

## Secondary succession in old-fields in the Transylvanian Lowland (Romania)

Sekundární sukcese na opuštěných polích v Transylvánské nížině v Rumunsku

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The main trends in spontaneous regeneration were studied in old-fields in the Transylvanian Lowland (Câmpia Transilvaniei) over a period of 40 years using the chronosequence method. Succession proceeds to grassland, because the establishment of woody vegetation is hindered by grazing and mowing of the old-fields and by the scarcity of woodlands in the vicinity. Community properties and population-level changes were recorded at different stages of succession and compared with semi-natural grassland in the surrounding landscape. Due to favourable soil conditions and temperate climate, vegetation cover develops quickly after the fields are abandoned. Annuals dominated only in the first year. After two years the fast growing clonal grass, *Elymus repens*, became dominant. After approximately 12 years, *Elymus* was replaced by *Festuca rupicola*, which is more resistant to stress and disturbance. In the later stages of succession various species, some typical of surrounding grassland, attained high cover values. A steady increase in species diversity, measured by the Shannon index, and richness was recorded at both the field (1.0–2.5 ha) and plot (4 × 4 m) scales. Species richness increased rapidly in early and middle stages and stabilized after the 14th year. Specific features of the succession in the old-fields in the Transylvanian Lowland can be attributed to the continued grazing and mowing of the fields after they are abandoned. This increases species richness because it arrests succession at a stage when species diversity is high. The management directs regeneration towards secondary grassland rather than species poor woodland.

**Key words:** abandoned fields, arrested succession, land-use, Romania, species diversity, spontaneous regeneration

### Introduction

Old-fields are suitable for studying secondary succession, because they occur abundantly in various landscapes throughout the world and the results can be used for large-scale comparisons of different regions. The study of successional processes is important for restoration ecology and restoration programs (Luken 1990, Prach et al. 2001).

Long-term changes in vegetation can be followed most accurately by using permanent plots (Bakker et al. 1996). If the time and necessary conditions for a long-term research project (e.g. undisturbed or private research area) are not available some form of compromise is necessary. Space-for-time substitution is an alternative of studying succession. Despite its weaknesses (Pickett et al. 2001) it can be used to delineate patterns in succession in landscapes or regionally (Foster & Tilman 2000) and gives results in a shorter time than permanent plots.

Much knowledge on succession in human-disturbed habitats in Europe has accumulated recently. By analysing the patterns in succession in several seres over a large region Prach et al. (1999) were able to construct an expert system that predicts the main changes

in vegetation that occur on human-made sites in Central Europe. There is a need for such expert systems and data on spontaneous regeneration processes on a regional scale for restoration projects. Currently there is very little information on the long-term spontaneous succession in Romanian old-fields (Bujorean 1930, Arsene & Chelu 2001) and the results of these studies are only informative in respect to vegetation types that appear throughout succession or that become a potential endpoint in different successional seres. In this study, the focus is on the main trends in spontaneous regeneration on abandoned fields in an old agricultural region of Romania, with the objective of identifying general successional trends and regional characteristics.

The primary questions addressed were: 1. What are the major trends in secondary succession on old-fields in the Transylvanian Lowland? 2. Are these trends similar to those recorded for secondary succession in comparable situations in the temperate zones of Europe and North America?

## Material and methods

### *Site description*

Old-fields were studied in the surroundings of the village Suatu (46°46'N, 23°58'E, 328–485 m a.s.l.), in the central part of the Transylvanian Lowland (Câmpia Transilvaniei) in Romania (Fig. 1). The climate in this area is temperate continental with precipitation maximum in summer (June, July, August); average yearly precipitation is around 550–600 mm, mean annual temperature is about 8.5 °C. The soil in this region is chernozemic brown forest soil on either a clay, marl or sandstone substrate (Jakab 1972). The natural vegetation is forest-steppe/forest. At present, small remnants of oak (*Quercus robur-Q. petraea*) and oak-hornbeam (*Quercus petraea-Carpinus betulus*) woods can be found on the tops of the hills or on northern facing slopes. Between the vast agricultural lands, there are well-conserved steppes dominated by *Stipa pulcherrima*, *Stipa lessingiana* on steep slopes with a SW, S or SE orientation, and meadow steppes dominated by *Festuca rupicola*, *Stipa tirsia*, *Bromus erectus* and *Brachypodium pinnatum* on slight slopes or bottoms. Mesoclimatic conditions are determined by the character of the relief. Remnants of semi-natural grassland are very diverse and of many types. Slope, exposure, and past and present land-use are the most important factors affecting the type of grassland that develops (Ruprecht 2000).

### *History of land-use*

The extensive deforestation of this region occurred more than 1000 years ago (Csűrös 1973). Only a few patches of woodland remained in the 1700s (Anon. 1769–1773) when the secondary extension of grasslands began. These grasslands were maintained up to the present by grazing and mowing and are species-rich and undegraded. Thus these remnants are important for nature conservation and restoring abandoned fields (Szabó & Ruprecht 2001).

Traditional agriculture and farming practices later became widespread which is still the case today. A few fields were abandoned in the 1970–1990 period, because the government policy was the permanent cultivation of land, even that with extreme edaphic conditions. More land was abandoned in the 1990s, mostly because of changes in ownership after the change in the political regime, lack of working capacity and the uncertain economic situation in agriculture.

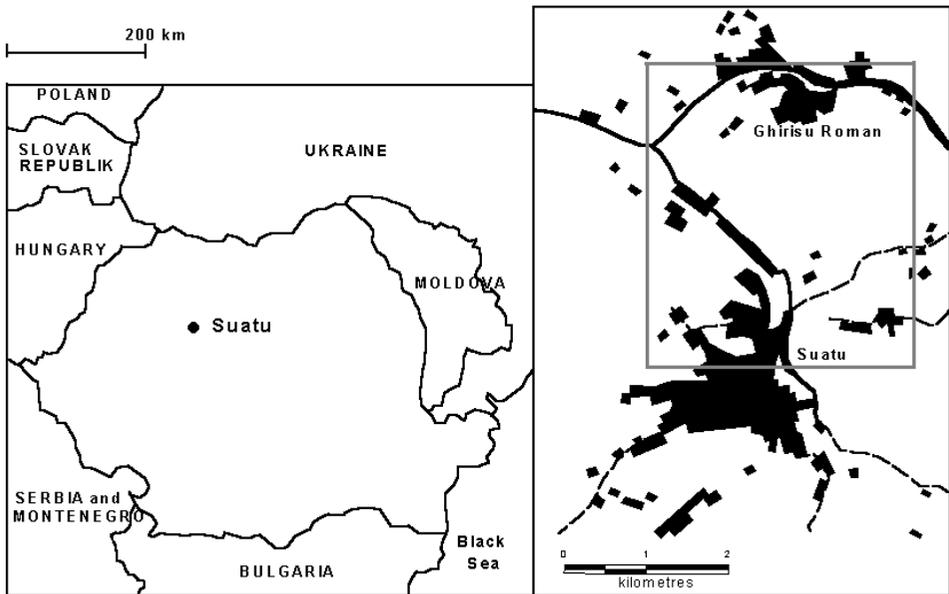


Fig. 1. – The location of the site in Romania and in the surroundings of the village Suatu, where abandoned fields were studied.

#### *Data on succession*

In 2000–2004, 41 old-fields abandoned 1–40 years ago were surveyed. Nine randomly chosen old-fields were re-examined two or three years later giving the total of 50 surveys. The size of the fields varied between 1–2.5 ha and the number of different ages is indicated in Fig. 2. All the fields and semi-natural grasslands studied were situated within a 2.25 km × 2.75 km area (Fig. 1). The date when the fields were abandoned and the last crop was obtained by asking the landowners. Percent cover by vascular plants was visually estimated in four 4 × 4 m plots per field. Because the vegetation of old-fields is heterogeneous, stratified sampling was used. Habitat type (in terms of soil type, exposure and slope) of the fields was similar, mainly transitional meso-xeric. Extremely dry and wet places were not sampled. The last crop was most frequently legumes (*Trifolium pratense*, *Medicago sativa*) planted for hay and cropped over a period of 3–4 years, in other cases it was maize, sunflower or grain (wheat, barley and oats). As a reference for the possible “endpoints” of the successional trends, five meso-xeric semi-natural grasslands were sampled. Grasslands were chosen, because succession proceeds towards this vegetation.

The secondary succession on abandoned agricultural fields was studied using space-for-time substitution or the chronosequence method, in order to determine the major trends in the spontaneous succession in this landscape.

#### *Data analysis*

For each field, total cover was calculated by summing the percentage cover of each species in a plot and mean cover per field by determining the mean of the four sample plots.

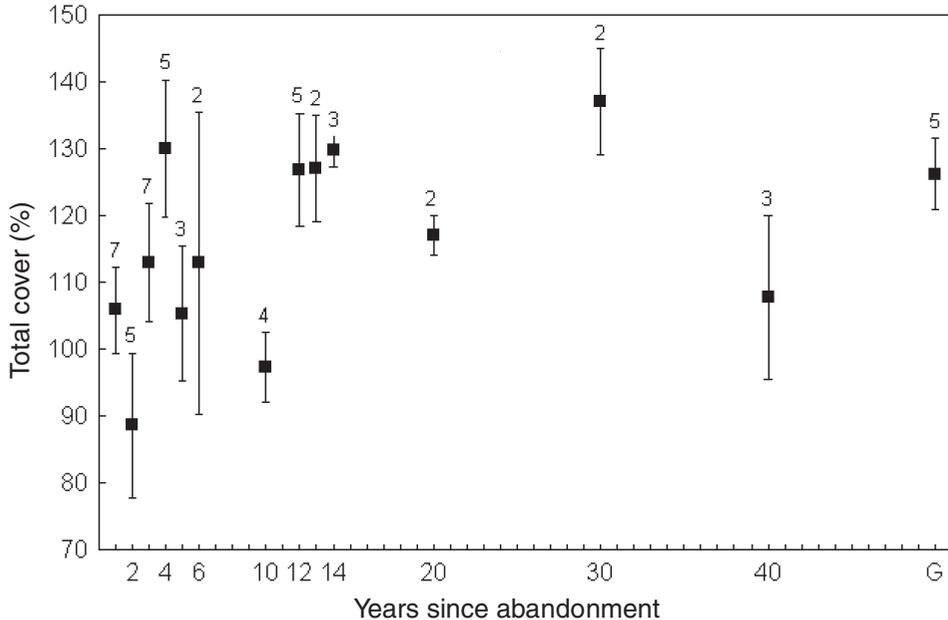


Fig. 2. – Changes in total cover in the course of the succession. Values are means and standard errors. Numbers above the whiskers are the number of fields in each age category; G = reference grassland. Note that the total cover exceeds 100% as the values are sums of the covers of all species present.

Species were classified into life form categories, as annuals, biennials and short-lived perennials, non-woody perennials and woody species (Sanda et al. 1983) and the relative cover of each category in each field was calculated. Biennials and short-lived perennials were lumped together because they play the same role in succession and in many cases are very difficult or even impossible to separate. This category represents a transition in life-history characteristics between annuals and long-lived perennials.

Changes in the dominant species in the course of succession were followed by using cover data. A species was considered to be dominant if it covered more than 25% of at least one old-field.

To obtain an overview of the main successional trends, averages of plots from a field or grassland, and the most important species were used as input data in the correspondence analysis (Podani 1997). Applying this ordination method often leads to a horseshoe-effect in the arrangement of the objects and variables on a figure. This effect is most often attributed to the non-linear structure of the data, which has biological meaning in this case. This is why, e.g. detrended correspondence analysis was not arbitrarily used to “linearize” the data (Podani 1997). Old-fields were grouped into three successional stages: early (fields

Table 1. – Species important in succession and surrounding grassland (with cover exceeding 10% on at least two old-fields or grasslands). Species numbers refer to Fig. 5. Species groups: w – weeds of agricultural fields, w-n – species common to agricultural fields and natural habitats, n – species of natural habitats, c – cultivated species. Life form: A – annual, B – biennial and short-lived perennial, P – non-woody perennial, W – woody species. G – reference grassland. Average covers of species (%) are given with the highest values in bold. ►

No	Species	Species group	Life form	Successional stage (years since abandonment)			G
				Early (1–6)	Middle (10–14)	Late (20–40)	
1	<i>Setaria pumila</i>	w	A	<b>1.84</b>	0	0	0
2	<i>Chenopodium album</i>	w	A	<b>1.38</b>	0	0	0
3	<i>Hibiscus trionum</i>	w	A	<b>0.71</b>	0	0	0
4	<i>Lapsana communis</i>	w-n	A	<b>0.31</b>	0	0	0
5	<i>Anthemis arvensis</i>	w	A	<b>2.63</b>	0.01	0	0
6	<i>Crepis setosa</i>	w	A	<b>2.33</b>	0.04	0	0
7	<i>Cirsium arvense</i>	w	P	<b>1.81</b>	0.54	0	0
8	<i>Conyza canadensis</i>	w	A	<b>1.63</b>	0.02	0	0
9	<i>Stachys annua</i>	w	A	<b>1.21</b>	0.01	0	0
10	<i>Sinapis arvensis</i>	w	A	<b>1.15</b>	0.01	0	0
11	<i>Symphytum officinale</i>	n	P	<b>0.97</b>	0.06	0	0
12	<i>Crepis foetida</i> subsp. <i>rhoeadifolia</i>	w	A	<b>0.73</b>	0.24	0	0
13	<i>Lathyrus tuberosus</i>	w	P	<b>0.69</b>	0.28	0	0
14	<i>Consolida regalis</i>	w	A	<b>0.53</b>	0.01	0	0
15	<i>Bromus inermis</i>	w-n	P	<b>0.38</b>	0.25	0	0
16	<i>Elymus repens</i>	w	P	<b>26.24</b>	12.11	0.13	0
17	<i>Medicago sativa</i>	c	P	<b>5.57</b>	0.03	0.08	0.3
18	<i>Convolvulus arvensis</i>	w-n	P	<b>5.06</b>	1.21	0.05	0.26
19	<i>Trifolium pratense</i>	w-n	P	<b>3.66</b>	0.38	1.05	0.78
20	<i>Poa angustifolia</i>	n	P	<b>2.64</b>	0.92	2.62	1.6
21	<i>Daucus carota</i>	w-n	B	<b>1.69</b>	1.15	0.19	0.17
22	<i>Echium vulgare</i>	w-n	B	<b>1.66</b>	0.16	0.01	0.05
23	<i>Medicago lupulina</i>	w-n	A	<b>1.46</b>	0.44	0.63	0.07
24	<i>Prunus spinosa</i>	n	W	<b>1.37</b>	0.13	0.82	0.03
25	<i>Rubus caesius</i>	w-n	W	2.78	<b>4.13</b>	0.04	0
26	<i>Trifolium repens</i>	w-n	P	0.90	<b>1.21</b>	0.13	0
27	<i>Mentha longifolia</i>	w-n	P	0.75	<b>0.89</b>	0.01	0
28	<i>Rapistrum perene</i>	w-n	B	0.47	<b>0.69</b>	0.32	0
29	<i>Festuca rupicola</i>	n	P	0.74	<b>29.22</b>	15.82	13.26
30	<i>Dorycnium pentaphyllum</i> subsp. <i>herbaceum</i>	n	P	2.00	<b>8.97</b>	8.75	3.85
31	<i>Leontodon hispidus</i>	n	P	1.17	<b>5.17</b>	4.01	0.91
32	<i>Lotus corniculatus</i>	w-n	P	0.36	<b>4.27</b>	0.98	1.26
33	<i>Achillea collina</i>	w-n	P	1.31	<b>4.10</b>	3.28	2.05
34	<i>Hieracium bauhini</i>	n	P	1.37	<b>3.18</b>	0.58	0.03
35	<i>Plantago lanceolata</i>	n	P	1.41	<b>2.66</b>	1.19	0.5
36	<i>Cichorium intybus</i>	w-n	B	2.22	<b>2.41</b>	0.26	0.03
37	<i>Potentilla argentea</i>	w-n	P	0.13	<b>2.27</b>	0	0.15
38	<i>Hieracium pilosella</i>	w-n	P	0.08	<b>1.40</b>	1.04	0.01
39	<i>Trifolium campestre</i>	w-n	A	0.11	<b>0.63</b>	0	0.02
40	<i>Poa trivialis</i>	n	P	0.78	0.28	<b>0.83</b>	0
41	<i>Arrhenatherum elatius</i>	n	P	0.24	0	<b>1.75</b>	0
42	<i>Salvia verticillata</i>	w-n	B	2.57	3.22	<b>6.75</b>	2.1
43	<i>Dactylis glomerata</i>	n	P	3.47	1.82	<b>5.07</b>	2.18
44	<i>Onobrychis vicifolia</i>	n	P	0.99	0.06	<b>5.93</b>	2.27
45	<i>Agrostis capillaris</i>	n	P	0.24	0.91	<b>2.22</b>	0.9
46	<i>Bromus erectus</i>	n	P	0.01	0.03	0	<b>10.25</b>
47	<i>Centaurea phrygia</i>	n	P	0.02	0.40	4.18	<b>6.98</b>
48	<i>Koeleria macrantha</i>	n	P	2.17	1.79	5.19	<b>5.81</b>
49	<i>Thymus spp.</i>	n	P	0.01	1.27	2.67	<b>4.70</b>
50	<i>Teucrium chamaedrys</i>	n	P	0.04	0.05	0.89	<b>3.53</b>
51	<i>Anthoxanthum odoratum</i>	n	B	0.02	0.02	0.31	<b>3.4</b>
52	<i>Festuca pratensis</i>	n	P	1.35	2.01	3.13	<b>3.35</b>
53	<i>Elymus hysspidus</i>	n	P	0	0.06	0.42	<b>3.1</b>
54	<i>Carex humilis</i>	n	P	0	0.06	1.12	<b>5.5</b>
55	<i>Adonis vernalis</i>	n	P	0	0	2.03	<b>4.5</b>
56	<i>Stipa tirsia</i>	n	P	0	0	0.04	<b>9.25</b>
57	<i>Carex tomentosa</i>	n	P	0	0	0	<b>3.41</b>

abandoned 1–6 years ago), middle (10–14 years) and late (20–40 years). Grasslands were included in the analysis as a reference. Species with cover values higher than 10% on at least two old-fields or grasslands were considered to be important in succession or grasslands. These species were classified into three groups according to Sanda et al. (1983): 1. species of natural habitats, 2. species common to agricultural fields and natural habitats, 3. weeds of agricultural fields (Table 1).

Species richness was calculated for each field and semi-natural grassland at two scales (plot and field). The Shannon index was used to calculate the species diversity on the field scale. For statistical analysis, Spearman rank correlation was applied (Zar 1999). Because at both scales a non-linear relationship was expected between age and species richness and diversity, respectively, the linear and non-linear relationships were tested by multiple regression. The best fit for the non-linear relationship was obtained using a logarithmic transformation.

Nomenclature follows Ciocârlan (2000).

## Results

Average total cover exceeded 100% in the initial years of succession. The total cover increased during the succession ( $R = 0.31$ ,  $t = 2.29$ ,  $N = 50$ ,  $p < 0.05$ ), despite the variation in cover of old-fields of different age. After the 12th year, the cover remained more or less stable (Fig. 2).

Annuals were dominant at the beginning, but their relative cover consistently decreased during the first 6 years. Biennials and short-lived perennials showed no clear trend and their average relative cover varied between 5 and 19%. In the second year, the relative cover of herbaceous perennials exceeded that of short-lived species (annuals, biennials and short-lived perennials) and their dominance continued to increase. The relative cover of woody species was always low and did not show a trend in the first 40 years (Fig. 3). Of the woody species, only the clonal *Rubus caesius* had a high cover in some fields in the first 10 years, whereas the bird-dispersed shrubs (*Rosa canina*, *Prunus spinosa* and *Crataegus monogyna*) had the highest cover and were also the most frequent later on.

*Setaria pumila* (annual grass), *Chenopodium album* (annual forb), *Anthemis arvensis* (annual forb), *Rubus caesius* (woody species) or *Elymus repens* (perennial grass) were dominant in the first year of the succession, *Rubus caesius* or *Elymus repens* in the second, *Plantago lanceolata* (perennial forb), *Echium vulgare* (biennial forb) or *Elymus repens* in the third. *Elymus repens* was the most frequently occurring dominant species in the 3rd to 12th year of succession (Fig. 4). From then on, *Festuca rupicola* became dominant up to the 14th year and on some fields for even longer. The cover of *Dorycnium pentaphyllum* subsp. *herbaceum*, another typical dominant of middle-aged fields, exhibited a temporal pattern similar to *Festuca* (Fig. 4). Older fields often lacked dominant species (none exceeded 25% cover); species with high cover values varied from field to field, but *Festuca rupicola* was always important. This species was also an important component of grassland, where it had high cover values or was dominant (Fig. 4). The grasslands sampled were often dissimilar in their dominant species possibly because of different land-use, history and habitat differences (e.g. microclimate, microgeomorphological factors). Some of the dominant species in grasslands (*Festuca rupicola*, *Thymus* spp., *Centaurea phrygia* and *Koeleria macrantha*) were already dominant in late successional old-fields.

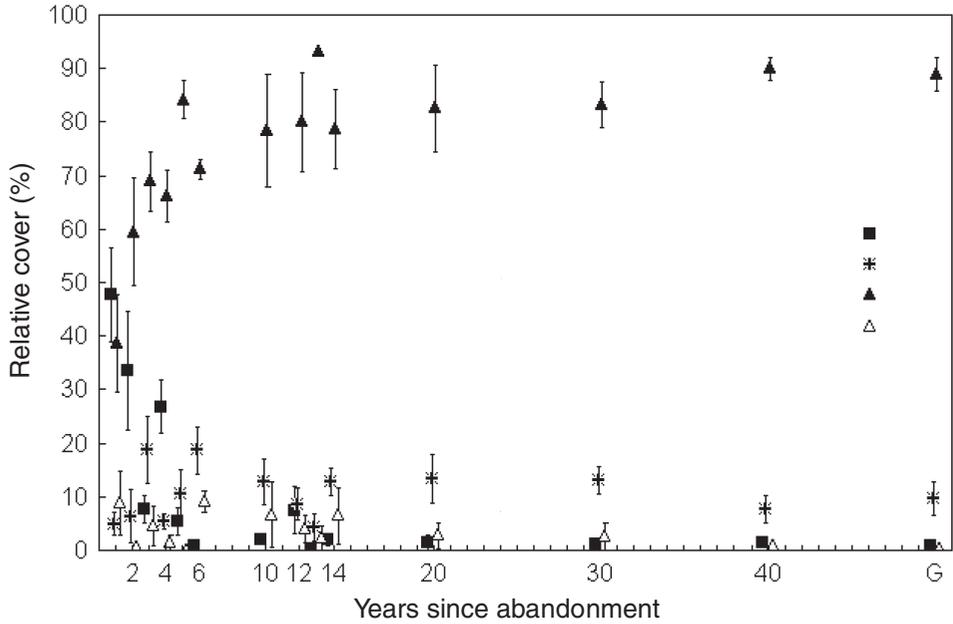


Fig. 3. – Change in the proportion of life-forms during succession. Values are means and standard errors. A = annuals, B = biennials and short-lived perennials, P = non-woody perennials, W = woody species, G = reference grassland.

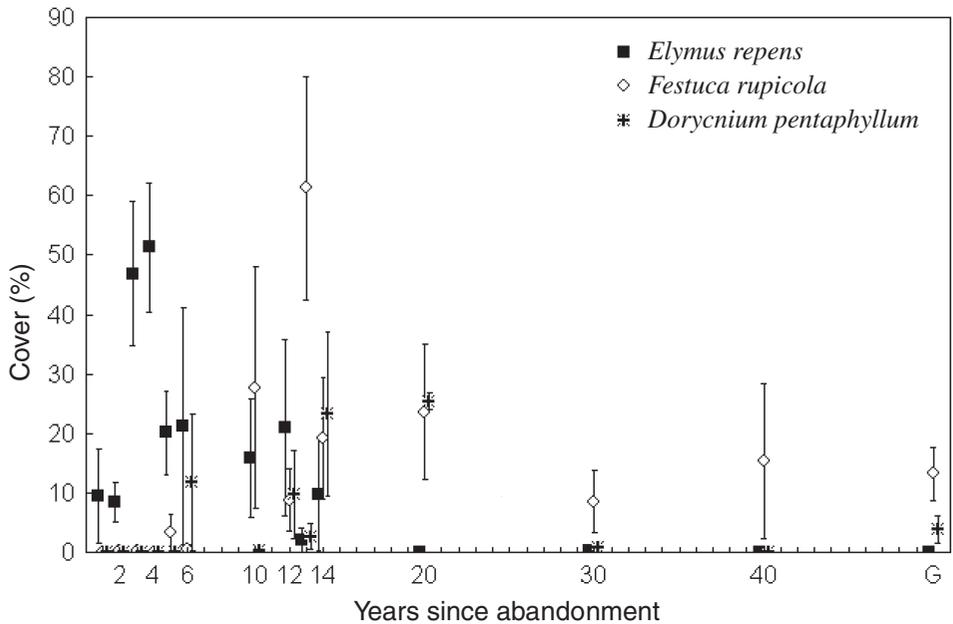


Fig. 4. – Changes in cover of dominant species during succession. Only species dominant (with cover exceeding 25%) on at least three old-fields are shown. Values are means and standard errors. G = reference grassland.

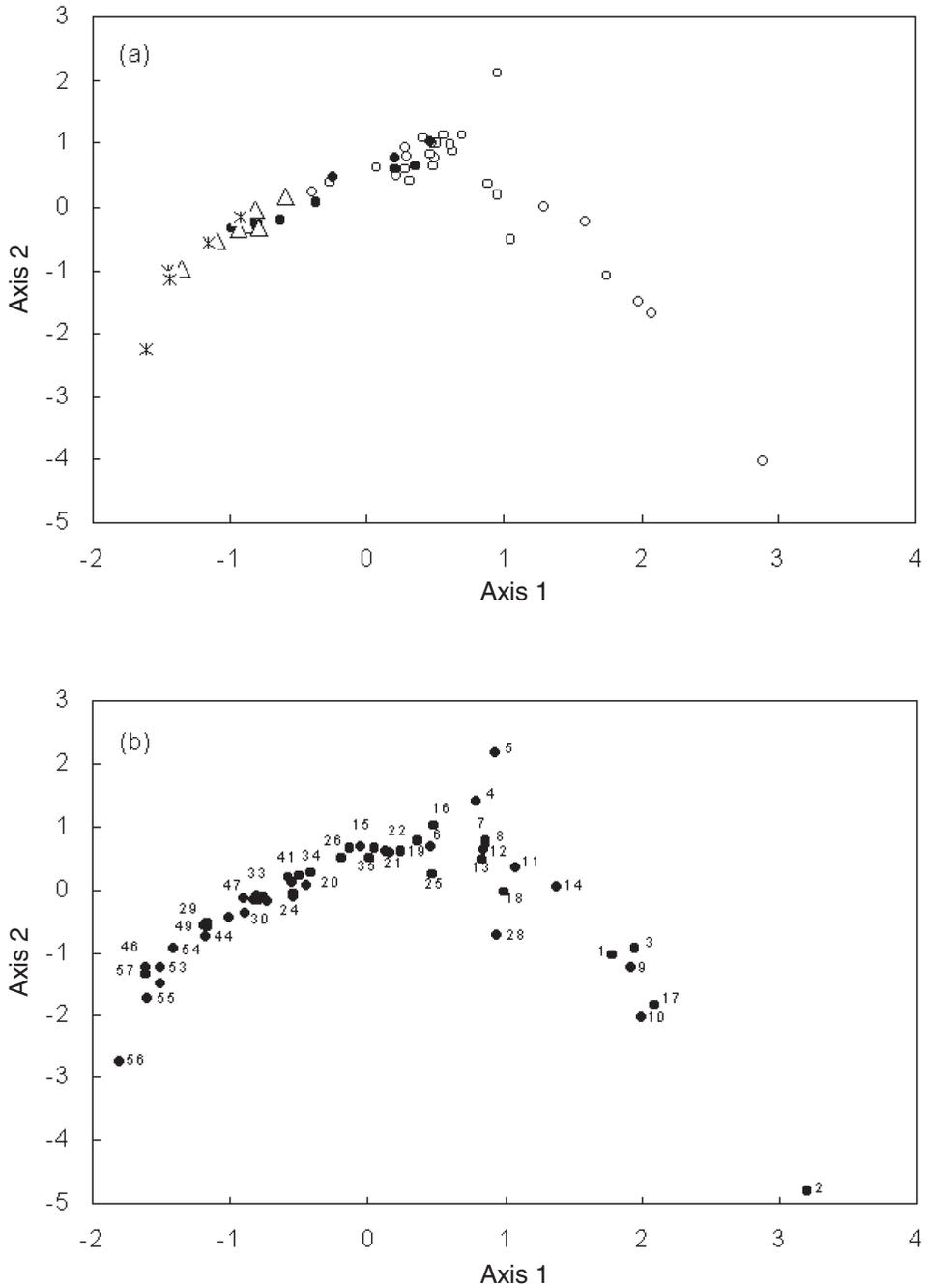


Fig. 5. – Correspondence analysis of (a) plots sampled in abandoned fields of different ages and grassland, and (b) the most important species. Open circles: fields abandoned 1–6 years ago; solid circles: fields abandoned 10–14 years ago; open triangles: fields abandoned 20–40 years ago; asterisks: grassland. Numbers in (b) are codes of individual species (see Table 1 for species names).

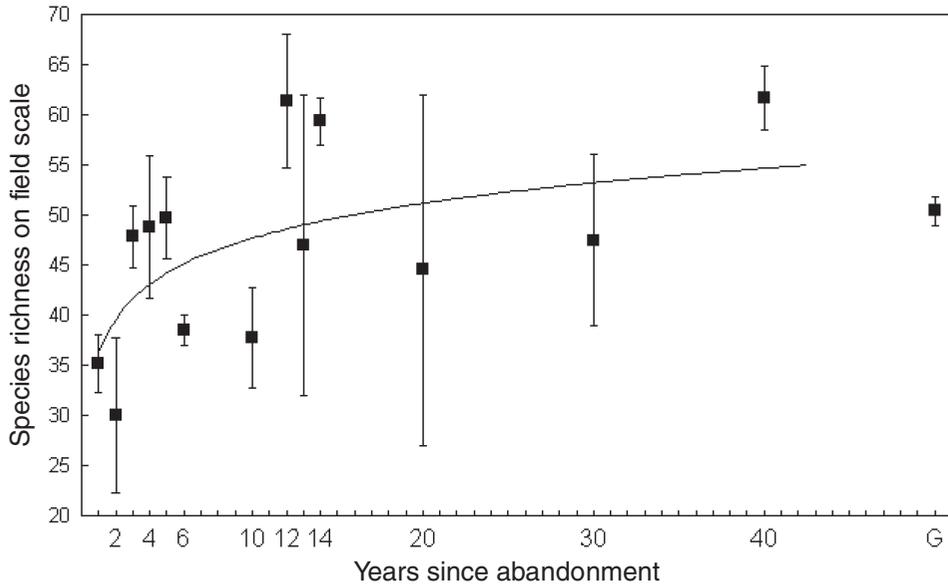


Fig. 6. – Relationship between species richness on the field scale and succession in old-fields. Values are means and standard errors. G = reference grassland.  $y = 35.17 + 14.66 \cdot \log_{10}(x)$

Despite the variation in the dominant species in old-fields it can be concluded that *Elymus repens* is the most typical dominant of early and middle successional stages, and *Festuca rupicola* of the later stage (Fig. 4).

On the ordination diagram, the old-fields form three groups corresponding to the early, middle and late successional stages (Fig. 5a). In spite of the horseshoe-effect (Podani 1997), time is represented by the first axis and the position of the old-fields along this axis reflects succession, with some overlap between the stages (Fig. 5a). The second axis does not reflect any clear pattern. Species are arranged according to their prevalence at different successional stages (Fig. 5b, Table 1). Species characteristic of the early stages are mainly agricultural weeds, to a lesser degree species common to agricultural fields and natural communities, and only few are typical of natural habitats (Table 1). Species common to agricultural fields and natural habitats, and to a lesser degree those of natural habitats were characteristic of the middle successional stages, and those characteristic of the late stages were almost exclusively species typical of natural habitats (Table 1).

On both field and plot scales, species richness increased significantly over time (field scale:  $R = 0.51$ ,  $t = 4.10$ ,  $N = 50$ ,  $p < 0.0005$ , plot scale:  $R = 0.45$ ,  $t = 3.51$ ,  $N = 50$ ,  $p < 0.001$ ). A logarithmic relationship between field age and species richness was found on the field scale [ $F_{2,47} = 6.77$ ,  $r^2 = 0.22$ ,  $p = 0.003$ , age,  $\beta = -0.09$  (SE = 0.26),  $t = -0.36$ ,  $p = 0.719$ ,  $\log(\text{age})$ ,  $\beta = 0.55$  (0.26),  $t = 2.10$ ,  $p = 0.041$ ], since species number increased rapidly in the first three years of succession, then slowed, and stabilized after the 14th year (Fig. 6). Species diversity, measured by the Shannon index, increased significantly through succession ( $R = 0.41$ ,  $t = 3.11$ ,  $N = 50$ ,  $p < 0.005$ ).

## Discussion

Vegetation cover developed quickly and closed shortly after the old-fields were abandoned. This is quite typical of regions with a wet to moderately wet climate and nutrient-rich soils (Pickett 1982, Bartha et al. 2003).

In terms of life-forms, annual species were dominant only in the first year after the fields were abandoned and then rapidly decreased. Biennials and short-lived perennials occurred at low to medium levels during the sere. This result corresponds with the finding of the present study about rapidly closing vegetation cover in the old-fields. Short-lived species require high light intensities, mainly at the time of germination, are often gap-colonizers (Bazzaz 1968, 1979, Brown & Southwood 1987) and the germinating seedlings are very sensitive to competition from neighbouring plants (Fenner 1978, Gross 1980). The establishment of a second generation of these annual plants is improbable due to the increase in vegetation cover, low light intensities at ground level and absence of bare soil (Bazzaz 1979, Fenner 1987). Increasing competition in this productive environment plays a major role early in succession when the short-lived species are displaced by perennial herbs (Fenner 1987, Osbornová et al. 1990, Grime 2001). Under such circumstances, biennials and short-lived perennials do not play a role in succession and are not represented by a distinct stage.

Few shrubs and trees established and survive, which cannot be attributed to insufficient water. The region is sufficiently moist to support a dense shrub cover. The few woody species in the later stages of succession are mostly due to the land-use techniques applied by landowners (mowing and grazing). However, the availability of seed may limit the establishment of seedlings of woodland trees in old-fields, as woodland is scarce in this landscape.

*Elymus repens*, a perennial grass, is the most frequent dominant up to the 12th year of succession. This is attributed to its ability to spread vegetatively rapidly and dynamically (active foraging) (Grime 1987). This species is the most important dominant of early successional stages not only at the study site but in most parts of Europe (Prach 1985, Osbornová et al. 1990) and some parts of North America (Tilman 1993). *Elymus* is outcompeted by *Festuca rupicola*, which is a slower-growing, tussock-forming grass species, which is more resistant than *Elymus* to stress and disturbance (e.g. draught or grazing). *Festuca* is reported to be an important mid- and late successional species in grassland seres in the drier parts of Central Europe (Baráth 1963, Osbornová et al. 1990, Molnár & Botta-Dukát 1998). The process of replacement in these two grasses involves a trade-off or interaction between competitive ability and tolerance to stress and disturbance (Bazzaz 1979, Grime 1987, Tilman 1990, 1993).

The lack of woody dominants at the end of the successional sequence can be considered to be a case of arrested succession, in which a stable proclimax (sensu Grime 1987, 2001) develops by the 40th year. Under the prevailing climatic conditions and in the absence of human intervention, woodland is expected to dominate abandoned fields in this region but it will take longer than 40 years.

Under continuous land-use it is probable that some competitively dominant grasses like *Festuca rupicola* will remain abundant, or dominants of the semi-natural grassland, like *Stipa tirsia*, will become dominant in some late secondary grasslands on former arable fields.

In ordination plots, fields are arranged along the first axis according to the old-field age and position of species reflects their prevalence in particular successional stages. The overlap between consecutive stages is probably due to the differences in the rate of succes-

sion in old-fields of identical age groups, e.g. some abandoned fields are closer or more distant from seed sources, or have habitat conditions favouring or retarding succession (Prach et al. 1993, Jongepierová et al. 2004). Weeds of agricultural fields are replaced relatively early by species of natural habitats, which dominate later stages of succession.

In several successional studies, various trends in diversity and species richness were reported (Nicholson & Monk 1974, Bazzaz 1975, Tramer 1975, Inouye et al. 1987, Osbornová et al. 1990, Molnár & Botta-Dukát 1998, Csecserits & Rédei 2001). These trends depend mostly on the temporal and spatial scales considered and the natural vegetation of the regions studied. Typically, diversity exhibits a unimodal relationship over time, if the time scale corresponds to that needed for the formation of the climax community (50–100 years) and the field size is appropriate (see Guo 2003 for review). The decrease in species richness in the later stages of succession can be attributed to competitive exclusion (Odum 1969). Management techniques, like grazing, reduce competitive pressure and create horizontal heterogeneity, which leads to increased species diversity (Hutchings & Booth 1996, Rebele & Lehmann 2002). In the present study, diversity and species richness on both plot and field scales increased over time. Species richness on the field scale rapidly increased over the first 12 years and then slowed and stabilized. There was no decrease in species richness and diversity in the oldest fields. This can be attributed to the short time-scale or land-use techniques that arrested succession at an intermediate stage, i.e. grassland instead of woodland (Grime 2001). Perhaps, given enough time, and in the absence of grazing and mowing, species richness would decline and woodland would develop. However, decreasing species richness is not the goal of nature conservation and revegetation.

### Conclusions and implications for nature conservation and management

The chronosequence method provided a general view of the main trends in the regeneration of abandoned arable fields on a regional scale and delineated the most important successional changes that occur over a short period of time.

Unfortunately, few old-fields in the later stages of succession were available for study. Thus the trends found in dominant species, diversity and species richness for the later stages are weaker than those found for the early and middle stages. As a consequence, predictions about the later stages of succession, based on this chronosequence, are only tentative.

After 14 years herbaceous perennials dominate abandoned fields, and total cover, species richness and diversity are similar to that in the semi-natural grassland in the surroundings. At this stage, some old-field dominants (*Festuca rupicola*, *Centaurea phrygia*, *Thymus* sp. div.) are also very abundant in the semi-natural grassland. This indicates that spontaneous regeneration in this region is fast, which could be important for nature conservation and restoration in the future.

Specific features of succession in the Transylvanian Lowland reflect that old-fields in this region are not abandoned completely; they continue to be used for grazing and mowing. This promotes species diversity and richness by arresting succession at the secondary grassland stage and prevents the development towards species poor woodland.

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## Souhrn

Hlavní trendy sukcese vegetace na opuštěných polích byly studovány v Transylvánské nížině; průběh sukcese po dobu 40 let byl rekonstruován srovnáním různých starých sukcesních stádií. Sukcese směřovala k travinným společenstvům, neboť uchycení dřevin je omezovalo pastvou a sečením a tím, že v okolí se vyskytuje málo lesů. Byly studovány změny v charakteristikách společenstva a v zastoupení populací jednotlivých druhů; sukcesní stádia na úhorech byla srovnána s přirozenými travinnými společenstvy v blízkém okolí. Díky příznivým půdním podmínkám a temperátnímu klimatu je vývoj vegetačního krytu na opuštěných polích rychlý; proto je období dominance jednoletých druhů omezeno pouze na první rok sukcese. Po dvou letech převládá rychle rostoucí tráva *Elymus repens*, která je po 12 letech nahrazena druhem *Festuca rupicola*; ten je odolnější vůči působení stresu a disturbancí. V pozdějších stádiích sukcese dosahuje vyšší pokryvnosti řada druhů, mezi nimi jsou i dominanty přirozených travinných společenstev. V průběhu sukcese stoupá počet druhů i druhová diverzita, vyjádřená Shannonovým indexem, a to jak v prostorovém měřítku celých úhorů (1.0–2.5 ha), tak ploch o velikosti 4 × 4 m. Počet druhů rychle stoupá v časných a středních stádiích sukcese, po 14. roce dochází k jeho stabilizaci. Specifické rysy sukcese v Transylvánské nížině jsou dány tím, že pole nejsou opuštěna úplně, nýbrž i po opuštění jsou využívána k pastvě nebo sečena. Tento management vede ke zvýšení druhové diverzity, protože sukcese je zablokována v druhově bohatých stádiích; směřuje tedy k druhotným travinným společenstvům namísto společenstev dřevin.

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