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Environmental drivers of species composition and richness in dry grasslands of northern and central Bohemia, Czech Republic

Bestimmende Umweltfaktoren für den Artenreichtum und die Artenzusammensetzung der Trockenrasen im nördlichen und mittleren Böhmen (Tschechien)

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Abstract

Central European dry grasslands are remarkably diverse plant communities that occur at the western edge of the Eurasian forest-steppe zone and harbour many species of continental distribution. Although their plant community types have been described in detail, the diversity patterns and their environmental determinants are still poorly known for these grasslands. Here, we study environmental drivers of species composition and richness in dry grasslands of northern Bohemia (České středohoří Mts) and central Bohemia (Křivoklát region), both in the Czech Republic. In vegetation plots of 100 m² we recorded all vascular plant species, measured soil chemistry variables, above-ground biomass production and nutrient concentrations in biomass. Species richness in these plots ranged from 13 to 55. The relationships between species composition and the environment were explored using detrended correspondence analysis and canonical correspondence analysis, while the relationships between species richness and the environment were assessed using univariate and multiple regression models. In both regions, species composition and richness strongly responded to the soil pH (ranging from 4.0 to 7.8), which was positively correlated with calcium and magnesium concentrations and negatively with annual precipitation. The response of species richness to soil pH was unimodal with a peak at pH of about 6.5 in the České středohoří Mts, and positive in the Křivoklát region. Plots on soils with a pH higher than 5 consistently contained more than 35 species. In the České středohoří Mts, species richness was positively related to the aboveground biomass production, whereas in the Křivoklát region, this relationship was only significant for graminoid species. In both areas, plots with soils deeper than 20 cm and with aboveground biomass dry weight above 200 g/m² harboured more than 40 species per 100 m². Moreover, in the České středohoří Mts, nitrogen concentrations in the biomass had considerable effects on both species composition and richness: species numbers were lower at sites with higher nitrogen concentration. This indicates a threat to diversity of these dry grasslands under currently high atmospheric nitrogen deposition coupled with the absence of management at most of the studied sites.

Keywords: biomass, diversity, nutrients, plant community, productivity, soil depth, soil pH, steppe

Erweiterte deutsche Zusammenfassung am Ende des Manuskripts

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1. Introduction

Continental dry grasslands and steppes are ecosystems with remarkable biological diversity and high species richness (Wilson et al. 2012). They also harbour many endangered species and, because of their vulnerability to land-use changes, are a major focus of nature conservation authorities in Europe (Veen et al. 2009, Werger & van Staalduinen 2012). The variability and distribution of Eurasian dry grasslands and steppes has been described in several syntheses and reviews (Horvat et al. 1974, Walter 1974, Royer 1991, Lavrenko et al. 1993, Werger & van Staalduinen 2012). It is generally accepted that the main factor that determines the variability of Eurasian dry grassland plant communities is moisture availability. It has strong effects on the ecosystem's productivity, and either independently, or through its effect on productivity, influences species composition and richness (Bai et al. 2007, Ma et al. 2010). Soil pH or base status is considered to be another important factor (Schuster & Diekmann 2003, Löbel et al. 2006, Chytrý et al. 2007). However, there are still many gaps in our understanding of the effects of environmental factors on dry grassland species composition and richness, both in general and in different local contexts. In central Europe, most dry grasslands are of secondary origin, developed after landscape deforestation and under the influence of long-term management such as grazing or hay-cutting, but there are also sites that may be natural remnants of the early Holocene steppes. The dry region in northern and central Bohemia, situated in the rain shadow of the Ore Mts (Erzgebirge, Krušné hory) and receiving less than 500 mm of annual precipitation, is one of the extrazonal outposts of the Eurasian continental forest-steppe (Martinovský 1984, Chytrý 2012). Patches of open steppe vegetation were most likely present there continuously throughout the Holocene, even on deep soils (Ložek 2007, 2011, Hejcman et al. 2013). Evidence includes a continuous fossil record of steppe snails throughout the Holocene (Juřičková et al. 2013a, b) and a large current species pool of steppe plants, including several species occurring at isolated sites far from their continuous range in continental Eurasia, e.g. *Helictotrichon desertorum*, *Stipa glabrata* and *S. smirnovii* (Holub 1962, Martinovský 1975, Kolbek & Boublík 2006, Kaplan 2012). The centre of this forest-steppe region is situated in the south-western České středohoří Mts and the lower Ohře valley. However, dry grasslands also occur in more precipitation-rich areas of the northern half of Bohemia, where they have less pronounced continental features and are probably of secondary origin, occurring mainly in previously forested areas (Chytrý 2007).

The aim of this study is to provide a basic description of vegetation-environment relationships in the dry grasslands of northern and central Bohemia. We selected two contrasting model regions: (1) České středohoří Mts, which include the driest part of Bohemia with vegetation corresponding to the forest-steppe biome; (2) Křivoklát region, which is characterized by higher precipitation and lower temperature. The latter region does not belong to the forest-steppe biome and forest is considered as the potential natural vegetation for most of this area, therefore its dry grasslands lack several specialist species of continental steppe. Primary dry grasslands are restricted to extreme habitats of steep slopes and rock outcrops, which occur in the deeply incised valley of the Berounka river, while secondary dry grasslands occur in areas of former pastures on deforested sites. Although species composition and selected site factors of dry grasslands in both regions have been extensively documented in numerous studies (e.g. Klika 1933, 1951, Kolbek 1975, 1978, 1979, Toman 1981, 1988, Kolbek et al. 2001, Chytrý 2007), the effects of environmental factors on plant species diversity have never been analyzed quantitatively or generalized, except in a local study focusing on a single model hill, Oblík in the České středohoří Mts (Slavíková et al. 1983).

In this study, we focus on two basic facets of plant community diversity: species composition and species richness. We ask which environmental variables are the most important drivers of each of them in the northern and central Bohemian dry grasslands. As the two study areas differ in many ways, we analyze them separately and compare the results. Moreover, we interpret the results in the context of previous knowledge of vegetation-environment relationships in Eurasian dry grasslands and steppes.

2. Study areas

The study areas in the České středohoří Mts (Böhmisches Mittelgebirge) and the Křivoklát region (Křivoklátsko Biosphere Reserve) are located, respectively, in northern and western-central Bohemia, Czech Republic (České středohoří Mts: 50°20’–50°40’ N, 13°40’–14°44’ E; Křivoklát region: 49°51’–50°07’ N, 13°41’–14°04’ E; Fig. 1).

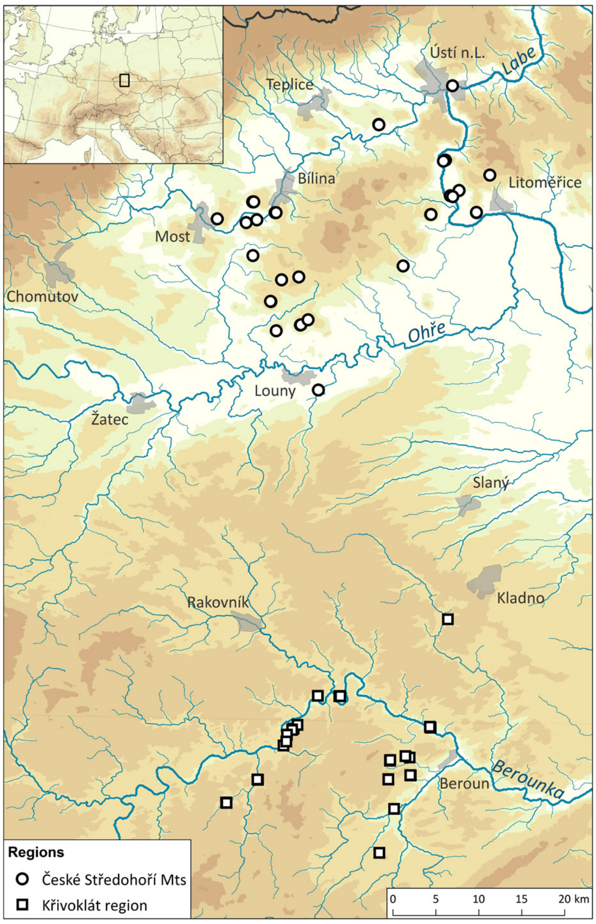


Fig. 1. Sites sampled in the České středohoří Mts and the Křivoklát region.

Abb. 1. Lage des Untersuchungsgebiets und der Untersuchungsflächen im Böhmischen Mittelgebirge (České středohoří Mts) und Pürglitz-Gebiet (Křivoklát region).

The České středohoří Mts are characterized by numerous solitary conical volcanic hills of Tertiary origin (SLAVÍKOVÁ et al. 1983). They are formed of either base-poor trachytic rocks (e.g. phonolites) or base-rich basalts. Dry grasslands typically occur in the naturally treeless upper parts of their south-facing slopes and summits (KOLBEK 1975, 1978, 1979). The Křivoklát region comprises a gently undulating landscape dissected by a deep valley of the Berounka river. The bedrock is of Palaeozoic and Proterozoic origin with a variable base content, e.g. shale, spilite, diabase, andesite, rhyolite or chert. Dry grasslands in this region typically occupy open patches on hilltops, upper edges of the deep Berounka river valley or south-facing valley slopes (KUČERA & MANNOVÁ 1998, KOLBEK et al. 2001).

Sites sampled in the České středohoří Mts are characterized by a mean annual temperature ranging from 7.3 to 9.1 °C, and in the Křivoklát region from 7.9 to 8.1 °C. Their mean annual precipitation ranges from 470 to 643 mm and from 527 to 562, respectively (interpolated values from the Climate Atlas of Czechia; TOLASZ et al. 2007). Altitude of the sites sampled in the České středohoří Mts ranges from 162 to 668 m and in the Křivoklát region from 226 to 476 m.

Despite substantial differences in landscape features, geology, climate and history of human impact, both regions host a wide range of dry grassland communities, scattered in areas of favourable mesoclimate (Fig. 2). Our data set includes dry grasslands of the *Festucion valesiacae*, *Koelerio-Phleion phleoidis*, *Hyperico perforati-Scleranthion perennis* and *Alysso-Festucion pallentis* alliances as delimited by CHYTRÝ (2007). These grasslands are typically dominated by *Carex humilis*, *Festuca ovina*, *F. rupicola*, *F. valesiaca*, *Koeleria macrantha*, *Stipa capillata* and *S. pennata*.

3. Methods

The dry grasslands were sampled in May and June 2007. The sampling sites were selected preferentially after preliminary landscape stratification with the aim to obtain a balanced representation of vegetation types on acidic and base-rich bedrock in both regions. Sampled sites in both regions were occasionally grazed by deer or sheep. We avoided both over-grazed sites and those abandoned for many years with visible signs of post-abandonment vegetation succession. A total of 62 sites were sampled (33 in the České středohoří Mts and 29 in the Křivoklát region).

At each site, we recorded all vascular plant species in a plot of 100 m², according to taxonomic concepts and nomenclature of DANIHELKA et al. (2012). In total, we found 273 species in the České středohoří Mts and 226 in the Křivoklát region, of which 162 species were shared. In each plot, we further measured environmental variables that might have affected species composition and richness (Table 1).

Using a soil probe, we estimated soil depth as a mean of ten measurements randomly located within each plot. Soils deeper than 30 cm were simply given a value of 30 cm, as we assumed that the influence of soil depth on dry grassland communities does not change much beyond this point. Soil samples were taken from three places within each plot at a depth of 2–10 cm and subsequently mixed for each plot. The composite samples were used to determine the following soil chemical properties: (1) soil pH was measured after 12-hour extraction in distilled water (soil/water ratio 2/5); (2) plant-available phosphorus, potassium, calcium and magnesium were determined from Mehlich III extracts by spectrophotometry (phosphorus) and atomic absorption spectrophotometry (potassium, calcium and magnesium); (3) C/N ratio was determined as the ratio of organic carbon approximated by loss on ignition and total nitrogen measured using the Kjehldahl method (ZBÍRAL 2005). The analyses were made in an accredited laboratory (AgroLab, Troubsko, Czech Republic).

Above-ground non-woody biomass was clipped in a quadrat of 0.25 m² placed within each plot of 100 m². This quadrat was selected based on visual assessment to represent mean biomass within the plot. Our pilot analyses showed that the variation in biomass parameters measured in a few 0.25-m²

Fig. 2. a) Basiphilous dry grassland with *Stipa capillata*, *Festuca valesiaca*, *Echium vulgare* and *Achillea collina* on a slope of Radobýl Hill in the České středohoří Mts, with Lovoš and Milešovka volcanic hills in the background (photo K. Merunková, 2007). **b)** Acidophilous dry grassland with *Koeleria macrantha*, *Rumex acetosella*, *Dianthus carthusianorum* and *Anthericum liliago* in the Velká Pleš National Nature Reserve in the Křivoklát region, surrounded by a thermophilous oak forest. Treeless cliffs of Čertova skála on the opposite side of the Berounka river valley are visible in the background (photo E. Hettenbergerová, 2005).

Abb. 2. a) Basiphiler Trockenrasen mit *Stipa capillata*, *Festuca valesiaca*, *Echium vulgare* und *Achillea collina* am Radobýl im Böhmischen Mittelgebirge mit den Vulkanhügeln Lovoš und Milešovka im Hintergrund (Foto: K. Merunková, 2007). **b)** Acidophiler Trockenrasen mit *Koeleria macrantha*, *Rumex acetosella*, *Dianthus carthusianorum* and *Anthericum liliago* im Naturschutzgebiet Velká Pleš im Pürglitz-Gebiet umgeben von thermophilem Eichenwald. Im Hintergrund auf der anderen Talseite des Berounka-Flusses sind die baumfreien Felsen des Čertova skála zu sehen (Foto: E. Hettenbergerová, 2005).

Table 1. Descriptive statistics for variables used in the analysis.

Tabelle 1. Deskriptive Statistik für die in den Analysen verwendeten Variablen.

	České středohoří Mts (n = 33)				Křivoklát region (n = 29)			
	Mean	SD	Min	Max	Mean	SD	Min	Max
Soil pH	5.6	1.3	4.1	7.7	5.1	1.2	4.0	7.8
Soil depth [cm]	14	7	5	30	11	5	3	26
P soil [ppm]	25	26	1	138	60	70	4	277
K soil [ppm]	517	380	117	2234	183	102	65	493
Ca soil [ppm]	4050	3450	506	14136	2799	3813	352	19236
Mg soil [ppm]	339	253	62	774	129	68	50	348
Organic C soil [%]	12	6	5	40	12	6	4	27
C/N soil	23	15	14	102	20	5	14	37
Biomass [g/m²]	167	112	2	454	83	59	10	242
Biomass herbs [g/m²]	80	67	0	308	37	29	0	99
Biomass graminoids [g/m²]	86	93	0	404	44	47	0	186
N biomass [%]	1.96	0.46	1.18	3.34	1.93	0.49	1.05	2.98
P biomass [%]	0.16	0.06	0.06	0.35	0.18	0.05	0.08	0.29
K biomass [%]	1.93	0.92	0.81	4.55	1.38	0.46	0.57	2.23
Ca biomass [%]	0.85	0.50	0.19	2.92	0.82	0.55	0.20	2.51
N biomass herbs [%]	2.20	0.49	1.38	3.34	2.25	0.45	1.59	3.33
P biomass herbs [%]	0.19	0.07	0.09	0.49	0.22	0.06	0.15	0.37
K biomass herbs [%]	2.32	0.84	0.75	4.55	1.86	0.46	0.91	2.77
Ca biomass herbs [%]	1.28	0.62	0.19	3.06	1.26	0.70	0.31	3.34
N biomass graminoids [%]	1.55	0.25	1.17	2.31	1.60	0.45	0.92	3.14
P biomass graminoids [%]	0.11	0.04	0.06	0.23	0.13	0.05	0.07	0.29
K biomass graminoids [%]	1.10	0.43	0.53	2.72	0.94	0.40	0.28	1.98
Ca biomass graminoids [%]	0.40	0.21	0.18	1.20	0.42	0.17	0.14	0.76
N/P biomass	13.4	3.9	4.5	23.3	11.3	2.4	7.1	16.9
N/P biomass herbs	12.4	3.6	3.3	19.8	10.5	2.5	5.7	16.1
N/P biomass graminoids	15.6	4.2	6.6	23.7	12.6	3.0	7.6	19.5
Annual precipitation [mm]	531	38	470	643	551	7	527	562
No. of vascular plant species	39.8	10.6	14	54	33.8	11.7	13	55
No. of herb species	28.1	9.8	7	43	24.4	9.1	5	39
No. of graminoid species	8.3	3.3	1	14	5.6	2.2	2	11

quadrats placed within the same 100-m² plot was rather low, therefore we used only one quadrat per plot. Biomass was separated into non-graminoid herbs (hereafter referred to as herbs), graminoids, and leaves of shrubs. Then it was oven-dried and weighed. The biomass dry weight was recalculated to g/m² and used as an estimate of annual primary productivity. The biomass was analyzed for nitrogen, phosphorus, potassium and calcium. For nitrogen determination, dry biomass was mineralized with sulphuric acid and hydrogen peroxide, and the nitrogen concentration was determined by the distillation method. For the determination of other elements (P, N, Ca), biomass was mineralized by microwave heating and determined using the same methods and in the same laboratory as mentioned above. We used biomass concentrations of these nutrients in addition to soil analysis as an alternative way of quantification of the ecosystem nutrient status. While soil analysis may not correctly reflect the nutrient availability for plants (especially for nitrogen), biomass concentrations measure the quantity of nutrients actually used by plants. However, biomass concentration is also not an ideal measure of available nutrients, because it may be affected by the dilution effect, i.e. decrease of nutrient concentrations as biomass grows, and by the specifics of the nutrient cycling patterns in the dominant species.

Soil depth, biomass weight and nutrient concentrations in soil and biomass were square-root transformed to achieve normal distributions. To visualize the major pattern in species composition unconstrained by relations to environmental variables, we used detrended correspondence analysis (DCA) and computed separately for each region. Percentage cover of species was square-root transformed for DCA. To test the relationships between species composition and environmental variables, we used canonical correspondence analysis (CCA), which was also computed separately for each region. First, gross effects of each variable on species composition were tested in models containing a single environmental variable each using Monte Carlo permutation tests with 999 permutations. Second, models of species composition including several environmental variables were prepared using the stepwise forward selection of variables in CCA. In the stepwise selection, variables were added to the model if they significantly ($p < 0.05$) increased the variation explained by the model in addition to the variables already included. Also in this case, p values were established using Monte Carlo tests with 999 permutations. DCA and CCA analyses were computed using CANOCO 4.5 (TER BRAAK & ŠMILAUER 2002).

Univariate relationships between species richness, environmental variables and biomass were quantified using regression analysis. In addition to linear relationships, we tested for quadratic relationships and included quadratic terms if they contributed significantly ($p < 0.05$) to the explanatory power of the linear terms. Finally, we calculated multiple regression models using forward stepwise selection of variables, in which both linear and quadratic terms were offered for selection. Also in this case, new variables were added if they significantly ($p < 0.05$) increased the variation explained by the model. All regression analyses were also calculated separately for each region, using STATISTICA 10 (www.statsoft.com).

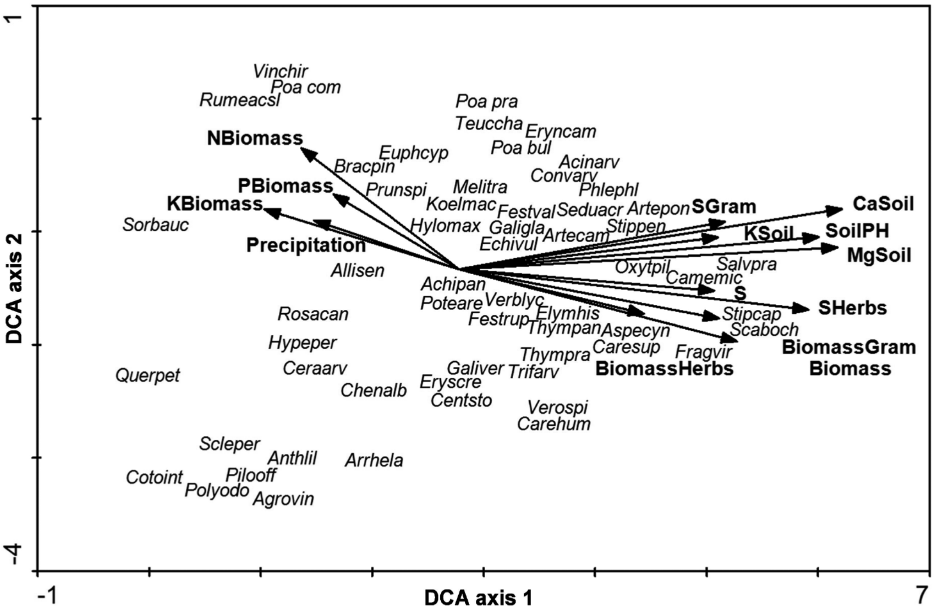
4. Results

4.1 Species composition

The main variation in species composition of dry grasslands in both study regions, as detected by the first DCA axis, was associated especially with soil pH, soil calcium and magnesium concentration, and in the Křivoklát region with the biomass calcium concentration in addition to those mentioned above (Fig. 3). In both regions, precipitation was negatively correlated with soil pH, calcium and magnesium concentrations along this gradient. The second most important gradient in species composition was poorly related to any environmental variable in the České středohoří Mts. In the Křivoklát region, the second compositional gradient extended from dry grasslands on rock outcrops towards more mesic grassland types, following the gradient of increasing soil depth and phosphorus in soil, which was positively correlated with biomass weight and negatively with soil organic carbon.

When we tested the effects of individual environmental variables separately in CCA, species composition was most strongly related to soil pH, calcium and magnesium, nutrient (nitrogen, phosphorus and potassium) concentrations in biomass, biomass weight and precipitation in the České středohoří Mts. In the Křivoklát region, nutrient concentrations in biomass had no significant effects, while most other variables that affected species composition in the České středohoří Mts were also important there; in addition, N/P ratios in biomass and soil depth appeared to be important factors to explain the variation in species composition (Table 2). In the CCA models with multiple environmental variables, species compositional variation in dry grasslands of the České středohoří Mts was best explained by the joint effect of soil pH, phosphorus in soil, nitrogen in biomass of all vascular plants, as well as in the

a) České středohoří Mts



b) Křivoklát region

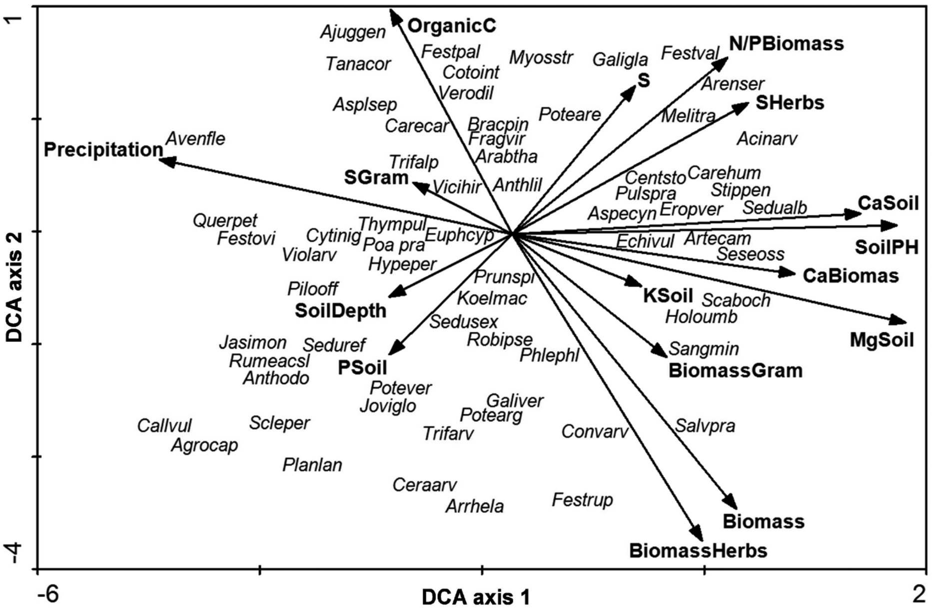


Fig. 3. Species diagrams of DCA ordination for the two study regions. Eigenvalues: **a)** České středohoří Mts – axis 1: 0.581, axis 2: 0.264, total inertia 5.739; **b)** Křivoklát region – axis 1: 0.540, axis 2: 0.329; total inertia 5.471. Number of all vascular plants (S), herbs (SHerbs) and graminoids (SGram) and environmental variables significantly related to species composition (according to the CCA tests with single variables; $p < 0.05$) are passively projected onto the DCA diagrams. For simplicity, nutrient concentrations in biomass of herbs and graminoids were omitted even if they were significant, because they gave very similar results as nutrient concentrations in total biomass. Only species with the highest weight in the analysis are shown. Acinarv, *Acinos arvensis*; Agrocap, *Agrostis capillaris*; Agrovin, *Agrostis vinealis*; Achipan, *Achillea pannonica*; Ajuggen, *Ajuga genevensis*; Allisen, *Allium senescens*; Anthlil, *Anthericum liliago*; Anthodo, *Anthoxanthum odoratum*; Arabtha, *Arabidopsis thaliana*; Arenser, *Arenaria serpyllifolia*; Arrhela, *Arrhenatherum elatius*; Artecam, *Artemisia campestris*; Artepon, *Artemisia pontica*; Aspecyn, *Asperula cynanchica*; Asplsep, *Asplenium septentrionale*; Avenfle, *Avenella flexuosa*; Bracpin, *Brachypodium pinnatum*; Callvul, *Calluna vulgaris*; Camemic, *Camelina microcarpa*; Carecar, *Carex caryophylla*; Carehum, *Carex humilis*; Caresup, *Carex supina*; Centsto, *Centaurea stoebe*; Ceraarv, *Cerastium arvense*; Chenalb, *Chenopodium album*; Convarv, *Convolvulus arvensis*; Cotoint, *Cotoneaster integerrimus*; Cytinig, *Cytisus nigricans*; Echivul, *Echium vulgare*; Elymhis, *Elymus hispidus*; Eropver, *Erophila verna*; Eryncam, *Eryngium campestre*; Eryscre, *Erysimum crepidifolium*; Euphcyp, *Euphorbia cyparissias*; Festovi, *Festuca ovina*; Festpal, *Festuca pallens*; Festrup, *Festuca rupicola*; Festval, *Festuca valesiaca*; Fragvir, *Fragaria viridis*; Galigla, *Galium glaucum*; Galiver, *Galium verum*; Holoumb, *Holosteum umbellatum*; Hylomax, *Hylotelephium maximum*; Hypeper, *Hypericum perforatum*; Jasimon, *Jasione montana*; Joviglo, *Jovibarba globifera*; Koelmac, *Koeleria macrantha*; Melitra, *Melica transsilvanica*; Myosstr, *Myosotis stricta*; Oxytpil, *Oxytropis pilosa*; Phlephl, *Phleum phleoides*; Pilooff, *Pilosella officinarum*; Planlan, *Plantago lanceolata*; Poa bul, *Poa bulbosa*; Poa com, *Poa compressa*; Poa pra, *Poa pratensis*; Polyodo, *Polygonatum odoratum*; Poteare, *Potentilla arenaria*; Potearg, *Potentilla argentea*; Potever, *Potentilla verna*; Prunspi, *Prunus spinosa* juv.; Pulspra, *Pulsatilla pratensis*; Querpet, *Quercus petraea* juv.; Robipse, *Robinia pseudoacacia* juv.; Rosacan, *Rosa canina* juv.; Rumeacsl, *Rumex acetosella*; Salvpra, *Salvia pratensis*; Sangmin, *Sanguisorba minor;* Scaboch, *Scabiosa ochroleuca*; Scleper, *Scleranthus perennis*; Seduacr, *Sedum acre*; Sedualb, *Sedum album*; Seduref, *Sedum reflexum*; Sedusex, *Sedum sexangulare*; Seseoss, *Seseli osseum*; Sorbauc, *Sorbus aucuparia* juv.; Stipcap, *Stipa capillata*; Stippen, *Stipa pennata*; Tanacor, *Tanacetum corymbosum*; Teuccha, *Teucrium chamaedrys*; Thympan, *Thymus pannonicus*; Thympra, *Thymus praecox*; Thympul, *Thymus pulegioides*; Trifalp, *Trifolium alpestre*; Trifarv, *Trifolium arvense*; Verblyc, *Verbascum lychnitis*; Verodil, *Veronica dillenii;* Verospi, *Veronica spicata*; Vicihir, *Vicia hirsuta*; Vinchir, *Vincetoxicum hirundinaria*.

Fig. 3. Arten-Diagramm nach einer DCA-Ordination für die beiden Untersuchungsgebiete. Eigenwerte: **a)** Böhmisches Mittelgebirge – DCA-Achse 1: 0,581, Achse 2: 0,264, total inertia 5,739; **b)** Pürglitz-Gebiet – Achse 1: 0,540, Achse 2: 0,329; total inertia 5,471. Der Artenreichtum aller Gefäßpflanzen (S), Kräuter (SHerbs) und Gräser mit Grasartigen (SGram) sowie die (nach CCA-Tests mit Einzelvariablen) signifikant ($p < 0,05$) mit der Artenzusammensetzung korrelierten Umweltvariablen wurden passiv in das DCA-Diagram projeziert. Der Übersichtlichkeit halber wurden die Nährstoffkonzentrationen der Biomasse der Kräuter und Gräser mit Grasartigen, auch wenn sie signifikant waren, weggelassen, da sie sehr ähnliche Ergebnisse wie die Nährstoffkonzentrationen der Gesamtbiomasse zeigten. Nur die Arten mit dem höchsten Gewicht in der Analyse sind dargestellt. Für die Bedeutung der Art-Kürzel siehe die englische Abbildungsunterschrift.

herb and graminoid fractions separately, and precipitation. Compositional variation in the Křivoklát region was best described by joint effects of soil pH, soil depth, phosphorus, magnesium and organic carbon in soil, biomass weight of all plants and potassium in herb biomass (Table 2).

Table 2. Variation in species composition explained by individual variables in separate CCA analyses, calculated as a percentage of the canonical eigenvalue to total inertia. p-values were established using Monte Carlo tests with 999 permutations. Bold values indicate significant ($p < 0.05$) effect on species composition. Shading indicates variables included in the models of environmental control of species composition for each of the two regions, built using forward stepwise selection of variables in CCA.

Tabelle 2. Durch Einzelvariablen in separaten CCA-Analysen erklärter Anteil der Variation in der Artenzusammensetzung in zwei Untersuchungsregionen. Errechnet wurde der Prozentsatz des kanonischen Eigenwerts an der *total inertia*. Die p-Werte stammen aus Monte-Carlo-Tests mit 999 Permutationen. Werte in Fettschrift zeigen signifikante ($p < 0{,}05$) Effekte auf die Artenzusammensetzung an. Umweltvariablen mit Effekt auf die Artenzusammensetzung auf Basis von *forward stepwise selection* der Variablen in der CCA sind grau hinterlegt.

	České středohoří Mts			Křivoklát region		
	% variation explained	*F*-value	*p*	% variation explained	*F*-value	*p*
Soil pH	**6.3**	**2.149**	**0.001**	**7.4**	**2.143**	**0.001**
Soil depth	3.4	1.134	0.159	**6.0**	**1.717**	**0.002**
P soil	3.9	1.296	0.075	**4.6**	**1.314**	**0.029**
K soil	**4.7**	**1.568**	**0.028**	**5.7**	**1.633**	**0.004**
Ca soil	**6.4**	**2.199**	**0.001**	**6.7**	**1.934**	**0.001**
Mg soil	**6.3**	**2.144**	**0.001**	**7.6**	**2.206**	**0.001**
Organic C soil	2.9	0.960	0.533	**4.6**	**1.298**	**0.037**
C/N soil	2.5	0.808	0.746	3.7	1.034	0.377
Biomass	**5.0**	**1.672**	**0.002**	**6.3**	**1.804**	**0.001**
Biomass herbs	**4.4**	**1.486**	**0.009**	**5.3**	**1.519**	**0.009**
Biomass graminoids	**4.9**	**1.643**	**0.001**	**4.8**	**1.367**	**0.018**
N biomass	**5.1**	**1.712**	**0.001**	3.9	1.093	0.257
P biomass	**4.1**	**1.351**	**0.044**	4.4	1.231	0.073
K biomass	**4.5**	**1.503**	**0.006**	3.7	1.027	0.361
Ca biomass	3.7	1.239	0.097	**5.6**	**1.608**	**0.003**
N biomass herbs	**5.1**	**1.717**	**0.019**	**4.7**	**1.325**	**0.044**
P biomass herbs	**5.0**	**1.690**	**0.013**	4.3	1.202	0.104
K biomass herbs	**4.7**	**1.561**	**0.019**	4.5	1.283	0.052
Ca biomass herbs	**5.0**	**1.668**	**0.004**	**7.0**	**2.034**	**0.001**
N biomass graminoids	**7.1**	**2.434**	**0.001**	3.2	0.887	0.719
P biomass graminoids	**6.4**	**2.174**	**0.001**	3.7	1.037	0.354
K biomass graminoids	**5.9**	**2.018**	**0.001**	3.8	1.079	0.265
Ca biomass graminoids	**6.2**	**2.131**	**0.001**	4.4	1.241	0.074
N/P biomass	2.8	0.927	0.669	**5.5**	**1.569**	**0.005**
N/P biomass herbs	3.8	1.275	0.061	**5.0**	**1.429**	**0.013**
N/P biomass graminoids	**5.6**	**1.912**	**0.001**	3.3	0.912	0.684
Annual precipitation	**5.5**	**1.869**	**0.002**	**6.8**	**1.982**	**0.001**
Model with multiple variables	**29.4**	**1.805**	**0.001**	**36.0**	**1.690**	**0.001**

4.2 Species richness

Plots in the České středohoří Mts contained 14–54 vascular plant species (median 43) per 100 m^2 and those in the Křivoklát region contained 13–55 species (median 35). In the České středohoří Mts, the number of all vascular plant species responded most strongly to soil pH, biomass weight of graminoids and calcium in soil (unimodal relationships), followed by nitrogen in biomass (negative linear relationship) and total biomass weight (positive linear relationship) (Table 3, Fig. 4). For the number of non-graminoid herb species the relationships were generally stronger than for the number of graminoids, though following a similar pattern. In the Křivoklát region, the response of vascular plant species richness to environ-

Table 3. Standardized regression coefficients (beta) for linear or quadratic terms and variation explained (adjusted R^2) in the univariate regression models of the relationship between the number of all vascular plant species, number of herb species and number of graminoid species in plots of 100 m^2, and environmental variables. All reported coefficients are significant at $p < 0.05$. Statistics for non-significant coefficients, as well as variables with no significant coefficients, are not shown.

Tabelle 3. Standardisierte Regressionskoeffizienten (Beta) für lineare und quadratische Zusammenhänge sowie der Anteil der erklärten Varianz (adjustiertes R^2) in den univariaten Regressionsmodellen für den Zusammenhang zwischen der Anzahl aller Gefäßpflanzenarten, Anzahl Krautarten und Anzahl Gräser mit Grasartigen auf 100 m^2-Flächen und den Umweltvariablen. Alle angegebenen Koeffizienten sind signifikant bei $p < 0,05$. Für nicht-signifikante Koeffizienten sowie nicht-signifikante Variablen sind keine statistischen Ergebnisse dargestellt.

	No. of all species			No. of herb species			No. of graminoid species		
	beta-linear	beta-quad.	adj R^2	beta-linear	beta-quad.	adj R^2	beta-linear	beta-quad.	adj R^2
České středohoří Mts									
Soil pH	7.15	-6.70	0.45	7.50	-6.98	0.55	5.92	-5.50	0.33
Soil depth	0.46	–	0.19	0.48	–	0.20	–	–	–
K soil	0.35	–	0.09	0.41	–	0.14	0.44	–	0.16
Ca soil	2.41	-1.96	0.36	2.68	-2.15	0.49	0.48	–	0.21
Mg soil	0.47	–	0.19	2.77	-2.26	0.33	0.55	–	0.28
C/N soil	-0.37	–	0.11	–	–	–	-0.38	–	0.12
Biomass	0.58	–	0.31	0.59	–	0.32	0.57	–	0.30
Biomass herbs	–	–	–	0.36	–	0.10	–	–	–
Biomass graminoids	1.62	-1.12	0.43	1.73	-1.23	0.46	0.58	–	0.31
N biomass	-0.61	–	0.35	-0.60	–	0.34	-0.50	–	0.22
P biomass	-0.37	–	0.11	-0.46	–	0.19	–	–	–
K biomass	-0.38	–	0.12	-0.48	–	0.21	–	–	–
N biomass herbs	-0.39	–	0.12	-0.44	–	0.16	–	–	–
K biomass herbs	–	–	–	-0.40	–	0.13	–	–	–
Ca biomass herbs	–	–	–	0.40	–	0.13	–	–	–
Křivoklát region									
Soil pH	0.41	–	0.13	4.81	-4.27	0.35	–	–	–
Soil depth	–	–	–	–	–	–	0.47	–	0.19
K soil	0.42	–	0.14	0.46	–	0.18	–	–	–
Ca soil	–	–	–	0.47	–	0.19	–	–	–
Mg soil	0.40	–	0.13	2.70	-2.18	0.35	–	–	–
Biomass graminoids	–	–	–	–	–	–	0.43	–	0.16
Ca biomass	–	–	–	2.35	-1.85	0.34	–	–	–
K biomass herbs	0.50	–	0.22	0.41	–	0.13	–	–	–
Ca biomass herbs	0.46	–	0.18	2.33	-1.75	0.42	–	–	–
Ca biomass graminoids	0.47	–	0.18	0.64	–	0.38	–	–	–

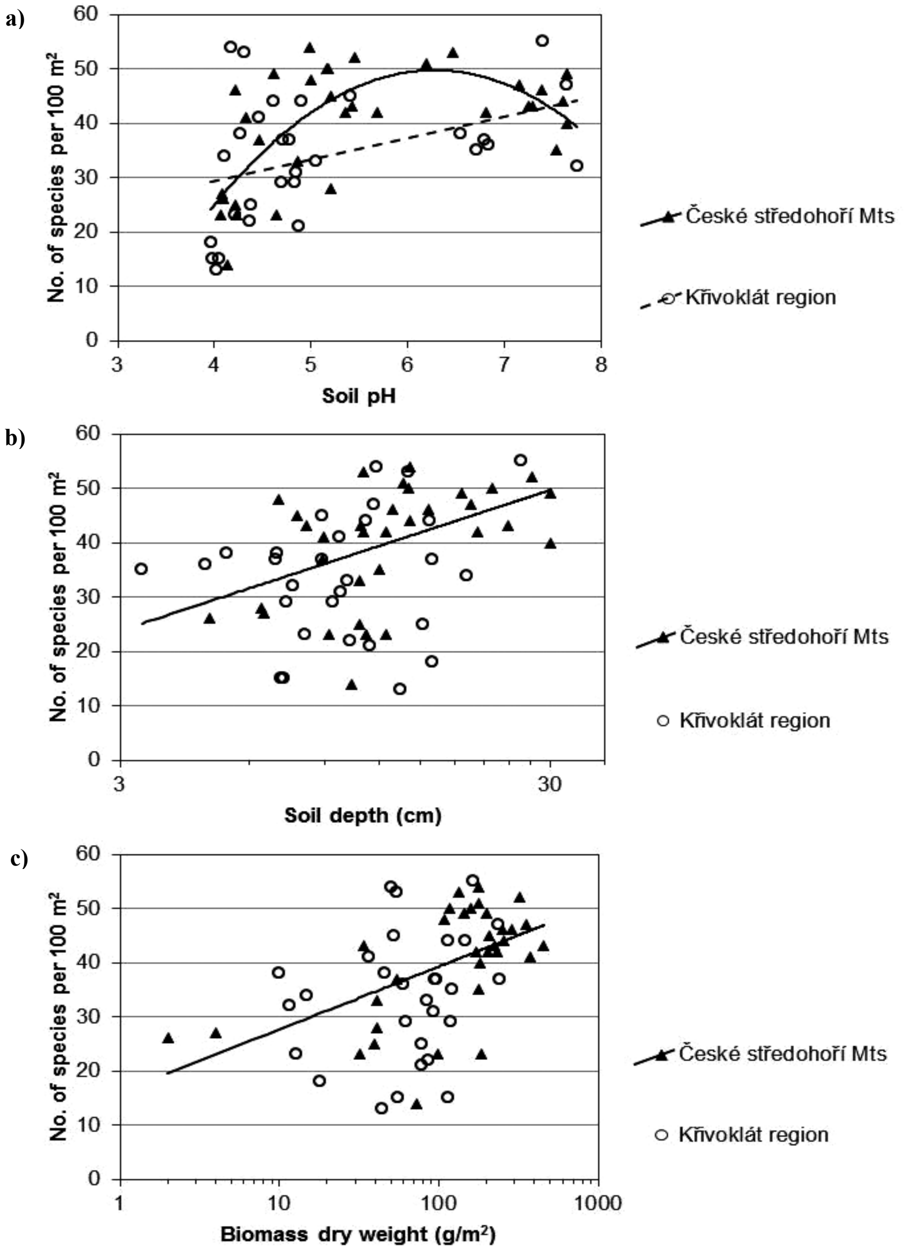


Fig. 4. Number of all vascular plant species recorded in dry grassland plots of 100 m^2 plotted against soil pH (a), soil depth (b) and productivity expressed as above-ground biomass dry weight without litter (c). Lines are fitted for significant (*P*p< 0.05) regressions only: non-significant relationships for the Křivoklát region in (b) and (c) are not shown.

Abb. 4. Auftragung der Anzahl aller Gefäßpflanzenarten auf 100 m^2-Flächen gegen den pH-Wert des Bodens (a), die Bodentiefe (b) und die Produktivität gemessen als Trockengewicht der oberirdischen Biomasse ohne Streu (c). Regressionsgeraden sind nur für signifikante ($p < 0,05$) Beziehungen dargestellt. Nicht-signifikante Beziehungen im Pürglitz-Gebiet (Křivoklát region) in (b) und (c) sind nicht dargestellt.

mental variables was weaker than in the České středohoří Mts, with the best predictors being potassium and calcium in biomass of herbs, and calcium in biomass of graminoids (positive linear relationships in all cases). For the number of herb species in the Křivoklát region, the relationship was stronger than for the number of all plant species, with the best predictors being calcium in biomass of herbs (unimodal relationship), calcium in biomass of graminoids (positive linear relationship), followed by soil pH and soil magnesium (unimodal relationship). The number of graminoids was correlated only with soil depth and biomass of graminoids (positive linear relationships). The best multiple regression models for the numbers of all species explained 47.6% of variation in the České středohoří Mts and 41.8% in the Křivoklát region (Table 4).

Table 4. Multiple regression models for species richness in the České středohoří Mts and Křivoklát regions, built using the forward stepwise selection with linear and quadratic terms of all variables as the input. Standardized regression coefficients (beta), adjusted coefficients of determination (adjusted R^2) and significances (*p*) are given.

Tabelle 4. Multiple Regressionsmodelle für den Artenreichtum der Trockenrasen im Böhmischen Mittelgebirge und Pürglitz-Gebiet auf der Grundlage von *forward stepwise selection* mit linearen und quadratischen Größen aller Variablen als Eingabe. Dargestellt sind standardisierte Regressionskoeffizienten (Beta), angepasste Bestimmtheitsmaße (adj R^2) und Signifikanzen (*p*).

České středohoří Mts

Number of all species = 0.402 Biomass - 0.455 [N biomass]^2 (adj $R^2 = 0.476$, $p < 0.001$)

Number of herb species = 3.193 Ca soil + 0.377 Biomass herbs - 2.752 [Ca soil]^2 + 0.306 [N/P biomass herbs]^2 (adj $R^2 = 0.680$, $p < 0.001$)

Number of graminoid species = 0.395 K soil (adj $R^2 = 0.121$, $p = 0.046$)

Křivoklát region

Number of all species = 0.483 Soil pH + 0.520 [Organic C soil]^2 + 0.474 [Biomass]^2 + 0.531 [K biomass]^2 (adj $R^2 = 0.418$, $p = 0.002$)

Number of herb species = 0.516 Mg soil + 0.342 Ca biomass herbs + 0.311 [Organic C soil]^2 + 0.611 [K biomass]^2 (adj $R^2 = 0.621$, $p < 0.001$)

Number of graminoid species = 0.474 [Soil depth]^2 (adj $R^2 = 0.191$, $p = 0.017$)

5. Discussion

Our study suggests that soil pH is a key environmental variable affecting species diversity of central European steppic grasslands. In both study areas, we captured a broad range of soil pH (approximately from 4 to 8), which constituted the most important gradient along which species composition changed. Importance of pH is well reflected in the common differentiation of high-rank phytosociological units of herbaceous vegetation into acidic and calcareous community types (Mucina & Kolbek 1993, Chytrý 2007, Dúbravková et al. 2010). In addition to toxic effects of Al^{3+} and H^+ ions released in low-pH soils, which severely restrict the pool of species tolerant to acidic environments (Tyler 1996, 2003), pH controls mineral nutrient availability across the whole gradient, causing e.g. low phosphate solubility in both alkaline and very acidic soils (Tyler & Olsson 2001). These effects influence competitive hierarchies among plant species with different nutritional requirements and nutrient uptake abilities.

Soil pH, along with associated soil properties (mainly calcium and magnesium concentrations), does not only affect species composition, but it also drives the pattern of species richness in the studied steppe plant communities. Species richness was found to be unimodally related to soil pH in the České středohoří Mts, with an increase from pH 4 to ~6.5 and a decrease from pH ~6.5 to 8. This relationship was especially strong for the numbers of herbs and weaker for the numbers of graminoids. Similar unimodal relationships were often found in grassland studies which encompassed a sufficiently broad pH gradient. For example, TYLER (1996) found a unimodal relationship with a peak at pH (KCl) of about 6.5 in southern Sweden. BECKER & BRÄNDEL (2007) reported a unimodal relationship, but with peak species richness around pH (H_2O) 7.5, in dry grasslands on soils rich in heavy metals in central Germany. KRATZERT & DENGLER (1999) found the peak species richness around pH (H_2O) 6.3 in dry grasslands in eastern Germany and LÖBEL et al. (2006) also reported a unimodal relationship from dry grasslands of southern Öland, Sweden. Although the range of soil pH sampled in the Křivoklát region was nearly identical to the range recorded in the České středohoří Mts, only the number of herbs displayed unimodal relationship there, whereas the total number of species was weakly positively related. The number of graminoids did not show any relationship with soil pH in the Křivoklát region. Different responses of various plant functional groups to pH, previously reported e.g. for bryophytes and lichens in contrast to vascular plants (LÖBEL et al. 2006), are one of the possible reasons for the differences in species richness-pH patterns across vegetation types (SCHUSTER & DIEKMANN 2003). Irrespective of vegetation type, linear relationships are usually found when studying short gradients that lack one or both extremes (GOUGH et al. 2001, PALMER et al. 2003, PIQUERAY et al. 2007, MERUNKOVÁ et al. 2012). Their direction depends on the position of the studied section on the entire pH gradient, on the differences in species pool size between various pH levels (PÄRTEL 2002, EWALD 2003) or on effects of interrelated factors. For example, CHYTRÝ et al. (2007), reporting a negative linear richness-pH relationship in the steppes of southern Siberia, suggested that the decrease in species richness towards high pH is caused by drought stress occurring on high-pH soils rather than by direct negative physiological effects of high pH. A pattern shared by both of our study regions is that up to pH 5, the species richness varied between 11 and 54 per plot, while plots with pH > 5 rarely had fewer than 35 species per 100 m^2. We suggest two explanations: (1) Although pH defines the main division of plots into groups with low vs. high average species richness, within plots on acidic soils, other factors apart from pH determine actual species richness. An exception was a group of plots with pH 4.0–4.1, where the constraining effect of extremely low pH kept the number of species consistently under 35 per 100 m^2 in all cases. (2) The soil of the species-rich plots in which low pH was measured may not have been acidic throughout the entire root zone. Some of these plots may have contained moderately base-rich bedrock with leached topsoil, supporting the occurrence of a rich mixture of plants with varied pH optima. Previous studies from dry grasslands in the České středohoří Mts indicate that proximity to bedrock and presence of scattered stones or rubble can considerably influence pH variation in soil (SLAVÍKOVÁ et al. 1983).

In steppes and related types of dry grasslands, water availability (usually approximated by surrogate variables such as precipitation or soil depth) has been identified as one of the most important drivers of plant species composition (MICHÁLKOVÁ 2007, DÚBRAVKOVÁ et al. 2010, DENGLER et al. 2012, REITALU et al. 2014) and productivity (LAVRENKO et al. 1993, BAI et al. 2007, MA et al. 2010). Productivity is considered as an important determinant of species richness (ROSENZWEIG 1995), but the positive correlation between species richness and productivity can also result from independent responses of each of these variables to other environmental variables, such as water availability in steppe vegetation (MA et al. 2010). Moreover, there can be considerable regional differences in the shape and strength of this relationship (KLAUS et al. 2013). In contrast to the hump-shaped relationship between species richness and productivity, frequently observed in mesic or wet grasslands of the Northern Hemisphere (OLDE VENTERINK et al. 2001, SCHAFFERS 2002, WEIHER et al. 2004, AXMANOVÁ et al. 2013), Eurasian steppes present a different picture. BAI et al. (2007) reported a predominance of positive linear relationships between species richness and productivity in the steppes of Inner Mongolia, and MA et al. (2010) described the same trend across a broad range of Chinese grasslands including various types of steppe. LAVRENKO et al. (1993) reported a similar pattern for the steppes of Eastern Europe and Central Asia. Our data from the České středohoří Mts, despite their limited geographical span compared to the above-mentioned studies, also show positive relationship between species richness and above-ground biomass dry weight (a measure of productivity in this study), accounting for 31% of variation in the number of species. This is in agreement with the results of a detailed ecological study of Oblík Hill in the České středohoří Mts, where the highest numbers of species was also found in steppe grasslands of high productivity (SLAVÍKOVÁ et al. 1983). In the Křivoklát region, which has a less pronounced steppic character and more links to western and central European dry grasslands than the České středohoří Mts, only graminoids exhibited a significant positive diversity-productivity relationship. Nevertheless, in both regions, plots with biomass dry weight higher than 200 g/m² and soil deeper than 20 cm nearly always contained more than 40 species per 100 m². Plots with lower productivity and on shallower soils were more variable in species numbers, suggesting importance of other factors at these sites. Contrary to large-scale studies (LAVRENKO et al. 1993, BAI et al. 2007, MA et al. 2010) that reported strong effects of precipitation on productivity and species richness of Eurasian steppes, in our regionally focused study, precipitation was unrelated to the above-ground biomass or species richness in both regions. The effect of precipitation on water availability was most likely overridden by variation in soil depth driven mainly by topography. Our data suggest that even though productivity is driven by water availability resulting from large-scale precipitation patterns in some cases, and from small-scale topographic patterns in other cases, the resulting species richness-productivity relationship is consistent with that reported in large-scale studies of Eurasian steppes.

Availability of nutrients such as nitrogen, phosphorus and potassium had less consistent effects on species composition and richness of the studied dry grasslands than soil pH (or calcium and magnesium) and productivity. Strong responses of both species composition and richness were found to biomass nitrogen concentration in the České středohoří Mts, but not in the Křivoklát region. Species richness in the České středohoří Mts declined with increasing concentration of nitrogen in the above-ground biomass. Nitrogen is often reported as the second factor limiting productivity in steppes and deserts, after water availability (VITOUSEK & HOWARTH 1991); however, its positive effect on biomass production is accompanied by acidification and base depletion (HORSWILL et al. 2008), effects on soil microbial processes (JOHNSON et al. 1998) and changes in interspecific competitive interactions (STEVENS et al. 2004). Higher biomass nitrogen concentration at some of our sites may be due to high atmospheric nitrogen deposition. Annual deposition of nitrogen in the study area has fluctuated between 10 and 25 kg/ha in recent decades, with even higher local peaks in some places (Czech Hydrometeorological Institute, http://portal.chmi.cz), which means that deposition levels are high enough to cause soil nitrogen accumulation over time. DUPRÉ et al. (2010) observed a strong decline in the number of plant species, especially dicots, and an increase in grasses in acidic grasslands of Great Britain and Germany in response to accumulated nitrogen deposition. Altered species composition and loss of species resulting from nitrogen deposition have been reported from grasslands in other areas of Eurasia (STEVENS et al. 2004, BAI et al. 2010, BOBBINK et al. 2010).

We conclude that species composition and richness of dry grasslands in northern and central Bohemia is driven especially by soil pH and primary productivity, with higher numbers of species at sites with soil pH above 5, soil depth above 20 cm and above-ground biomass dry weight above 200 g/m². However, availability of nutrients, especially nitrogen is also important.

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Erweiterte deutsche Zusammenfassung

Einleitung. Die mitteleuropäischen Trockenrasen an der westlichen Verbreitungsgrenze der Eurasischen Waldsteppengebiete stellen bemerkenswert artenreiche Vegetationstypen dar und enthalten zahlreiche Pflanzenarten mit kontinentalem Verbreitungsschwerpunkt. In dieser Studie befassen wir uns mit den Trockenrasen des Böhmischen Mittelgebirges (Nord-Böhmen; České středohoří) und des Pürglitz-Gebietes (Mittel-Böhmen; Křivoklátsko) in der Tschechischen Republik (Abb. 1, 2). Das Böhmische Mittelgebirge umfasst den Kern der nördlichen und zentralen böhmischen Waldsteppen-Zone (MARTINOVSKÝ 1984, CHYTRÝ 2012) mit einer jährlichen Niederschlagsmenge von stellenweise weniger als 500 mm. Die dort vorkommenden primären Steppenrasen existieren höchstwahrscheinlich bereits seit Beginn des Holozäns (JUŘIČKOVÁ et al. 2013a, b). Das Pürglitz-Gebiet befindet sich dagegen ausserhalb der Waldsteppen-Zone mit höheren jährlichen Niederschlagsmengen. Trockenrasen kommen in diesem Gebiet vorwiegend an Felsbändern vor oder stellen Ersatzgesellschaften auf vorherigen Waldstandorten dar. Die Artenzusammensetzung und Syntaxonomie der Trockenrasen wurde in der Vergangenheit ausgiebig untersucht (z. B. KLIKA 1933, 1951, KOLBEK 1975, 1978, 1979, TOMAN 1981, 1988, KOLBEK et al. 2001, CHYTRÝ 2007). Dagegen sind ihre Diversitätsmuster mit den zugrundeliegenden ökologischen Faktoren weitgehend unbekannt. Sie wurden bislang nur exemplarisch am Oblík, einem vulkanischen Hügel des Böhmischen Mittelgebirges quantifiziert (SLAVÍKOVÁ et al. 1983). In der vorliegenden Studie analysieren wir den Einfluss bestimmter Umweltfaktoren auf die Artenzusammensetzung und Artenvielfalt der Trockenrasen im Böhmischen Mittelgebirge und im Pürglitz-Gebiet.

Material und Methoden. Auf 100 m²-Aufnahmeflächen wurden sämtliche Gefäßpflanzenarten, verschiedene bodenchemische Parameter und die oberirdische Biomasseproduktion sowie der Nährstoffgehalt der Biomasse erfasst (Tabelle 1). Beziehungen zwischen Artenzusammensetzung und Umweltvariablen wurden mit multivariaten Methoden (DCA und CCA) untersucht, Beziehungen zwischen Artenvielfalt und Umweltvariablen hingegen mit univariaten und multiplen Regressionsmodellen.

Ergebnisse. In den 100 m²-Aufnahmeflächen kamen zwischen 13 und 55 Pflanzenarten vor. Der Boden-pH (H_2O) mit einer Spanne von 4,0 bis 7,8 war in beiden Regionen positiv mit dem Kalzium- und Magnesiumgehalt des Bodens und negativ mit der jährlichen Niederschlagsmenge korreliert (Tabelle 2, Abb. 3). Die Artenzusammensetzung der Trockenrasen hing vom pH-Wert des Bodens ab. Im Böhmischen Mittelgebirge folgte die Beziehung der Artenvielfalt zum pH-Wert des Bodens einem unimodalen Model mit der höchsten Artenvielfalt um pH 6,5. Im Pürglitz-Gebiet war die Artenvielfalt der Trockenrasen hingegen mit dem pH-Wert des Bodens linear positiv korreliert. Flächen auf Böden mit einem pH-Wert über 5 beherbergten durchgehend mehr als 35 Pflanzenarten (Abb. 4a). Zusätzlich waren Trockenrasen auf tiefgründigen Böden (> 20 cm) und mit einer Biomasseproduktion von mehr als 200 g Trockengewicht pro m² mit durchgehend mehr als 40 Pflanzenarten pro 100 m² sehr artenreich (Abb. 4b). Während in den Trockenrasen des Böhmischen Mittelgebirges die Artenvielfalt positiv mit der oberirdischen Biomasseproduktion korreliert war, zeigte sich dieses Muster im Pürglitz-Gebiet nur für die Artenvielfalt der Gräser (Abb. 4c). In den Trockenrasen des Böhmischen Mittelgebirges nahm die Artenvielfalt zudem mit zunehmender Stickstoffkonzentration der Biomasse ab (Tabelle 3, 4).

Diskussion. Unsere Studie impliziert, dass der Boden-pH in Verbindung mit weiteren Bodenparametern (vorwiegend dem Kalzium- und Magnesiumgehalt) eine Schlüsselrolle für die Artenvielfalt und Artenzusammensetzung der nördlichen und zentral-Böhmischen Trockenrasen spielt. Eine unimodale Beziehung zwischen pH-Wert und Artenvielfalt, wie wir sie in den Trockenrasen der Böhmischen Mittelgebirge vorfanden, steht im Einklang mit zahlreichen anderen Studien aus Nord- und Mitteleuropa (z. B. TYLER 1996, KRATZERT & DENGLER 1999, LÖBEL et al. 2006, BECKER & BRÄNDEL 2007). Lineare Beziehungen zwischen Artenvielfalt und pH-Wert des Bodens, wie wir sie in den Trockenrasen des Pürglitz-Gebietes fanden, wurden hingehen in Studien mit kürzeren pH-Gradienten gefunden. Ein weiteres wichtiges Merkmal der Artenvielfalt im Grasland ist dessen Produktivität. Im Gegensatz zum Grasland auf mittleren oder nassen Standorten der Nordhemisphäre, in denen häufig eine unimodale Beziehung zwischen Produktivität und Artenvielfalt herrscht, ist dieser Zusammenhang in den Eurasischen Steppen normalerweise linear positiv (BAI et al. 2007, MA et al. 2010). Dies war in den Trockenrasen des Böhmischen Mittelgebirges ebenso. Die Produktivität dieser Trockenrasen scheint vorwiegend von der Wasserverfügbarkeit abzuhängen, welche unter anderem von der Menge der Niederschläge und der Bodentiefe abhängt. Die Artenvielfalt der Trockenrasen wird somit negativ (entweder direkt oder indirekt durch die höhere Produktivität) von der verfügbaren Wassermenge beeinflusst. Die Nährstoffgehalte an Stickstoff, Phosphor und Kalium im Boden hatten in den untersuchten Trockenrasen hingegen kaum einen Effekt auf die Artenvielfalt und Artenzusammensetzung. Die Abnahme der Artenvielfalt mit ansteigender Stickstoffkonzentration der Biomasse lässt jedoch auf eine Gefährdung der Diversität der Trockenrasen des Böhmischen Mittelgebirges durch derzeit hohe atmosphärische Stickstoffdepositionen in Verbindung mit fehlender Landnutzung schließen.

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