .	. . . . . .
Veronica chamaedrys	. 2 . 1 2	. . . . .	2 **3** 2 1 . 1 . . .	. 2 . .	. 1 2 2 . .	. . . .	. . . . .	. 1 . . .	. . . . . .
Alchemilla sp.	1 1 . . 1	. . . . .	**2** **3** . 1 **2** . 1 . **2**	1 . . .	**2** . . 1 **2** .	. . . .	. . **2** . .	. . . . .	. . . . . .
Picea abies	. . **2** . .	. . . **2** **2**	. . **2** **2** **2** **2** . . .	. . . 1	. 1 **2** . **2** .	. . . 1	. . . 1 1	. 1 . . .	. . . . . .
Galium verum	. . . 2 2	. . . . .	2 . 2 **3** 2 . . . **3**	2 . . 2	. . 1 . . .	. . . .	. . . . .	. . . . .	. . . . . .
Danthonia decumbens	. . . . .	. **3** **3** **3** **3**	. 2 2 2 2 **3** 2 2 2	. 2 2 2	. . 2 . . .	1 . . 2	. 2 . **3** .	. . . . .	. . . . . .
Nardus stricta	. . 2 . .	**8** **7** **7** **8** **7**	. 2 2 2 2 **5** 2 . 2	. 2 2 3	. 2 1 1 2 .	. 2 2 2	. . . 2 .	. . . . .	. . . . . .
Festuca rubra	. 2 2 . .	2 2 2 2 2	2 . 2 2 2 2 2 2 2	**3** 2 2 2	2 . 1 2 2 2	2 . . 1	. . . . .	. . . . .	. . . . . .
Potentilla aurea	. . . . .	2 2 2 2 .	. 2 . 2 2 . 1 **3** 2	. . 2 2	. . 2 1 2 .	1 2 . 2	. . . . .	. . . . .	. . . . . .
Cruciata glabra	. 2 . . .	. 2 . 2 2	2 2 2 2 2 2 1 2 .	**3** 2 2 .	1 2 2 1 2 1	1 . 2 2	. . 2 . .	. 1 . . .	. . . . . .
Carlina acaulis	. . 1 1 .	2 2 2 2 **3**	1 2 2 **3** **3** **3** 1 2 2	. 2 2 **3**	. 2 . 1 1 .	. . 2 1	1 . . 2 2	. . . . .	. . . . . .
Luzula luzuloides	. 2 . 2 .	**3** **5** **5** **3** **3**	2 . 2 2 **5** **3** . **3** .	**3** **3** 2 2	. . 2 2 2 2	2 . 2 2	2 . 2 2 2	2 2 . 2 .	. . 2 . . .
Carex pilulifera	 2	2 **3** 2 **3** 2	. 2 2 **5** . . **3** 2 2	2 . 2 **3**	2 **3** 2 1 2 2	2 2 2 **3**	2 2 . 2 2	2 2 2 2 .	. 2 . . . .

T a b l e 1. (Continued)

Veronica officinalis	. . . 2 .	2 2 . . **3**	2 . 2 2 2 2 2 2 2	. 2 **3** **3**	1 2 2 2 2 2	1 2 2 1	. 2 2 1 .	2 2 2 1 .	. . . . . .
Pilosella officinarum	 1	. . 2 2 2	. . 2 2 . . **3** . 2	. 2 . 2	. 2 2 2 2 .	**3** . 1 1	. . . . .	2 1 1 2 .	. . . . . .
Agrostis capillaris	2 3 2 3 2	2 3 3 **5** **5**	**7** **6** **5** **5** **5** **5** 3 **7** **7**	. **5** **5** **5**	2 2 3 2 **5** 2	3 2 3 3	2 3 2 2 2	. 1 . 2 2	2 . . . . .
Hypericum maculatum	3 3 3 3 2	2 2 3 3 3	**6** **5** **5** **6** 3 **5** 3 **7** **5**	**5** 3 . 3	3 3 . 2 3 2	3 2 **5** 3	2 3 2 3 2	2 . 1 1 2	. . . . . .
Avenula planiculmis	. . 2 2 2	2 2 2 2 3	3 2 **7** **5** **7** **7** **5** 3 3	**8** **8** **8** **7**	2 2 2 . 3 .	3 3 **5** 2	2 3 2 **5** .	. 1 . . .	. . . . . .
Potentilla erecta	2 2 2 2 2	**5** **5** **5** **5** **5**	3 3 3 **5** 2 3 **6** 3 3	**5** 3 **5** 3	2 3 3 2 **5** 2	**6** 3 **5** **5**	2 3 2 3 3	2 2 . 2 .	. . . . . .
Rhytidiadelphus squarrosus	**8** **6** 5 3 **7**	. . . . .	**8** **9** **7** **7** **6** **6** **7** **8** **8**	5 . 2 3	5 **6** 5 **6** **7** **6**	3 **6** 5 2	3 **6** **7** . 5	. 3 . . 2	2 . . . 2 .
Fragaria vesca	2 . 2 2 .	. . . . .	**3** . . **3** **3** **5** 2 2 .	. . . 2	**3** **5** **5** **6** **3** 2	1 . . .	2 . **3** . 2	. . . 1 .	. . . . 2 2
Pimpinella saxifraga	. . 2 2 2	. . . . .	2 2 2 2 . 2 . 2 2	2 2 2 .	**3** **5** **3** . 2 **3**	2 . . .	. . 1 2 2	. . 1 . .	. . . . . .
Acer pseudoplatanus	. . 1 . .	 1	. 1 . 1 . . **2** 1 .	. . 1 1	1 1 1 . 1 1	**2** 1 1 1	. . . . .	1 . . 1 1	. . . . . .
Ajuga reptans	2 . 2 . 2	. . 2 . 2	**3** **3** 2 **5** . 2 **6** 2 2	. . **3** 2	**5** **7** **6** **5** **6** **5**	**3** 2 2 .	. 2 **3** . 3	1 2 2 . .	**3** **3** . 2 . 2
Pleurozium schreberi	. . 3 5 2	**8** **7** **7** **7** **7**	5 2 **7** 5 **6** **7** **6** **6** **7**	5 **7** **7** **8**	**6** **7** **7** **6** **6** **6**	3 **7** **7** 5	3 **7** **7** **7** **7**	5 3 5 2 2	2 2 2 2 . .
Avenella flexuosa	. . . 2 3	**5** **6** **6** **3** **5**	2 2 . **5** 2 3 **7** . **6**	3 3 3 2	3 3 4 2 **5** 2	**7** **8** **7** **7**	3 3 2 **5** **5**	2 2 2 3 3	. . 2 . 2 2
Hylocomium splendens	. . . . .	3 2 5 6 **7**	. . 5 **7** 2 5 **7** . .	3 . 2 **7**	**7** **7** **7** 6 6 6	**8** **7** **8** **8**	**8** . 3 3 3	**9** **9** **8** **9** **8**	5 3 3 3 2 2
Plagiomnium affine	3 2 3 2 2	. . . . .	. 2 . 2 3 **5** 2 2 .	. 2 3 .	3 **5** 3 **5** 2 **6**	. 2 2 3	3 **6** 2 3 2	3 . 3 2 3	**8** **8** **7** **8** **6** **7**
Dicranum polysetum	. . . . .	. . . 3 3	. . . .	. . . .	. . . . 2 2	**5** . 3 .	. . . . .	. . . 2 3	. . . . . .
Ranunculus auricomus agg.	1 **2** . . .	. . . . .	. . . . 1	. . . .	. . . . . .	. . . .	. . . . .	. . . . .	. . . . . .
Primula elatior	2 2 . . .	. . . . .	**3** **3**	. . . .	 1	. . . .	. . . . .	. . . . .	. . . . . .
Lathyrus pratensis	. 2 . . .	. . . . .	. 2	. . . .	. . . . . .	. . . .	. . . . .	. . . . .	. . . . . .
Arrhenatherum elatius	2	. . . . .	. **6**	. . . .	. . . . 2 .	. . . .	. . . . .	. . . . .	. . . . . .
Vicia cracca	1 2 . . .	. . . . .	2 2 . . 2	. . . .	. . . . . .	. . . .	. . . . .	. . . . .	. . . . . .
Leucanthemum vulgare agg.	. . . 1 .	2	. . . .	. . . .	. . . 2 . .	. . . .	. . . . .	. . . . .	. . . . . .
Plantago lanceolata	. . . . .	2	2	. . . .	. . . . . .	. . . .	. . . . .	. . . . .	. . . . . .
Carex caryophyllea	. . . . .	2	. . 2	. . . .	. . . . . .	. . . .	. . . . .	. . . . .	. . . . . .
Quercus petraea agg.	. . . . .	. . . 1 .	 1	. . . .	. . . . . .	. . . .	. . . . .	. . . . .	. . . . . .
Poa pratensis agg.	. . . . .	. . . . .	2 . . . . . . 2 .	**3** . . .	. . . . . .	. . . .	. . . . .	. . . . .	. . . . . .
Poa chaixii	. . **3** . .	. 2 2 . .	. . . . . 2 **3** . .	. . . .	. 2	. . . .	. . . . .	. . 1 . .	. . . . . .
Rumex acetosa	 1	. **2** **2** . .	. . . 1 **2** **2** . . .	**2** . . .	. . 1 1 **2** .	. . . .	. . . . .	. . . . .	. . . . . .
Dactylis glomerata	. 1 . . .	. . . . .	**3** . . 1	. . . .	. . 2 . . .	. 2 . .	. . . . .	. . . . .	. . . . . .
Carex pallescens	. **2** . . .	. . . . .	**2**	**2** . . .	 1	. . . 1	. . . . .	. . . . .	. . . . . .
Viola riviniana	. . . . .	. . . . .	. **2** . 1	. . . .	 1	. . . 1	. . . . .	. . . . .	. . . . . **2**
Campanula persicifolia	. . . . .	. . . . .	. . . . . 1 . . .	. 1 . .	. 1 **3** . . .	. . . .	. . . . .	. . . . .	**2** . . . . .
Thymus pulegioides	. . . . .	. . . . .	. . . . . **2** 1 . .	. . . .	. . 1 . 1 .	. . . .	. . . . .	. . . . .	. . . . . .
Quercus cerris	. . . . .	. . . . .	. . . . . . 3 . .	. . . .	. . . . . .	1 . . .	. . . . .	. . . . .	. . . . . .
Padus avium	. . . . .	. . . . .	. . . 1	. . . .	. . 1 1 . .	1 . . .	. . . . .	. . . . .	. . . . . .
Senecio ovatus	. . . . .	. . . . .	. . . .	. . . .	. . . 1 . .	. . . .	. . . . .	. . 1 . .	. . . . . .
Oxalis acetosella	. . . . .	. . . . .	. . . .	. . . .	. . . 2 . .	. . . .	. . . . .	. . . . .	. . . . 2 .

Species represented in one relevé only (Table 1)

E₀: *Ambystegium serpens* rel. 31: 2, *Climatium dendroides* 3: 2, *Dicranum scoparium* 24: 2, *Polytrichum juniperinus* 28: 2, *Rhodobryum roseum* 29: 5.

E₁: *Asarum europaeum* rel. 48: 1, *Astragalus glycyphyllos* 13: 1, *Cardamine pratensis* agg. 26: 1, *Carex montana* 8: 2, *Chaerophyllum aromaticum* 14: 1, *Colchicum autumnale* 15: 1, *Corylus avellana* 28: 1, *Festuca pratensis* 11: 2, *Galium mollugo* agg. 11: 2, *Geum urbanum* 11: 2, *Juniperus communis* 9: 1, *Rubus idaeus* 24: 2, *Stellaria graminea* 20: 2, *Trifolium repens* 11: 2, *Viburnum opulus* 41: 1.

Legend: cover values in bold – species with dominance values above the average; light shading – constancy ≥ 50% in current vegetation type; dark shading – optimum zone of current species (with high constancy and relatively the highest cover values).

43, H) and *Jungermannia leiantha-Plagiomnium affine* agg. (44–49, I). Differentiation of the types according to species composition is shown in Table 1. These types represent the whole scale of non-forest field layer vegetation variability that occurs depending on changing ecological conditions (mainly light and nutrients; cf. Fig. 4) and duration of succession. Within the types, we detected three groups according to the prevailing species domi-

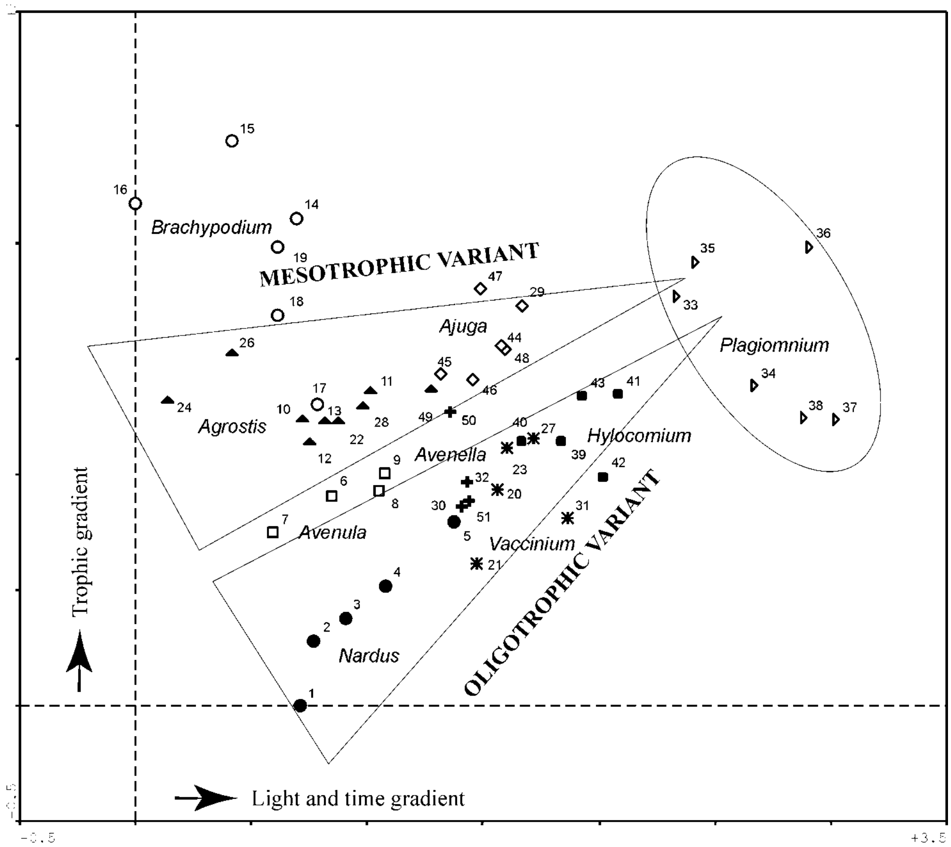
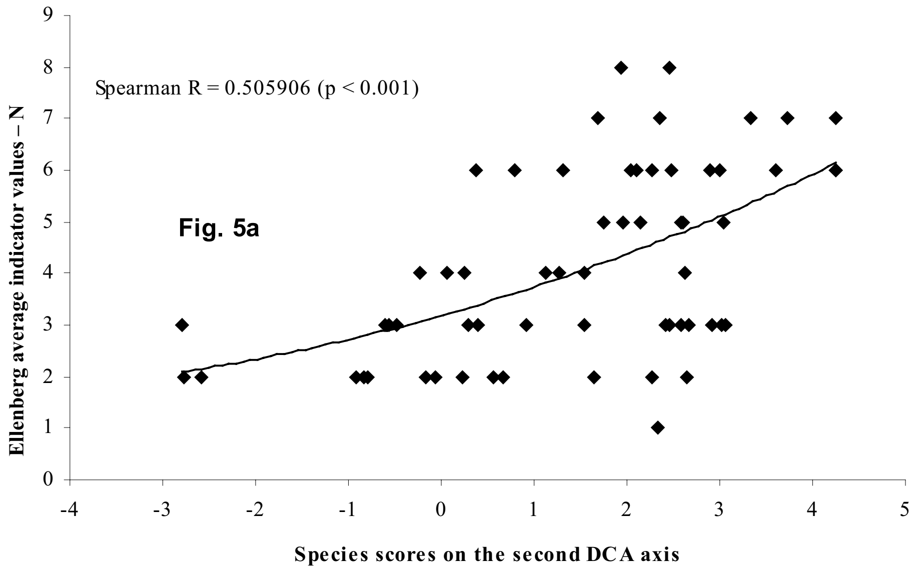


Fig. 4. DCA analysis of phytosociological relevés and schematic indication of variants of succession series (total inertia: 2.855; lenghts of gradient: AX1 – 2.886, AX2 – 2.760; eigen values: AX1 – 0.293, AX2 – 0.221; percentage variance of species data: AX1 – 10.3, AX2 – 7.7).
Legend: ○ *Brachypodium – Trifolium medium-Brachypodium pinnatum* type of vegetation (type A in tables), ● *Nardus – Antennaria dioica-Nardus stricta* (B), ▲ *Agrostis – Phyteuma spicatum-Agrostis cappilaris* (C), □ *Avenula – Knautia arvensis-Avenula* sp. (D), ◇ *Ajuga – Prunella vulgaris-Ajuga reptans* (E), + *Avenella – Platanthera bifolia-Avenella flexuosa* (F), * *Vaccinium – Vaccinium myrtillus* (G), ■ *Hylocomium – Hylocomium splendens* (H) and ▷*Plagiomnium – Jungermannia leiantha-Plagiomnium affine* agg. (I).



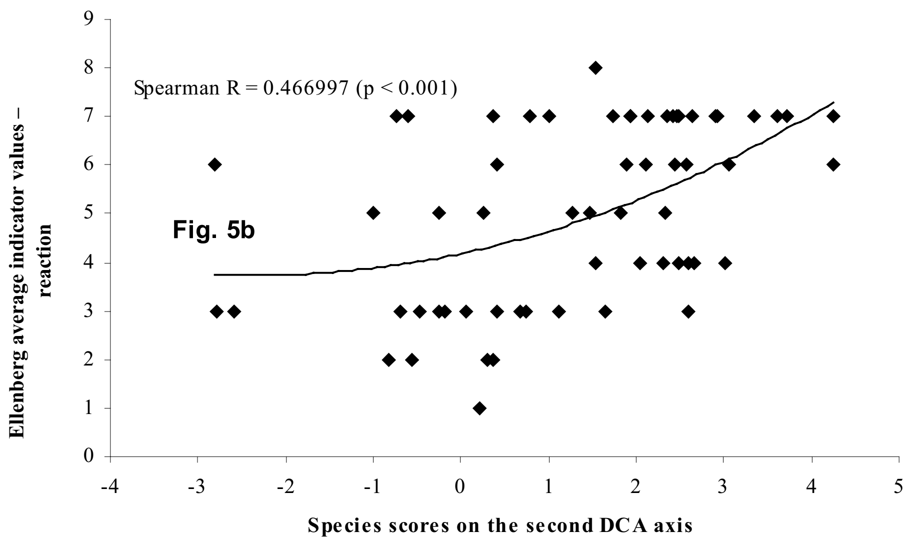


Fig. 5. Correlation between species scores on the second DCA axis and average Ellenberg indicator values for nitrogen (N; Fig. 5a) and pH (Fig. 5b).

nance: i) types with one strongly dominant species (A, B, D, F, G), ii) species-rich types with more dominant species (C, E), iii) species-poor types with the dominance of mosses and with the occurrence of 1 or 2 dominant species (H, I).

The course of successional changes within the transect can easily be observed in the ordinantion graph, where the first axis can be considered to follow the light and temporal gradient of succession, and the second axis the trophic gradient (Fig. 4). Light input decreases towards the margin of the original forest, where the old spruce individuals were planted. These trees served as source for the spread of spruce seeds to the abandoned grassland. On the contrary, the length of duration of the succession process increases towards to this margin. This relationship is confirmed by the correlation between the scores of relevés along the first DCA axis and the distances from the forest margin (Spearman's rank correlation coeficient $R = 0.623$, $p < 0.001$). Along the second DCA axis, types of vegetation were differentiated mainly according to the trophic gradient (Fig. 4). With increasing species score on the second DCA axis, the average eco-numbers for both nitrogen (quantifying the accessibility of N for plants during vegetation period) and soil reaction increase (Fig. 5a, b).

Succession series

The order of types according to average sample score on the first DCA axis is following (Fig. 4) – B (0.3), D (0.5), C (0.6), F (1.1), E (1.3), G (1.4), H (1.6), I (2.7). The variability of second axis show, that it is impossible to order all recorded types to one single temporal series. We suppose that the trophic gradient of the second axis is related to partly different stand development after the mowing cessation. The scheme of the supposed development

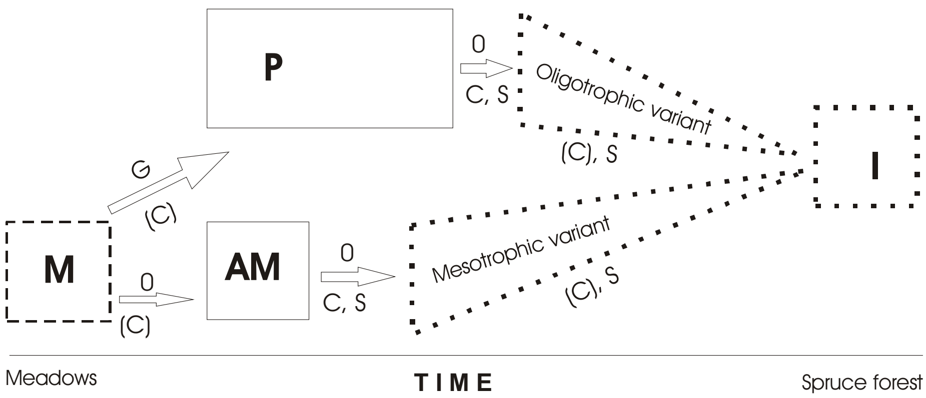


Fig. 6. Succession scheme of a divergent development of field layer vegetation in the study site caused by grazing and spruce colonization.
Legend: M – mowed tall-grass meadows (*Polygono-Trisetion*; relevé signed as A in text), P – oligotrophic pastures (O2 in the Table 3), AM – abandoned tall-grass meadows (O1 in the Table 2), I – *Jungermannia leiantha-Plagiomnium affine* agg. type of vegetation, 0 – withount utilization (abandoned), G – grazing, C – colonization of spruce, S – shading by trees.

is shown in Fig. 6. The horizontal axis symbolizes temporal changes associated with site modifications caused by subsequent spruce colonization. In the vertical direction, two variants are differentiated according to a different length of the grazing period and/or the absence of grazing. The changes of field layer vegetation that we recorded are marked by dashed line; vegetation changes caused by the utilization change and a subsequent influence of irregular low-intensity cattle grazing are displayed by full line.

The common starting point ("origin" stage) of both variants was most likely mowed meadow community, which have been preserved until present days only on the nearby locality Šútovka (1.3 km ENE from the transect, see Fig. 1). The locality has similar site conditions. The species composition is documented by the following relevé A:

Relevé A: Poľana, Šútovka, the first meadow on the way from Príslopy to the Kyslinky settlement; mesophilous meadow community on relatively milder part of an undulated slope; mowed once per year, not fertilized; the *Polygono-Trisetion* allianace; cambisol, volcanic bedrock; relevé area 20 m^2; altitude 970 m; aspect 35°; slope 10°; cover total 97%; E_1 95%; E_0 60%; height of herb layer 65 cm; author K. Ujházy; 21. 6. 2001.

E_1: *Festuca rubra* 2b, *Luzula luzuloides* 2b, *Poa chaixii* 2b, *Trifolium pratense* 2b, *Primula elatior* 2b, *Briza media* 2a, *Agrostis capillaris* 2a, *Leontodon hispidus* 2a, *Tragopogon orientalis* 2a, *Hypericum maculatum* 2a, *Crepis mollis* 2a, *Cruciata glabra* 2a, *Arrhenatherum elatius* 1, *Rhinanthus minor* 1, *Carlina acaulis* 1, *Veronica chamaedrys* 1, *Achillea millefolium* 1, *Campanula serrata* 1, *Chaerophyllum aromaticum* 1, *Viola canina* 1, *Dactylis glomerata* +, *Festuca pratensis* +, *Carex pallescens* +, *Nardus stricta* +, *Anthoxanthum odoratum* +, *Avenula adsurgens* +, *Trifolium repens* +, *Trifolium montanum* +, *Ranunculus auricomus* agg. +, *Taraxacum* sp. +, *Ranunculus acris* +, *Vicia cracca* +, *Colchicum autumnale* +, *Polygonatum verticillatum* +, *Lotus corniculatus* +, *Geranium sylvaticum* +, *Acetosa pratensis* +, *Potentilla erecta* +, *Vicia sepium* +, *Trifolium flexuosum* +, *Plantago lanceolata* +, *Alchemilla* sp. +, *Phyteuma spicatum* +, *Listera ovata* +, *Galium pumilum* +, *Carum carvi* +, *Leucanthemum vulgare* agg. +, *Galium verum* +, *Luzula campestris* r, *Lathyrus pratensis* r, *Campanula patula* r, *Plantago media* r, *Botrychium lunaria* r, *Acer pseudoplatanus* r, *Potentilla aurea* r, *Thymus pulegioides* r, *Ranunculus polyanthemo* r, *Tussilago farfara* r, *Geum rivale* r, *Fragaria vesca* r, *Myosotis palustris* agg. r, *Knautia arvensis* r.

E_0: *Rhytidiadelpus squarrosus* 3, *Plagiomnium* sp. 2b, *Brachythecium* sp. 2a, *Climacium dendroides* +.

Variants of the series

We distinguished two basic variants within the "spruce-beech" succession series (cf. Ujházy, 2003) – a mesotrophic and an oligotrophic one (Tables 2, 3; diagnostic and constant species for each variant are bold-faced; Fig. 4, 6). They are characterised by a specific species composition, and both the temporal and the spatial sequence types of vegetation (Tables 2, 3).

The **mesotrophic variant** (Table 2, Fig. 4) – the point of origin of this variant is an abandoned tall-grass mountain meadow (*Agrostis capillaris* comm., Table 2, O1), the succession continues by the type of vegetation C, next the type E and the last stage with a total shading by spruce is the type I. The **oligotrophic variant** (Table 3, Fig. 4) – the succession starts from (hemi-)oligotrophic pastures (*Cynosurion* all., *Anthoxantho-Agrostietum tenuis* subas. *nardetosum*), which probably gradually developed after the conversion of mowed tall-grass meadows of the *Polygono-Trisetion* all. to extensively managed short-grass pastures during 1950s to 1980s (Table 3, O2). Consequently, they gradually change under the shading by trees and the absence of grazing to the types B, F, G, and H, and their changes are finished in the moss type of vegetation I. Type of vegetation I is the common final

T a b l e 2. Synoptic table of the phytosociological relevés of mesotrophic variant

Vegetation type		I	E	C	O1	I	E	C	O1
Number of relevés		6	6	9	4	6	6	9	4
		constancy [%]				**fidelity (phi coef.)**			
Differential species of the vegetation types									
Lophocolea heterophylla	[E0]	50	.	.	.	65.7	---	---	---
Jungermannia leiantha	[E0]	33	.	.	.	52.5	---	---	---
Vaccinium myrtillus	[E1]	17	.	.	.	36.3	---	---	---
Asarum europaeum	[E1]	17	.	.	.	36.3	---	---	---
Plagiothecium denticulatum	[E0]	33	17	.	.	36.9	8.1	---	---
Fagus sylvatica	[E1]	17	50	.	.	1.0	52.1	---	---
Sorbus aucuparia	[E1]	17	50	22	.	---	34.2	---	---
Campanula persicifolia	[E1]	17	33	11	.	1.0	26.6	---	---
Hieracium murorum	[E1]	17	83	11	.	---	69.3	---	---
Abies alba	[E1]	.	33	.	.	---	52.5	---	---
Dicranum polysetum	[E0]	.	33	.	.	---	52.5	---	---
Prunella vulgaris	[E1]	.	83	11	.	---	78.1	---	---
Fraxinus excelsior	[E1]	.	33	11	.	---	36.9	---	---
Trifolium medium* subsp. *flexuosum	[E1]	.	33	11	25	---	26.6	---	10.7
Acer pseudoplatanus	[E1]	.	83	44	25	---	49.7	6.8	---
Danthonia decumbens	[E1]	.	17	89	.	---	---	82.6	---
Phyteuma spicatum	[E1]	.	17	89	50	---	---	67.8	5.3
Carex hirta	[E1]	.	.	56	.	---	---	66.7	---
Platanthera bifolia subsp. *latiflora*	[E1]	.	.	44	.	---	---	58.2	---
Aulacomnium palustre	[E0]	.	.	33	.	---	---	49.2	---
Primula elatior	[E1]	.	17	22	75	---	---	---	52.1
Arrhenatherum elatius	[E1]	.	17	11	75	---	---	---	60.0
Carex pallescens	[E1]	.	17	11	75	---	---	---	60.0
Cardamine pratensis	[E1]	.	17	.	75	---	1.0	---	70.2
Leucanthemum vulgare agg.	[E1]	.	17	.	50	---	8.1	---	51.0
Plantago media	[E1]	.	.	22	75	---	---	4.2	60.0
Plantago lanceolata	[E1]	.	.	11	75	---	---	---	70.2
Ranunculus auricomus agg.	[E1]	.	.	11	75	---	---	---	70.2
Festuca pratensis	[E1]	.	.	11	75	---	---	---	70.2
Colchicum autumnale	[E1]	.	.	11	75	---	---	---	70.2
Briza media	[E1]	.	.	11	75	---	---	---	70.2
Poa pratensis agg.	[E1]	.	.	22	50	---	---	12.7	40.5
Campanula patula	[E1]	.	.	22	50	---	---	12.7	40.5
Trifolium repens	[E1]	.	.	11	50	---	---	---	51.0
Lathyrus pratensis	[E1]	.	.	11	50	---	---	---	51.0
Brachythecium species	[E0]	.	.	.	100	---	---	---	100.0

T a b l e 2. (Continued)

Luzula campestris	[E1]	.	.	.	75	---	---	---	84.6
Knautia arvensis	[E1]	.	.	.	75	---	---	---	84.6
Trifolium pratense	[E1]	.	.	.	75	---	---	---	84.6
Carum carvi	[E1]	.	.	.	75	---	---	---	84.6
Viola canina	[E1]	.	.	.	75	---	---	---	84.6
Anthoxanthum odoratum	[E1]	.	.	.	50	---	---	---	67.6
Trifolium montanum	[E1]	.	.	.	50	---	---	---	67.6
Crepis mollis	[E1]	.	.	.	50	---	---	---	67.6
Stellaria graminea	[E1]	.	.	.	50	---	---	---	67.6
Taraxacum species	[E1]	.	.	.	50	---	---	---	67.6
Geum rivale	[E1]	.	.	.	50	---	---	---	67.6
Rhinanthus minor	[E1]	.	.	.	50	---	---	---	67.6
Myosotis scorpioides agg.	[E1]	.	.	.	50	---	---	---	67.6
Alopecurus pratensis	[E1]	.	.	.	50	---	---	---	67.6
Listera ovata	[E1]	.	.	.	50	---	---	---	67.6
Vicia sepium	[E1]	.	.	.	50	---	---	---	67.6
Widely distributed species									
Oxalis acetosella	[E1]	17	17	.	.	18.0	18.0	---	---
Brachypodium pinnatum	[E1]	33	17	11	.	26.6	1.0	---	---
Viola riviniana	[E1]	17	17	22	.	1.0	1.0	12.7	---
Hylocomium splendens	[E0]	100	100	56	.	38.5	38.5	---	---
Plagiomnium affine	[E0]	100	100	67	75	24.5	24.5	---	---
Ajuga reptans	[E1]	67	100	89	25	---	31.6	22.6	---
Avenella flexuosa	[E1]	50	100	78	.	---	42.1	21.5	---
Fragaria vesca	[E1]	33	100	67	25	---	45.9	10.2	---
Pleurozium schreberi	[E0]	67	100	100	25	---	28.1	37.5	---
Rhytidiadelphus squarrosus	[E0]	33	100	100	75	---	28.1	37.5	---
Carex pilulifera	[E1]	17	100	67	.	---	54.0	22.0	---
Luzula luzuloides	[E1]	17	67	67	25	---	21.0	28.0	---
Veronica officinalis	[E1]	.	100	89	25	---	45.9	44.2	---
Padus avium	[E1]	.	33	11	.	---	36.9	---	---
Thymus pulegioides	[E1]	.	33	22	25	---	18.7	4.2	5.5
Pimpinella saxifraga	[E1]	.	83	78	25	---	35.2	38.7	---
Pilosella officinarum	[E1]	.	67	44	.	---	41.8	20.0	---
Picea abies	[E1]	.	50	44	.	---	27.5	27.5	---
Nardus stricta	[E1]	.	67	78	50	---	16.5	38.7	---
Carlina acaulis	[E1]	.	50	100	50	---	---	66.5	---
Poa chaixii	[E1]	.	17	22	25	---	1.0	12.7	10.7
Potentilla erecta	[E1]	.	100	100	75	---	35.0	46.8	2.9
Avenula planiculmis	[E1]	.	67	100	100	---	---	51.4	29.9
Hypericum maculatum	[E1]	.	83	100	100	---	14.2	46.8	27.2

Table 2. (Continued)

Agrostis capillaris	[E1]	17	100	100	100	---	28.1	37.5	21.8
Cruciata glabra	[E1]	.	100	89	100	---	35.0	28.2	27.2
Festuca rubra	[E1]	.	83	89	75	---	22.6	38.9	10.0
Ranunculus polyanthemos	[E1]	.	33	56	50	---	---	30.6	12.7
Alchemilla species	[E1]	.	50	67	100	---	---	22.0	41.9
Ranunculus acris	[E1]	.	50	22	100	---	16.4	---	58.2
Rumex acetosa	[E1]	.	50	33	100	---	11.5	---	53.5
Potentilla aurea	[E1]	.	50	67	75	---	2.2	28.0	23.6
Achillea millefolium	[E1]	.	33	100	100	---	---	61.2	35.6
Veronica chamaedrys	[E1]	.	50	56	100	---	2.2	11.3	45.4
Lotus corniculatus	[E1]	.	33	44	75	---	---	13.2	35.5
Galium verum	[E1]	.	17	56	75	---	---	30.6	35.5
Dactylis glomerata	[E1]	.	17	22	50	---	---	4.2	32.7
Deschampsia cespitosa	[E1]	.	.	44	50	---	---	35.9	26.6
Vicia cracca	[E1]	.	.	33	25	---	---	35.5	10.7
Chaerophyllum aromaticum	[E1]	.	.	11	25	---	---	8.6	27.3

phase of grass-stand changes for both succession variants, occurring in totally closed spruce stands. In the next phase, field layer vegetation is completely suppressed by spruce (shading, thick litter layer). This is the end of the non-forest stages development. Subsequent phases of forest communities succession were not recorded within the transect.

Types with the dominance of strongly competitive clonal grasses *Brachypodium pinnatum* and *Avenula* sp., which are relatively poor in species, occupy a specific position beyond the mentioned variants of the succession series (Fig. 4).

Changes of cover and number of field-layer species

During the succession, the cover of herb and grass species (E_1) decreases strongly, and the number of these species declines gradually. On the other hand, the cover of mosses (E_0) increases to the point, when the canopy of the tree layer is closed. The highest values of moss cover were detected within the types of vegetation E and G, partially also within the type F. Total vegetation cover, as well as species richness, exhibit a decreasing tendency (Fig. 7–8). A strong decrease of herb and grass cover is associated with an increasing abundance of tree and shrub seedlings. The highest number of woody species in E_1 was detected within the types of vegetation E to H (the values can be partly affected by differences in the sample plot area), where the cover of the herb layer (E_1) dropped down to 35–50% and that of moss layer (E_0) was approx. 80 % (cf. Fig. 7–8). These findings can be explained by a low competitive ability of tree seedlings compared to the herbaceous E_1 species and their need of sufficient moisture.

T a b l e 3. Synoptic table of the phytosociological relevés of oligotrophic variant

Vegetation type		I	H	G	F	B	O2	I	H	G	F	B	O2
No. of relevés		6	5	5	4	5	5	6	5	5	4	5	5
		Constancy [%]						**Fidelity (phi coef.)**					
Differential species of the vegetation types													
Jungermannia leiantha	[E0]	33	.	.	.	.	.	53.5	---	---	---	---	---
Asarum europaeum	[E1]	17	.	.	.	.	.	37.1	---	---	---	---	---
Oxalis acetosella	[E1]	17	.	.	.	.	.	37.1	---	---	---	---	---
Lophocolea heterophylla	[E0]	50	20	20	25	.	.	37.5	---	---	4.9	---	---
Plagiothecium denticulatum	[E0]	33	.	40	.	.	.	29.4	---	35.1	---	---	---
Vaccinium myrtillus	[E1]	17	.	100	50	20	.	---	---	68.3	17.1	---	---
Acer pseudoplatanus	[E1]	.	60	.	100	20	.	---	33.7	---	65.0	---	---
Platanthera bifolia ssp. *latiflora* [E1]	.	20	20	75	.	.	---	4.0	4.0	61.4	---	---	
Aulacomnium palustre	[E0]	.	.	20	25	60	.	---	---	4.0	8.8	52.0	---
Poa chaixii	[E1]	.	20	.	.	40	.	---	14.9	---	---	44.7	---
Veronica chamaedrys	[E1]	.	20	.	.	.	100	---	---	---	---	---	89.4
Lotus corniculatus	[E1]	.	.	20	.	.	100	---	---	---	---	---	89.4
Alchemilla species	[E1]	.	.	20	.	.	100	---	---	---	---	---	89.4
Carex pallescens	[E1]	.	.	.	25	.	80	---	---	---	8.8	---	76.0
Plantago lanceolata	[E1]	.	.	.	.	20	80	---	---	---	---	4.0	76.0
Campanula persicifolia	[E1]	17	.	.	.	.	80	---	---	---	---	---	76.0
Thymus pulegioides	[E1]	.	.	.	.	.	100	---	---	---	---	---	100.0
Poa angustifolia	[E1]	.	.	.	.	.	100	---	---	---	---	---	100.0
Campanula patula	[E1]	.	.	.	.	.	100	---	---	---	---	---	100.0
Ranunculus acris	[E1]	.	.	.	.	.	100	---	---	---	---	---	100.0
Prunella vulgaris	[E1]	.	.	.	.	.	80	---	---	---	---	---	87.7
Cardamine pratensis	[E1]	.	.	.	.	.	80	---	---	---	---	---	87.7
Trifolium pratense	[E1]	.	.	.	.	.	80	---	---	---	---	---	87.7
Vicia cracca	[E1]	.	.	.	.	.	60	---	---	---	---	---	74.5
Ranunculus auricomus	[E1]	.	.	.	.	.	60	---	---	---	---	---	74.5
Galium verum	[E1]	.	.	.	.	.	60	---	---	---	---	---	74.5
Primula elatior	[E1]	.	.	.	.	.	60	---	---	---	---	---	74.5
Euphrasia rostkoviana	[E1]	.	.	.	.	.	60	---	---	---	---	---	74.5
Plantago media	[E1]	.	.	.	.	.	60	---	---	---	---	---	74.5
Knautia arvensis	[E1]	.	.	.	.	.	60	---	---	---	---	---	74.5
Festuca rupicola	[E1]	.	.	.	.	.	60	---	---	---	---	---	74.5
Polytrichum formosum	[E0]	.	.	.	.	.	60	---	---	---	---	---	74.5
Trifolium repens	[E1]	.	.	.	.	.	60	---	---	---	---	---	74.5
Climacium dendroides	[E0]	.	.	.	.	.	40	---	---	---	---	---	59.8
Lathyrus pratensis	[E1]	.	.	.	.	.	40	---	---	---	---	---	59.8
Cladonia species	[E0]	.	.	.	.	.	40	---	---	---	---	---	59.8
Trifolium medium ssp. *flexuosum*	[E1]	.	.	.	.	.	40	---	---	---	---	---	59.8
Rosa canina agg.	[E1]	.	.	.	.	.	40	---	---	---	---	---	59.8
Polygala vulgaris	[E1]	.	.	.	.	.	40	---	---	---	---	---	59.8
Stellaria graminea	[E1]	.	.	.	.	.	40	---	---	---	---	---	59.8
Widely distributed species													
Brachypodium pinnatum	[E1]	33	20	.	25	.	.	29.4	8.8	---	13.5	---	---
Fragaria vesca	[E1]	33	20	60	25	.	40	3.6	---	29.3	---	---	9.8
Hieracium murorum	[E1]	17	20	20	.	40	40	---	---	---	---	17.6	17.6
Ajuga reptans	[E1]	67	60	60	75	40	60	6.8	---	---	12.0	---	---
Plagiomnium affine	[E0]	100	80	100	75	40	100	22.4	---	20.0	---	---	20.0
Hylocomium splendens	[E0]	100	100	80	100	100	100	9.3	8.3	---	7.3	8.3	8.3
Pleurozium schreberi	[E0]	67	100	100	100	100	100	---	12.0	12.0	10.5	12.0	12.0
Avenella flexuosa	[E1]	50	100	100	100	100	60	---	20.0	20.0	17.5	20.0	---
Rhytidiadelphus squarrosus	[E0]	33	40	80	100	.	100	---	---	21.1	34.3	---	39.1

T a b l e 3. (Continued)

Pilosella officinarum	[E1]	.	80	.	75	60	80	---	29.9	---	22.3	12.0	29.9
Potentilla erecta	[E1]	.	60	100	100	100	100	---	---	27.0	23.7	27.0	27.0
Agrostis capillaris	[E1]	17	60	100	100	100	100	---	---	24.7	21.6	24.7	24.7
Luzula luzuloides	[E1]	17	60	80	75	100	100	---	---	9.8	4.3	29.3	29.3
Carex pilulifera	[E1]	17	80	80	100	100	100	---	3.5	3.5	21.6	24.7	24.7
Veronica officinalis	[E1]	.	80	60	100	60	100	---	15.5	---	29.8	---	34.0
Hypericum maculatum	[E1]	.	80	100	100	100	100	---	3.5	24.7	21.6	24.7	24.7
Carlina acaulis	[E1]	.	.	60	50	100	80	---	---	12.0	2.6	47.8	29.9
Avenula planiculmis	[E1]	.	20	80	100	100	100	---	---	15.5	29.8	34.0	34.0
Cruciata glabra	[E1]	.	20	20	75	60	100	---	---	---	25.1	15.0	51.1
Picea abies	[E1]	.	20	40	25	40	40	---	---	13.5	---	13.5	13.5
Pimpinella saxifraga	[E1]	.	20	60	25	.	100	---	---	25.3	---	---	63.2
Ranunculus polyanthemos	[E1]	.	.	20	.	.	40	---	---	14.9	---	---	44.7
Fagus sylvatica	[E1]	17	.	.	25	40	.	4.9	---	---	13.5	35.1	---
Dicranum polysetum	[E0]	.	40	.	50	40	60	---	9.8	---	17.1	9.8	29.3
Potentilla aurea	[E1]	.	.	.	75	80	100	---	---	---	28.0	36.5	54.8
Nardus stricta	[E1]	.	.	20	75	100	100	---	---	---	22.3	47.8	47.8
Danthonia decumbens	[E1]	.	.	40	50	80	100	---	---	---	5.3	33.1	51.1
Festuca rubra	[E1]	.	.	.	50	100	100	---	---	---	8.0	54.8	54.8
Achillea millefolium	[E1]	.	.	.	25	60	100	---	---	---	---	29.3	68.3
Antennaria dioica	[E1]	.	.	.	.	60	60	---	---	---	---	44.7	44.7
Anthoxanthum odoratum	[E1]	.	.	.	.	60	80	---	---	---	---	38.8	59.9
Rumex acetosa	[E1]	.	.	.	.	40	80	---	---	---	---	22.4	67.1
Viola canina	[E1]	.	.	.	.	60	100	---	---	---	---	33.7	74.2
Luzula campestris agg.	[E1]	.	.	.	.	40	100	---	---	---	---	17.6	81.1
Briza media	[E1]	.	.	.	.	40	100	---	---	---	---	17.6	81.1
Carex caryophyllea	[E1]	.	.	.	.	20	40	---	---	---	---	14.9	44.7
Leucanthemum vulgare agg.	[E1]	.	.	.	.	20	40	---	---	---	---	14.9	44.7

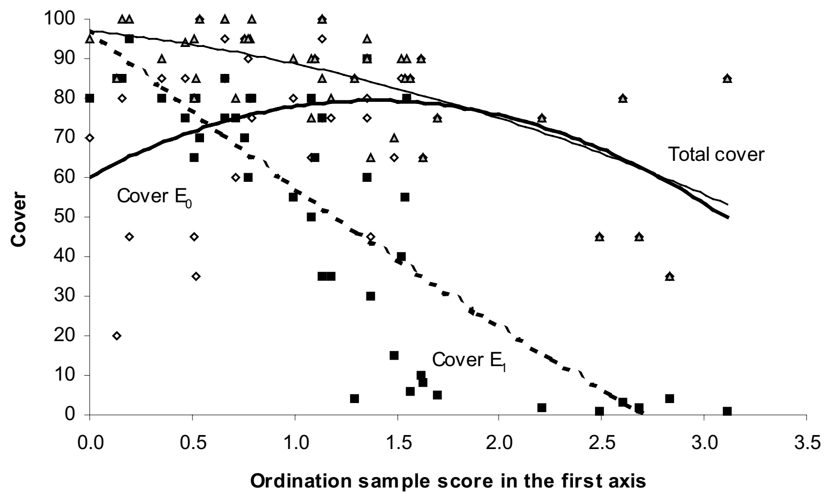


Fig. 7. Relation between relevé scores on the first DCA axis and the cover of the moss and herb layer (▲ and full trend line – total cover of E_1 and E_2, ◇ and bold trend line – cover of E_0, ■ and dashed trend line – cover of E_1).

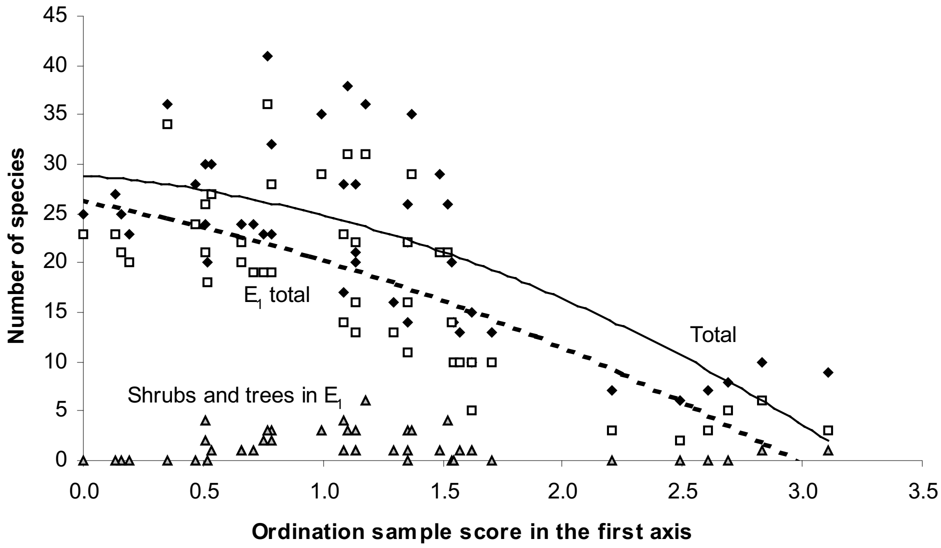


Fig. 8. Relation between relevés scores on the first DCA axis and the number of species in both moss and herb (including young shrubs and trees) layers (♦ and full trend line – total number of species, □ and dashed trend line – number of species in E_1, ▲ number of shraubs and trees in E_1).

Discussion

The colonization of abandoned grasslands by forest trees in the investigated locality has taken place since approximately 50 years (cf. Ujházy, 2003). Types of vegetation were best differentiated according to light, trophic gradient and duration of succession (Fig. 4).

Supposed succession scheme (Fig. 6) shows a regular series of recorded types (mesotrophic – *Agrostis capillaris* comm. > C > E > I and oligotrophic – *Anthoxantho-Agrostietum tenuis nardetosum* > B > F > G > H > I). However, these two basic variants need not follow always the same type sequence, according to our field observations. The whole process can be markedly modified by strong competitive species, which can (but need not) expand into the abandoned stands of the original stage or in any of the later types. They are mainly clonal species (*Avenula* sp., *Brachypodium pinnatum*, *Vaccinium myrtillus*, *V. vitis-idaea*) or dense tussock species *Calamagrostis arundinacea*. Only *Avenula* sp. and *Brachypodium pinnatum* are involved in the mesotrophic variant. However, *Avenula* sp. expands well into the stands of the oligotrophic variant as well. *Vaccinium myrtillus* enters the development process within the oligotrophic variant later, after side shading. Similarly, but less frequently or on smaller patches occur *Vaccinium vitis-idaea* or *Calamagrostis arundinacea.*

According to several authors (e.g. Svoboda, 1939; Miadok, 1976, 1983, 1985; Ružičková, 1991), during the succession, the cover of *Nardus stricta* decreases, while the proportion of herbs like *Avenella flexuosa*, *Luzula luzuloides*, *Vaccinium myrtilus*, or woody species *Juniperus communis*, *Picea abies* increase in stands of the association *Anthoxantho-Agrostietum tenuis* subass. *nardetosum*. This is identical with our finding, namely concerning the oligotrophic variant of succession series at Príslopy. The examples are the stands with the dominance of *Nardus stricta* on mountain meadows. *Nardus stricta* withdraws under the pressure of taller grasses (e.g. *Avenula* sp., *Calamagrostis arundinacea*, *Deschampsia cespitosa*), but also some lower species like *Avenella flexuosa* or *Hypericum maculatum*, and due to shading of spruce trees (cf. Regal, 1953; Jeník, 1983; Blažková, 1988, 1996; Blažková, Březina, 2003; Krahulec, 1996). On the other hand, the succession of the *Polygono-Trisetion* all. is not well documented in the literature. Ružičková (1991) described the species composion of abandoned meadows of the *Polygono-Trisetion* all in the Zamagurie region. She classified *Gladiolus imbricatus*, *Platanthera bifolia*, *Fragaria vesca*, *Trifolium medium* and *Gymnadenia conopsea* among the species of abandoned meadows. The second and the fourth species occur more frequently in the types of vegetation C, E within the mesotrophic variant of the studied series, *Fragaria vesca* has even the optimum of its occurrence here (Tables 1, 2). A gradual decrease of species diversity and cover of herb species is typical for the succession rather than a spread of new species (other than those typical for these communities; cf. Ružičková, 1991). Within the later overshaded herbal phases of succession, mainly vegetatively reproducing species (e.g. *Ajuga reptans*, *Fragaria vesca*, *Prunella vulgaris*) are able to survive (Table 2).

The types of vegetation with the dominance of clonal grasses (*Avenula* sp., *Brachypodium pinnatum*) fall beyond the scheme of variants of succession series. This fact is apparently connected with the specific way of dispersal of these species, as well as their strong competitive ability. Development of these stands is probably regulated more by the population dynamics of these species and their tolerance to limiting factors (mainly light), than by gradual changes in species composition (what can be observed for the other types of vegetation). *Brachypodium pinnatum* is considered to be an indicator of abandoned meadows and pastures (Perez-Chacon, Vabre, 1985; Dutoit, 1996; Krahulec, 1996; Ujházy, 2003) and a strong competitive species (CS strategist sensu Grime, 1979), which is able to modify soil properties (Richelot, 1997). The taxa of genus *Avenula*, which spread within the sub-mountain and mountain meadows and pastures in Veľká Fatra and Poľana Mts, possess similar properties (Kliment, 1994, 1997; Uhliarová et al., 2000). These types of vegetation do not directly conform with any described variant of the succession series in the Príslopy area.

Conclusion

Spruce is the most important species, whose expansion clearly determined the direction and speed of field layer changes on the study site. The development from an abandoned meadow grass stand towards a pure spruce stand lasted approx. 30–50 years. This relatively short period could be characterised by a sequence of dominant species stands (as proposed, e.g., by Prach, 1990), or a sequence of types of vegetation, which are mostly characterised by 1 to 3 dominant species (see Tables 1–3).

However, vegetation in field layer developed differently near the forest edge (where grazing was less intense after mowing was abandoned, and where there was a fast colonization by spruce) than at the places, where meadows had changed substantially by grazing before the spread of spruce began. This is why two parallel variants of successional development exist. The oligotrophic variant is less species rich compared to the mesotrophic one (see Table 1) and has more modifications given by alternative expansion of competitive clonal (mostly) species. Divergence of the successional development as described by Waddington (1977) or Míchal (1992) is only temporary here and finishes after the closing of canopy within the spruce layer in species-poor stages (type of vegetation I – *Jungermannia leiantha-Plagiomnium affine* agg.).

The change of types of vegetation during a relatively short period (initial stage of the spruce-beech succession series sensu Ujházy, 2003) cannot be explained by known models like that of Connel, Slatyer (1977). Species composition has not changed much; most species occurred here already in non-shaded stands of abandoned grassland. We observed a gradual change of one set of species and a regression of the other ones as a reaction to the modification of ecological conditions during the spruce expansion. Only a few new herb species join the process. Five strong competitive taxa expand to abandoned grasslands (not-shaded or partly shaded). The typical forest ones (e.g. —*Oxalis acetosella, Asarum europaeum*) were detected rarely, after the regression of grasses under the spruce canopy.

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Hrivnák R., Ujházy K.: **Zmeny vegetácie horských lúk a pasienkov po opustení a kolonizácií smrekom.**

Zmeny nelesnej vegetácie počas kolonizácie opustených horských lúk a pasienkov smrekom sme sledovali na pásovom transekte (20 x 170 m) v pohorí Poľana. Transekt predstavuje prechod od otvorených trávnych porastov s ojedinele roztrúsenými mladými jedincami smreka a borievky ku 40–50 ročnému smrekovému porastu hraničiacemu s umelo založeným smrekovým lesným okrajom.

Zmeny v nelesnej vegetácii začali po ukončení kosenia lúk, začatí nepravidelného a mozaikovitého pasenia a následnej kolonizácii smrekom. Na transekte sme identifikovali 9 typov vegetácie, charakterizovaných špecifickou druhovou kombináciou a dominanciou niektorých druhov bylín a tráv: *Trifolium medium-Brachypodium pinnatum* (A), *Antennaria dioica-Nardus stricta* (B), *Phyteuma spicatum-Agrostis capillaris* (C), *Knautia arvensis-Avenula* sp. (D), *Prunella vulgaris-Ajuga reptans* (E), *Platanthera bifolia-Avenella flexuosa* (F), *Vaccinium myrtillus* (G), *Hylocomium splendens* (H) a *Jungermannia leiantha-Plagiomnium affine* agg. (I). Diferencovali sme ich pomocou divizívnej polytetickej klasifikácie a ordinačných metód (Twinspan a DCA).

Prvé dve ordinačné osi DCA môžeme interpretovať ako svetelný a časový gradient (prvá os), resp. trofický gradient (druhá os). Na základe tejto analýzy sme odlíšili dva paralelné sukcesné varianty v rámci tej istej sukcesnej série – mezotrofný (spol. *Agrostis capillaris* spol. > C > E > I) a oligotrofný (*Anthoxantho-Agrostietum tenuis nardetosum* > B > F > G > H > I). Pri oboch variantoch sú východiskovým typom vegetácie kosené horské lúky a finálnou fázou druhovo chudobný machový typ vegetácie (I). Okrem uvedených dvoch základných variantov s odlišným priebehom existuje ešte v rámci každého variantu viacero modifikácií spôsobených najmä konkurenčne silnými druhmi tráv.

Počas tohto relatívne krátkeho sukcesného vývoja nedochádza k výraznejším zámenám druhov. Pokryvnosť a počet druhov v bylinnej etáži postupne klesá. Machorasty majú najvyššiu pokryvnosť v rámci typov vegetácie E, F a G. Tu je redukované zastúpenie bylín a tráv a zároveň ešte nie je zapojená krovinová a stromová etáž. V týchto typoch vegetácie sme zároveň zaznamenali aj najvyššiu druhovú pestrosť semenáčikov a juvenilných jedincov drevín.