History or abiotic filter: which is more important in determining the species composition of calcareous grasslands?

Které parametry jsou odpovědné za druhové složení suchých vápnomilných trávníků – historie nebo stanovištní podmínky?

Petr K a r l í k[1,2] & Peter P o s c h l o d[1]

[1]*Institute of Botany, Faculty of Biology and Preclinical Medicine, University of Regensburg, D-93040, Germany; e-mail: peter.poschlod@biologie.uni-regensburg.de* [2]*Department of Dendrology and Forest Tree Breeding, Faculty of Forestry and Wood Sciences, Czech University of Life Sciences, Kamýcká 1176, CZ-165 21, Praha 6, Czech Republic; e-mail: pkarlik@seznam.cz*

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Dry calcareous grassland is one of the most species-rich and endangered ecosystem in Central Europe. Despite the dramatic loss of grassland in the second half of the 20th century due to abandonment of agricultural land or afforestation, new grasslands developed on former arable land. The main objective of this study was to assess the effect of age on the vegetation and habitat properties of calcareous grasslands. We found that the history (former land use, age of habitats) of grassland localities has had a fundamental effect both on the species composition of the vegetation and habitat properties. Significant differences were found, especially in soil reaction and water-holding capacity. Therefore, we can state that both history and habitat properties determine the recent species composition pattern. Consequently, it was possible to identify species indicating the historical status of the grasslands. Indicators of ancient grassland (i.e., patches continuously used as pastures at least since 1830) could be assigned to typical *Festuco-Brometea* species but also more widespread grassland species such as *Carex flacca, Buphthalmum salicifolium, Carlina vulgaris, Cirsium acaule, Hippocrepis comosa* and *Scabiosa columbaria*. Indicators of recent grasslands (i.e., patches temporarily farmed as arable fields after 1830) belong to different phytosociological classes: *Festuco-Brometea*, *Molinio-Arrhenatheretea, Trifolio-Geranietea sanguinei* and *Secalietea cerealis*. *Festuco-Brometea* species restricted to recent grasslands were e.g. *Thymus pulegioides* subsp. *carniolicus, Stachys alpina*, *Rhinanthus alectorolophus* and *Onobrychis viciifolia*. The two latter species are survivors from the former arable cultivation, the first was an arable weed and the second a widespread fodder plant, but are now considered to be characteristic species of calcareous grasslands. Therefore, we claim that the occurrence of these species indicate calcareous grasslands that were previously arable fields and that recent grasslands are a monument to historical land use. Rare and/or endangered species were not only found in ancient but also in recent grasslands. Furthermore, recent grasslands have a high species diversity. Thus both, ancient and recent calcareous grasslands should be considered equally valuable from a nature-conservation point of view.

K e y w o r d s: ancient grasslands, biodiversity, calcareous grasslands, Central Europe, historical ecology, historical land use indicators, recent grasslands, Swabian Alb

Introduction

Most calcareous grasslands are so-called semi-natural grasslands influenced and formed by husbandry. Their existence dates back at least to the Neolithic (Dutoit et al. 2009) or Bronze Age (Körber-Grohne & Wilmanns 1977, Thorley 1981, Ložek 1988, Ložek & Cílek 1995, Wilmanns 1997, Baumann & Poschlod 2008, Poschlod & Baumann 2010).

Before the Neolithic Age dry grassland species were restricted to small patches on rocky outcrops, although in some more continental regions of Central Europe dry grasslands might have been formed from still existing steppic vegetation due to early colonization and continuous settlement (Gradmann 1933, Pokorný 2005, Ložek 2007).

Furthermore, some non-forest species currently occuring in dry grasslands might have survived there throughout the Holocene due to grazing by wild animals (Vera 2000). Periods of dry grassland extension started probably in the Bronze Age but also the Roman Age and especially the High and Late Medieval Ages and the 18th and 19th century of Modern Times (Baumann 2006, Poschlod & Baumann 2010). The decrease started at the end of the 19th century (Quinger et al. 1994) with the strongest decline during the 1960s and 1970s (Mattern et al. 1980, 1992, Mauk 2005) due to changes in farming practices and increased imports of sheep wool from e.g., Australia and New Zealand, which resulted in a decline in sheep numbers (Poschlod & Wallis de Vries 2002). Since calcareous grasslands are among the most species-rich habitats in Central Europe (Korneck et al. 1998, Wallis de Vries et al. 2002, Sádlo et al. 2007) they are now the focus of conservation efforts and listed in the Annex I of the Natura 2000 Habitats Directive (92/43/EEC).

However, grasslands replaced former arable fields from the middle of the 19th century when agricultural techniques were improved (Hard 1964, Baumann et al. 2005, Mailänder 2005). Furthermore, after the wine-pest (*Phylloxera*) epidemic in the 19th century grasslands also replaced abandoned vineyards (Illyés & Bölöni 2007). Hard (1964) even states that they were artificially established by sowing hayseed. A large proportion of recent grasslands developed in the middle and second half of 20th century at less agriculturally favourable sites in numerous regions in Central Europe when arable farming was abandoned because of socioeconomical and political changes (Osbornová et al. 1990, Ruprecht 2005, 2006, Illyés & Bölöni 2007, Poschlod et al. 2008). Therefore, we may differentiate ancient and recent calcareous grasslands. We define ancient grasslands as those that are at least 180 years old and recent grasslands as those that are marked as arable fields at least on the first detailed maps published at the beginning of the 19th century of the Central European landscape (first cadaster maps available from 1820s and 1830s) or on some younger maps (Mailänder 2005, Baumann 2006, Poschlod et al. 2008).

The effect of habitat continuity on species richness and composition and habitat properties is recorded for forests (Peterken 1974, 1976, Peterken & Game 1981, 1984, Kubíková 1986, Koerner et al. 1997, Graae & Sunde 2000, Bellemare et al. 2002, Jacquemyn et al. 2003, Verheyen et al. 2003, Vojta 2007). A comparison of studies from different parts of Europe revealed a set of indicator species for ancient and recent forests (Wulf & Kelm 1994). The absence of ancient forest indicators in recent forests is attributed to either their dispersal limitation (Ehrlén & Eriksson 2000, Graae & Sunde 2000) or the lack of dispersal processes in the current landscape (Poschlod & Bonn 1998).

There are only a few comparisons of the species composition, habitat properties and indicator species of ancient and recent grasslands (Ejrnæs & Bruun 1995, Chýlová & Münzbergová 2008, Poschlod et al. 2008). There are, however, some studies of populations of single species (Geertsema et al. 2002, Becker 2003, Herben et al. 2006) and species diversity (Austrheim et al. 1999, Bruun 2000, Bruun et al. 2001, Gustavsson et al. 2007, Pärtel et al. 2007, Waesch & Becker 2009). Other studies are related to the establishment of grasslands after abandonment of arable fields and restoration of afforested grasslands. Succession resulting in the establishment of grassland on former arable land is described, e.g. by Knapp (1979), Schmidt (1981), Soukupová (1984), Osbornová et al. (1990) and Ruprecht (2005, 2006). Gibson & Brown (1991), Verhagen et al. (2001), Pywell et al. (2002) and Kiehl & Pfadenhauer (2007) studied the establishment of grasslands on former arable fields after restoration management. Von Blanckenhagen & Poschlod (2005) investigated the establishment of calcareous grasslands after clear-cutting afforestations. Hirst et al. (2005) report the resilience of calcareous grasslands to disturbance by military vehicles in military training areas.

As in recent forests, the dispersal potential of grassland species, both in space and time, limit species composition after reestablishment or restoration (Hutchings & Booth 1996). Grazing by domestic livestock is the key factor in the dispersal of grassland species (Fischer et al. 1996, Stender et al 1997, Cosyns et al. 2005, Bugla 2008). Wells et al. (1976) emphasized that the time that has elapsed since the arable fields were abandoned is another key factor in the reestablishment of grasslands.

Summarizing, there is a lack of studies on how land use history affects species composition and habitat properties of grasslands. The following questions are addressed in the present paper: (i) What are the differences between ancient and recent calcareous grasslands in species richness and composition, and the physical and chemical characteristics of the soil? (ii) If there are any differences in vegetation are they caused by differences in land use history, environmental factors or both? (iii) Are there any plant indicators of ancient and recent grasslands?

Material and methods

Study area

This study was carried out in the nature reserve "Kaltes Feld" located in the central part of the Jurassic mountains, Swabian Alb, in southwestern Germany (Fig. 1). Altitude ranges from 650 to 781m a.s.l. The climate is temperate, with a mean annual precipitation of 1050 mm and mean annual temperature of 7°C (Deutscher Wetterdienst 1979). Geological substrate consists of Jurassic bedrock (Malm) containing hard and soft layers resulting in a relief of steep slopes around a plateau (Landesamt für Geologie, Rohstoffe und Bergbau in Baden-Württemberg 2002, Geyer & Gwinner 2008; see also Table 1). Soils are shallow, both on the slopes and the plateau (Table 2). The main soil type is rendzina.

During the 18th and beginning of the 19th century there was a great increase in area of arable land due to the increasing human population after the strong decrease in the 17th century (the Thirty Years' War, pest epidemies). Cultivation of marginal areas, however, was very labour-intensive. In the case of "Kaltes Feld", the fields the farmers were cultivating were located some 200 to 300 altitudinal meters higher than their farms. Therefore, arable farming of distant and less fertile fields was abandoned in the middle of the 19th century when the first railways were constructed connecting rural areas with central market places and farm products were imported from more fertile regions (Mailänder 2005). At the same time, the "golden age" of sheep breeding in Wuerttemberg started, which means that arable fields were turned rapidly into grasslands. Later in the 19th century, mineral fertilizers were introduced, which caused further abandonment of marginal areas (Poschlod et al. 2010). The last massive abandonment of arable fields in the study area occurred after World War II when the economic situation improved (Poschlod & Wallis de Vries 2002, Mailänder 2005).

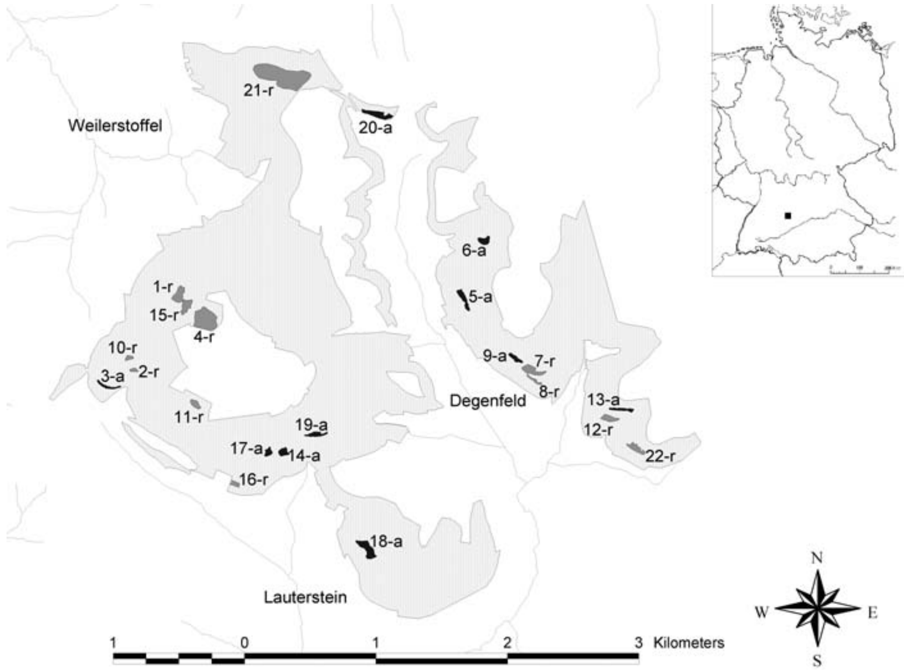

Fig. 1. – Location of "Kaltes Feld" in Germany and that of the investigated ancient (dark grey, a) and recent (grey, r) grasslands in the study area. Bright grey area is the nature conservation area. Position of brooks and villages are also shown.

Crops most cultivated in the past in the study region were spelt (*Triticum spelta*), oats (*Avena sativa*), potatoes (*Solanum tuberosum*), clover (*Trifolium pratense* but also *Medicago sativa*) and sainfoin (*Onobrychis viciifolia*) (Königliches statistisch-topographisches Bureau 1870, Gradmann 1950). The grasslands belong to the broadly conceived association *Gentiano-Koelerietum* (alliance *Mesobromion erecti*), which is a typical example of mesophilous Central-European calcareous grassland (Oberdorfer 2001, Chytrý 2007). The flora and vegetation of the study area is described by Alexejew et al. (1988) and Jandl (1988).

Study sites

Ancient and recent grasslands were selected using cadastral maps for 1830 and land-use maps for 1953 and 2002, which were made available by Mailänder (2005). The ancient grasslands were those grasslands continuously designated as pastures since 1830. Recent grasslands were defined as patches that were designated as arable land at least on one of the older maps (1830, 1952) and as grassland at least on the most recent map (2002).

Ten ancient and 12 recent grasslands were selected. A higher number of recent grasslands was chosen because they are generally more variable (e.g., in inclination, age, see also Table 2 and Fig. 2). Four recent grasslands on the plateau were exactly 150 years old (category "very old" grassland), four others between 55 and 150 years ("old" grassland) and four only about 50 to 60 years old ("young" grassland). The ancient and recent grasslands selected were roughly similar in terms of environmental characteristics like slope, exposure and soil depth.

Table 1. – Geology of the localities.

Geology	Number of ancient grassland plots	Number of recent grassland plots
Kimmeridgian marl-stone (ki1)	32	20
Oxfordian marl stone (ox1)	10	5
Solid limestone (ox2)	1	15
Hard reef-limestone (joMu)	0	20
Run-of-hill scree (qu)	7	0

Table 2. – Data of environmental variables in different age classes of grasslands (with the year of the beginning of continuous existence as grassland indicated in parentheses). One-way ANOVA was applied to test for significant differences between at least two groups followed by Tukey HSD multiple comparisons. Means bearing different letters row-wise were significant different between the age classes. SD – standard deviation; P – significance value; EIV – Ellenberg indicator value.

Variable	Ancient (n = 50)		Very old (1855; n = 20)		Old (<< 1953; n = 20)		Young (> 1937, > 1953; n = 20)		One-way ANOVA	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	F	P
Mean species number	37.5^{a}	6.5	40.6^{a}	4.3	38.1^{a}	8.6	38.8^{a}	6.1	1.10	0.352
Shannon-Wiener index	3.15^{a}	0.22	3.18^{a}	0.20	3.03^{a}	0.38	3.10^{a}	0.25	1.44	0.234
Altitude (m a.s.l.)	665^{ac}	15	773^{b}	6	666^{ac}	30	650^{c}	37	131.33	< 0.001
Exposure (°)	210^{a}	32	222^{a}	100	229^{a}	70	189^{a}	15	1.98	0.122
Inclination (°)	17.8^{a}	5.7	2.8^{b}	2.2	14.8^{ac}	8.3	12.2^{c}	5.0	33.53	< 0.001
Soil depth (average;cm)	18.6^{a}	7.3	13.6^{b}	3.3	18.8^{a}	5.9	13.1^{b}	3.8	6.73	< 0.001
Cover herb layer (%)	77.2^{a}	10.1	77.4^{a}	11.1	84.4^{a}	13.4	80.9^{a}	11.2	2.31	0.081
Cover moss layer (%)	9.2^{a}	6.2	15.1^{ab}	11.0	12.4^{a}	12.9	7.3^{ac}	5.3	3.53	0.017
Cover of stones (%)	2.7^{a}	5.2	0.0^{bc}	0.0	0.9^{ac}	2.0	0.0^{bc}	0.0	4.12	0.008
PDSI 21. December	3.30^{a}	0,88	1.72^{b}	0.19	2.74^{a}	1.30	3.01^{a}	0.57	16.57	< 0.001
PDSI 21. March	6.26^{a}d	0.58	5.13^{b}	0.17	5.83^{c}d	0.93	6.08^{ac}d	0.41	18.29	< 0.001
WHC (weight %)	59.9^{a}	9.1	81.6^{b}	9.3	67.2^{a}	10.1	73.1^{b}	15.95	21.29	< 0.001
pH(H_2O)	7.60^{a}	0.08	6.84^{b}	0.58	7.57^{ac}	0.10	7.40^{c}	0.25	39.31	< 0.001
pH($CaCl_2$)	7.28^{a}	0.06	6.58^{b}	0.61	7.27^{a}	0.10	7.11^{a}	0.26	30.63	< 0.001
H_2O-$CaCl_2$	0.32^{a}	0.09	0.26^{a}	0.13	0.29^{a}	0.10	0.29^{a}	0.09	2.17	0.096
Conductivity (µS)	130^{a}	16	86^{b}	31	117^{a}	15	133^{a}	25	24	< 0.001
K (mg/kg soil)	158^{a}	46	54^{b}	29	160^{a}	49	143^{a}	51	28	< 0.001
P (mg/kg soil)	18.5^{a}	6.4	8.2^{b}	3.5	19.0^{a}	6.5	17.4^{a}	6.7	15.69	< 0.001
EIV Light	7.4^{a}	0.08	7.3^{b}	0.08	7.3^{b}	0.05	7.3^{b}	0.12	9.71	< 0.001
EIV Temperature	5.5^{a}	0.08	5.4^{a}	0.10	5.5^{b}	0.11	5.7^{c}	0.05	23.37	< 0.001
EIVcontinentality	3.7^{a}	0.10	3.6^{b}	0.15	3.9^{c}	0.13	3.9^{c}	0.15	21.24	< 0.001
EIV Moisture	3.9^{a}	0.14	4.1^{b}	0.15	3.9^{a}	0.21	3.9^{a}	0.11	10.77	< 0.001
EIV Soil reaction	7.5^{a}	0.09	6.9^{b}	0.25	$7. 5^{a}$	0.13	7.4^{a}	0.17	71.70	< 0.001
EIV Nutrients	2.9^{a}	0.18	3.5^{b}	0.29	3.0^{a}	0.17	3.4^{b}	0.20	53.37	< 0.001

Vegetation data

Vegetation was recorded in five 2 × 2 m plots placed semi-randomly (avoiding rocks, bushes and strongly disturbed patches) in each grassland during July–August in 2006 and 2007 using the Braun-Blanquet's (1964) nine-grade abundance-dominance scale. For data processing the scale classes were transformed into percentage values: 1 (r), 2 (+), 3 (1), 5

(2a), 8 (2m), 18 (2b), 38 (3), 63 (4), and 88 (5). For each plot species diversity based on the number of species (species richness) and the Shannon-Wiener index were calculated. The Shannon–Wiener index of diversity (Begon et al. 1990) was calculated in CanoDraw (ter Braak & Šmilauer 2002).

Species occurring only in one plot (see Electronic Appendix 1) were excluded from the multivariate analysis because they do not determine the vegetation patterns, which was the case for 21 of the total of 163 taxa. In addition, four species (*Rhinanthus minor, R. glacialis, Polygala vulgaris, P. comosa*) were omitted, because they could not be identified to the species level in this case as they did not flower. The hybrid *Ononis spinosa* × *repens* was also omitted. Therefore, 137 taxa were included in the analysis.

Nomenclature follows Rothmaler (2005) for species and Oberdorfer (2001) for syntaxa.

Environmental data

Data on the following environmental parameters were collected for each plot: geological substrate, altitude, inclination, exposure, cover of herb- and moss-layer, cover of stones, occurrence of ant-hills and two categories of current management (grazing or no grazing; shrubs cleared or present). Most of the localities of both the ancient and recent grasslands are underlain by marlstone. Some localities occurred on solid limestone and other rocks (Table 1).

Data on latitude, inclination and exposure were used to calculate the potential direct solar radiation (PDSI). This was done by adding the cosines of angles between the sun and the plot surface at 15-minute intervals over a whole day. The calculation was done on the 21st day of each month between December and June following the description of Jeník & Rejmánek (1969). Most of the variability in species data was explained by winter months (December to March) probably due to the effect of the thickness and duration of the snow cover. Furthermore, the following soil physical and chemical properties were measured for each plot: soil depth, water holding capacity (WHC), pH(H_2O), pH($CaCl_2$), conductivity, concentration of available potassium (K) and phosphorus (P) in the soil.

Soil depth was estimated by repeatedly (8 ×) thrusting an iron rod, 0.6 cm in diameter, into the soil. Water holding capacity was measured by collecting soil cores using a metal borer of a standard volume of 100 cm^3 (diameter 56.4 mm, height 40 mm). After collecting each sample, soil within metal borer was saturated with water by placing on a permanently wet filter paper for 24 hours. Then, the saturated samples were dried at 105°C until a constant weight. Water holding capacity was calculated using the following formula: WHC = (weight of water saturated soil – weight of dry soil) × 100/ weight of dry soil.

For measuring the chemical properties of the the soil it was collected from a depth of 5–10 cm at three points within each plot and then mixed. These soil samples were air dried and sieved through a 2 mm sieve before the analysis. The chemical analysis followed the standards given by Verband Deutscher Landwirtschaftlicher Untersuchungs- und Forschungsanstalten (1991). Soil reaction (pH) was measured in a 1: 2.5 suspension of dry soil and distilled water (active soil acidity) or 0.01 M $CaCl_2$ (exchangeable soil acidity) after 1 hour using a universal pH meter WTW SenTix41. Conductivity was measured in a 1: 5 suspension of dry soil and distilled water using a WTW LF340 apparatus. Plant-available P and K were extracted using calcium acetate lactate (CAL). Phosphorus was measured photometrically after making the P content visible with ammoniumhepta-molybdate. K was measured using an atomic absorption spectrometer. Other variables were geographical coordinates and their combinations. This analysis was done to filter out possible spatial distribution effects on samples (Fortin & Dale 2009).

Data analysis

Differences between the environmental parameters recorded in the different grassland-age classes were analysed using one-way analysis of variance (ANOVA) followed by a Tukey HSD test in SPSS 12.0 Program (Bühl & Zöfel 2000). Unweighted mean Ellenberg indicator values (Ellenberg et al. 1992) for particular plots were calculated to test for additional variables using the JUICE 6.5 Program (Tichý 2002). Juvenile trees and shrubs were omitted from this calculation.

Ordination techniques were applied to determine the difference between the vegetation of ancient and recent grasslands and the influence of environmental factors. Methods based on the linear species response were chosen, which was supported by the length of the gradient in the DCA analysis (less than 3 S.D. units; ter Braak & Šmilauer 2002). Thus, Principal Components Analysis (PCA) and its constrained counterpart, Redundancy Analysis (RDA) were applied using the CANOCO for Windows 4.5 program package (ter Braak & Šmilauer 2002).

To estimate the influence of environmental factors, the eigenvalues of the corresponding ordination axes from unconstrained (PCA) and constrained (RDA) analyses were compared (Lepš & Šmilauer 2003). Scaling is focused on inter-species correlations in order to facilitate visibility of species positions in biplots. Species scores were divided by their standard deviation. Species covers (in percent) were transformed using the formula $y = (\ln x + 1)$. Samples (vegetation plots) were neither centered nor standardized. Centering, but not standardization was used for species. Statistical significance of the first canonical axis in the RDAs was determined using the Monte Carlo permutation test, with 1999 permutations and a reduced model. Permutations were restricted to the split-plot design. Five vegetation plots within each grassland were not permuted split plots. Particular grasslands represent whole plots and were permuted completely at random. Floristic differences between ancient and young grasslands were analysed using RDA (length of gradient in DCA: 2.292). We used only one explanatory variable, which was "history". Other variables were used as covariables in the RDA in order to filter out different environmental variables and spatial gradients and obtain only the effect of history on species composition. Significance of all potential covariables was at first tested by manual forward selection with the P-value = 0.05 (Monte Carlo test, 499 permutations). The following environmental variables were selected applying the forward-selection function: altitude, inclination, soil depth (average), grazing, three variables for geology (joMu, ox2, ki1), PDSI on 21 December, PDSI on 21 February, phosphorus, pH(H_2O), conductivity, cover of herb layer and geographical coordinates X and Y.

All variables were quantitative except geology and management (grazing). Geology and management data were categorical. Due to a strong correlation with other variables (high inflation-index in CANOCO) altitude and PDSI on 21 February were excluded from further analyses. Therefore, in total 13 covariables were used in the direct gradient analysis (RDA).

Various methods, such as regression coefficients, scores on the first canonical axis in $RDA_{history}$ and others were applied to detect indicator species for both, ancient and recent grasslands. These methods offered similar results, therefore, only the results from the fidelity calculation expressed as a phi-coefficient (Sokal & Rohlf 2001, Chytrý et al. 2002) are presented in this paper (Table 4). Significance of fidelity for species belonging to ancient or recent grassland was calculated using Fisher's exact test ($P = 0.05$). Data were processed using the JUICE 6.5 Program (Tichý 2002).

Results

Vegetation patterns

There were strong differences between the ancient and recent grasslands, both in vegetation and environmental variables. The assesment of the basic vegetation pattern was performed using PCA, which revealed distinct differences between plots of ancient and recent grasslands (ordination diagram not shown). The majority of plots were well separated. The main floristic variability (gradient along the first axis, AX1) can be interpreted by the variables geology and history (see also Figs 2–4). The vegetation pattern can be differentiated into three groups (PCA diagram not shown, see Electronic Appendix 1). Nearly all plots of the ancient grasslands and only a few of those of recent grasslands are characterized by many basi- and calciphilous grassland species, such as *Carex flacca*, *Buphthalmum salicifolium*, *Carlina acaulis* subsp. *caulescens*, *Hippocrepis comosa* and *Ligustrum vulgare*. The plots that include species of this group are from sites located on marlstone substrates (ki1-Lacunosamergel). There are two groups of recent grasslands. The first is characterized by many mesophilous grassland species, such as *Avenula pubescens*, *Cynosurus cristatus*, *Dactylis glomerata*, *Festuca pratensis*, *Trisetum flavescens*, *Cerastium holosteoides*, *Trifolium pratense*, *T. repens* and *Veronica chamaedrys,* some acidophilous species, such as *Agrostis capillaris* and *Luzula campestris* and a few arable weeds and ruderals. This group is related to the 150 year old grasslands on the plateau underlain by slowly weathered reefstone. The other group of recent grasslands can be identified by its occurrence on mainly solid limestone and by the presence of calciphilous species, such as *Salvia pratensis, Melampyrum arvense, Centaurea scabiosa* and the hemerophilic species *Medicago sativa* and *Convolvulus arvensis* .

When the analysis of the grasslands was constrained by the factor "history" and differentiated into four age classes, the general pattern was similar (Fig. 4). A synoptic table of the original floristic data is provided in Electronic Appendix 1.

Environmental variables

Although there were no differences in species diversity, there were clear differences in habitat properties (except cover of herb layer and exposure) of ancient and recent grasslands (Table 2), which is already obvious from the PCA that included the largest number of environmental variables (Fig. 2).

Ancient grasslands exhibited a higher inclination than recent grasslands. Accordingly, solar radiation was also higher at ancient grassland sites. Soil was a little bit deeper at ancient than recent grassland sites. Soils at recent grasslands sites were more acidic. More information is presented in Table 2.

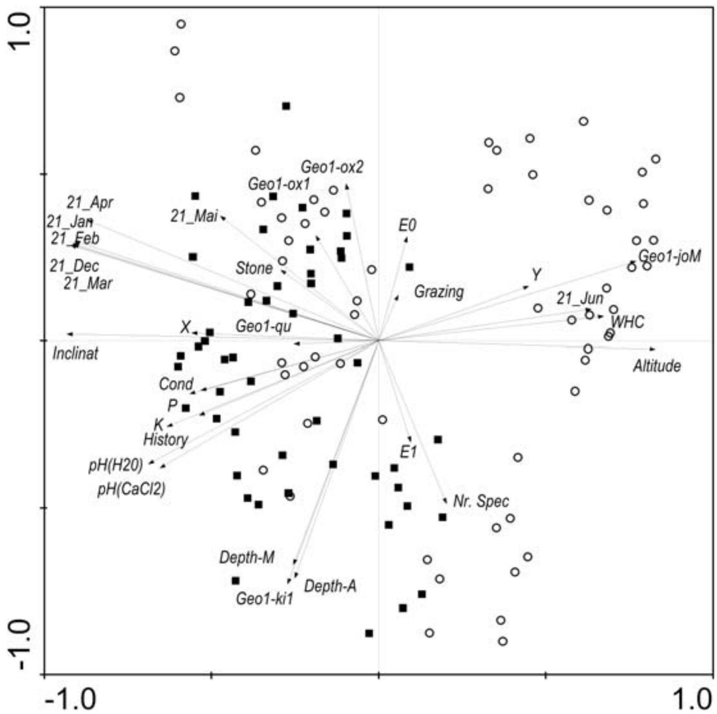

Fig. 2. – Principal components analysis (PCA) presenting the correlations between many environmental variables (geology [joMu, ox 1, ox2, ki1, qu; see Table 1 for details], history, altitude, inclination, PDSI for all seven months, soil depth (average and median), pH(H_2O), pH($CaCl_2$), conductivity, plant available potassium (K) and phosphorus (P), number of species, cover of herb (E1) and moss (E0) layer, cover of stones, grazing and geographical coordinates X and Y in an ordination diagram (■ ancient grasslands, ○ recent grasslands). Environmental variables were treated like “species”.

Both standard deviations of most environmental parameters (Table 2) and the multivariate analysis (Fig. 2) show clearly that the environment of recent grasslands is much more heterogenous than that of ancient grasslands. If recent grasslands are divided into three age classes, a more differentiated pattern appeared showing that the oldest recent grasslands are situated on the plateau with strong differences in several environmental parameters, whereas the younger recent grasslands (60 to 150 and 50 to 60 years old) are more similar to ancient grasslands (Table 2).

History

The influence of land-use history was calculated using direct linear analysis (RDA). History ($RDA_{history}$) explains 2/3 of variability along the main floristic gradient compared to RDA with all variables. However, history is correlated with other environmental variables when the results of AX1 in both RDA’s, $RDA_{history}$ and $RDA_{history+covariables}$, are compared. Therefore, the eigenvalues of the first ordination axes (AX1) from PCA and $RDA_{history+covariables}$ were compared, which showed that 21% of the vegetation pattern along the main floristic gradient could be attributed to the net influence of history. The permutation test of the first axis was highly significant (Table 3).

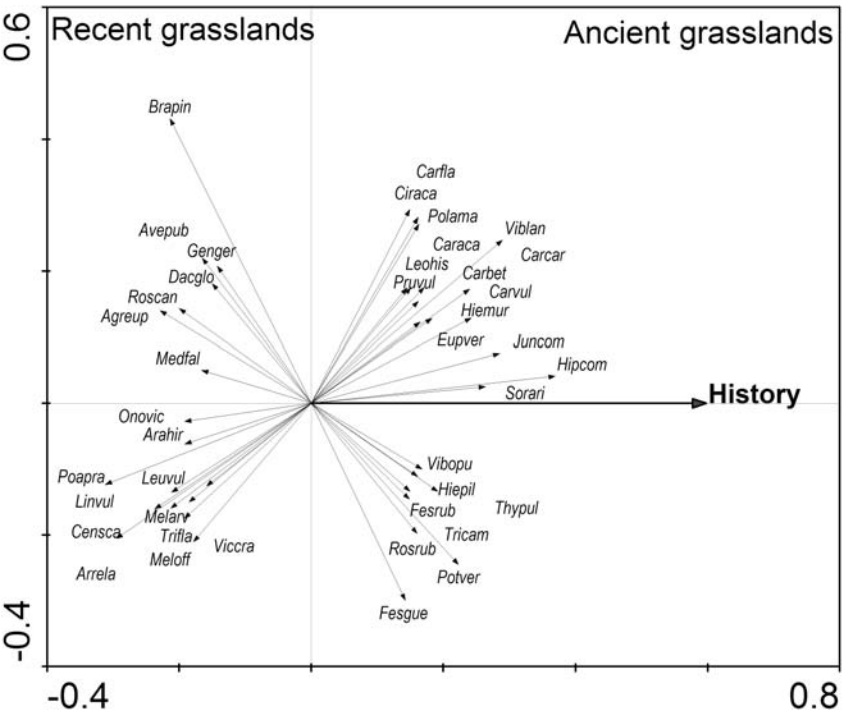

Fig. 3. – RDA$_{\text{history+covariables}}$ analysis constrained by the factor "history", reflecting the continuous ancient grasslands and discontinuous recent grasslands. The effect of 13 covariables was subtracted. Only the 44 most correlated species (species fit range > 10%) are presented. For the full species names see Electronic Appendix 1.

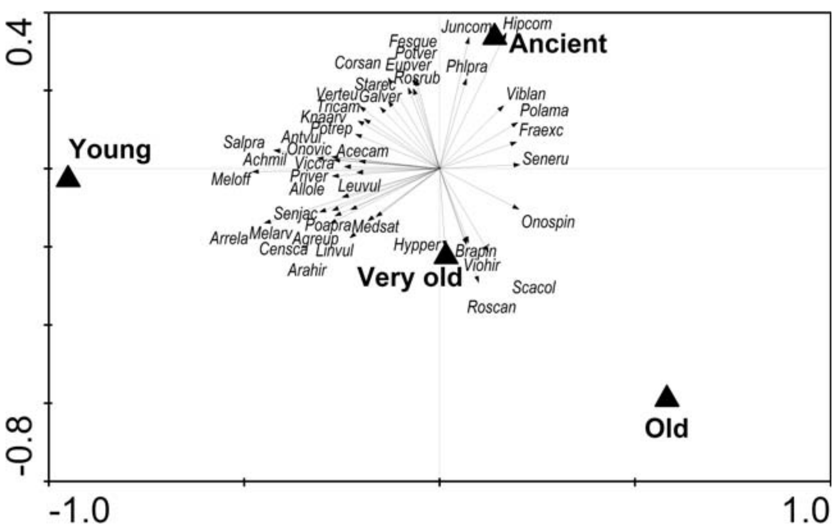

Fig. 4. – RDA$_{\text{age groups+covariables}}$ analysis constrained by four variables representing the different age-groups of grasslands. "Ancient" grassland are continuously used as pastures at least since 1830. Category "very old" are 150 year old grasslands, "old" are grasslands between 55 and 150 years old and "young" are grasslands only about 50 to 60 years old. The effect of covariables was subtracted. Only the 43 most correlated species (species fit range > 4%) are presented. For full species names see Electronic Appendix 1.

Table 3. – Results of the ordination analysis (PCA, RDA). Plots n = 110, species n = 137, environmental variables and covariables n = 14 (history, three variables for geology, inclination, PDSI on 21 December, average soil depth, pH(H_2O), conductivity, phosphorus, cover of herb layer, grazing and geographical coordinates X and Y). For detailed explanation see text and Figs 2–4; % variance: cumulative percentage variance of species data explained by four ordination axes, % all AX: variance explained by all the canonical axes, F-statistics and significance (p-value) of Monte Carlo permutation test of significance of first canonical axis (1.999 permutations under reduced model).

Ordination analysis	Environ-mental variables	Cova-riables	% variance				% all AX	F-stat	p-value
			AX1	AX2	AX3	AX4			
PCA	–	–	16.3	26.2	33.3	38.6	–	–	–
RDA	14	0	13.7	22.2	26.6	30.5	42.7	15.118	< 0.001
$RDA_{history}$	1	0	9.4	20.1	29.6	35.7	9.4	11.162	< 0.001
$RDA_{history+covariables}$	1	13	3.5	10.4	16.5	21.5	3.5	3.481	< 0.001
$RDA_{age\ groups}$	4(3)	0	12.7	18.8	21.1	30.5	21.1	15.490	< 0.001
$RDA_{age\ groups+covariables}$	4(3)	13	3.9	6.9	8.7	14.8	8.7	3.763	< 0.001

Indicators for ancient and recent grasslands

On the $RDA_{history+covariables}$ biplot (Fig. 3) species are shown according to their position along the first canonical axis constrained by history. On the left side of the diagram species typical of recent grasslands are displayed and on the right side are species typical of ancient grasslands. Using different analyses to calculate the indicator values of species related to history such as fidelity expressed by the phi-coefficient, regression coefficients or scores on the first canonical axis in $RDA_{history,}$ provided similar results. Therefore, only the results from the fidelity analysis are presented (Table 4). This analysis clearly shows that the indicators of ancient grasslands were rarely exclusive, which was, however, the case for recent grasslands.

Strong indicators of ancient grasslands are *Carex caryophyllea*, *C. flacca, Bupthalmum salicifolium, Carlina vulgaris, Cirsium acaule, Hippocrepis comosa* and *Scabiosa columbaria*. Species exclusively indicating recent grasslands are *Anthoxanthum odoratum, Avenula pubescens*, *Cynosurus cristatus*, *Dactylis glomerata*, *Cerastium holosteoides*, *Medicago sativa*, *Melampyrum arvense*, *Onobrychis viciifolia*, *Rhinanthus alectorolophus* and others. The RDA indicated a different indicator strength for some species when environmental covariables were subtracted due to the preference/non-preference of species for specific environmental conditions. Such substraction allows a better detection of the real effect of history. When covariables are substracted the following species of both ancient and recent grasslands had a remarkably lower indicating power: *Achillea millefolium*, *Agrostis capillaris, Cynosurus cristatus*, *Galium molugo* and *Trifolium pratense* (all growing in the recent grasslands on the plateau), *Daucus carota* and *Scabiosa columbaria* (found in ancient grasslands growing on soils with a high pH and relatively high content of nutrients, especially potassium). However, for other species their indicating power increased after substraction of covariables. These were species growing under intermediate environmental conditions, such as e.g., *Thymus pulegioides* s. str. and *Viburnum lantana* in ancient grasslands or *Centaurea scabiosa, Medicago sativa*, *Melampyrum pratense* and *Onobrychis viciifolia* in recent grasslands.

Table 4. – Synoptic table including indicator species of both ancient and recent grasslands. Species are sorted by a fidelity measure (presence/absence data) expressed in terms of the Phi coeficient (calculation by JUICE 6.5 Program; Tichý 2002). Only those species with significant fidelity to each group are listed (P = 0.05; Fischer's exact test). Number of plots n = 50 for ancient and 60 for recent grasslands. The percentage frequency of each species in each group is given.

Species	Indicators of ancient grasslands					Indicators of recent grasslands			
	Fidelity ancient	Fidelity recent	Frequency ancient	Frequency recent		Fidelity ancient	Fidelity recent	Frequency ancient	Frequency recent
Hippocrepis comosa	76.2	–	94	18.3	*Trisetum flavescens*	–	65.6	4	66.7
Buphthalmum salicifolium	50.7	–	74	23.3	*Veronica chamaerdys*	–	56.0	2	51.7
Carlina vulgaris	48.4	–	60	13.3	*Poa pratensis* subsp. *angustifolia*	–	44.0	26	70.0
Carex flacca	44.7	–	100	66.7	*Dactylis glomerata*	–	43.8	16	58.3
Prunella vulgaris	43.1	–	82	40.0	*Festuca pratensis*	–	43.5	4	40.0
Juniperus communis	42.9	–	44	6.7	*Cerastium holosteoides*	–	40.6	.	28.3
Carex caryophyllea	38.2	–	98	70.0	*Avenula pubescens*	–	39.2	.	26.7
Hieracium pilosella	37.4	–	50	15.0	*Cynosurus cristatus*	–	39.2	.	26.7
Cirsium acaule	36.1	–	96	68.3	*Vicia cracca*	–	38.2	2	30.0
Scabiosa columbaria	34.6	–	90	60.0	*Anthoxanthum odoratum*	–	37.8	.	25.0
Daucus carota	31.7	–	76	45.0	*Salvia pratensis*	–	37.8	.	25.0
Briza media	31.2	–	94	70.0	*Agrostis capillaris*	–	36.3	.	23.3
Viburnum lantana	29.5	–	16	.	*Arrhenatherum elatius*	–	36.3	.	23.3
Senecio erucifolius	28.0	–	40	15.0	*Cirsium eriophorum*	–	34.9	.	21.7
Carlina acaulis subsp. *caulescens*	27.0	–	62	35.0	*Trifolium pratense*	–	33.4	44	76.7
Linum catharticum	27.0	–	98	81.7	*Luzula campestris*	–	33.3	.	20.0
Leontodon hispidus	26.7	–	84	60.0	*Ononis repens*	–	32.1	2	23.3
Gymnadenia conopsea	26.1	–	38	15.0	*Senecio jacobea*	–	32.1	2	23.3
Polygala amarella	25.5	–	28	8.3	*Agrimonia eupatoria*	–	31.4	48	78.3
Koeleria pyramidata	23.9	–	48	25.0	*Trifolium repens*	–	30.4	2	21.7
Ligustrum vulgare	23.9	–	48	25.0	*Rhinanthus alectorolophus*	–	30.2	.	16.7
Potentilla neumanniana	23.7	–	76	53.3	*Hypericum perforatum*	–	29.1	18	45.0
Euphorbia verrucosa	23.0	–	14	1.7	*Galium verum*	–	28.0	8	30.0
Rosa rubiginosa	22.9	–	10	.	*Convolvulus arvensis*	–	26.7	.	13.3
Thymus pulegioides subsp. *pulegioides*	20.9	–	100	91.7	*Thymus pulegioides* subsp. *carniolicus*	–	26.7	.	13.3
Aster amellus	20.5	–	12	1.7	*Galium mollugo* s.l.	–	26.1	14	36.7
Sorbus aria agg. – juv.	20.5	–	12	1.7	*Euphrasia* sp.	–	25.2	2	16.7
Gentiana verna	20.4	–	8	.	*Galium pumillum*	–	25.1	20	43.3
Brachypodium pinnatum	19.2	–	92	78.3	*Cerastium arvense*	–	24.9	.	11.7
Vincetoxicum hirundinaria	18.3	–	60	41.7	*Potentilla reptans*	–	24.9	.	11.7
					Medicago lupulina	–	24.0	50	73.3
					Acer campestre – juv.	–	23.3	10	28.3
					Arabis hirsuta	–	23.3	2	15.0
					Arenaria serpyllifolia	–	22.9	.	10.0
					Centaurea scabiosa	–	22.9	.	10.0
					Melampyrum arvense	–	22.9	.	10.0
					Melilotus officinalis	–	22.7	6	21.7
					Taraxacum sect. *Ruderalia*	–	21.5	10	26.7
					Medicago sativa	–	20.9	.	8.3
					Onobrychis vicifolia	–	20.9	.	8.3
					Trifolium campestre	–	20.9	.	8.3

Discussion

Vegetation pattern, history and environmental parameters

There was no difference in the species richness of ancient and recent grasslands, however, their species compositions differed. This difference could be assigned to both habitat properties and history. Percentages of the variability explained by particular variables on AX1 of the RDA analysis that did not include covariables were: geology (marlstone × other) 10.9; geology (hard reef-limestone × other) 10.7; altitude 9.5; history (ancient × recent) 9.4; pH(H_2O) 9.1; inclination 8.5; PDSI 21.March 7.0 (see also Fig. 2 for correlations between variables).

The relationship between the vegetation of grasslands and former land use was still very clear and significant if the influence of other variables was subtracted (Table 3). The influence of history was even stronger, 4.8 instead of 3.5%, when the four recent grasslands situated on the plateau, which is strongly affected by other environmental parameters such as geology, were omitted. A similar strong effect of history on the composition of the vegetation is reported by Hermy et al. (1999), who compared ancient and recent forests.

The geomorphological and soil parameters of the ancient and recent grasslands also differed. Arable field use was correlated often with a lower inclination – although some recent grasslands occurred on steep (> 20°) slopes – which are not only easier to plough but also are less affected by soil erosion. Despite this soil depth is significantly lower in recent grasslands, which clearly shows that soil erosion occured during the arable field phase. There was a slight positive correlation between soil depth and slope inclination (Pearson correlation coefficient $r = 0.229$, $P = 0.016$, $n = 110$). Based on many local studies, Bork et al. (1998) reveal that soil erosion occurred in historical times to a much greater extent than today and argue that this is because (i) the area of arable fields was much greater and (ii) the plant cover of arable fields was less dense.

Whereas there were no differences in the cover of the herb and moss layers, cover of stones was significantly different, reflecting the fact that during the period of arable field use stones were removed by hand, often still visible at the edges of recent grasslands or in recent forests, where there are deposits of long heaps of stones.

In terms of soil physical and chemical properties those of recent grasslands have a higher water holding capacity than those of ancient grasslands. This fact can be explained by the geological substrate of most of the ancient grasslands, which is marlstone, and the resultant soil dense and loamy. Higher water holding capacity may explain the higher number of mesic grassland species. Contents of potassium and phosphorus, the latter often the limiting factor on calcareous soils (Janssens et al. 1998, Carroll et al. 2003), were significantly lower in the very old grasslands due to the specific abiotic conditions prevailing on the plateau (Table 2). However, other authors report high nutrient levels in soil even after almost 2000 years of arable field use (Dupouey et al. 2002). In our case nearly no fertilizer was applied, because of the great altitudinal difference between farms and fields, except that provided by occasional hurdling by sheep during the stubble phase, which was still the case even during the 1950s (Mailänder 2005). Finally, tillage caused the decomposition of humus and harvesting of crops continuously extracted nutrients. This pattern, however, contrasts with the vegetation pattern of recent grasslands, where there are more species indicating rather high nutrient supply (N-value, Table 2). These indicators are particularly associated with the plateau (“very old” grasslands). This might be explained by the fact that highly productive species are also able to thrive at low phosphorus concentrations (from 20 mg P/kg soil; Hejcman et al. 2007, 2009) and that the indicator values for terrestrial plants only take into account nitrogen and ignore the fact that P and K may be limiting under certain conditions (Schaffers & Sýkora 2000, Niinemets & Kull 2005, Chytrý et al. 2009).

Vegetation patterns and flora

Differences in vegetation patterns were associated with ecological or phytosociological plant species groups. Recent grasslands were phytosociologically more heterogenous and, unlike ancient grasslands, could not clearly be assigned to a certain community. Ancient grassland species could be clearly assigned to *Festuco-Brometea* (Oberdorfer 2001, Chytrý & Tichý 2003), whereas recent grassland species belong to different classes, namely *Festuco-Brometea* but also *Molinio-Arrhenatheretea, Trifolio-Geranietea sanguinei* and *Secalietea cerealis* or even crop plants.

The occurrence of arable weed species in recent grasslands, such as *Convolvulus arvensis*, *Cerastium arvense* and the hemiparasitic species, *Melampyrum arvense* and *Rhinanthus alectorolophus*, strongly feared in former times since they strongly decreased crop yield (Gradmann 1950), is reported by other authors (Dutoit & Alard 1995, Poschlod & Wallis de Vries 2002, Dutoit et al. 2004). However, formerly cultivated plants like *Dactylis glomerata*, *Medicago sativa*, *Melilotus officinalis*, *Onobrychis viciifolia* and/or *Trifolium pratense*, still occur in recent grasslands; the last one, however, is also frequent in ancient grasslands (Table 4, Electronic Appendix 1). Some of these species are not indigenous. *Melilotus officinalis* is an archaeophyte and was probably introduced with unclean seed (Lohmeyer & Sukopp 1992). *Onobrychis viciifolia* is a neophyte and was introduced as a fodder plant (Kowarik 2003). Cultivation of *Dactylis glomerata* started in the 18th century (Stebler & Schröter 1902). *Medicago sativa* and *Trifolium pratense* were widely grown as fodder plants on nutrient-poor soils and are even mentioned as cultivated in the study region (Königliches statistisch-topographisches Bureau 1870, Gradmann 1950). *Melilotus officinalis* was often sown because of its medicinal properties, as a bee plant and to improve soil conditions. The medical power of field melilot was well known even in prehistorical times. In certain regions it was delivered in huge quantities to pharmacies and drugstores (Hegi 1966). The cultivation of *Onobrychis viciifolia* started in France during the 15th century and in Germany at the beginning of the 18th century, especially on nutrient-poor calcareous soils, which made it possible for the first time to transform calcareous grassland into more productive arable fields for fodder production (Stebler & Schröter 1902).

The largest proportion of recent grassland species are either mesotrophic (*Molinio-Arrhenatheretea*) or calcareous (*Festuco-Brometea*) grassland species like *Anthoxanthum odoratum*, *Arrhenatherum elatius*, *Avenochloa pubescens*, *Cerastium holosteoides*, *Cynosurus cristatus*, *Dactylis glomerata*, *Festuca pratensis*, *Poa pratensis*, *Trisetum flavescens*, *Trifolium pratense*, *Vicia cracca* or *Arabis hirsuta*, *Ononis repens*, *Salvia pratensis* and *Thymus pulegioides* subsp. *carniolicus*. *Salvia pratensis* and *Centaurea scabiosa*, both diagnostic species of *Festuco-Brometea,* occurred only in the most recent grasslands, which are 50–60 years old. The absence in ancient grassland can be explained by the fact that these species rarely naturally occur at higher altitudes such as in the study area. Their occurrence in recent grasslands may be explained by tradition of hayseed application after abandonment of arable field use, which was applied extensively during the 19th and beginning of the 20th century, the period of the famous grassland construction schools in Germany (Häfener 1847, Hard 1964, Schröder-Lembke 1983, Poschlod & Wallis de Vries 2002). In contrast to recent grasslands, characteristic species of ancient grasslands were mainly typical calcareous grassland species (Table 4). These indicator species patterns correspond to those reported by Röder et al. (2006) based on a comparison of one ancient and one recent grassland located at Garchinger Haide north of Munich.

As there are species of plants that are exclusive indicators of ancient forests (Wulf & Kelm 1994) it is surprising that there are no such indicators for old grasslands. However, this may be due to the fact that recent grasslands were not strongly isolated from ancient grasslands and sheep grazing in the study area maintained a continuous seed input from ancient to recent grasslands. Sheep are known to be one of the most important and effective dispersal vectors in Central-European man-made landscapes (Fischer et al. 1996, Poschlod et al. 1996, Poschlod & Bonn 1998). There are, however, many exclusive species of recent grasslands, which may be simply explained by their former conversion into arable fields, which resulted in the establishment of new species and once established they have persisted even though the habitat has changed.

Conclusions and perspectives

Summarizing, history affects the vegetation pattern more than environment, except for the recent grasslands on the plateau. Therefore, future vegetation studies should include the results of not only floristic and environmental but also historical analyses. Contrary to the commonly held opinion that more recent habitats have little or no nature conservation value (Waesch & Becker 2009), recent grasslands may contain rare and/or endangered species such as *Gentianella germanica, Gymnadenia conopsea* and in the case of *Melampyrum arvense* even an exclusive species. Furthermore, a part of the regional calcareous grassland species pool was also restricted to recent grasslands (e.g., *Thymus pulegioides* subsp. *carniolicus, Rhinanthus alectorolophus, Stachys alpina*). Therefore, recent grasslands may have a high conservation value and should be considered in future management plans of calcareous grassland landscapes.

See http://www.preslia.cz for Electronic Appendix 1.

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Souhrn

Suché vápnomilné trávníky jsou jedním z druhově nejbohatších, avšak i nejohroženějších biotopů střední Evropy. Navzdory dramatickému poklesu jejich rozlohy během druhé pol. 20. stol. v důsledku ukončení obhospodařování nebo záměrného zalesňování však došlo také ke vzniku nových ploch na opuštěné orné půdě. Hlavním tématem naší studie bylo porovnání starých („kontinuálních“) a nově vzniklých trávníků a zjištění vlivu stáří na vegetační skladbu a stanovištní charakteristiky. Zjistili jsme, že historie lokalit (tj. způsob využití půdy v minulosti a stáří porostů) je klíčovým faktorem, který se promítá jak do aktuální vegetace, tak i do stanovištních charakteristik dnešních trávníků. Zjistili jsme výrazné rozdíly ve vegetaci mezi starými a mladými trávníky, které byly průkazné i poté, co jsme odfiltrovali vliv ostatních proměnných prostředí (kovariát). Polní hospodaření ovlivnilo fyzikální a chemické vlastnosti půd, které jsou i po řadě desetiletí, co jsou plochy proměněny v trávníky, stále výrazně patrné. Výrazné rozdíly byly nalezeny zejména v maximální vodní kapacitě a v pH půdy. Obsah živin nebyl poněkud překvapivě v mladých trávnících vyšší, někdy byl dokonce i výrazně nižší, což lze vysvětlit jako důsledek dřívějšího velmi extenzivního polního hospodaření s minimálním hnojením. Mezi indikátory bývalých polí se vyskytují cenologicky nevyhraněné druhy jako *Poa pratensis, Veronica chamaedrys*, druhy mezofilní, např. *Trisetum flavescens, Cerastium holosteoides,* bývalé plodiny či polní plevele jako *Onobrychis viciifolia* a *Rhinanthus alectorolophus* nebo i typické druhy suchých trávníků, jako je *Salvia pratensis* či *Centaurea scabiosa.* U posledně jmenovaných se domníváme, že se jedná o důsledek výsevu, protože konkrétně šalvěj se jinak ve zdejší, výše položené a poněkud chladnější oblasti vyskytuje jen vzácně. Mezi dobré indikační druhy kontinuálních trávníků patří vesměs diagnostické druhy svazu *Mesobromion erecti*, jako jsou *Carex flacca, Bupthalmum salicifolium, Carlina vulgaris, Cirsium acaule, Hippocrepis comosa* a *Scabiosa columbaria.* V území jsme nalezli řadu vzácných a ohrožených druhů (např. *Gentianella germanica, Gymnadenia conopsea*), které se vyskytovaly jak ve starých, tak i mladých trávnících. Na mladé trávníky je vázána část regionální květeny (*Thymus pulegioides* subsp. *carniolicus, Rhinanthus alectorolophus, Stachys alpina*), která vytváří specifická společenstva. Mladé trávníky mají i velmi vysokou druhovou diversitu. Proto by při ochraně biodiversity suchých trávníků měl být kladen důraz nejen na staré, ale i na historicky mladé trávníky.

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