Past land use co-determines the present distribution of dry grassland plant species

Využití krajiny v minulosti spoluurčuje současné rozšíření druhů

Tereza C h ý l o v á[1] & Zuzana M ü n z b e r g o v á[1,2*]

[1]*Department of Botany, Faculty of Science, Charles University, Benátská 2, CZ-128 01 Praha 2, Czech Republic;* [2]*Institute of Botany, Academy of Sciences of the Czech Republic, Zámek 1, CZ-252 43 Průhonice, Czech Republic, email: zuzmun@natur.cuni.cz*

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Landscapes are constantly changing and, for plant species, this means that some suitable patches disappear while others emerge. Distribution of species in the landscape depends, therefore, not only on actual distribution of suitable habitat patches but also on a species' ability to persist in habitats that are already unsuitable and disperse to habitats that have become suitable. Distribution of species in such landscapes thus strongly depends on the spatio-temporal structure of the landscape and species traits. The present study aims to determine to what degree past land use affects the present distribution of dry grassland plant species at a regional scale. We studied the distribution of 52 dry grassland species in 215 grassland patches. Data on bedrock, slope, potential irradiation, area and past land use for two periods (1950s and 1980s) were collected from maps. Multivariate analysis was performed to assess the relative contribution of environmental and historical factors on present species distribution. In addition, analyses were carried out to reveal the relationship between past land use and occurrence of single species. This study shows that dry grasslands are habitats with rapid land-use changes. Distribution of species in these habitats is largely determined by environmental conditions, but past land-use also has a significant effect. In many species, the effect of past land use is even more important than the effect of environmental conditions. For the species investigated, those restricted both to former pastures and fields could be identified. Only a minority of species are restricted to continuous grasslands. This indicates that many species colonized places cultivated in 1950 within 50 years, suggesting that the dynamics of these species is relatively fast. The results suggest that many dry grassland communities in the region are of recent origin and the distribution of species in these habitats is partly determined by past land use. In addition to information on environmental conditions, detailed knowledge of land use history, landscape structure and species attributes is needed in order to understand the distribution of species in dry grassland communities.

K e y w o r d s: abandoned agricultural land, grazing, habitat fragmentation, habitat occupancy, habitat suitability, metapopulation dynamics, plant population, seed dispersal, time lag

Introduction

Landscapes are constantly changing and, for plant species, this means that some suitable patches disappear while others emerge. Distribution of species in the landscape depends, therefore, not only on actual distribution of suitable habitat patches but also on a species' ability to persist in habitats that are already unsuitable and disperse to habitats that have become suitable (Eriksson 1996, Ehrlén & Eriksson 2000). Distribution of species in such landscapes thus strongly depends on the spatio-temporal structure of the landscape

* corresponding author

(Fahrig 1992, Quintana-Ascencio & Menges 1996) and on species traits (Dupré & Ehrlén 2002, Maurer et al. 2003, Tremlová & Münzbergová 2007).

Many studies dealing with land-use history show that time since habitat change is the key factor for understanding the distribution pattern of certain species at a regional scale (Peterken & Game 1984, Bellemare et al. 2002, Jacquemyn et al. 2003). Most of these studies have been done in forests. Peterken & Game (1984), Motzkin et al. (1996), Graae & Sunde (2000), Bellemare et al. (2002) and Jacquemyn et al. (2003) conclude that some species occur almost exclusively in primary forests whereas others tend to occur more often in secondary forests. Moreover, according to Koerner et al. (1997), the different distribution patterns observed in some secondary forests depend on past land use.

Most typical forest species are poor at dispersal, which could explain the considerable effect of past land use on the distribution of forest plant species. Graae & Sunde (2000) show that species with heavy seeds, a transient seed bank, ant-dispersed seeds, a short flowering period, low stature and vigorous lateral spread are more common in primary forests while those with small, short-lived seeds, epizoochorous dispersal, a longer period of flowering and poor lateral spread are more common in secondary forests.

Studies of these patterns in grasslands are much less common and some concentrate only on one or a few species (Geertsema et al. 2002, Herben et al. 2006). Studies focusing on more species include e.g., Wells et al. (1976), Quintana-Ascencio & Menges (1996), Austrheim & Olsson (1999), Pärtel et al. (1999), Norderhaug et al. (2000), Cousins & Eriksson (2001, 2002) and Dutoit et al. (2004). Most of these studies, however, deal with overall vegetation changes in the course of secondary succession. Studies exploring the effect of past land use on single species, comparable in scope with the above-mentioned studies on forests, are relatively rare. Also, very few of these studies are of Central European dry grassland communities, which represent a unique species-rich habitat. Grasslands are among the biotopes with the highest diversity of plants in Europe and host many rare species (Willems et al. 1993, Cousins & Eriksson 2002, Poschlod & WallisDeVries 2002). Land-use changes, as important as those in forests, have also occurred in grasslands.

In current grasslands, different past land use has three main consequences for species distribution. First is the physical and chemical alteration of the soil that affects biotic interactions among species. Second is the already mentioned effect of possible time lag between emergence of a patch and its colonization by species. According to the studies on the effect of history on species distribution in forests and grasslands (Peterken & Game 1984, Peterken 1993, Eriksson 1995, Bruun et al. 2001, Bellemare et al. 2002, Cousins & Eriksson 2002) these two types of effect of past land use can persist for at least several decades. There is also a third option. This is the possibility that the habitat patches host species that belong to the the previous community, forming so-called remnant populations (Eriksson 1996).

The present study aims to determine to what degree past land use affects the present distribution of dry grassland plant species at a regional scale. Analysis based on topographical and historical data collected from maps and information on the occurrence of 52 species in 215 patches of grassland was performed to answer the following questions: (i) What were the main changes in land use of the areas of current dry grasslands during the second half of the 20th century? (ii) What is the importance of past land use for species distribution in dry grasslands? (iii) Is it possible to separate effects of past land use from that of the environmental conditions in the grasslands?

Material and methods

Study area

The study was carried out in N Bohemia, Czech Republic. This region is characterized by a high diversity of geology, geomorphology and past land use, and there are several hundred patches of dry grassland scattered throughout a mainly agricultural landscape. Most patches were used for agricultural purposes at least until the 1950s. Nowadays, they are all abandoned and in many places are in the process of secondary succession. If undisturbed, these patches will eventually revert to oak or hornbeam forests. Nevertheless, some patches situated on steep marl slopes are strongly affected by erosion and will follow a different successional sequence. The successional process, however, is slow at all these habitats. At present, these patches host species-rich dry grassland communities; patches overgrown by shrubs were not included in this study. The dry grasslands can be classified as belonging to the *Bromion erecti* Koch 1926 community (Ellenberg 1988).

Data collection

Based on the mapping of habitats within the NATURA 2000 project (Chytrý et al. 2001) 215 dry grassland patches were chosen for the study that quite evenly covered an area of approximately 120 km^2 delimited by the river Labe (Elbe) in the south and the villages Štětí, Křešice u Litoměřic, Tuhaň and Úštěk (see also Tremlová & Münzbergová 2007). Patch size ranged from 0.005 to 21.2 ha, with a mean size of 7.3 ha.

A new digital vector map of inventoried patches was then created based on orthophotomaps from the Czech Office of Surveying, Mapping and Cadastre. Coordinates of patch corners were measured using GPS and identified on the orthophotomaps based on a knowledge of the terrain. A grassland patch is defined as continuous grassland with visually homogenous vegetation separated from other grassland patches by an unsuitable area (arable fields, patches of shrubs etc.). If an abrupt vegetation change occurred within the continuous grassland, the parts with different vegetation were treated as different patches. These cases were uncommon; in all of them there was a visual topographic barrier between the patches such as a small ditch or change of slope from very steep to flat.

For every patch, a number of environmental parameters apparent on the digital maps were recorded. From digital geological maps from the Geological Institute of Czech Academy of Sciences we calculated the proportion of different bedrock types present beneath every patch. Digital contour maps from the Military Geographic and Hydrometeorological Institute were used to collect data on slope and aspect of the patches within a 10 m × 10 m grid. We used median value of slope and aspect to describe the conditions at each patch. For a preliminary analysis, we also used maximum and minimum values and their ranges. Because similar conclusions were recorded using these values it was decided to work only with median values. Information on the slope and aspect was also used to compute potential direct solar irradiation at patches for the 21st day of every month from December to June (Münzbergová 2004). Only the two least correlated months determined using PCA analysis of our data (December and May) were used in the subsequent analyses.

Another option is to describe the environmental conditions of the patches using direct measurements of e.g., soil conditions. These conditions could, however, be influenced by past land use (Peterken 1993, Motzkin et al. 1996) and studying them would thus answer a different question from that asked here.

Table 1. – Correlations among environmental and historical variables determined using simple pair-wise correlation analysis and data on the proportion of each land use type (50–1950s; 80–1980s) at each locality. Significant correlations (P < 0.05) are in bold.

		Field 50	Grass-land 50	Vine-yard 50	Forest 50	Road 50	Ridge 50	Field 80	Grass-land 80	Vine-yard 80	Forest 80	Road 80	Ridge 80
	Slope	**0.17**	–0.01	0.11	–0.11	**–0.15**	**–0.24**	**–0.15**	0.02	0.06	**0.18**	0.04	**–0.24**
Bedrock	Limestone	0.01	0.10	–0.02	–0.11	–0.01	–0.10	–0.05	0.00	0.06	**0.17**	–0.12	–0.10
	Sandstone	0.09	–0.09	–0.06	–0.07	0.05	0.02	0.00	0.09	–0.04	**–0.16**	0.07	0.02
	Marl	**–0.18**	–0.03	0.00	**0.31**	–0.08	**0.26**	0.00	–0.05	–0.03	–0.06	0.00	**0.26**
	Bazaltoid	–0.02	0.02	**0.16**	–0.04	–0.03	–0.04	0.02	0.00	–0.02	–0.05	0.08	–0.04
	Loess	0.05	–0.03	–0.04	0.00	0.06	–0.05	0.05	0.03	–0.03	–0.11	0.09	–0.05
	Sediment	–0.01	0.04	0.04	0.01	–0.01	–0.06	0.02	–0.08	0.03	0.13	–0.03	–0.06
PDSI	December	0.12	–0.12	**0.18**	–0.09	–0.06	–0.04	0.00	0.08	0.09	–0.12	0.06	–0.04
	May	0.09	–0.12	0.11	–0.05	–0.01	0.02	0.06	0.09	0.08	**–0.19**	0.04	0.02

Table 2. – Species used in the study and their abbreviations. The nomenclature follows Tutin et al. (1964–1983).

Abbr.	Name	Abbr.	Name
Agri eu	*Agrimonia eupatoria*	Glo elo	*Globularia elongata*
Ane syl	*Anemone sylvestris*	Hel gra	*Helianthemum nummularium* subsp. *grandiflorum*
Ant ram	*Anthericum ramosum*	Hie pil	*Hieracium pilosella*
Ant vul	*Anthyllis vulneraria*	Inu sal	*Inula salicina*
Asp cyn	*Asperula cynanchica*	Leo his	*Leontodon hispidus*
Asp tin	*Asperula tinctoria*	Lin ten	*Linum tenuifolium*
Ast ame	*Aster amellus*	Lot cor	*Lotus corniculatus*
Ast cic	*Astragalus cicer*	Med fal	*Medicago falcata*
Ast gly	*Astragalus glycyphyllos*	Mel arv	*Melampyrum arvense*
Bra pin	*Brachypodium pinnatum*	Mel nem	*Melampyrum nemorosum*
Bro ere	*Bromus erectus*	Ono spi	*Ononis spinosa*
Bup fal	*Bupleurum falcatum*	Peu cer	*Peucedanum cervaria*
Cax fla	*Carex flacca*	Pot are	*Potentilla arenaria*
Cax hum	*Carex humilis*	Pot hep	*Potentilla heptaphylla*
Cax tom	*Carex tomentosa*	Pru gran	*Prunella grandiflora*
Car vul	*Carlina vulgaris*	Sal pra	*Salvia pratensis*
Cen jac	*Centaurea jacea*	Sal ver	*Salvia verticillata*
Cen sca	*Centaurea scabiosa*	San min	*Sanguisorba minor*
Cir aca	*Cirsium acaule*	Sco his	*Scorzonera hispanica*
Cir eri	*Cirsium eriophorum*	Ses alb	*Sesleria albicans*
Cir pan	*Cirsium pannonicum*	Sta rec	*Stachys recta*
Cor var	*Coronilla varia*	Tan cor	*Tanacetum corymbosum*
Ery cam	*Eryngium campestre*	Thy pre	*Thymus praecox*
Fes rup	*Festuca rupicola*	Tri med	*Trifolium medium*
Fra vir	*Fragaria viridis*	Tri mon	*Trifolium montanum*
Gen cru	*Gentiana cruciata*	Ver teu	*Veronica austriaca* subsp. *teucrium*

Data about land use in the 1950s and 1980s come from a special set of maps that combine topographical and cadastral information. These maps were provided by the Czech Office of Surveying, Mapping and Cadastre in paper format and were digitized, geo-referenced and vectorized in GIS. Using information on past land use, we calculated the proportion of patches with histories of different land use. Land use included arable fields, grasslands (including pastures, meadows, orchards), vineyards (including hop gardens), forests, roads and unploughed ridges. Data on environmental conditions and land use history were processed using ArcView 8.3 (ESRI 2002), ArcInfo 9.1 (ESRI 2004) and DiGeM (Conrad 1998) software.

Correlations among all the independent variables were estimated using simple regression analyses and are shown in Table 1. The results indicate relatively low correlation coefficients between the independent variables. It is thus possible to separate the effect of past land use from that of environmental conditions.

At every patch an inventory of species was made based on a list of selected species (Table 2). For each species, we recorded its presence/absence. The list comprises species that occur in dry grasslands in the region with neither a too high nor too low frequency and that are almost exclusively bound to this type of habitat in the study area. The reason for excluding the very common and very rare species (occurring in almost all or very few habitats) from the study was that it would not be possible to obtain reliable estimates of their response to habitat conditions for the subsequent analyses. In total, the occurrence of 52 species was recorded in 2003 and 2004. Nomenclature of the species follows Tutin et al. (1964–1983).

Because it is often assumed that a species' dispersal ability could be the key factor determining its response to land-use history, the species were classified according to their dispersal mode into those with wind- and animal-dispersed seeds (there was only one endozoochorous species), and unspecific dispersal. Classification was done using a database of Grime et al. (1989). For species not included in the database, dispersal mode was deduced from closely related species with similar propagules. We are aware that these data are quite crude. More detailed data on all these species, however, are unavailable. We thus use them only to discuss the patterns in species distribution.

Data analysis

To reveal the importance of environmental and historical factors for the occurrence in the patches of the species studied, a series of canonical correspondence analyses (CCA, ter Braak 1986) were performed. First, single environmental factors (bedrock type, slope, potential solar irradiation) were used as independent variables and the occurrence of species in patches as dependent variables. All the levels within one environmental factor were treated together as one environmental factor, e.g. all the bedrock type levels.

Next, all the significant environmental factors were used as covariates and all past land-use types were used as independent variables. First, only land use in the 1980s was used as an independent variable. Afterwards, land use in the 1980s was used as another covariate and land use in the 1950s as an independent variable. In this way, it was possible to explore whether knowledge of land use in the 1950s contributed additional information to that of land use in the 1980s. These results were compared with results of analyses in which land use in both time periods was included as independent variables and analyses exploring the effect of land use in the 1950s without using the land use in the 1980s as a covariate (see Table 3). All multivariate analyses were done using CANOCO for Windows (ter Braak & Šmilauer 1998) and rare species were down-weighted. Proportion of area accounted for by each past land use and bedrock type was expressed for each patch. We also explored the alternative coding using only presence absence of each land use and bedrock type per patch. Because the former coding had a better predictive power, only the former coding is used in the results.

Table 3. – Effect of environmental and historical factors on occurrence of the dry grassland species studied in the patches identified using CCA analyses. For detailed explanation see text; % variation explained by all the canonical axes together; Env. vars. – environmental variables; 50–1950s, 80–1980s.

	Bedrock	Irradiation	Slope	Log area	Env. vars together	Land use 80+50	Land use 80	Land use 50	Land use 50–80
Covariates	–	–	–	–	–	Env. var.	Env. var.	Env. var.	Env var. and land use 80
d.f.	5	2	1	1	9	10	5	5	5
F-ratio	2.759	6.569	2.854	1.719	3.133	1.768	1.902	1.783	1.574
P	0.002	0.002	0.002	0.008	0.002	0.002	0.002	0.002	0.002
% variation	7.36	5.86	1.35	0.79	12.22	7.92	4.75	4.43	3.25

Response of the individual plant species to the studied factors was modelled using logistic regression. First, for every species the best statistical model based on environmental conditions was created using a stepwise backward selection. Afterwards, land use in the 1980s was added to the variables selected in the preceding step and the significant land-use types were selected using stepwise backward selection. As environmental conditions are considered to be the primary factor, these remained fixed in these analyses. Inclusion of a term into a model was decided by using a penalized log likelihood analyses as in S-PLUS (2000). In the same way, past land use in the 1950s was added to the previous model. The three types of model were then compared to determine if the more complex models are really significantly better than the simpler ones. This was done using a function to compare models in S-PLUS (2000) using χ^2 criteria. When performing logistic regression analysis it is important to check for possible overdispersion of the data. We thus compared the residual deviance in all our models with the residual degrees of freedom. This comparison indicated that in most cases the residual deviance is smaller than the residual degrees of freedom. In those cases where it was larger, it was never bigger than 1.6× the number of degrees of freedom. This suggests that overdispersion of the data is not a major problem.

The final type of analyses should reveal species response to selected individual types of past land use. Previously selected environmental conditions served as a basis for the models to which individual past land use classes were added. In the analyses used to test the effects of land use in the 1950s, land use in the 1980s was included into the models as a covariate. These analyses were done to study only major land-use types (field, grasslands or forests). In addition, we studied the effect of continuous grasslands, i.e. grassland patches that were grasslands both in the 1950s and 1980s. All univariate analyses were done using S-PLUS (2000).

Because we show in our previous study (Tremlová & Münzbergová 2007) that occurrence of dry grassland species in these habitats depends on patch size, we used logarithm of patch area as another independent variable. We used logarithm of patch area because it proved to have better predictive power than the untransformed values in the preliminary analyses.

Results

Of the total patch area (165 ha) only 23% was used in the same way in the 1980s and 1950s, and only 7% has been grassland continuously since the 1950s (described by category pasture or meadow on the 1950s and 1980s maps). The most important change concerns the arable fields that were turned into grasslands, afforested or abandoned. Vineyards and hop gardens were also mainly abandoned. These processes caused an emergence of new patches suitable for the dry grassland species in the region (Fig. 1).

Results of CCA analyses exploring the effect of environmental factors on species distribution indicate that bedrock type explained the highest proportion of total variation (7.4%) in occurrence of the species studied. In total, environmental conditions explained 12.2% of the variation in occurrence. Historical factors explained an additional 7.9% and contribute significantly to understanding species distribution patterns. Land use in the 1980s explained 4.7% of the total variation and adding information on land use in the 1950s explained an additional 3.2% (Table 3).

The strongest dichotomy in the 1980s analysis (shown by the 1st ordination axis) is the distinction between species occurring in habitats classified as forests in 1980s, and arable fields and grasslands in the 1980s. Species restricted to patches classified as forests in the 1980s are e.g., *Anthericum ramosum*, *Cirsium pannonicum*, *Melampyrum nemorosum* and *Peucedanum cervaria* (Fig. 2a). The response to land use in the 1950s reveals a field-grassland polarity on the first ordination axis. Many species seem to be restricted to localities that used to be grasslands in 1950s (*Anemone sylvestris*, *Anthericum ramosum*,

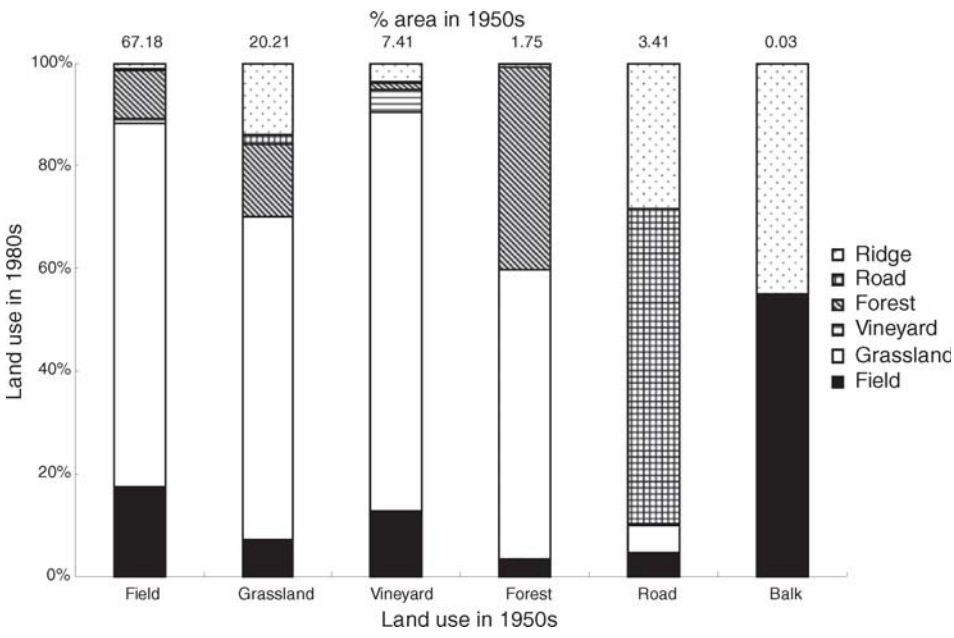

Fig. 1. – Transitions among land use classes between the 1950s and 1980s on current dry grasslands. Numbers above columns indicate area of each habitat type in 1950s in hectares.

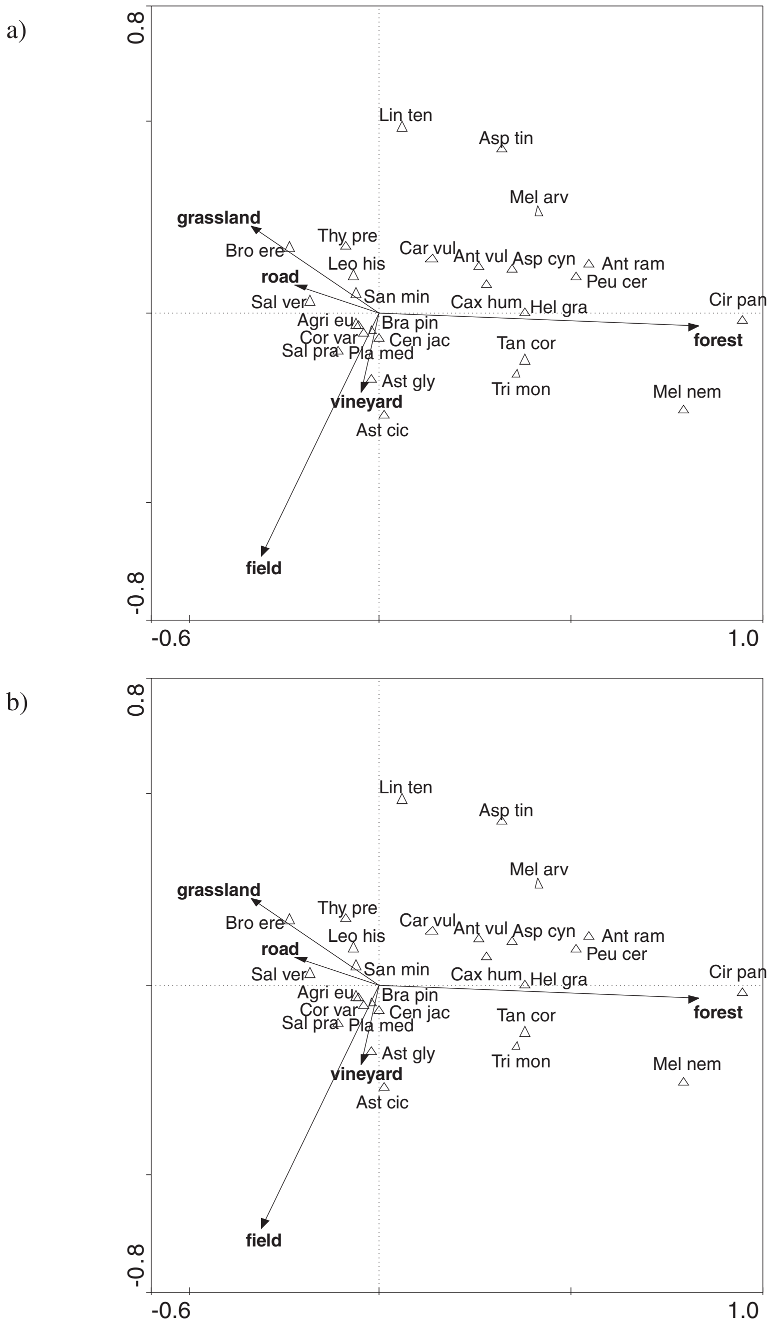

Fig. 2. – Effect of past land use on the occurrence of the studied dry grassland species in patches estimated using CCA analyses (see also Table 3). Environmental variables are (a) land use in the 1980s and (b) land use in the 1950s. Environmental conditions in the patches were used as covariates in both cases; in graph (b) also land use in the 1980s was used as covariate. For species abbreviations see Table 2. The first canonical axis explained 1.98 of the total variation in the dataset in graph A and 1.19 % in graph B, the second explained 0.95 and 0.79 %, respectively.

Carlina vulgaris, *Linum tenuifolium*, *Prunella grandiflora* and *Scorzonera hispanica*, Fig. 2b). In this case, the 2nd ordination axis shows also a relatively strong distinction between fields and the other habitats.

When exploring the effect of environmental conditions on the occurrence of individual species, a statistically significant model could be created for 51 species out of the 52 species analyzed. The exception was *Linum tenuifolium*. The significant models explained between 2% and 41% of variance in species occurrence (median 9.7, S.D. 7.7).

Comparison of models based on environmental conditions with those that also included historical factors showed that the type of land use in the 1980s is important for 28 species (54%) and land use in the 1950s for 28 species. For 12 species both periods have a significant influence. Seven species do not show any significant response to past land use (Table 4).

Relative importance of environmental and historical factors strongly differs among species (Fig. 3). Of 45 species whose occurrence is at least partly determined by past land use, 17 are influenced more by past land use than by environmental conditions (e.g., *Asperula cynanchica*, *Cirsium pannonicum*, *Melampyrum nemorosum* and *Trifolium montanum*). On the other hand, species such as *Anthericum ramosum*, *Sesleria albicans*, *Cirsium eriphorum* and *Carex flacca* depend more on environmental conditions than on past land use (Fig. 3).

Twelve species avoid patches that were arable fields in the 1980s. None of the species prefer patches that used to be arable fields in the 1980s. Thirteen species avoid patches that used to be fields in 1950s, while only one species prefers them. Four species avoid patches that were fields both in the 1980s and 1950s. Three species prefer patches that used to be

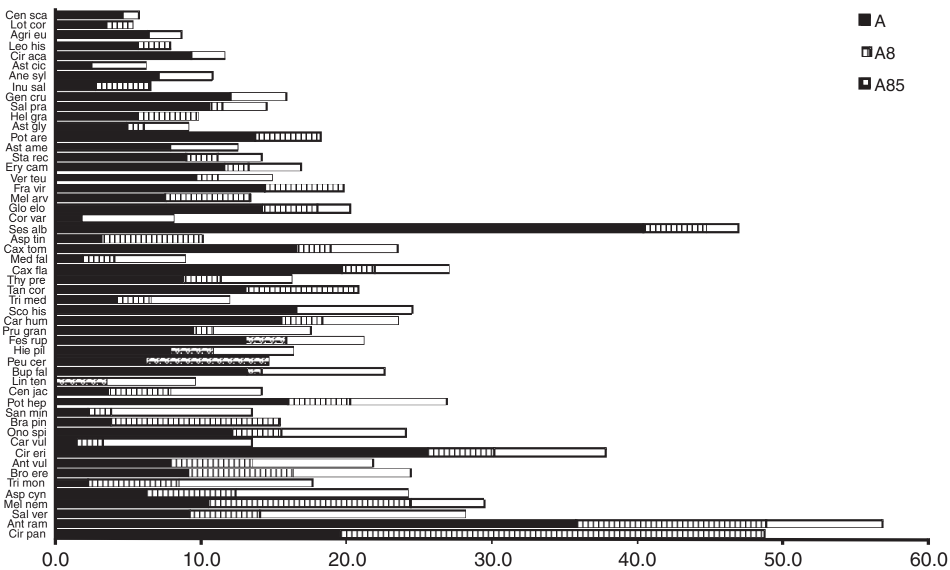

Fig. 3. – Percentage of deviance explained by environmental and historical factors. A is the best statistical model based on environmental conditions, A8 is the model that included environmental conditions and land use in the 1980s, A85 includes also the land use in the 1950s. For species abbreviations see Table 2. Species are sorted by increasing percentage of deviance explained by past land use.

Table 4. – Effect of past land use in the 1980s and/or 1950s on distribution of individual species. Species are ranged into columns according to their significant response to land use in none, one or both time periods. Combination = model including the land use in the 1980s and 1950s is significantly better than that based only on environmental conditions, although neither the effect of the 1980s nor the 1950s is significant on its own. The effect of land use in the 1950s was estimated using a model in which land use in 1980s was used as a covariate. The underlined species are wind dispersed, the species in bold are animal dispersed and the remaining have unassisted dispersal.

Only 1980s	Only 1950s	Both 1980s and 1950s	Combination	No effect
Asperula tinctoria	*Anemone sylvestris*	*Anthericum ramosum*	***Festuca rupicola***	***Agrimonia eupatoria***
Brachypodium pinnatum	*Aster amellus*	*Anthyllis vulneraria*		*Astragalus cicer*
Bromus erectus	*Astragalus glycyphyllos*	*Asperula cynanchica*		*Centaurea jacea*
Cirsium eriophorum	*Bupleurum falcatum*	*Carlina vulgaris*		*Centaurea scabiosa*
Cirsium pannonicum	*Carex tomentosa*	*Carex flacca*		***Globularia elongata***
Fragaria viridis	*Cirsium acaule*	*Carex humilis*		*Lotus corniculatus*
Helianthemum grandiflorum	*Coronilla varia*	*Hieracium pilosella*		*Veronica teucrium*
Leontodon hispidus	***Eryngium campestre***	*Medicago falcata*		
Linum tenuifolium	*Gentiana cruciata*	***Melampyrum nemorosum***		
Melampyrum arvense	*Inula salicina*	*Ononis spinosa*		
Peucedanum cervaria	***Prunella grandiflora***	*Potentilla heptaphylla*		
Potentilla arenaria	***Salvia pratensis***	***Salvia verticillata***		
Sesleria albicans	*Sanguisorba minor*			
Stachys recta	*Scorzonera hispanica*			
Tanacetum corymbosum	*Thymus praecox*			
Trifolium montanum	***Trifolium medium***			

grasslands in 1980s, while another three species tend to avoid them. After taking into account land use in 1980s, 19 species seem to be restricted to patches that used to be grassland in the 1950s. Probability of occurrence of 13 species significantly increases with increasing proportion of forest in the 1980s, while probability of occurrence of two species decreases with the increasing proportion of forest in the 1980s (Table 5).

Discussion

Results of this study show that the occurrence of dry grassland plant species depends not only on the environmental conditions of the sites but also on the type of past land use and time since the land-use change. Although there has been a great turnover in land use since the 1950s, the imprint of the previous management in terms of species distribution is still traceable and knowledge of past land use can help in accounting for the species distribution patterns in these patches.

Many species in our dataset seem to be restricted to patches that were classified as forests in the 1980s. Since the patches that were afforested according to the maps sometime between the 1950s and 1980s were not forests when inventoried for the purpose of this study, the afforestation seems to be rather an intention that failed. Traces of afforestation efforts are still visible at many of these sites but there is no real forest. It can thus be assumed that the signs for forest were used in the maps at the time of planting trees, regardless of the real state of the stand. Forests in the 1980s (with the exception of several small patches that were classified as forests even in 1950s) can be thus considered as abandoned land with occasional disturbance during afforestation work. Such disturbance supported many species that still prefer these habitat patches.

Table 5. – Relationship of individual species with single types of past land use. Direction of response is shown for species with a significant ($P < 0.05$) effect determined using a χ^2 test comparing the frequency of occurrence in habitats with and without a given land use. Continuous grasslands are grassland patches that were grasslands both in the 1950s and 1980s. Species that did not show a significant response are not shown in the table. The underlined species are wind dispersed, the species in bold are animal dispersed and the remaining have unassisted dispersal.

	Field 1980s	Field 1950s	Grassland 1950s	Grassland 1980s	Forest 1980s	Continuous grassland
Anthericum ramosum	–	–	+		+	
Asperula cynanchica	–	–	+		+	
<u>*Carlina vulgaris*</u>	–	–	+		+	
Ononis spinosa	–	–	+		+	
Carex humilis	+	–	+			
Carex flacca	–		+			
Stachys recta	–		+			
<u>*Cirsium pannonicum*</u>	–			–	+	–
Potentilla heptaphylla	–			+		
<u>*Anthyllis vulneraria*</u>	–				+	
Asperula tinctoria	–					
<u>*Hieracium pilosella*</u>	–					
Linum tenuifolium	–					
<u>*Anemone sylvestris*</u>		–	+			+
Thymus praecox		–	+			+
<u>*Aster amellus*</u>		–	+			
Bupleurum falcatum		–	+			
Carex tomentosa		–	+			
Medicago falcata		–	+			
Prunella grandiflora		–	+			
<u>*Scorzonera hispanica*</u>		–	+			
Astragalus glycyphyllos		+				
<u>*Cirsium acaule*</u>			+			
Eryngium campestre			+			
Melampyrum nemorosum		+	–	+		
Sanguisorba minor			+			
Tanacetum corymbosum				–	+	–
<u>*Cirsium eriophorum*</u>				+		
Trifolium medium				+		
Bromus erectus					–	
Salvia verticillata					–	
Helianthemum grandiflorum					+	
Melampyrum arvense					+	
Peucedanum cervaria					+	
Trifolium montanum					+	

Past land use in our dataset depends only weakly on the environmental conditions of patches. This finding is important because otherwise it would not be possible to separate the effect of history from the effect of habitat conditions. The idea that habitat conditions determine the type of land use was also refuted by Motzkin et al. (1996), Bellemare et al. (2002) and Gerhardt & Foster (2002).

Among the environmental variables bedrock and potential direct solar irradiation influenced the occurrence of the dry grassland species most. Apart from that, occurrence of the species studied was also significantly affected by past land use. This influence remained significant even if the effect of environmental variables was removed. Many species were restricted to patches classified as forests in the 1980s and pastures in the 1950s, and many species were absent from patches classified as fields in both periods. These patterns are revealed by both the multivariate analyses and the analyses of single species. This indicates that the multiple tests on single species did not increase the numbers of significant relationships.

The advantage of the individual species analyses is that they yielded more in-depth results. The effect of environmental variables on the occurrence of species varies greatly. While for several species (e.g., *Sesleria albicans* and *Cirsium eriophorum*) a relatively large proportion of variance in occurrence can be explained by environmental conditions, for others (e.g., *Linum tenuifolium*, *Medicago falcata*, *Trifolium montanum*, *Sanguisorba minor*) it is almost negligible. *Asperula tinctoria*, *Cirsium pannonicum*, *Linum tenuifolium* and *Stachys recta* avoid in patches that were arable fields in the 1980s. Without an experiment, it is impossible to decide whether they were not able to colonize these patches or whether these patches are unsuitable for the species. This would require sowing seeds of these species in these patches and monitoring the recruitment and growth of the plants over several years. If the plants could establish viable populations there, the unsuitability of the patch could be ruled out and the absence of the species explained by limited seed-dispersal ability (Ehrlén & Eriksson 2000, but see Ehrlén et al. 2006). Such an experiment was done for *Aster amellus*, *Cirsium pannonicum, Globularia elongata*, *Linum tenuifolium* and *Scorzonera hispanica* by Münzbergová (2004) in the study area. The results of this 3-year study indicate that these species are able to grow well in such patches suggesting that it is their dispersal ability that limits their distribution.

Two of the species, *Cirsium pannonicum* and *Tanacetum corymbosum*, avoid sites that were grasslands in the 1980s. These two species are large and lack defense mechanisms and could thus be attractive to grazers. Absence of these species from grasslands could thus be a result of animal grazing. The only species that prefers patches that were grasslands in 1980s is *Cirsium eriophorum*. This unpalatable thistle can outcompete other species. In comparison to the other species bound to habitat patches that were grasslands in 1950s, this thistle has a higher dispersal ability, not only due its pappus (the same holds true for *Cirsium acaule*), but mainly its high stature, which also positively affects the distance they can disperse. According to Fisher et al. (1996) plant height also affects the capacity to attach to animal fur, which increases the probability of long-distance dispersal by animals.

Species responding only to the 1950s land use (*Anemone sylvestris*, *Aster amellus*, *Bupleurum falcatum*, *Carex tomentosa*, *Prunella grandiflora*, *Scorzonera hispanica* and *Thymus praecox*) typically do not occur in patches that used to be fields and are present in patches that used to be grasslands. This group contains species with different dispersal modes. It thus does not support the expectation that these species have poor dispersal and good persistence ability. A similar persistence with a little higher dispersal ability could be expected for species that are only associated with grassland (*Cirsium acaule*, *Eryngium campestre* and *Sanguisorba minor*). This group, however, again includes species with very different dispersal strategies.

The only species that prefers patches that were fields in the 1950s is *Astragalus glycyphyllos*. Its ability to colonize newly abandoned fields is also apparent from its high occurrence on present fallow land. The very competitive stature of this species is probably more important than its dispersal capacity because it has unassisted dispersal and relatively large seeds.

Among species responding to land use both in the 1980s and 1950s, there is only one obvious tendency: *Anthericum ramosum*, *Asperula cynanchica*, *Carlina vulgaris* and *Ononis spinosa* do not occur on former arable fields and mainly occur in patches that used to be forest in the 1980s and grassland in the 1950s. These species seem to need grazing for establishment and are able to survive after grazing ceases. The survival of species in habitat patches classified as forest in 1980s was probably due to the disturbance during afforestation (see above). Except for *Carlina vulgaris*, these are species with unassisted dispersal and a low dispersal capacity.

Thus it is clear that different species respond differently to past land use. Our rough data on the dispersal capacity of these species did not account for these between-species differences. Finding an explanation clearly requires much more detailed data on many dispersal- and growth-related traits of all the species (Tremlová & Münzbergová 2007).

Limitations of using old maps

Use of historical cadastral maps in botanical research has become quite standard (Cousins & Eriksson 2002) because they contain valuable information on past land use and usually cover the whole area of a country. They provide an opportunity to gather data from large areas easily. As with other maps, however, they present only a simplified and sometimes distorted model of reality. To avoid a serious misinterpretation, it is, therefore, of crucial importance to take into account the accuracy of the maps, especially when working with different kinds of maps.

Maps used in this study were geodetically accurate. The only potential problem is with the content of the maps used for gathering data about land use in 1950. With respect to the map creation process (these were derived from topographical and cadastral maps from different periods of the first half of the 20th century) it is unlikely that the land was really used exactly in this way in 1950. Though this may seem to be a serious disadvantage, for the purpose of this research it is not so significant because we were not particularly interested in the year 1950. Our aim was to detect the state of land use before the great agriculture transformation that began in the late 1950s. Nevertheless, it is important to bear this in mind when interpreting the results of the study.

As previously mentioned, the area of the parcels of land in the 1950s was often of limited extent and most present grassland patches consist of several former parcels of land with different past land uses. The variable "history" therefore expresses the relative proportion of the area in a patch used in a given way and can only be interpreted as increased probability of occurrence with increasing proportion of the area in a patch of the given land-use class. A more straightforward interpretation would be possible if the units were of uniform history. Jacquemyn et al. (2001) adopted such an approach. They divided the patches consisting of parcels of land with different past land use into smaller patches of uniform history. Although this is an elegant method, it cannot be applied to an area with very fine-grained parcels of land as in this study. Another approach was adopted by Cousins & Eriksson (2001) who randomly chose several points in semi-natural grasslands according to a land-cover map. They located each point in a field and created a 5 m × 5 m plot around it and then recorded the vegetation composition within the plot. Afterwards, they determined its history, which was probably uniform, given the area of the plot. The disadvantage of this method is that it does not consider the effect of adjacent areas. If the randomly chosen plot lies within an arable field, the situation will not be the same as if grasslands surrounded the plot. In this respect, the approach adopted in this study is more realistic.

Conclusions

This study shows that dry grasslands are communities occurring in places with a high turnover of past land use. Distribution of species in these habitats depends not only on the environmental conditions at the sites but also past land use. In many species, the effect of past land use is even more important than the effect of the abiotic conditions in the habitat patches. Of the investigated species, some were restricted to former pastures and others to former fields. Only a minority of the species, however, occurred only in continuous pastures. This indicates that many species were able to colonize places cultivated in 1950 within 50 years, suggesting that the dynamics of these species is relatively fast. The results suggest that many dry grassland communities in the region are of recent origin and the distribution of species in these habitats is determined not only by the environmental conditions of the sites but also past land use. Detailed knowledge of land-use history, landscape structure and of species attributes is, thus, needed to understand the distribution of species in grassland communities.

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Souhrn

Krajina se neustále mění a pro rostliny to znamená mizení a objevování se vhodných stanovišť. Rozšíření druhů proto závisí nejen na aktuálním rozšíření vhodných stanovišť v krajině, ale také na schopnosti druhů přežívat na stanovištích, která jsou nevhodná, a šířit se na nová vhodná stanoviště. Rozšíření druhů na stanovištích proto silně závisí na časové a prostorové struktuře krajiny a na vlastnostech druhů. Cílem této studie bylo zjistit, do jaké míry určuje historická struktura krajiny současné rozšíření druhů suchých trávníků na krajinné úrovni. Studovaly jsme rozšíření 52 druhů suchých trávníků na 215 lokalitách. Data o podloží, sklonu, osluněnosti, rozloze a hospodaření ve dvou časových obdobích (1950 a 1980) byla získána z existujících map. Za pomoci mnohorozměrné analýzy jsme stanovily význam historických a stanovištních faktorů pro současné rozšíření druhů. Navíc jsme za pomoci jednorozměrných analýz zjistily závislosti mezi rozšířením jednotlivých druhů a historickým využitím lokalit.

Výsledky ukazují, že studovaná stanoviště se velmi rychle mění. Rozšíření druhů na těchto stanovištích je silně ovlivněno stanovištními podmínkami, nicméně i hospodaření v minulosti má průkazný vliv na výskyt druhů. Pro řadu druhů je vliv hospodaření v minulosti dokonce silnější než vliv stanovištních podmínek. Ve skupině studovaných druhů se vyskytuje řada druhů omezených na bývalé pastviny a druhů vyskytující se i na bývalých polích. Pouze velmi malý počet druhů je však striktně vázaný na kontinuální pastviny. Výsledky ukazují, že některé druhy suchých trávníků byly schopné během 50 let kolonizovat stanoviště využívaná v roce 1950 jako pole a že dynamika těchto druhů je tedy relativně rychlá. To naznačuje, že společenstva suchých trávníků ve studované oblasti jsou relativně mladá a že rozšíření těchto druhů je kromě stanovištních podmínek určeno i historickým využitím krajiny. Pro pochopení rozšíření druhů je tedy kromě znalosti stanovištních podmínek nezbytná i podrobná znalost využití krajiny, krajinné struktury a vlastností druhů.

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