



Tuexenia 31: 283–299. Göttingen 2011.

## Impact of hoofed game and weather on the vegetation of endangered dry grasslands in the Křivoklátsko Biosphere Reserve (Czech Republic)

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### Abstract

Using four exclosures, the impact of mouflon grazing and weather on plant communities of the phytosociological alliances *Koelerio-Phleion phleoidis* and *Hyperico perforati-Scleranthion perennis* occurring on shallow soils within a forest landscape was studied in the Křivoklátsko Biosphere Reserve (Czech Republic) during seven years. In the years 2004–2010, the vascular plant species composition was recorded annually on a total of eight fenced and eight control plots, each 2 m × 1 m in size. Treatment, time, and weather data were used as explanatory variables in ordination and correlation analyses. Cover values of different life forms and indicator values varied significantly in dependence on the weather conditions of the preceding five months; however, correlations varied according to the vegetation type and were rather rarely detected. The effect of fencing appeared important in all study plots; however, the temporal trends were significant only in half of them. We did not find a significant interaction between treatment and time in the total dataset. A successional change was detected in one fenced plot only; in all other cases, the species composition fluctuated – a phenomenon that is not directly attributable to weather conditions. In the fenced plots, the herbaceous vegetation cover decreased, mainly due to litter accumulation and partly due to shrub encroachment. At least some parts of the valuable and species-rich habitats could be maintained under high game density, but some parts are endangered by eutrophication and game grazing. Nature conservation management should balance both mechanisms.

### Zusammenfassung: Auswirkung des Schalenwildes und der Wetterbedingungen auf die Vegetation der gefährdeten Trockenrasen im Biosphärenreservat Křivoklátsko (Tschechische Republik)

Die Auswirkungen von Mufflonbeweidung und Wetterbedingungen auf Pflanzengesellschaften der Verbände *Koelerio-Phleion phleoidis* und *Hyperico perforati-Scleranthion perennis* auf flachgründigen Böden innerhalb einer Waldlandschaft wurden im Biosphärenreservat Křivoklátsko (Pürglitzer Wald), Tschechische Republik, in vier Auszäunungen untersucht. Von 2004 bis 2010 wurde die Artenzusammensetzung der Gefäßpflanzen jährlich auf je acht Plots (2 m × 1 m) innerhalb und außerhalb der Auszäunung erfasst. Beweidung und Wetterdaten wurden als erklärende Variablen für Ordinations- und Korrelationsanalysen verwendet. Die Deckung verschiedener Lebensformen sowie Indikatorwerte schwankten signifikant in Abhängigkeit von den Wetterbedingungen der vorhergehenden fünf Monate. Die Auszäunung hatte nur bei einer Untersuchungsfläche einen wesentlichen Einfluss auf die Artenzusammensetzung. In den Auszäunungen nahm die Deckung der krautigen Vegetation kontinuierlich ab, teilweise bedingt durch Verbuschung und Streuakkumulation. Wir schließen, dass ein Teil der wertvollen und artenreichen Habitate auch unter einem erhöhten Wildbesatz erhalten werden kann, wobei allerdings die Gefahr von Eutrophierung und Wildverbiss besteht. Das Naturschutzmanagement sollte diese beiden Einflüsse gegeneinander abwägen.

**Keywords:** browsing, *Festuco-Brometea*, game impact, *Koelerio-Corynephoretea*, long-term research, succession.

### 1. Introduction

Dry grasslands are among the most endangered habitats in the world (BOBBINK et al. 1998, ZAVALLETTA et al. 2003), and due to the high conservation value, they are of central interest for many researchers (e.g. ENYEDI et al. 2008, JANDT et al. 2010). They are endangered by urbanisation, cessation of traditional management (e.g. shepherding), and environmental pollution (BAKKER 1989, KAHMEN et al. 2002, JACQUEMYN et al. 2003). The existence





of dry grasslands and their seasonal dynamics are predominantly driven by habitat and weather extremes and to a lesser extent by wildlife or livestock grazing (DONIČA et al. 2003). In Central Europe, however, shepherding has currently stopped in many of these habitats due to the low profit, but in some places it has been substituted by high game impact. With the abandonment, plant species richness usually decreases but not that of invertebrates (WIEZIK et al. 2011). The alien mouflon (*Ovis musimon* Pallas) is frequently distributed in the study region and may have a different impact on the vegetation (i.e. via disturbance, feeding damage, eutrophication) in comparison with native herbivores (CÔTÉ et al. 2004).

Weather conditions influence the fitness of vascular plants differently (DE BELLO et al. 2005). Extreme events may have lethal effect on many species in open habitats such as dry grasslands. On the other hand, a higher precipitation in the previous vegetation period may support the species re-emergence in the following growing season (FITTER & HAY 2001). To better understand vegetation development under climate change and game impact, data on long-term monitoring are urgently needed (LENGYEL et al. 2008, BAASCH et al. 2010). Despite the well-known population dynamics of many endangered grassland species, long-term monitoring of their habitats is rather scarce (but see RŮSIŇA & KIEHL 2010) or at least without evidence of interannual dynamics.

In this paper, we aim to answer the following questions: (i) What was the effect of game grazing (mainly by mouflons and less by deers) on the dynamics of dry grassland species in the period 2004–2010? (ii) Can changes in vegetation attributes be connected with the weather conditions?

## 2. Material and methods

### 2.1. Study sites

The two study sites (Velká Pleš – 49° 59' 23" N, 13° 48' 11" E, 440 m a.s.l.; Týřovické skály – 49° 59' 02" N, 13° 47' 42" E, 420 m a.s.l.) are located in the Křivoklátsko Protected Landscape Area and Biosphere Reserve in the western part of Central Bohemia (approx. 45 km W of Prague; see Fig. 1a). Forest steppes and surrounding dry oak forests are typical of south-exposed slopes of the Berounka River, which has shaped an approx. 200 m deep valley. The study site Velká Pleš is oriented to S–WSW with 12–18° inclination, while Týřovické skály is situated on a slope with S aspect and an inclination of 18–26°. The soils at the study sites are shallow Leptosols developed from andesite bedrock.

The mean annual temperature is about 8 °C, and the mean annual precipitation reaches approx. 550 mm (TOLASZ et al. 2007). For Central Bohemia, there are data available from tens of climatological stations (see [www.chmu.cz](http://www.chmu.cz)). In Appendix 1 we present the mean monthly air temperatures and the mean monthly precipitation, averaged over these stations. We point out to extremely dry periods in July 2006 (recorded also by RŮSIŇA & KIEHL 2010 in Latvia) as well as Aprils 2007 and 2009. The temperatures of the last three years exceeded the long-term 30-years average by up to 1.6 °C. The year 2003 was also low in precipitation, but in 2004 a large amount of precipitation (203 % of climatological normal 1961–1990) fell in January. Other precipitation-rich periods were: September 2007, January and September 2010 (over 180% of climatological normal 1961–1990 each), August 2010 (over 200% of that normal).

From the phytosociological point of view, the study sites are dominated by dry grasslands classified into the *Hyperico perforati-Scleranthion perennis* Moravec 1967 and the *Koelerio-Phleion phleoidis* Korneck 1974. Communities of the *Hyperico perforati-Scleranthion perennis* are dominated mostly by *Hieracium pilosella*, *Rumex acetosella* and *Agrostis capillaris*. Within the *Koelerio-Phleion phleoidis*, *Festuca valesiaca* and *Pseudolysimachion spicatum* prevail. The studied plant communities contain endangered species (e.g. *Anthericum liliago*, *Aster linosyris*, *Cerastium brachypetalum*, *Filago minima*, *Gagea villosa*, *Medicago minima*) listed in the Czech Red List (HOLUB & PROCHÁZKA 2000).



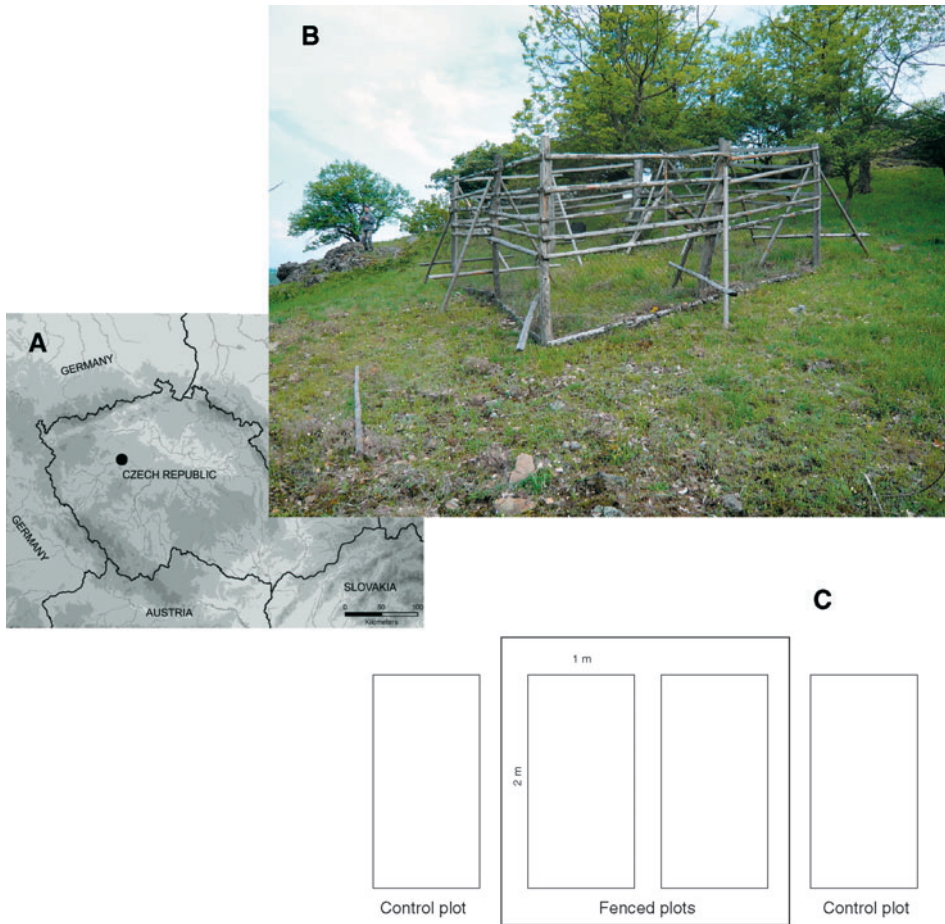


Fig. 1: A – Position of the study area within the Czech Republic. B – An enclosure at Týřovické skály, plots T1–T2 (Photo T. Černý, 2010). C – Sampling design.

Abb. 1: A – Lage des Untersuchungsgebietes in der Tschechischen Republik. B – Eine der eingezäunten Flächen T1–T2 in Týřovické skály (Foto T. Černý, 2010). C – Datenerfassungsdesign.

## 2.2. Field work

Yearly in spring (2004–2010), we recorded the vascular plant species composition using the semi-quantitative 9-degree modified version of the Braun-Blanquet scale proposed by WESTHOFF & VAN DER MAAREL (1973) (see Tables 1 and 2). At each of the two study sites, two enclosures (approx. 3.5 m × 3.5 m in size) were established in January 2004 (see Fig. 1b). Their distance was approx. 35 m at both study sites. Each enclosure contained two 1 m × 2 m plots (see also Fig. 1c for the sampling design). Immediately adjacent to the fenced plots, unfenced control plots influenced by grazing through free ranging game were set up. All subplots were marked in the field using iron nails and coded at the Velká Pleš site as P1–P4 and at the Týřovické skály site as T1–T4 (always in fenced and unfenced variants). Unfenced plots were located as close as possible to the fenced plots (the maximum distance was about 3 m) in places with similar species composition (assessed as Euclidean distance in the first year of observation) and environmental conditions. Each 2-m<sup>2</sup> plot was documented by photographs every year (see Fig. 2 for an example).





### 2.3. Data treatment and analysis

Vegetation data were stored in TURBOVEG for Windows (HENNEKENS & SCHAMINÉE 2001). In the programme JUICE 7.0 (TICHÝ 2002), the synoptic table with 28 pairs of relevés and 80 species recorded at both study sites (Tables 1 and 2) was further edited. To reduce the random noise in the statistical analyses, species occurring only once and twice were omitted. As a result, only 58 species at Velká Pleš entered the further analysis and 56 at Týřovické skály. For comparison of the grazing effect, the annual data from fenced plots and those from control plots (coded as T1–T2, T3–T4 and P1–P2, P3–P4) were merged separately within a site, and their averaged cover (total cover values after BARKMAN [1989]) were used for the statistical analyses.

For the ordination, the semi-quantitative scale was translated to percentage covers, which were subsequently square-root transformed. After that, the default options according to LEPS & ŠMILAUER (2003) were followed in the CANOCO 4.5 programme. Supplementary variables were derived from species data and used in constrained ordinations: life forms according to Raunkiaer (used from BiolFlor database, see www.biolflor.de, calculated as sum of the species cover values in percentage); Ellenberg indicator values (ELLENBERG et al. 2001, calculated as unweighted means) for light, soil moisture, temperature, soil nutrients, soil reaction, and continentality; Shannon diversity index; number of species; cover of the herb (shrub) layers.

In the species data, the Detrended Correspondence Analysis (DCA) revealed short lengths of gradients (the longest was about 3 SD). Thus, for the assessment of changes in species composition, a Redundancy Analysis (RDA) was performed, firstly for the total dataset (sites joined), where we tested the vegetation variability constrained by the interaction of treatment and time. In all these tests, the interaction of time with treatment proved no significant trend in species composition. Hence, we continued with individual RDA analyses for each of the pairs of fenced/control plots – separately for each site because of their different vegetation types (see section 2.1). For the assessment of the grazing effect, the pure temporal effect, the fencing effect, and their interaction were tested in forward selection using 999 Monte Carlo permutation tests of canonical axes (following the split-plot structure of the experimental design, LEPS & ŠMILAUER 2003) and accepting factors to be significant at a level of  $p < 0.001$ . Supplementary variables were used passively (*post-hoc* correlations) to avoid cyclic reasoning.

Relations between weather characteristics and plant species composition attributes (cf. supplementary variables above) were analysed by pairwise Spearman rank correlations (a nonparametric method was used due to the low sample size). Also, an analysis of covariance (ANCOVA) with weather parameters and treatment as independent variables was carried out in STATISTICA 9.1 (StatSoft, Inc.) to identify important predictors of vegetation attributes. In this analysis, the interaction term was found to be insignificant in all cases. We used mean monthly temperatures and sums of precipitation for the period January–May, derived from the weather data in Appendix 1. This period was selected as we considered it is crucial for the phenological development of dry grasslands with respect to the recording dates. In the ANCOVA, only precipitation was used since it resulted in the same and stronger relations than temperature. The nomenclature of vascular plants follows KUBÁT et al. (2002).

## 3. Results

### 3.1. General patterns

The RDA of the interaction between time and treatment performed with the total dataset proved no significant vegetation change. Hence, we did not find a systematic effect of game exclusion on the temporal development of stands across fenced plots and sites. The same insignificant result was found when analysing time and treatment interaction separately within Velká Pleš and Týřovické skály sites.

During the time of monitoring (see Tables 1 and 2), *Veronica hederifolia* agg. and *Trifolium alpestre* occurred as new species in Velká Pleš, and *Lamium amplexicaule* and *Gagea villosa* emerged in Týřovické skály. *Rosa canina* increased its cover in the fenced plot T3 in Týřovické skály and grew into the shrub layer. *Galium glaucum* increased its cover in the fenced plots T3 and T4 in Týřovické skály. On the other hand, *Cerastium brachypetalum*, *Potentilla tabernaemontani* (Velká Pleš) and *Festuca rupicola* (Týřovické skály) disappeared.





Table 1: Vegetation development in Velká Pleš as sampled during 2004–2010 in plots of 2 m × 1 m on fenced and control plots. The vegetation was recorded with a modified Braun-Blanquet scale (2m = m, 2a = a, 2b = b).

Tab. 1: Vegetationsentwicklung von 2004 bis 2010 auf eingezäunten und Kontroll-Dauerflächen von 2 m × 1 m in Velká Pleš. Die Vegetation wurde mit einer verfeinerten Braun-Blanquet Skala (2m = m, 2a = a, 2b = b) aufgenommen.

Management	fenced	control	fenced	control	fenced	control	fenced	control
Code of the plot	PPPPPP	PPPPPP	PPPPPP	PPPPPP	PPPPPP	PPPPPP	PPPPPP	PPPPPP
Year of observation (20..)	111111	111111	222222	222222	333333	333333	444444	444444
Cover of herb layer (%)	000000	000000	000000	000000	000000	000000	000000	000000
Number of vascular plant species	456789	456789	456789	456789	456789	456789	456789	456789
-----								
E <sub>1</sub> - herb layer								
<i>Agrostis capillaris</i>	++m1m1	++1+1+	aa33mbm	+++11+	r+++++	++11+1	+1a11m	+11+++
<i>Anthoxanthum odoratum</i>	++111+	m1111+	+1a11	r	m11+1+	3ma+1+	m1m+1+	bbalm+1
<i>Koeleria macrantha</i>	++11+1	111a11	+11111	m1a111	+m1m+	r+++++	+1+m+	+1+1+
<i>Thymus pulegioides</i>	r+++++	r+++++	r+++++	r+++++	r+++++	r+++++	r+++++	r+++++
<i>Anthericum liliago</i>	+1+1+	+11+1+	+1+1+	+1+1+	+1+1+	+1+1+	+1+1+	+1+1+
<i>Hypericum perforatum</i>	.rrr+	+++++	.r++++	r+++++	+b++++	++r1+	++a1+	++m1+
<i>Hieracium pilosella</i>	11mmab3	m1mbb33	b1abb44	m1aab33	r+.r.	r.	+1+1+	m1m+1+
<i>Rumex acetosella</i> s.l.	bb+rr+	aaa++++	aaa.r.	aaa++++	1bar1+	++1.r	mba.+1	+1a.r+
<i>Dianthus carthusianorum</i>	1+m+11	+++++	+++++	+++++	1++++	.r.	+++++	r+++++
<i>Veronica verna</i> agg.	rr.	r.	rr.	r.	r.	rr.	rr.	rr.
<i>Jasione montana</i>	rr+++++	rr+++++	r+++++	r+++++	r+++++	r+++++	r+++++	r+++++
<i>Potentilla arenaria</i>	.....	r.	rr.	r.	amabbbm	amaam1	mmmmmm	+1+1+
<i>Scleranthus perennis</i>	abrr111	mm.r+	1mr.r.	++r+	r+	.....	r.	rr.
<i>Arabis thaliana</i>	.....	r.	.....	r.	11r1+	++r+	1.	1+1+
<i>Festuca pallens</i>	11m1+	++1+rr	111+rr	+++++	.....	.....	.....	.....
<i>Pseudolysimachion spicatum</i>	.....	.....	.....	.....	.....	.....	.....	.....
<i>Fraxinus excelsior</i>	.r+	r.	r.	r.	r.	r.	r.	r.
<i>Myosotis ramosissima</i>	.....	r.	.....	r.	1r1+	++r+	1.	1+1+
<i>Euphorbia cyparissias</i>	.....	r.	.....	r.	.....	.....	.....	.....
<i>Luzula campestris</i> agg.	.....	r.	.....	r.	.....	.....	.....	.....
<i>Festuca valesiaca</i>	.....	.....	.....	.....	.....	.....	.....	.....
<i>Allium senescens</i> subsp. montanum	rr+	r+	rr+	+++++	.....	.....	.....	.....
<i>Filago minima</i>	.....	r.	.....	r.	.....	.....	.....	.....
<i>Valerianella locusta</i>	.....	r.	.....	r.	.....	.....	.....	.....
<i>Myosotis stricta</i>	.....	r.	.....	r.	.....	.....	.....	.....
<i>Hypochaeris radicata</i>	.....	r.	.....	r.	.....	.....	.....	.....
<i>Phleum phleoides</i>	.....	r.	.....	r.	.....	.....	.....	.....
<i>Festuca ovina</i>	.....	r.	.....	r.	.....	.....	.....	.....
<i>Ajuga genevensis</i>	.....	r.	.....	r.	.....	.....	.....	.....
<i>Veronica hederifolia</i> agg.	.....	r.	.....	r.	.....	.....	.....	.....
<i>Helianthemum grandiflorum</i>	.....	r.	.....	r.	.....	.....	.....	.....
<i>Pyrethrum corymbosum</i>	.....	r.	.....	r.	.....	.....	.....	.....
<i>Trifolium arvense</i>	.....	r.	.....	r.	.....	.....	.....	.....
<i>Geranium columbinum</i>	.....	r.	.....	r.	.....	.....	.....	.....
<i>Brachypodium pinnatum</i>	.....	r.	.....	r.	.....	.....	.....	.....
<i>Genista germanica</i>	r.	r.	.....	r.	.....	.....	.....	.....
<i>Carex caryophylla</i>	.....	r.	.....	r.	.....	.....	.....	.....
<i>Ranunculus bulbosus</i>	.....	r.	.....	r.	.....	.....	.....	.....
<i>Potentilla filiformis</i>	.....	r.	.....	r.	.....	.....	.....	.....
<i>Poa angustifolia</i>	.....	r.	.....	r.	.....	.....	.....	.....
<i>Allium oleraceum</i>	.....	r.	.....	r.	.....	.....	.....	.....
<i>Quercus petraea</i>	.....	r.	.....	r.	.....	.....	.....	.....
<i>Sedum reflexum</i>	.....	r.	.....	r.	.....	.....	.....	.....
<i>Cerastium brachypetalum</i>	.....	r.	.....	r.	.....	.....	.....	.....
<i>Geranium sanguineum</i>	.....	r.	.....	r.	.....	.....	.....	.....
<i>Prunus spinosa</i>	.....	r.	.....	r.	.....	.....	.....	.....
<i>Erophila verna</i>	.....	r.	.....	r.	.....	.....	.....	.....
<i>Vicia sativa</i> agg.	.....	r.	.....	r.	.....	.....	.....	.....
<i>Galium verum</i>	.....	r.	.....	r.	.....	.....	.....	.....
<i>Cytisus nigricans</i>	.....	r.	.....	r.	.....	.....	.....	.....
<i>Potentilla tabernaemontani</i>	.....	r.	.....	r.	.....	.....	.....	.....
<i>Saxifraga granulata</i>	.....	r.	.....	r.	.....	.....	.....	.....
<i>Gagea villosa</i>	.....	r.	.....	r.	.....	.....	.....	.....
<i>Galium *pomeranicum</i>	.....	r.	.....	r.	.....	.....	.....	.....
<i>Trifolium alpestre</i>	.....	r.	.....	r.	.....	.....	.....	.....
<i>Poa compressa</i>	.....	r.	.....	r.	.....	.....	.....	.....
<i>Cardaminopsis arenosa</i>	.....	r.	.....	r.	.....	.....	.....	.....
<i>Carpinus betulus</i>	.....	r.	.....	r.	.....	.....	.....	.....
<i>Taraxacum</i> sp.	.....	r.	.....	r.	.....	.....	.....	.....
<i>Vicia</i> sp.	.....	r.	.....	r.	.....	.....	.....	.....
<i>Betula pendula</i>	.....	r.	.....	r.	.....	.....	.....	.....
<i>Koeleria pyramidata</i>	.....	r.	.....	r.	.....	.....	.....	.....
<i>Veronica arvensis</i>	.....	r.	.....	r.	.....	.....	.....	.....
<i>Fallopia</i> sp.	.....	r.	.....	r.	.....	.....	.....	.....
<i>Taraxacum</i> sect. <i>Erythrosperma</i>	.....	r.	.....	r.	.....	.....	.....	.....
<i>Medicago minima</i>	.....	r.	.....	r.	.....	.....	.....	.....
<i>Veronica</i> sp.	.....	r.	.....	r.	.....	.....	.....	.....
<i>Genista tinctoria</i>	.....	r.	.....	r.	.....	.....	.....	.....
<i>Poa nemoralis</i>	.....	r.	.....	r.	.....	.....	.....	.....
<i>Vicia tetrasperma</i>	.....	r.	.....	r.	.....	.....	.....	.....

Species occurring in one relevé only:  
 E<sub>1</sub> - herb layer: *Fagus sylvatica* fenced P1 09: r, *Festuca rupicola* control P1 04: r, *Quercus* sp. fenced P2 10: r, *Galeopsis* sp. control P2 06: r, *Trifolium* sp. control P2 10: r, *Valerianella* sp. control P3 05: r, *Crataegus* sp. control P3 07: r, *Taraxacum* sect. *Ruderalia* control P3 08: r, *Cardamine* cf. *flexuosa* control P3 10: r, *Lactuca serriola* fenced P4 04: r, *Sorbus torminalis* fenced P4 10: r, *Acer platanoides* control P4 08: r.







### 3.2. Vegetation development at the Velká Pleš site

A significant change with time was detected only in P1–P2 (Figs. 3 and 4). Generally, the cover of *Rumex acetosella* s.l. (geophyte) strongly decreased, and so did the cover of the hemicryptophytes *Anthoxanthum odoratum*, *Potentilla arenaria* and *Scleranthus perennis*. *Hieracium pilosella* (hemicryptophyte) increased its cover in both fenced and control plots, but not so in P4, where it retreated (see also Table 1). *Hypochaeris radicata* was restricted to the fenced plots. Other species suppressed by the increased cover of competitive species included *Veronica verna* agg., *Potentilla tabernaemontani*, *Euphorbia cyparissias*, and *Festuca pallens*, but the trend was rather weak (Fig. 4). *Potentilla filiformis* retreated being competed out by *Potentilla arenaria* and *Helianthemum grandiflorum*. We did not observe any strong temporal shift in species composition during seven years in P3–P4 (compare also Fig. 3). *Pseudolysimachion spicatum* fluctuated similar to *Festuca valesiaca* during 2006–2008.

Considering all fenced and control plots, the treatment-based trends in traits for light, moisture, soil reaction and selected life forms (i.e., geophytes and phanerophytes) were significant (see Fig. 4). After the establishment of the study plots, the cover of light-demanding species decreased. This trend was reversed due to the warm and dry winter and spring 2006/2007, particularly on control plots, where it proved to be significant (see negative cor-

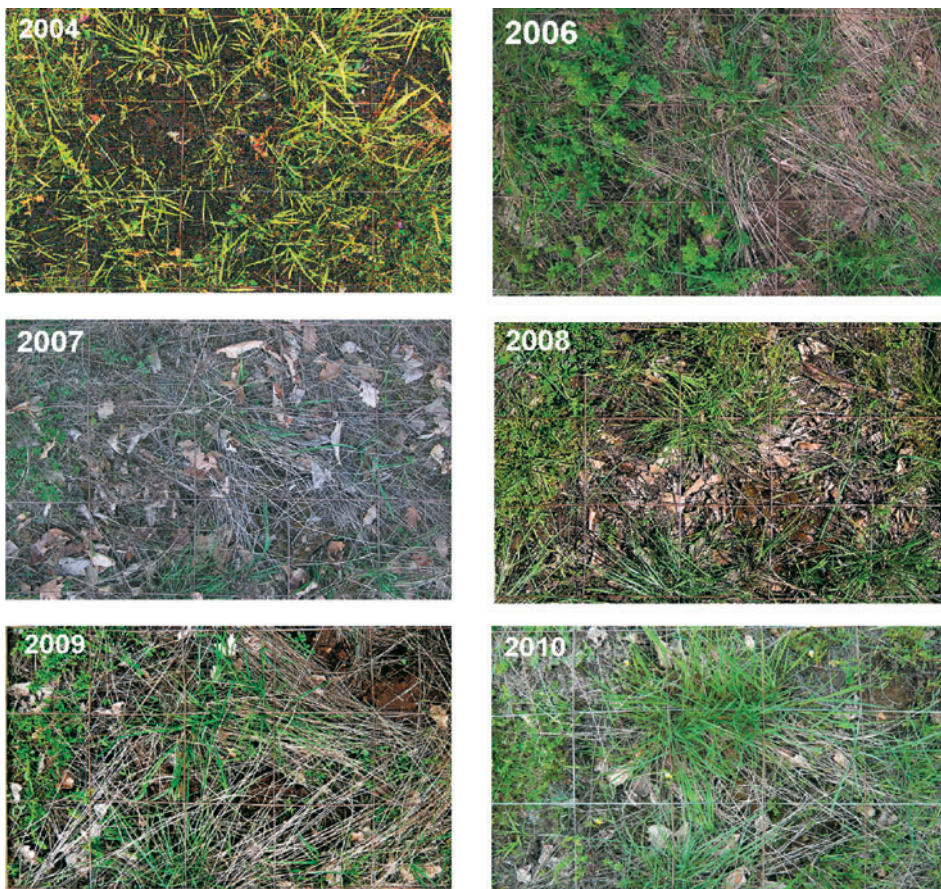


Fig. 2: Example of the vegetation development (year 2005 excluded) in a segment of the fenced plot P4 at Velká Pleš (Photos: T. Černý).

Abb. 2: Ein Beispiel der Vegetationsentwicklung (ohne 2005) in einem Teil der eingezäunten Fläche P4 in Velká Pleš (Fotos: T. Černý).



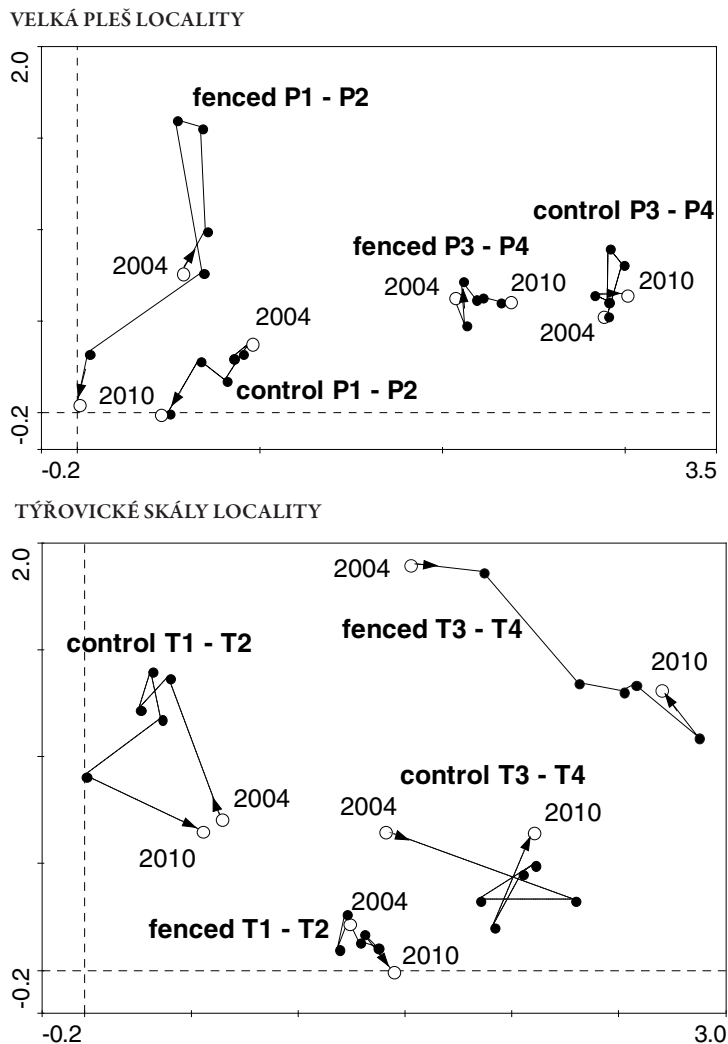


Fig. 3: Temporal trend of vegetation composition on fenced and control plots at two study sites revealed by Detrended Correspondence Analysis. The first and the last year of each observation series are highlighted.

Abb. 3: Vegetationsentwicklung auf den eingezäunten und Kontrollparzellen in zwei Untersuchungsflächen, dargestellt mit Hilfe von einer *Detrended Correspondence Analysis*. Das erste und letzte Jahr der Beobachtungsserien sind hervorgehoben.

relation with cover of geophytes and temperature in Table 3). The trend in traits for moisture and soil reaction revealed to be significant only for fenced plots, however, this trend did not interact with the weather conditions (Table 4). The cover of phanerophytes was still small, but significantly different between treatments (Table 4). The retreat of the hemiphanerophyte *Thymus pulegioides* was an example for the decreasing cover of phanerophytes in fenced plots.

Contrary to other plots, there was a remarkably higher cover of hemicryptophytes in the fenced plots P1–P2 (see above). In the first years, we observed an increase of their cover, followed by a rapid decrease as of 2005 (2006); on the control plots, however, the cover remained stable during the last four years. The Shannon diversity index decreased with time on the fenced plots, but the total number of species surviving on fenced plots did almost not change.



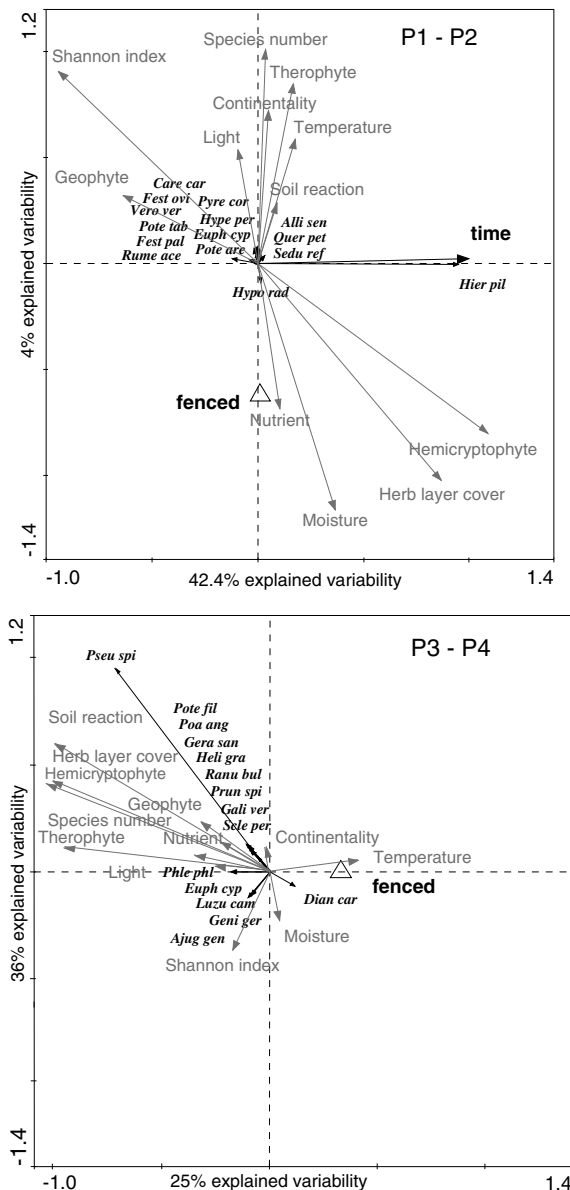


Fig. 4: Temporal vegetation change at Velká Pleš, based on Redundancy Analysis (RDA). Pairs of fenced and control plots were analysed separately. Only statistically significant variables are shown (printed in black). Supplementary variables (printed in grey) were passively projected into the ordination space. Only species (for full names, see Appendix 2) with the strongest linear fit to factors are plotted. The percentage of explained variability for ordination axes is shown.

Abb. 4: Ergebnisse der Redundancy Analysis (RDA) von Vegetationszeitveränderungen in Velká Pleš. Beide Paare der eingezäunten und Kontrollflächen wurden getrennt analysiert. Nur die statistisch signifikanten Variable werden gezeigt (schwarz). Die zusätzlichen Variablen (ökologische Zeigerwerte nach Ellenberg, Arteeigenschaften, Shannon-Diversitätsindex, Artenzahl, Deckung der Kraut- und Strauchschicht – grau) sind passiv in den Ordinationsraum projiziert. Nur die Arten mit der stärksten linearen Reaktion auf einzelne Faktoren werden dargestellt (siehe Anhang 2 für vollständige Namen). Bei den Achsen ist der Anteil erklärter Varianz angegeben.





Table 2: Vegetation development in Týřovické skály as sampled during 2004–2010 in plots of 2 m × 1 m on fenced and control plots. The vegetation was recorded with a modified Braun-Blanquet scale (2 m = m, 2a = a, 2b = b).

Tab. 2: Vegetationsentwicklung von 2004 bis 2010 auf eingezäunten und Kontroll-Dauerflächen von 2 m × 1 m in Týřovické skály. Die Vegetation wurde mit einer verfeinerten Braun-Blanquet Skala (2 m = m, 2a = a, 2b = b) aufgenommen.

Management	fenced	control	fenced	control	fenced	control	fenced	control
Code of the plot	TTTTTT	TTTTTT	TTTTTT	TTTTTT	TTTTTT	TTTTTT	TTTTTT	TTTTTT
Year of observation (20..)	111111	111111	222222	222222	333333	333333	444444	444444
Cover of shrub layer (%)	000000	000000	000000	000000	000000	000000	000000	000000
Cover of herb layer (%)	4655453	5877763	4454454	3888874	7635474	5764533	7546374	5663632
Number of vascular plant species	2222212	2111111	2222212	11 1 1	2222222	2222222	2322222	2221212
	2211290	0742818	5100294	1186190	2685806	0622225	9083668	1524199
-----								
E <sub>2</sub> - shrub layer								
<i>Rosa canina</i>	.....	.....	.....	.....	..11aab	.....	.....	.....
E <sub>1</sub> - herb layer								
<i>Festuca valesiaca</i>	11mmaal	a4333aa	abbbbba	b4444bb	43am+m1	mmmmmm	3bbannm	111111
<i>Potentilla arenaria</i>	mabamal	b44343b	bbbbabm	ab3b33b	am++++	3bbmaa	bamm+1	b33mbaa
<i>Veronica verna</i> agg.	1m1m++	111111	1m1m1+	+1r11+	11+r+++	+am+mam	1mm+11	+1am1aa
<i>Arabidopsis thaliana</i>	+r1+++	+1.1+++	+1+1+1+	+1.1r++	++++++	+1+11+	+++++1	+m1111
<i>Myosotis stricta</i>	+r.r.+	+r.r.+	+1++++	+r.r.+	+.r.+	.1.r.r+	+r.r.r+	+1+r.r+
<i>Centaurea stoebe</i>	+r.r.+	+r.r.+	+r.r.+	+r.r.+	+r.r.+	+1+1+r	+1+1+r	+1+1+r
<i>Rumex acetosella</i> s.l.	1mal+++	+r1.1+	+1+r++	+r.r.+	.r.r.+	.r.r.+	.r.r.+	.r.r.+
<i>Viola tricolor</i> subsp. <i>saxatilis</i>	+r.r.+	+r.r.+	+r.r.+	+r.r.+	+r.r.+	+r.r.+	+r.r.+	+r.r.+
<i>Thymus pulegioides</i>	+r.r.+	+r.r.+	+r.r.+	+r.r.+	+r.r.+	+r.r.+	+r.r.+	+r.r.+
<i>Ajuga genevensis</i>	+r.r.+	+r.r.+	+r.r.+	+r.r.+	+r.r.+	+r.r.+	+r.r.+	+r.r.+
<i>Hypericum perforatum</i>	+1a11+	+r.r.+	+r.r.+	+r.r.+	+r.r.+	+r.r.+	+r.r.+	+r.r.+
<i>Erophila verna</i>	+r.r.+	+r.r.+	+r.r.+	+r.r.+	+r.r.+	+r.r.+	+r.r.+	+r.r.+
<i>Poa pratensis</i> agg.	+r.r.+	+r.r.+	+r.r.+	+r.r.+	+r.r.+	+r.r.+	+r.r.+	+r.r.+
<i>Scleranthus perennis</i>	+r.r.+	+r.r.+	+r.r.+	+r.r.+	+r.r.+	+r.r.+	+r.r.+	+r.r.+
<i>Echium vulgare</i>	+r.r.+	+r.r.+	+r.r.+	+r.r.+	+r.r.+	+r.r.+	+r.r.+	+r.r.+
<i>Euphorbia cyparissias</i>	+r.r.+	+r.r.+	+r.r.+	+r.r.+	+r.r.+	+r.r.+	+r.r.+	+r.r.+
<i>Vicia hirsuta</i>	+r.r.+	+r.r.+	+r.r.+	+r.r.+	+r.r.+	+r.r.+	+r.r.+	+r.r.+
<i>Hieracium pilosella</i>	bbalaaa	+++1++	+++1mm	.....	.....	.....	.....	.....
<i>Veronica hederifolia</i> agg.	.....	.....	.....	.....	.....	.....	.....	.....
<i>Anthericum liliago</i>	+1111+	+r.r.+	+r.r.+	+r.r.+	+r.r.+	+r.r.+	+r.r.+	+r.r.+
<i>Trifolium arvense</i>	+r.r.+	+r.r.+	+r.r.+	+r.r.+	+r.r.+	+r.r.+	+r.r.+	+r.r.+
<i>Koeleria macrantha</i>	+r.r.+	+r.r.+	+r.r.+	+r.r.+	+r.r.+	+r.r.+	+r.r.+	+r.r.+
<i>Myosotis ramosissima</i>	+r.r.+	+r.r.+	+r.r.+	+r.r.+	+r.r.+	+r.r.+	+r.r.+	+r.r.+
<i>Dianthus carthusianorum</i>	.....	.....	.....	.....	.....	.....	.....	.....
<i>Artemisia absinthium</i>	.....	.....	.....	.....	.....	.....	.....	.....
<i>Rosa canina</i>	.....	.....	.....	.....	.....	.....	.....	.....
<i>Jasione montana</i>	rr.r.r.	.r.r.r.	.r.r.r.	.r.r.r.	.r.r.r.	.r.r.r.	.r.r.r.	.r.r.r.
<i>Galium glaucum</i>	.....	.....	.....	.....	.....	.....	.....	.....
<i>Fragaria viridis</i>	.....	.....	.....	.....	.....	.....	.....	.....
<i>Galium verum</i>	.....	.....	.....	.....	.....	.....	.....	.....
<i>Melica transsilvanica</i>	.....	.....	.....	.....	.....	.....	.....	.....
<i>Valerianella locusta</i>	.....	.....	.....	.....	.....	.....	.....	.....
<i>Ranunculus bulbosus</i>	.....	.....	.....	.....	.....	.....	.....	.....
<i>Veronica arvensis</i>	.....	.....	.....	.....	.....	.....	.....	.....
<i>Potentilla argentea</i>	.....	.....	.....	.....	.....	.....	.....	.....
<i>Agrostis vinealis</i>	+1111+	+r.r.+	+r.r.+	+r.r.+	+r.r.+	+r.r.+	+r.r.+	+r.r.+
<i>Gagea villosa</i>	.....	.....	.....	.....	.....	.....	.....	.....
<i>Geranium columbinum</i>	.....	.....	.....	.....	.....	.....	.....	.....
<i>Brachypodium pinnatum</i>	.....	.....	.....	.....	.....	.....	.....	.....
<i>Arenaria serpyllifolia</i> agg.	.....	.....	.....	.....	.....	.....	.....	.....
<i>Thymus praecox</i>	.....	.....	.....	.....	.....	.....	.....	.....
<i>Senecio viscosus</i>	.....	.....	.....	.....	.....	.....	.....	.....
<i>Allium oleraceum</i>	.....	.....	.....	.....	.....	.....	.....	.....
<i>Hieracium rothianum</i>	.....	.....	.....	.....	.....	.....	.....	.....
<i>Filago arvensis</i>	.....	.....	.....	.....	.....	.....	.....	.....
<i>Vincetoxicum hirundinaria</i>	+r++++	+r.r.+	+r.r.+	+r.r.+	+r.r.+	+r.r.+	+r.r.+	+r.r.+
<i>Festuca ovina</i>	1mmmal	r.r.r.	r.r.r.	r.r.r.	r.r.r.	r.r.r.	r.r.r.	r.r.r.
<i>Geranium sanguineum</i>	.....	.....	.....	.....	.....	.....	.....	.....
<i>Polygonum aviculare</i> agg.	.....	.....	.....	.....	.....	.....	.....	.....
<i>Verbascum lychnitis</i>	.....	.....	.....	.....	.....	.....	.....	.....
<i>Aster linosyris</i>	.....	.....	.....	.....	.....	.....	.....	.....
<i>Vicia tetrasperma</i>	.....	.....	.....	.....	.....	.....	.....	.....
<i>Agrostis capillaris</i>	.....	.....	.....	.....	.....	.....	.....	.....
<i>Avenula pubescens</i>	.....	.....	.....	.....	.....	.....	.....	.....
<i>Lamium amplexicaule</i>	.....	.....	.....	.....	.....	.....	.....	.....
<i>Festuca rupicola</i>	+r.r.+	+r.r.+	+r.r.+	+r.r.+	+r.r.+	+r.r.+	+r.r.+	+r.r.+
<i>Trifolium campestre</i>	.....	.....	.....	.....	.....	.....	.....	.....
<i>Quercus petraea</i>	.....	.....	.....	.....	.....	.....	.....	.....
<i>Medicago</i> sp.	.....	.....	.....	.....	.....	.....	.....	.....
<i>Fraxinus excelsior</i>	.....	.....	.....	.....	.....	.....	.....	.....
<i>Veronica</i> sp.	.....	.....	.....	.....	.....	.....	.....	.....

Species occurring in one relevé only:

E<sub>1</sub> - herb layer: *Pseudolysimachion spicatum* control T1 04: r, *Galium pumilum* control T1 04: r, *Sonchus* sp. fenced T2 06: r, *Veronica serpyllifolia* fenced T2 10: +, *Achillea millefolium* agg. fenced T2 10: r, *Prunus spinosa* control T3 04: r, *Avenula pratensis* control T3 06: r, *Agrostis* sp. control T3 07: r, *Filago minima* control T3 10: r, *Fallopia dumetorum* fenced T4 04: +, *Taraxacum* sp. fenced T4 04: r, *Crataegus* sp. fenced T4 08: r, *Medicago cf. minima* fenced T4 09: r, *Arrhenatherum elatius* fenced T4 09: r, *Melica nutans* fenced T4 10: +, *Cynoglossum officinale* fenced T4 10: r, *Epilobium* sp. control T4 10: r, *Galium aparine* control T4 10: r.





Table 3: Correlations between weather characteristics (mean temperatures and sums of precipitation for the months January to May preceding the vegetation recording) and vegetation attributes, separated with respect to treatment. Only dependent variables with significant effects at least in one case are shown: light = mean Ellenberg indicator value for light, temp = mean Ellenberg indicator value for temperature, moist = mean Ellenberg indicator for moisture, geo = cover of geophytes. Each correlation is based on 28 observations (4 relevés  $\times$  7 years). Spearman rank correlation coefficients and their significance are given (ns = non-significant, \*\*  $p < 0.01$ , \*  $p < 0.05$ ).

Tabelle 3: Korrelationen zwischen Wetterparametern (Niederschlagssummen und Mitteltemperaturen der Monate Januar bis Mai, die der jeweiligen Vegetationsaufnahme vorausgingen) und Vegetationsattributen, getrennt für beweidete und unbeweidete Flächen. Nur abhängige Variablen mit signifikanten Effekten sind dargestellt: light = mittlere Lichtzahl, temp = mittlere Temperaturzahl, moist = mittlere Feuchtezahl, geo = Deckung der Geophyten. Jede Korrelation beruht auf 28 Beobachtungen (4 Aufnahmen  $\times$  7 Jahre). Es sind die Spearman Rang-Korrelationskoeffizienten und die statistische Signifikanz angegeben (ns = nicht signifikant, \*\*  $p < 0.01$ , \*  $p < 0.05$ ).

	light	temp	moist	geo
<b>VELKÁ PLEŠ, fenced</b>				
temperature	ns	ns	ns	-0.55**
precipitation	ns	ns	ns	ns
<b>VELKÁ PLEŠ, control</b>				
temperature	ns	ns	ns	-0.52**
precipitation	-0.44**	ns	0.41*	0.39*
<b>TÝŘOVICKÉ SKÁLY, fenced</b>				
temperature	ns	ns	ns	ns
precipitation	ns	ns	ns	ns
<b>TÝŘOVICKÉ SKÁLY, control</b>				
temperature	-0.45*	0.40*	ns	ns
precipitation	0.38*	ns	ns	ns

### 3.3. Vegetation development at the Týřovické skály site

The species composition did not change much within the control plots T1–T2 (see Fig. 3); however, the effect of fencing was significant (Fig. 5 and Table 4). A significant change over time in the interaction with the treatment was observed in the plots T3–T4 (Fig. 5). This is indeed the only result revealing the effect of wildlife grazing. Here, an increase of the cover of chamaephytes and geophytes, a decrease of the cover of hemicryptophytes, and higher values of diversity parameters on fenced plots could be observed (Table 4). Vegetation changes also indicate the increase in soil moisture, soil reaction, and rising cover of light-demanding species (in contrast to T1–T2; Tables 3 and 4). The last-mentioned attribute changed due to the impact of weather conditions (mainly precipitation), irrespective of the treatment (Table 4). There were no significant correlations between changes in weather and plant traits on the fenced plots (Table 3).

There was a significant decrease in the cover of hemicryptophytes (e.g. *Festuca valesiaca*, *Potentilla arenaria*, and *Scleranthus perennis*) in both fenced (stronger) and unfenced (less pronounced) plots, contrary to the increase of *Rosa canina* in fenced plots, but its decrease outside (see Table 2). Similarly, *Fragaria viridis*, *Galium glaucum*, and *G. verum* increased their cover in fenced plots, likely being influenced by decomposed litter or due to their ability to grow through a litter layer. On the other hand, some species reacted differently depending on season (e.g. *Hieracium pilosella*, *H. rothianum*, and *Potentilla argentea*). As opposed to Velká Pleš, geophytes increased their cover in fenced plots. The trend was not significant, but clearly different from that in the control plots (Table 4). The occurrence of



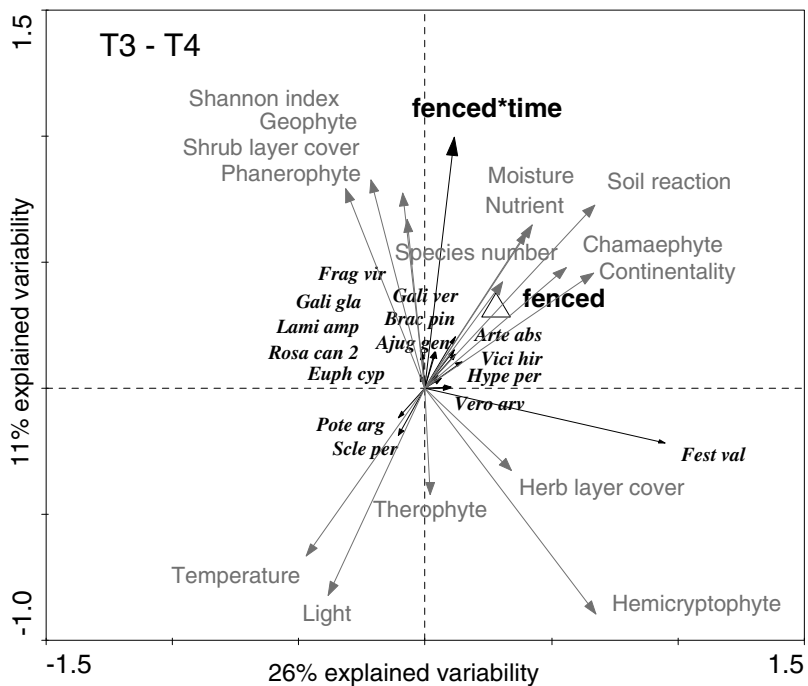
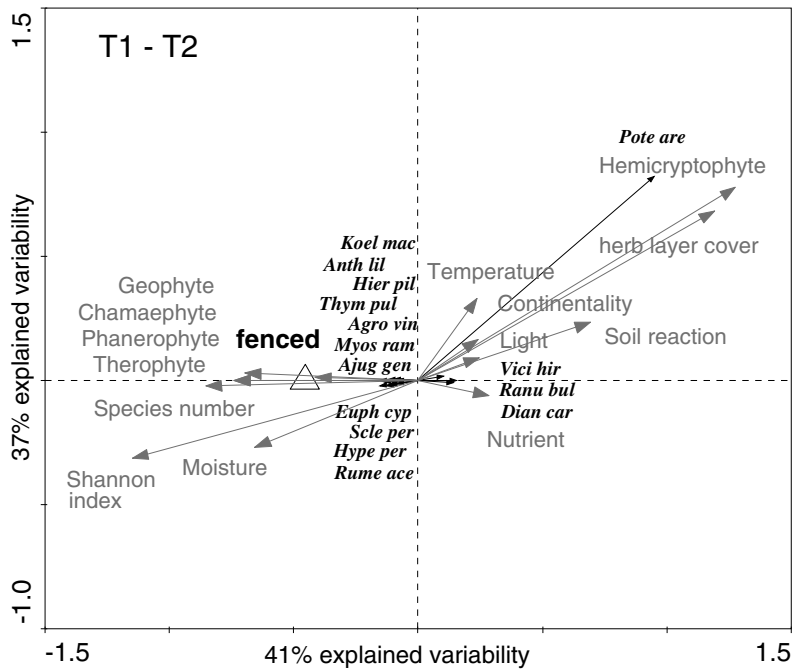


Fig. 5: Redundancy Analysis (RDA) results of temporal vegetation change on the permanent plots at Týřovické skály. For details, see Fig. 4.

Abb. 5: Ergebnisse der Redundancy Analysis (RDA) von Vegetationszeitveränderungen in der Nähe der Týřovické skály. Erklärungen siehe Abb. 4.



Table 4: Results of ANCOVA, where individual vegetation attributes were used as response variables and treatment “manag” (fencing vs. control) and precipitation “precip” (see Methods) were used as factors. *F*-ratios and significance levels are shown (ns = non-significant, \*\*\*  $p < 0.001$ , \*\*  $p < 0.01$ , \*  $p < 0.05$ ).

Tabelle 4: Resultate der ANCOVA, in der individuelle Attribute als abhängige Variablen sowie Behandlung „manag“ (Umzäunung vs. Kontrolle) und Niederschlagssumme „precip“ (s. Methoden) als Faktoren genutzt wurden. Angegeben sind *F*-Werte und Signifikanzen (ns = nicht signifikant, \*\*\*  $p < 0.001$ , \*\*  $p < 0.01$ , \*  $p < 0.05$ ).

Vegetation attributes	Velká Pleš		Týřovické skály	
	manag	precip	manag	precip
<b>Ellenberg indicator values</b>				
Light	ns	ns	14.2***	9.3**
Temperature	ns	ns	8.8**	ns
Continentality	ns	ns	5.5*	ns
Moisture	8.6**	ns	6.1*	ns
Soil reaction	6.1*	ns	5.8*	ns
<b>Life form cover</b>				
Geophytes	ns	7.2**	11.6**	ns
Therophytes	12.8***	ns	ns	ns
Hemicryptophytes	ns	ns	4.0*	ns
Phanerophytes	8.2**	ns	ns	ns
Chamaephytes	ns	ns	21.0***	ns
<b>Shannon index</b>	11.7**	ns	23.1***	ns
<b>Species richness</b>	45.9***	ns	26.2***	ns

therophytes is obviously not related to the treatment (see Table 4). An increase of therophytes occurred after the wet winter 2004/2005 and after the cold and snow-rich winter 2009/2010. Contrary, after the severe winter 2005/2006, the cover of therophytes decreased.

A trend of a decreasing cover of the herb layer is typical here; however, peaks occurred in 2005 for the control plot and in 2009 for the fenced plot after a wet end of winter 2008/2009 and a very warm April 2009. It seems this has to be attributed to the direct influence of weather conditions (and its interaction with litter decomposition and nutrient supply); however, the weather data used did not confirm this assumption. The increase in the herb layer cover in fenced plots as compared to control plots in the last two years was most likely caused by the absence of game disturbance, in particular when the vegetation at the whole site was stressed by drought.

## 4. Discussion

### 4.1. Effect of game grazing on life forms

The absence of grazing in the fenced plots resulted in accumulated biomass and influenced seedling recruitment in vegetation gaps (see BARBARO et al. 2001). The renewal of certain plant species within gaps in the sward of hemicryptophytes in fenced plots was enhanced after warm winters, as was found by STERNBERG et al. (1999). In our study, rather than being influenced by treatment, hemicryptophytes likely depended on seasonal precipitation (as indicated by positive correlation between geophyte cover and precipitation and moisture in Table 3 and Table 4). In continental steppes, hemicryptophytes were reported to dominate on both grazed and abandoned plots (ENYEDI et al. 2008), whereas in other parts





of Europe, their retreat with both heavy grazing and abandonment has been shown (KAHMEN et al. 2002, ŠKORNIK et al. 2010). At Týřovické skály, this retreat was also observed, irrespective of the treatment (but stronger on fenced plots, see Table 4) and apparently not influenced by weather conditions. The accumulation of biomass in abandoned grasslands can cause an increase in the cover of geophytes – a life form with an effective strategy to cope with this stress factor (KAHMEN et al. 2002).

Contrary to the hemicryptophytes, the therophytes reflected very likely the common effect of seasonal weather conditions and gap dynamics rather than an influence of hoofed game (compare results from Týřovické skály). The long-lasting and thick snow cover during the winter 2009/2010 caused the intensive disintegration of litter accumulated so far, together with seed germination (see also STERNBERG et al. 1999).

Similarly as in the 7-year monitoring study on dry grasslands by DOSTÁLEK & FRANTÍK (2008), we hardly detected any significant changes in plant traits caused by grazing. In addition, the intensity of grazing could not be assessed as we did not quantify the game density.

#### 4.2. Correlation between weather conditions and vegetation changes

The observed changes of vegetation attributes might covary with the course of weather characteristics in the season, thus obscuring the effect of game grazing. However, only less than 10% of all listed pairs of environmental variables were significantly correlated, a phenomenon that was also found in a study on permanent plots in dry grasslands in Central Bohemia (DOSTÁLEK & FRANTÍK 2011). This indicates the minor role of weather conditions compared to the more important (but not systematic) changes caused by the impact of hoofed game. The reaction of vegetation on seasonal weather fluctuations is first of all community-specific; thus future trends can be generalised only within the context of particular vegetation units and also separately for different functional species groups (EVINER & CHAPIN 2003). For example, the species-poorer vegetation at the Týřovické skály site reflected precipitation and temperature only through the proportion of light-demanding species, irrespective of the treatment effect, whereas at the species-richer Velká Pleš site, such pattern was detected only for geophytes. The relatively important influence of precipitation on the development of plant traits was also proved by a 9-year monitoring study in Central Bohemia (DOSTÁLEK & FRANTÍK 2011).

We need longer observation times for rigorous statements about which fluctuations are weather-based and which are successional trends. For this purpose, we have installed two automatic detectors for monitoring temperature and soil humidity at the study sites in 2010.

#### 4.3. Overall development of the dry grasslands studied and implications for nature conservation

Based on our results, we can forecast the vegetation change in dependence of varying game densities as follows: If game grazing stops completely, a gradual encroachment of shrubs and a temporary increase of species richness will start. Litter accumulation and soil humus will increase as well. Such a scenario has been described for Romanian steppe-like grasslands (RUPRECHT et al. 2009). These changes are connected with the increase of nutrient stocks within communities accelerating the rate of succession (KNOPS & TILMAN 2000). In the final stage, trees growing sporadically in mosaics with open grassland patches and small scrub thickets will occur. We have shown that these successional changes will be neither quick nor systematic. Their rate is strongly habitat-dependent within a scale of a few metres, with some patches being more resistant than others. Nevertheless, it seems that the proportion of these open steppe-like grasslands within forests will be rather constant over time and that only the spatial pattern might vary in the course of decennia (described as shifting mosaics), as recently found by I. Husáková and Z. Münzbergová (unpublished manuscript) from the same localities.

A significant shift in stand composition occurred in all fenced plots, but with different patterns at both study sites. Besides the grazing of mouflons, there was a clear effect of interannual weather variability. Both weather extremes in the previous year and mean values







were very likely the key factors for the development of forest steppes, regardless the effect of grazing. The vegetation returned after some diversion into the stage observed at the beginning of our study. The same pattern was observed on south Moravian dry calciphilous grasslands in the course of 13 years of periodic monitoring (HÉDL & DANIHELKA 2006). On fenced plots, there is a continuous, yet slow accretion of dead above-ground biomass, which may diminish the importance of climatic extremes on open plots. STERNBERG et al. (1999) pointed out that habitat extremeness should be seen as important for keeping ungrazed vegetation relatively open.

Even though we can see the changes (yet overall insignificant) in vegetation structure and composition as described above and hypothesize further trends based on them, seven years of monitoring are still insufficient to validate them. OZINGA et al. (2007) described that most species growing in grasslands “have a half-life expectation over 15 years”. However, based on our results, it is clear that at least some parts of similar species-rich habitats could be kept open and maintained under high game density, but some parts are endangered by grazing and eutrophication by mouflon feces and litter accumulation. Nature conservation management should balance both mechanisms (hunting of mouflons or cutting of woody species).

### Acknowledgement

The fieldwork was supported by the institutional long-term research plan AV0Z60050516 of the Academy of Sciences of the Czech Republic. P.P. was supported by the Biodiversity Research Centre (grant no. LC 06073; Ministry of Education, Youth, and Sports). K.B. was supported by the grant no. 42900/1312/3114 of the Internal Grant Agency of the Faculty of Environmental Sciences of the Czech University of Life Sciences Prague. C. Renetzeder and J. Danihelka kindly proofread our German. We are indebted to the administration of the Křivolátsko Biosphere Reserve and the Protection Landscape Area for the establishment of the studied plots and the support of our research. We thank M. Adámek for the preparation of the map in Fig. 1. We thank J. Dengler (formal and linguistic editing), A. Huckauf (English editing), M. Janišová (co-ordinating editor), K. Ujházy (reviewer) and one anonymous reviewer for help with improvement of previous versions of the paper.





**Appendix 1:** Weather conditions 2004–2010 (from www.chmu.cz) in Central Bohemia. Mean monthly precipitation (in mm) and mean monthly air temperatures (in °C).

Appendix 1: Wetterbedingungen 2004–2010 (Daten von www.chmu.cz) aus Mittelböhmen. Niederschlagssummen (in mm) und mittlere Monatstemperaturen (in °C) sind angegeben.

Month	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Sum Jan–May
<b>Precipitation (mm)</b>													
2004	65	33	38	25	53	94	55	54	46	25	60	16	214
2005	50	54	19	24	69	54	134	72	42	11	17	47	216
2006	22	32	61	61	90	84	31	110	14	35	25	24	266
2007	55	33	32	3	66	72	78	73	87	20	64	21	189
2008	30	19	40	49	55	55	73	65	22	51	35	33	193
2009	18	42	53	20	87	83	95	44	16	51	30	57	220
2010	58	16	27	33	96	58	99	150	84	8	59	38	230
<b>Temperature (°C)</b>													
2004	-3.4	1.7	3.3	9.3	11.9	15.7	17.7	18.8	13.5	9.4	3.8	-0.2	4.56
2005	0.6	-3.0	2.0	9.7	13.7	16.7	18.5	16.4	14.7	9.6	2.5	-0.4	4.60
2006	-5.4	-2.2	1.0	8.7	13.3	17.5	22.0	15.7	16.3	10.5	6.1	2.9	3.08
2007	4.1	3.6	5.8	11.0	15.0	18.7	18.9	18.2	12.0	7.8	2.0	0.0	7.90
2008	2.0	3.1	3.7	8.3	14.2	17.9	18.5	18.2	12.6	8.6	4.6	1.1	6.26
2009	-3.9	-0.3	4.1	12.8	14.0	15.4	18.5	19.2	15.4	7.9	6.3	-0.6	5.34
2010	-4.4	-1.3	3.6	8.9	12.1	17.3	20.9	17.8	11.9	6.9	5.2	-5.1	3.78

**Appendix 2:** Full species names used as abbreviations on ordination plots.

Appendix 2: Die vollen Namen für die Abkürzungen aus den Ordinationsgraphen.

*Agro vin* – *Agrostis vinealis*, *Ajug gen* – *Ajuga genevensis*, *Alli sen* – *Allium senescens* subsp. *montanum*, *Anth lil* – *Anthericum liliago*, *Arte abs* – *Artemisia absinthium*, *Brac pin* – *Brachypodium pinnatum*, *Care car* – *Carex caryophylla*, *Dian car* – *Dianthus carthusianorum*, *Euph cyp* – *Euphorbia cyparissias*, *Fest ovi* – *Festuca ovina*, *Fest pal* – *Festuca pallens*, *Fest val* – *Festuca valesiaca*, *Frag vir* – *Fragaria viridis*, *Gali gla* – *Galium glaucum*, *Gali ver* – *Galium verum*, *Geni ger* – *Genista germanica*, *Gera san* – *Geranium sanguineum*, *Heli gra* – *Helianthemum grandiflorum* subsp. *obscurum*, *Hier pil* – *Hieracium pilosella*, *Hype per* – *Hypericum perforatum*, *Hypo rad* – *Hypochaeris radicata*, *Koel mac* – *Koeleria macrantha*, *Lami amp* – *Lamium amplexicaule*, *Luzu cam* – *Luzula campestris*, *Myos ran* – *Myosotis ramosissima*, *Pble pbl* – *Phleum phleoides*, *Poa ang* – *Poa angustifolia*, *Pote are* – *Potentilla arenaria*, *Pote arg* – *Potentilla argentea*, *Pote fil* – *Potentilla filiformis*, *Pote tab* – *Potentilla tabernaemontani*, *Prun spi* – *Prunus spinosa*, *Pyre cor* – *Pyrethrum corymbosum*, *Quer pet* – *Quercus petraea* juv., *Ranu bul* – *Ranunculus bulbosus*, *Rosa can 2* – *Rosa canina* (shrub layer), *Rume ace* – *Rumex acetosella* s.l., *Scle per* – *Scleranthus perennis*, *Thym pul* – *Thymus pulegioides*, *Vero arv* – *Veronica arvensis*, *Vero ver* – *Veronica verna* agg., *Vici hir* – *Vicia hirsuta*.





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Co-ordinating editor: Monika Janišová  
 Manuscript received: 06.11.2010; accepted: 14.03.2011



