

Restoring grassland on arable land: an example of a fast spontaneous succession without weed-dominated stages

Obnova lučních porostů na orné půdě: příklad rychlé spontánní sukcese bez stádia s plevely

Ivana Jongepierová¹, Jan W. Jongepier² & Leoš Klimeš³

¹Administration of the Protected Landscape Area Bílé Karpaty, Bartolomějské nám. 47, CZ-698 01 Veselí nad Moravou, Czech Republic; ²Národních mučedníků 948, CZ-698 01 Veselí nad Moravou, Czech Republic; ³Institute of Botany, Academy of Sciences of the Czech Republic, Dukelská 135, CZ-379 01 Třeboň, Czech Republic, email: klimes@butbn.cas.cz

Jongepierová I., Jongepier J.W. & Klimeš L. (2004): Restoring grassland on arable land: an example of a fast spontaneous succession without weed-dominated stages. – Preslia, Praha, 76: 361–369.

Vegetation succession was studied for 12 years on an abandoned nutrient-poor small field surrounded by a strip of natural grassland. No fertilizers or herbicides were applied. Few weeds or annuals were present during this period. Only two plants, i.e. *Agrostis capillaris* and *Festuca rubra*, dominated during the 12 years. At two spatial scales (0.04 and 0.4 m²) a dramatic increase in species richness was recorded during the first two years. However, no further trend in species richness occurred after the sixth year of succession. Successional changes were directed and continuous. The rate of succession depended on the distance from the neighbouring meadow. Vegetation at the margins of the transect developed more slowly and diverged from the middle during the succession.

Key words: Czech Republic, divergent succession, grassland restoration, long-term dynamics, monitoring, mowing, oldfield, rate of succession, secondary succession, species richness

Introduction

Restoration of species-rich grassland is a long-term process which is not always fast or successful. A lack of diaspores of plants typical of late successional stages of grassland vegetation and high concentrations of nutrients in the soil are repeatedly identified as crucial factors hampering grassland restoration on arable land (Willems & Bobbink 1990, Muller et al. 1998). Moreover, seeds of weedy plants prevail in seed banks of abandoned fields whereas grassland species are poorly represented (McDonald et al. 1996, Willems 2001). Virtually all reports on grassland restoration in oldfields describe a relatively fast establishment of an initial successional stage dominated by weeds. Without human intervention subsequent development towards grassland is slow or even prevented for a long time if tall weedy perennials dominate (Klötzli & Grootjans 2001, Willems 2001).

If former grasslands or pastures are farmed only for several years, diaspores of some grassland plants can persist in the seed bank and germinate after farming ceases. Diaspore availability can be further improved if the arable field is small and surrounded by natural grasslands. High nutrient levels do not cause problems on sandy soils where nutrients are leached out within a few weeks or months. Therefore, in some situations grassland restoration could be fast and the initial domination by weeds avoided.

Unfortunately, there are very few examples showing how restoration proceeds if diaspore availability and high nutrient levels do not restrict succession. Even on sandy soils where nutrients are at very low levels, the first stages of succession are dominated by weeds for several decades (Falinski 1986). Also, the spread of natural steppe vegetation into abandoned fields in dry and nutrient-poor conditions can be slow and affect only the margins of the field (Buisson & Dutoit 2002). However, very few observations are available for non-fertilized arable fields farmed for only a few years and where the persisting seed bank is likely to contain seed of species of the former grassland.

Here we report such a case. In the central part of the Bílé Karpaty Protected Landscape Area people in the past cultivated small pieces of land around their farms, which were usually surrounded by orchards, pastures or hay meadows and situated in clearings within woodland (Nekuda 1982). Due to a lack of fertilizers the fields were fertilized only moderately. As the size of the harvest usually decreased after several years, such sites were abandoned or changed to grasslands. Because of the shortage of arable land small arable fields were often established in the middle of meadows and pastures (Kunz 1955, 1956). Therefore, the arable fields were usually transient, always small, and isolated from each other by grasslands and woodlands.

In this note we refer to spontaneous succession in an area previously managed in the traditional way. From 1989 to 1999 we studied succession on an abandoned field to answer the following questions: 1. Can the initial weedy stage in succession be avoided and the restoration process speeded up? 2. Does the rate of succession slow down in time? 3. Does the speed of succession at a particular spot depend on the proximity of grassland?

Material and methods

Study plot

The study plot was situated in the Bílé Karpaty Mountains, SE Moravia, Czech Republic, in a nature reserve called “Rubaniska” (48°44' N, 17°15' E), located in a highland area with extensive saddles and deep valleys. The study area, 15.4 ha in size, consists of an 80 m wide strip of pasture with several springs and brooks, at altitudes ranging from 460 to 530 m. The locality slopes at 8–10° to the north, the mean annual temperature is 7.9 °C, and annual precipitation 808 mm (1951–1980, Kuča et al. 1992). The pastures were mown once a year and up until the 1960s occasionally grazed by cattle and sheep in autumn. In the centre of the pasture, an area of 20 × 100 m, perpendicular to the slope, was ploughed in 1985 and maize cultivated there for two seasons. No fertilizer was applied. The maize field was abandoned after the harvest in 1986 and since then the whole area, including the study plot, was mown once a year in summer. Only once, in 1992, it was grazed by sheep.

Sampling and analyses

Two fixed transects, parallel to the shorter side of the former arable field in the centre of the abandoned area, were set up in June 1989. Their length was 10 m, and width 4 cm. Each of them consisted of 50 segments, each 20 cm long. The amount of work is substantially reduced by using transects rather than permanent quadrats, while the number of spe-

cies recorded remains high. As one of the transects was damaged, data for only one transect is presented. From 1989 to 1999 the presence of vascular plants was recorded along the transect every year in late June, before the grassland was mown. Species richness was evaluated at two scales: the whole transect (0.4 m²; called plot) and 1 m long plots (0.04 m²; called sub-plots), consisting of five continuous segments, each 20 cm long. In addition, in 1999 the species composition was recorded in ten sub-plots, placed randomly, in a nearby pasture that was not ploughed. Rates of change in species composition were assessed (1) by comparing data from pairs of subsequent years using three coefficients of similarity (Similarity ratio, Soerensen and Jaccard's coefficients of similarity), which differ in the weighting of rare and frequent plants (for details see Jongman et al. 1987), and (2) using the time-lag analysis developed by Collins et al. (2000). The latter method utilises Euclidean distance, calculated using all possible pairs of years. They are plotted against time lag for all lags below the diagonal in the triangular matrix of resemblance coefficients. The Euclidean distances were calculated using the percentage of 0.2 m long segments in each 1 m long segment of the transect occupied by individual species. The slope of the regression line indicates the pattern of succession. In stable communities the slope is close to zero, in those with directional change it is positive, and in those with cyclical dynamics negative (Collins et al. 2000). This was done for ten 1 m long segments along the transect to determine whether the successional pattern was the same along the whole transect. We did not estimate the significance of the regressions because not all the data points were mutually independent.

The effect of distance from the ends of the transect on species composition was evaluated using Canonical Correspondence Analysis (CCA) with recording year defined as a covariable and distances from either end of the transect, respectively, defined as environmental variables. Using this coding the sub-plots at the centre of the transect had the same codes. Testing the distance effect was performed using 999 Monte Carlo simulations restricted for time series (ter Braak & Šmilauer 1998). Nomenclature of vascular plants follows Marhold & Hindák (1998).

Results

Altogether 74 species were recorded along the transect from 1988 to 1999. Total species numbers in the plot (0.4 m²) more than doubled from the first (14 species) to the second year (33 species) and then increased linearly with a mean increment of 1.7 species per year, until 1997 (49 species). During the last two years (1998 and 1999) several species disappeared (Fig. 1A). A similar trend was observed in the sub-plots (0.04 m²; Fig. 1B). There were considerable differences in species richness between the upper and other parts of the transect, with less species accumulating in the upper part in 1990 and more in 1997–1998. However, in other years there were no such differences (Fig. 1B).

Species composition along the transect evaluated using sub-plots changed considerably during the succession. However, the greatest changes were observed during the first two years; later, species composition did not change much. This accords with the results of the analysis of the numbers of newly recorded species and species that disappeared in subsequent years, which did not change from 1989 to 1999 (colonization: $y = -0.1x + 200.9$, $R^2 = 0.009$, $P > 0.05$; extinction: $y = 0.33x - 64.6$, $R^2 = 0.2$, $P > 0.05$) and were about the

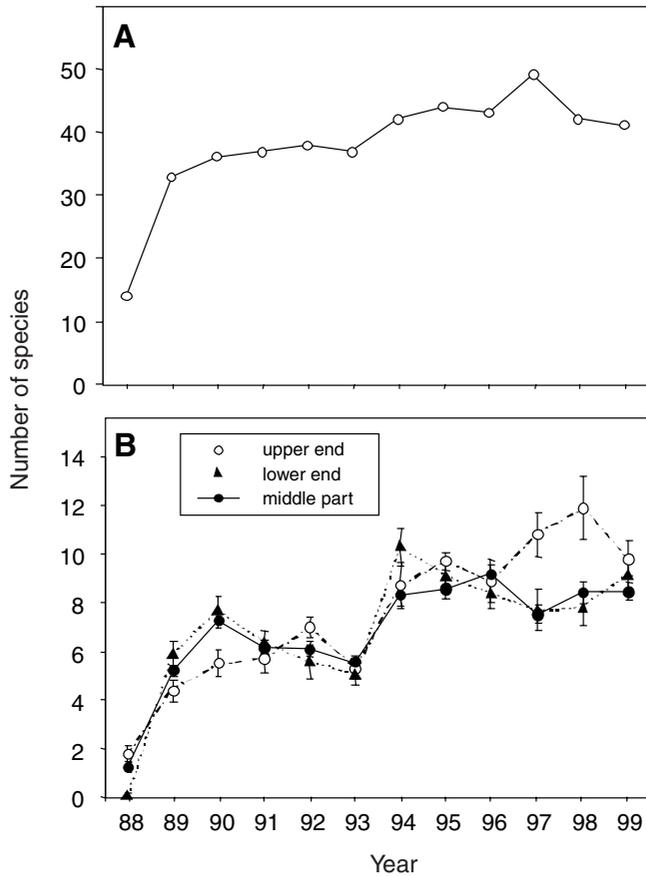


Fig. 1. – Species richness (mean \pm SE) in 0.4 m² plots (A) and in 0.04 m² subplots (B) along a transect across the study site.

same in individual years ($P = 0.5$; paired t-test). The fast convergence of the transect to unploughed pasture accords with the fact that with the exception of *Koeleria pyramidata*, all species found in the pasture with a frequency of 20% or more were already recorded in the transect in 1990.

Species composition was not the same along the transect. CCA showed a strongly significant effect of the distance from both ends of the transect on species composition ($\text{Lambda} = 0.24$, $F = 17.78$, $P < 0.001$). An analysis of individual species showed that very few species occurred preferentially at the ends of the transect at the beginning of the study, whereas after 11 years more species significantly concentrated there and their frequencies were much higher (Table 1). None of the species concentrated at the ends of the transect occurred there preferentially over the whole period of the study, even if the number of species recorded every year from 1990 (3rd year) to 1999 (12th year) was as high as 19. Virtually all species recorded in 1999 were recorded before 1995. This indicates relatively small and slow changes in species composition of the grassland during the last 10 years.

Table 1. – Percentage of 0.2 m long transect segments occupied by individual species from 1988 to 1999. Species significantly concentrated at lower (a) or upper (b) ends of the transect or in its middle part (c) are labelled with superscripts (tested by χ^2 test). Species recorded in 4 or less years are omitted.

	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999
<i>Acetosa pratensis</i>		6	14	8	14	6	14	16	20	14 ^b	24	16
<i>Achillea millefolium</i>	28	46	76	64	62	56	82	88	88	76	66	62
<i>Agrostis capillaris</i>	14	84	76	94	96	84	76	66	60	74	92	84
<i>Alchemilla vulgaris</i>		8	10	2	4	2				4 ^a		2
<i>Anthoxanthum odoratum</i>		4	16 ^b	18 ^b	8	12	20	26	48	38	8	26
<i>Aquilegia vulgaris</i>		2	2	6	6	6	4	14	8	4	8	6
<i>Brachypodium pinnatum</i>			2	10	4	2	8	12	14	28 ^c	32 ^c	34
<i>Bromus erectus</i>	2			2		2	10			4	2	
<i>Campanula patula</i>				2	2		24 ^b	12	6	10	10 ^a	14 ^a
<i>Carex montana</i>				8	4	2	10	4				
<i>Carex pallescens</i>				4 ^a			8 ^a	2	2	12 ^a	14 ^a	12 ^a
<i>Carex pilulifera</i>		4	10	6	10	10	4	12	36	32	38	50
<i>Cerastium holosteoides</i>		14 ^b	38 ^b	18	14	12 ^b	36 ^b	16	20	4	2	10
<i>Cirsium arvense</i>		22	26	10		4	6	12	10	2		
<i>Cruciata glabra</i>				8			4	10	20 ^f	28	32	42
<i>Dactylis glomerata</i>							2	4	6	4	6	4
<i>Danthonia decumbens</i>			2	8 ^a	18	20 ^a	22	32 ^a	32 ^a	24 ^a	24 ^a	26 ^a
<i>Festuca rubra</i>		2	8	50	70	60	68	84	86	94	92	94
<i>Filipendula vulgaris</i>		6	2	6	4	4	10	6	10	2	4	4
<i>Helianthemum grandiflorum</i> subsp. <i>obscurum</i>					2	4	2		2		2	2
<i>Holcus lanatus</i>		68	76	54	26	10	6	12	8 ^b	4 ^b	6 ^b	
<i>Hypericum maculatum</i>		6	2				4			2	2	4 ^b
<i>Hypochaeris radicata</i>					4	2	16 ^a	6 ^a		4 ^a		4 ^a
<i>Jacea phrygia</i>								4	2	4	4	6
<i>Leontodon hispidus</i>			14 ^b			4				2	2	4
<i>Leucanthemum ircutianum</i>	8	38	42 ^a	40 ^a	40 ^a	38 ^a	46 ^a	38 ^a	14 ^a	2		
<i>Lotus corniculatus</i>		2	6	4	2		6	2	2			
<i>Luzula campestris</i>		4	6	14	32	28	46	46	62	52	58	60
<i>Pimpinella saxifraga</i>		14	6	6	2	6	6		6		6	2
<i>Plantago lanceolata</i>		18	28	36	46	54	84	84	70	44 ^a	40 ^a	52
<i>Polygala vulgaris</i>							8	2	4 ^a	2	2	
<i>Potentilla alba</i>		8	26		4	4	4	6	2	6	4	4 ^a
<i>Potentilla erecta</i>		44	50	36	38	12	32	24	18	20	30	16
<i>Ranunculus polyanthemos</i>		6	28	10			22	6	18	18	20 ^a	20
<i>Sanguisorba officinalis</i>		30	28	18	10	6	40	24	26	28	30	32
<i>Stellaria graminea</i>			10	6	2 ^b	4 ^b	14 ^b	18	24 ^b	12	28 ^b	30 ^b
<i>Taraxacum sect. Ruderalia</i>		8	32	12	10	6	10	6	2	6 ^b	2	2
<i>Thesium linophyllum</i>		2	4	2	2	4	2	4	4	2		4
<i>Trifolium medium</i>				30	4	18		28	20	6	18	20
<i>Trifolium pratense</i>		34	34		6					2	2	
<i>Trisetum flavescens</i>					2		2	4	4 ^b	8 ^b	14 ^a	8 ^b
<i>Veronica chamaedrys</i>				4	4	8 ^{ab}	18 ^b	20 ^b	16	14 ^a	8 ^{ab}	8
<i>Veronica officinalis</i>		8	4	2	6	8	24	38 ^c	50 ^c	54 ^c	66	52
<i>Viola canina</i>		2	12	6	8	20	36	40	52	38	44	40

The number of weedy species was very low during the whole study. Even during the first years of succession only two annual weeds typical of initial successional stages were recorded, *Persicaria* sp. and *Veronica arvensis*. Moreover, they were found only once. The only perennial weed was *Cirsium arvense*, which persisted until 1997 but never became abundant.

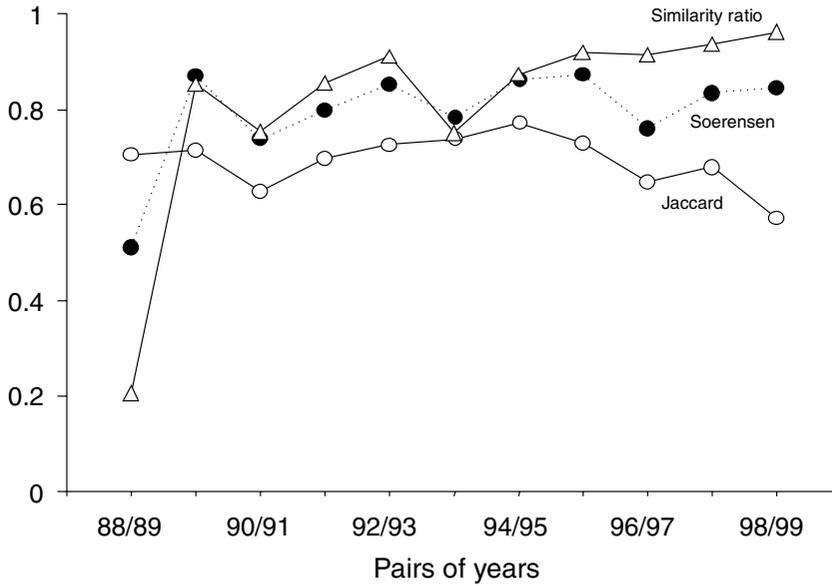


Fig. 2. – Similarity coefficients calculated for pairs of subsequent years

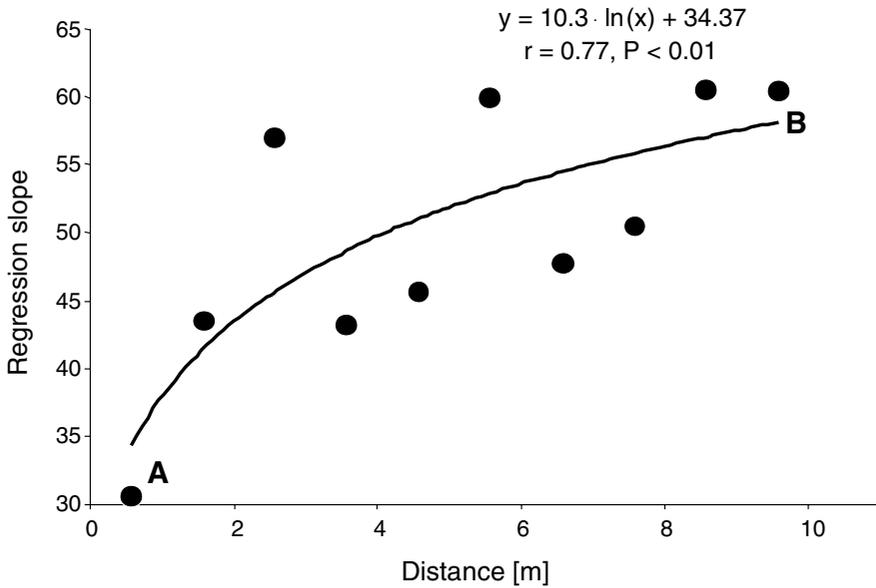


Fig. 3. – Slopes of the regressions calculated for the relationships between time lags and Euclidean distances along the transect.

Only two species were recorded as dominant during the whole study period. *Agrostis capillaris* became dominant as early as 1989 (2nd year). It kept its position for several years but was later gradually replaced by *Festuca rubra*. This replacement was not completed until the end of this study when *Festuca rubra* was the main species along the whole transect, followed by *Agrostis capillaris* with a slightly lower frequency.

The changes in the rate of succession, expressed by similarity coefficients, strongly depended on the nature of individual coefficients. While the values of Jaccard's coefficient did not change until 1995 and then decreased slightly, Soerensen's coefficient was constant after an initial strong increase and the similarity ratio gradually increased to a constant rate, after a big initial increase (Fig. 2). The time-lag analysis calculated for the first and last 1 m long segments along the transect resulted in regression lines with positive slopes. This indicates that the succession in these sub-plots was directional, i.e., no cyclicity or chaotic behaviour was found (Fig. 3). The slope calculated for the first segment of the transect was larger than that for the last segment. Therefore, the rate of succession was not uniform along the transect. The slowest rate occurred at the lower end of the transect (Fig. 3), whereas in the middle and at the upper end it was higher.

Discussion

We found that restoration of species-rich grassland on abandoned land can be fast, and successional stages dominated by weeds can be avoided, if the arable field is small, farmed for a few years only, not fertilized and surrounded by natural vegetation. This is interesting and may be useful in applied ecology. However, the preconditions are rather strict and unlikely to apply to most situations.

The most important difference between our results and those in the literature is the missing initial successional stages dominated by weedy plants. Weeds are usually well-represented not only in vegetation developing in the first years after an arable field is abandoned (Numata 1982, Falinski 1986) but also in the seed bank (Lopez-Marino et al. 2000), so their regeneration may negatively affect the process of restoration even at later successional stages. The results of the time-lag analysis of an oldfield succession presented by Collins et al. (2000) are similar to ours, i.e. directional change without cyclicity and much stochasticity, except in the first years when his plots behaved rather chaotically, due to great changes in the species composition of annuals, which were then very abundant. In our case, as indicated by Fig. 3, this first stage of succession was absent and directional succession started immediately after the field was abandoned. This speeded up the successional development. This difference probably resulted from an absence of weed seeds in the seed bank in this field. Thus, weedy plants are uncommon at the onset of succession only if they are absent from the seed bank and uncommon in the surrounding land.

Various procedures have been suggested for suppressing weeds in the initial stages of succession or avoiding these stages completely. The seed bank of arable fields can partly be exhausted of weeds if they are allowed to germinate and establish, but then cut before flowering (Míchal & Petříček 1999). If this procedure is repeated several times, the number of seeds in the soil can be reduced. In some cases herbicides are utilized to prevent the established weeds in abandoned fields from flowering (Wilson & Gerry 1995, Biedenbender & Roundy 1996). As weedy plant assemblages include species adapted to

a wide range of environmental conditions, they cause serious problems not only in nutrient-rich localities but also nutrient-poor conditions, such as sandy soils (Falinski 1986, but see Csecserits & Redei 2001). Therefore, the dominance of weedy plants in the early stages of succession on abandoned fields is difficult to suppress.

A fast rate of succession appears to benefit restoration. This is certainly true if there is a single weedy stage before real grassland is established. However, in other cases a high rate of succession can be associated with a larger number of initial stages each dominated by different species. In that case a high rate of succession does not necessarily imply that grassland is achieved within a shorter period. In our particular case the slow rate of succession was beneficial. As most of the important grassland plants were already present in the former arable field early in the succession only slight changes in species composition were required to establish grassland similar to that in the surrounding landscape.

The estimated rate of succession depends partly on the method of its calculation. There are several methods, the simplest of which is that of Prach et al. (1993) who used year-to-year changes in the cover of the dominant species. They found that succession on nutrient-poor and dry sites is slower than on nutrient-rich and wet sites and that the rate of succession decreases strongly at the beginning and more slowly later in the succession. Similar results were obtained by Myster & Pickett (1994), based on species composition of the whole plant assemblage. Our results cannot be directly compared with those of Prach et al. (1993), as we did not estimate plant cover. However, assuming a correlation between frequency and plant cover, a tentative comparison can be made. In our study only two dominant species were recorded in the first 12 years of the succession. Therefore, the succession rate was extremely low. Our observation contrasts with that reported for other oldfields where the succession was usually very fast in the first five years or so, after which it decreased in the following decade or so (e.g. Bornkam 1981, Molnár & Botta-Dukát 1998). This difference is associated with the generally low rate of succession in the grassland studied. The extremely low proportion of annuals (3 species, i.e. 4% of the species recorded during 12 years) is largely responsible for the pattern observed in this study. As perennials grow more slowly than annuals, the rate of succession was lower. Moreover, even among the perennials there were hardly any characteristics of early successional stages. Therefore, the pattern was largely caused by a step-by-step increase in plants typical of late successional stages and largely stochastic extinction of already established species.

Acknowledgements

We would like to thank Vlastimil Kostkan, Libor Ambrozek and Michal Hájek for assistance with the fieldwork. Karel Prach provided some literature and commented on a draft of the paper. L.K. was financially supported by grant no. 206/01/1037 from the Grant Agency of the Czech Republic, and institutional long-term research plan no. AV0Z6005908 and grant no. KSK6005114, both from the Academy of Sciences of the Czech Republic AV ČR. Tony Dixon kindly improved our English.

Souhrn

Sukcese vegetace byla studována na živinami chudém, opuštěném poli uprostřed lesního porostu, které bylo obklopeno přirozenou pastvinou. Naše dvanáctileté sledování jsme zahájili po opuštění pole, které bylo kultivováno pouze dva roky. Počet druhů plevelů a jejich pokryvnost byly během celé sledované doby pozoruhodně nízké. Pouze dva druhy, *Agrostis capillaris* a *Festuca rubra*, dominovaly během sledovaných 12 let. Od 6. roku sledování se již neměnil počet druhů. Sukcesní změny byly během celého sledování kontinuální, směřovaly jedním směrem a od druhého roku byly jen malé.

References

- Biedenbender S. H. & Roundy B. A. (1996): Establishment of native semidesert grasses into existing stands of *Eragrostis lehmanniana* in southeastern Arizona. – *Restor. Ecol.* 4: 155–162.
- Bornkamm R. (1981): Rates of change in vegetation during secondary succession. – *Vegetatio* 47: 213–226.
- Buisson E. & Dutoit T. (2002): Can grassland species colonize ex-cultivated fields from the margins (La Crau steppic area, Southeastern France)? – In: de Patta Pillar V. (ed.), Abstracts of the 45th symposium of the International Association for Vegetation Science, p. 148, Department of Ecology and Botany, Porto Alegre.
- Collins S. L., Micheli F. & Hartt L. (2000): A method to determine rates and patterns of variability in ecological communities. – *Oikos* 91: 285–293.
- Cseceserits A. & Redei T. (2001): Secondary succession on sandy old-fields in Hungary. – *Appl. Veg. Sci.* 4: 63–74.
- Falinski J. B. (1986): Vegetation succession on abandoned farmland as a dynamics manifestation of (an) ecosystem liberal of long continuance anthropopression. – *Wiadom. Ekol.* 30: 25–50 & 115–126.
- Jongman R. H., ter Braak C. J. F. & van Tongeren O. F. R. (1987): Data analysis in community and landscape ecology. – Pudoc, Wageningen.
- Klötzli F. & Grootjans A. P. (2001): Restoration of natural and semi-natural wetland systems in Central Europe: Progress and predictability of developments. – *Restor. Ecol.* 9: 209–219.
- Kuča P., Majský J., Kopeček F. & Jongepierová I. (eds.) (1992): Chránená krajinná oblasť Biele/Bílé Karpaty. – *Ekológia*, Bratislava.
- Kunz L. (1955): Staré zemědělství na Valašsku I. – *Valašsko* 4: 14–23.
- Kunz L. (1956): Staré zemědělství na Valašsku II. – *Valašsko* 5: 6–21.
- Lopez-Marino A., Luisscalabuig E., Fillat F. & Bermudez F. F. (2000): Floristic composition of established vegetation and the soil seed bank in pasture communities under different traditional management regimes. – *Agr. Ecosyst. Env.* 78: 273–282.
- Marhold K. & Hindák F. (eds.) (1998): Zoznam nižších a vyšších rastlín Slovenska. – Veda, Bratislava.
- McDonald A. W., Bakker J. P. & Vegelin K. (1996): Seed bank classification and its importance for the restoration of species-rich flood-meadows. – *J. Veg. Sci.* 7: 157–164.
- Michal I. & Petříček V. (eds.) (1999): Péče o chráněná území. Vol. 1–2. – Agentura ochrany přírody a krajiny ČR, Praha.
- Molnár Z. & Botta-Dukát Z. (1998). Improved space-for-time substitution for hypothesis generation: secondary grasslands with documented site history in SE-Hungary. – *Phytocoenologia* 28: 1–29.
- Muller S., Dutoit T., Alard D. & Grevilliot F. (1998): Restoration and rehabilitation of species-rich grassland ecosystems in France: a review. – *Restor. Ecol.* 6: 94–101.
- Myster R. W. & Pickett S. T. A. (1994): A comparison of rate of succession over 18 yr in 10 contrasting old fields. – *Ecology* 75: 387–392.
- Nekuda V. (ed.) (1982): Uherskohradišsko. – Muzejní a vlastivědná společnost, Brno.
- Numata M. (1982): Experimental studies on the early stages of secondary succession. – *Vegetatio* 48: 141–149.
- Prach K., Pyšek P. & Šmilauer P. (1993): On the rate of succession. – *Oikos* 66: 343–346.
- ter Braak C. J. F. & Šmilauer P. (1998): CANOCO reference manual and user's guide to "Canoco for Windows" software for canonical community ordination, version 4. – Microcomputer Power, Ithaca.
- Willems J. H. (2001): Problems, approaches, and results in restoration of Dutch calcareous grassland during the last 30 years. – *Restor. Ecol.* 9: 147–154.
- Willems J. H. & Bobbink R. (1990): Spatial processes in the succession of chalk grassland on old fields in the Netherlands. – In: Krahulec F., Agnew A. D. Q., Agnew S. & Willems J. H. (eds.), Spatial processes in plant communities, p. 237–249, Academia, Praha.
- Wilson S. D. & Gerry A. K. (1995): Strategies for mixed-grass prairie restoration: Herbicide, tilling, and nitrogen manipulation. – *Restor. Ecol.* 3: 290–298.

Received 16 January 2004
Revision received 14 July 2004
Accepted 18 August 2004