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Testing the validity of successional predictions on an old-field chronosequence in Hungary

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Abstract: We studied the vegetation of 54 sandy old-fields abandoned at different times. We first surveyed the vegetation in 1998 and developed predictions about the spontaneous succession using the chronosequence approach. Afterwards, we repeated the survey in 2000, 2001, 2002 and 2003, and based on this monitoring we tested the predictions of the chronosequence study. For both approaches, we analysed the changes in functional group composition during succession. According to the chronosequence study, the most important changes occurred in the youngest old-fields, abandoned 1-4 years ago: the species number and abundance of annuals, disturbance-requiring and anthropogenic species decreased, and those of perennials, grassland generalists, and species with low disturbance-tolerance increased. No changes were predicted for the older fields. The monitoring confirmed the predictions for the youngest old-fields. However, during the 5 years of monitoring several functional groups changed in their species number or abundance even on the older abandoned fields. Both of the methods showed that secondary succession on sandy old-fields is relatively fast. The chronosequence study provided a more static view of the processes, while the multi-year monitoring revealed that there were considerable inter-annual changes as well. With the yearly monitoring we can detect the effect of additional factors, such as land use changes (e.g., changes in grazing intensity) and yearly climate fluctuations on the direction and rate of secondary succession.

Nomenclature: Simon 2000.

Abbreviations: PFT – Plant Functional Type; BSS – Blue-Small Successional Study.

Introduction

Vegetation succession represents the process of species replacement over time (Pickett et al. 1987), and succession on abandoned fields provides a model system for examining this process (e.g., Osbornová et al. 1990, Prach and Pysek 2001). Basically, there are two ways to study the course of succession: to follow the development of vegetation from the abandonment of the field (continuous monitoring) or to examine old-fields abandoned at different times and consider them as parts of a chronosequence (space-for-time substitution analysis) (Pickett 1989, Bakker et al. 1996, Foster and Tilman 2000). Examples can be found for both methods in Europe and North America, but most of the long-term studies take place in habitats where the succession leads to forest (e.g., Inouye et al. 1987, Pickett 1982, Myster and Pickett 1994, Bornkamm 1985, Osbornová et al. 1990, Schmidt 1998). Only a few old-field succession studies can be found in the literature from the Eurasian forest-steppe or steppe zone, and even less long-term research has been carried out in this biome. So far, short-term studies have shown that the natural regeneration ability of abandoned fields is relatively good in Eastern Europe given the available propagule sources in the surrounding areas (Molnár and Botta Dukát 1998, Csecserits and Rédei 2001, Halassy 2001, Prach and Pysek 2001, Hölzel et al. 2002, Ruprecht 2006). In Hungary, just like in other parts of Europe, large areas of agricultural land have been abandoned, mainly on soils with low productivity; and this process is likely to continue into the future. It is important to know what kind of vegetation can spontaneously develop on these abandoned fields, because it determines their further management. Interventions (e.g., planting native and non-native woody species) are often planned right after the abandonment, and the interventions can be influenced only by quick expert opinion. For these reasons, it is important to know what kind of results can be expected by examining the succession for a single year and how they are verified on the long run. In our earlier paper (Csecserits and Rédei 2001), we reported a study on the landscape history and secondary succession of sandy old-fields carried out with the chronosequence method. In the present study, we had two aims:

AIM 1. To describe the successional trends of sandy old-fields by using different plant traits. The difficulty in investigating succession is finding the general pattern in the development of species composition. In the case of abandoned fields, different history, different local species pool, and the dependence of species establishment on the different abiotic conditions (Pickett 1989, Török et al. 2000) are the main causes of variation. The use of species groups based on life history traits can reduce the noise, help find patterns in vegetation development and enhance the comparability of different old-fields (Noble and Slatyer 1980, Lavorel and Garnier 2002). For example, Prach and Pyšek (1999) compared the traits of dominant successional species with non-dominants and with the total of Central European flora. Based on a dataset of 15 different types of successional series, they found that species dominating during the first decades of succession (up to 76 years) are typically tall, mainly wind-pollinated, have intensive lateral spread, require nutrient-rich conditions and high site moisture.

From the large variety of plant traits, functional traits are biological characteristics of plant species that can be related to their response to the dominant environmental conditions (Noble and Gitay 1996, Lavorel et al. 1997, Grime 2001). Species possessing the same functional traits are classified into plant functional types (PFTs), which are “groups of organisms that respond in a similar way to a syndrome of environmental factors” (Gitay and Noble 1997, Lavorel et al.1997, Lavorel et al. 2002). In Hungary, the knowledge concerning the traits of several species is incomplete, but the species’ ecological behaviour and response to different disturbances are well known through field experience. Therefore, we created plant functional types based on life form, habitat preference and disturbance-tolerance of the species (furthermore we use the term species groups for the PFTs). The importance of these species groups is expected to change during succession, thus their use in the analysis enables us to describe the process of secondary succession and to create hypotheses concerning the mechanism behind the successional changes.

AIM 2. To compare the chronosequence approach and monitoring in assessing successional trends. Both methods have advantages and disadvantages: the *chronosequence approach* can be carried out quickly (usually in one year) and provide information about the general trends and already existing vegetation development already existing for 100 or more years. The great benefit of monitoring is that it gives more accurate results as it shows the actual successional changes in a particular area. Monitoring permanent quadrats helps to separate trends and fluctuations in the species composition (Pickett et al. 2001). However, it is difficult to generalise the result, as the history of the site determines the successional process to a large extent. Moreover, monitoring requires a lot of time, which often represents the main constraint of the study. It can be useful to know the relationship between the results obtained by the two methods in the same site, because

- Theoretically, re-sampling of a chronosequence can provide insight into successional processes that are not accessible by a single chronosequence survey (Foster and Tilman 2000); thus the predictions based on the chronosequence study can be tested.
- Practically, in many cases (e.g., before planning nature conservation measures), it is not possible to conduct long-term research, thus decisions concerning the management of an abandoned field have to be made in one or two years. For this reason, it is essential to know the reliability level of the chronosequence study.

So far only a few studies have assessed the validity of the chronosequence approach by re-sampling each site in the chronosequence to see if the predicted successional changes do actually occur (Debussche et al. 1996, Foster and Tilman 2000, Pickett et al. 2001). In our paper we compare the validity of a chronosequence study to real time-series monitoring describing the secondary succession of a vegetation community adapted to an extreme abiotic environment in the Eurasian forest-steppe zone. Our questions are:

1.When comparing old-fields with the chronosequence approach, how did the species richness and abundance of certain species groups change (based on life form, disturbance-tolerance, and habitat preference)?

2.What are the main trends of succession based on monitoring in terms of life form, disturbance- tolerance and habitat preference?

3.Are the results of the 5-year monitoring approach and the predictions based on the chronosequence study similar?

Material and methods

Study site

The research was carried out in the Kiskunság National Park near Fülöpháza located in the Danube-Tisza Interfluve, central Hungary (46°55'N, 19°30'E, 105 m a.s.l.). The area has a semi-arid, subcontinental-submediterranean climate, and is covered by coarse calcareous sand soil. The potential vegetation is a mosaic-like forest – forested steppe. For the detailed climatic, geographical and vegetation description of the site, see Csecserits and Rédei (2001).

Fifty-four abandoned agricultural fields of different age were chosen within a 60 hectare area. In 1997, we delineated the former boundaries of abandoned agricultural fields using archived aerial photographs and persistent landscape features (e.g., forest patches, ploughed ditches). The type of previous cultivation was ignored, since in all cases ploughing, sowing, and hoeing heavily disturbed the sandy soil surface. The boundaries of fields changed during the period of cultivation. We delineated the fields based on the boundaries existing in the last year of cultivation because the last cultivation practice strongly influences the recolonization patterns of the vegetation (Keever 1979, Myster and Pickett 1990).

We reconstructed the history of the study area over the past 200 years using old maps, archived aerial photographs and written records (Csecserits and Rédei 2001). The first farms in the study area were set up around 1900. Traditional, moderately intensive agricultural methods were used here until abandonment: no pesticides, herbicides or chemical fertilizers were applied, only animal manure. The exact treatment and last crops of each field could not be determined since there were no records made by the owners or authorities, and local people could provide only vague, oral information. However, over the whole study site the owners used the same agricultural methods.

On the scale of the whole study site we assumed landscape history to be homogeneous, therefore the area was suitable for the space-for-time substitution method. We used aerial photographs from 1965, 1975, 1989 and 1994 to create four age-groups based on the time since abandonment (Table 1, Fig. 1). Each abandoned agricultural field was considered as a sample unit because it was cultivated uniformly. There were areas occupied by black locust trees (*Robinia pseudo-acacia)* or other invasive tree species not suitable for sandy grassland species, thus they were omitted during the delineation of fields. The size of fields varied between 0.13 and 1.3 ha.

The fields were interspersed with forest plantation patches and small remnants of former vegetation. Plantations were mainly composed of black locust tree (*Robinia pseudo-acacia),* and tree of heaven (*Ailanthus altissima),* with thin undergrowth. These trees have recently spread clonally into some abandoned fields from the adjacent plantations where secondary forest vegetation has developed. The growth of such forest patches cannot be considered as part of natural succession, but rather a type of disturbance which is caused by the planted stands. Based on the aerial photographs, several patches between the fields were identified that have been covered by native woodland (hawthorn, *Crataegus monogyna,* and poplar, *Popu-*

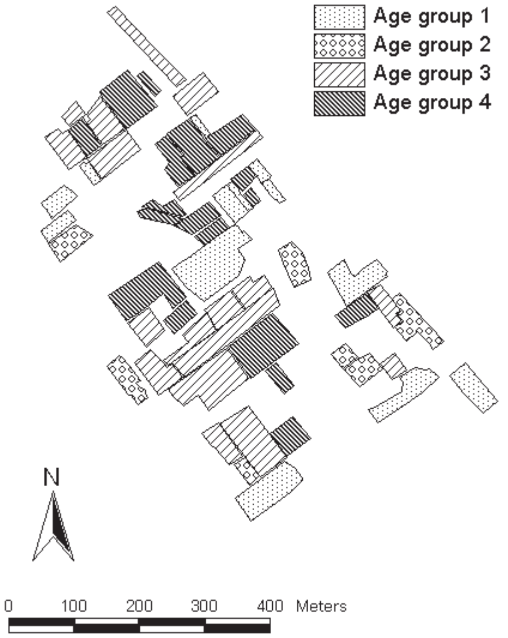

Figure 1. Map showing the localization of the four age-groups of old-fields studied.

Table 1. The last known date of cultivation, age range of fields at the beginning of the study and the number of fields in each age-group.

	Last known year of cultivation (Date of the arial photos)	Age of abandonment in 1998	Number of fields
Age-group 1	1994	1-4	11
Age-group 2	1988	5-10	7
Age-group 3	1975	11-23	18
Age-group 4	1965	24-33	18

lus alba) or open sandy grassland as far back as the 1960s. These were considered to be propagule sources for the abandoned fields. Northwest from the fields there are large, semi-natural, slightly grazed, open, sandy grasslands, which can also serve as propagule sources for our study site.

The study area was grazed by approximately 50 sheep under the supervision of the National Park Administration from the 1980s until 2003. The exact extent of the grazing on each old-field could not be determined because there are no recorded data about the grazing regime. The sheep used 200 ha including our study site, but the grazing regime was not homogeneous. For this study we assumed that the grazing regime is not dependent upon the age of the old-fields.

Data collection

In 1998, we recorded the complete species list of vascular plants in each field twice (in June and September) and we combined the two samples to obtain one single dataset. To characterise species abundance, percentage canopy cover was estimated for each species in each field. June and September data were merged on the basis of the highest cover value per species per year. This sampling was used as the input data for the chronosequence analysis. Sampling was repeated in 2000, 2001, 2002, and 2003 with the same methodology, providing the dataset for the monitoring approach.

Species groups

We classified the species according to three different grouping factors, which we considered important in describing the succession. This category system was previously developed for the Kiskunság region, reflecting the ecological demand and traits of the species typical for the region based on the results and experience of several regional studies (Szujkó-Lacza and Kovács 1993, Horváth et al. 1995, Bartha et al. 1998**,** Kovács-Láng et al. 2000, Csecserits and Rédei 2001). The three grouping factors selected for this study were life form, disturbance-tolerance and habitat preference of the species.

Life form is generally used to describe succession because species with different life forms colonise open space with different speed, success and durability. Naturalness represents a plants tolerance to human disturbance (i.e., ploughing, overgrazing, planting non-indigenous species). Ruderal elements require some kind of disturbance for their establishment which creates gaps in closed vegetation (Jutila and Grace 2002), whereas species of natural and semi-natural communities hardly tolerate regular human disturbance. The second grouping factor, disturbance-tolerance, describes this property. Habitat preference – the third grouping factor – reflects if the succession moves towards the "desired" target community (in our case, from ruderal to open or closed sandy grassland vegetation). The three groupings are not independent of each other. For example, most of the annuals have high disturbance-tolerance and are mainly anthropogenic, but some annuals can be connected to the sandy grassland and other grasslands as well.

We used four categories for *life form*: annuals, biennials, perennials and woody species. Species were classified following the systems of Horváth et al. (1995) and Simon (2000). Categories of *disturbance-tolerance* included in the analyses were: species requiring human disturbance for their establishment or presence, species with high disturbance-tolerance and species with low disturbance-tolerance. *Habitat preference* categories were based on the coenological character of species developed for the Hungarian flora (Soó 1980, Borhidi 1995), but tailored to reflect species behaviour in the sand dune region, in the Kiskunság. The following categories were distinguished according to the frequency of occurrence in different habitat types within the Kiskunság region: species connected to anthropogenic habitats (anthropogenic); species characteristic of xeromesic closed grasslands (closed grassland); species usually found in a wide range of dry grasslands (grassland generalist); species characteristic to the open sandy grassland (sandy grassland); species characteristic of sandy forest vegetation (forest); species characteristic of black locust and tree of heaven plantations (plantation). For the list of species and their classification into species groups, see Appendix A.

Data analysis

First, we analysed the data from 1998. In the second step, we made predictions about successional trends for the next years based on these data. Then, we analysed the data of the time period 1998-2003. Finally, we compared the prediction made from the first year study with the results of the monitoring. For all statistical tests we used a significance level of $p=0.05$.

In case of *chronosequence analysis*, the comparison of different age-groups was carried out using the Kruskal-Wallis test (Sokal and Rohlf 1981), which is not sensitive to different sample sizes. The old-fields differed in size, so in order to remove the effect of plot size on the species number we calculated with the Arrhenius species-area relation. On some old-fields (on 5-10% of the area) non-native forest (*Robinia pseudo-acacia, Ailanthus altissima,* and *Acer negundo*) developed from the trees planted along the edges, where the grassland species could not colonise. This area of the plantation was subtracted from the total area of the old-field because we were only concerned with the spontaneous succession of the grasslands. The number of species was assumed to depend on the area of the grassland component of the old fields according to Arrhenius' species-area relation:

$$\log S = c + z \cdot \log A \qquad (1)$$

where S is the number of species, A is the area and, c and z are constants (MacArthur and Wilson 1967). For each species group, the logarithm of the species number was plotted as a function of the logarithm of the sample unit area for all 54 old-fields. We fit a line to the entire dataset (54 old-fields) and compared the difference of each age-group (residuals) from the common line using the Kruskal-Wallis test. If there was a significant difference, we considered that the species number between the different age-groups changed.

To allow comparisons among species groups, we divided the percentage cover of each species group by the total plant abundance in the old-field. We evaluated differences in the abundance of the species groups in the four age-groups by using the Kruskal-Wallis test.

We made *predictions* on the course of succession based on the survey in 1998 comparing the younger age-groups with the older. First, we compared only the adjacent age-groups; for example, if the species number or abundance of a certain species group was higher in age-group 2 than in age-group 1 according to the space-for-time method. Then, we predicted that the species number or abundance of this species group would increase in age-group 1 within 5 years. For age-group 2, we made the predictions in the same way as in the comparison of age-groups 2 and 3. In the second step we also analysed the expected changes for longer time period; i.e., age-group 1 was compared to age-group 3, age-group 2 was compared to age-group 4. Concerning age-group 4, we made a hypothetical prediction that it would not change within 5 years because the species number and abundance in this age-group was always the same as in age-group 3.

In case of the 5-year-monitoring approach, in order to detect changes in species numbers or abundances during the 5-year period, we performed linear regressions of the species numbers and abundances against the time from the first sampling. By means of the Wilcoxon-test, we determined if the slope parameters of the regression equations differed from zero. Finally, we compared the results of the 5-year monitoring approach with the predictions based on the chronosequence.

Results

Chronosequence approach

In the case of the chronosequence study we compared the species numbers and abundances of four age-groups for each species group (Table 2). We found significant differences in the following cases: in the life form categories, the species number of the annuals was significantly higher in age-group 1 than in the others, while the species number of perennials was lower in age-group 1 compared to the others. In categories based on disturbance-tolerance, the species number of disturbance-requiring species was higher in age-group 1 than in age-groups 2, 3 and 4. The number of high disturbance-tolerant species did not differ among age-groups, but the number of low disturbance-tolerant species was lower in age-group 1 compared to the others. In the case of the species groups based on habitat preference, there was a difference at the anthropogenic, grassland generalist, sandy grassland and forest species. The number of anthropogenetic species was highest in age-group 1, while the species number of the other 3 groups was lower in these age-groups. The total species number among the four age-group did not change.

The changes in abundance of species groups showed similar trends to changes in species numbers (Table 2). In case of life form categories, the abundance of annuals was lower in age-group 3 than in age-group 1; the abundance of perennials was higher in age-group 3 than in age-group 1 and the abundance of woody species was higher in age-group 2 compared to age-group 1. The abundance of disturbance-requiring species was the highest, while the abundance of low disturbance-tolerant species was the lowest, in age-group 1. In the case of species groups based on habitat preference, the differences were in the abundance of anthropogenic, grassland generalist, sandy grassland and forest species among the species groups. The abundance of anthropogenic species in age-group 1

Table 2. The medians and results of comparison of the (**a**) species number and (**b**) abundance in 1998 for the chronosequence study. In case of species number, we fit a line to the species-area data and tested whether there was a difference between the residuals (distance from the line in the *y* direction) of the 4 age-groups. In case of abundance, we compared the group-participation (which was calculated by dividing the percentage cover of each species group by the total plant abundance of the old-field). The age-groups with significantly different species numbers are indicated with different letters, "a" always signifies the species group with less species (Kruskal-Wallis test, $p < 0.05$). * means not studied. 'p' is the result of Kruskal-Wallis test.

	a. Species number					**b.** Abundance				
	Age-group 1	Age-group 2	Age-group 3	Age-group 4	p	Age-group 1	Age-group 2	Age-group 3	Age-group 4	p
Life form										
Annual	25^{b}	18^{a}	17.5^{a}	17.5^{a}	0.0013	0.604^{b}	0.463^{ab}	0.338^{a}	0.376^{a}	0.0009
Biennial	6	6	6	5.5	0.1422	0.023	0.022	0.018	0.02	0.7445
Perennial	20^{a}	32^{b}	33^{b}	27^{b}	0.0039	0.352^{a}	0.488^{ab}	0.628^{b}	0.57^{b}	0.006
Woody	2	6	4	4	0.1129	0.0004^{a}	0.031^{b}	0.028^{b}	0.02^{b}	0.0159
Disturbance tolerance										
Requiring	16^{b}	10^{a}	8.5^{a}	8.5^{a}	0.0033	0.244^{c}	0.097^{bc}	0.034^{ab}	0.033^{a}	0.0000
High	32	37	35	33.5	0.2316	0.684	0.744	0.785	0.782	0.178
Low	5^{a}	13^{b}	16.5^{b}	13.5^{b}	0.0026	0.030^{a}	0.066^{b}	0.15^{b}	0.147^{b}	0.0011
Habitat preference										
Anthropogenic	9^{b}	5^{a}	4^{a}	4.5^{a}	0.0014	0.182^{c}	0.107^{b}	0.022^{a}	0.011^{a}	0.000
Closed grassland	13	16	14.5	11.5	0.0604	0.118	0.144	0.131	0.077	0.5709
Grassland generalist	8^{a}	10^{b}	12^{b}	9^{b}	0.0254	0.081^{a}	0.238^{ab}	0.309^{b}	0.187^{b}	0.0002
Sandy grassland	22^{a}	24^{ab}	25.5^{b}	26.5^{b}	0.0382	0.462^{a}	0.399^{a}	0.441^{a}	0.588^{b}	0.0387
Forest	1^{a}	3^{b}	3^{b}	2^{b}	0.041	0.00019 a	0.0004^{b}	0.0013^{b}	0.0008^{b}	0.0251
Plantation	2	3	1.5	2	0.9309	0.0006	0.0007	0.0008	0.0195	0.368
Total	55	67	58.5	56.5	0.1727	*	*	*	*	-

was the highest, while in age-group 2 it was lower and in age-groups 3 and 4 it was the lowest. The abundance of grassland generalist species was the lowest in age-group 1; significantly lower than in age-groups 3 and 4. The abundance of forest species in age-group 1 was the lowest. The abundance of sandy grassland species in age-group 4 was the highest.

Predictions based on the chronosequence study

The predictions can be seen in the first part of Table 3. There were many "no change" predictions; positive or negative directional changes were expected only in age-group 1, except for the decrease in abundance of anthropogenic species and disturbance-requiring species in age-group 2. We expected a decrease in species number only for annuals, disturbance-requiring species and anthropogenic species, only in age-group 1. An increase in species number of perennials, low disturbance-tolerant species, grassland generalists, sandy grassland and forest species was expected.

The predicted changes in abundance were similar; we expected a decrease in abundance of annuals, disturbance-requiring and anthropogenic species, while an increase in perennials, woody species, low disturbance-tolerant species and grassland generalists was expected. We predicted changes in species number and abundance in the same categories as well, except for the sandy grassland, forest and woody species.

Continuous monitoring

Changes in species numbers within age-groups based on the monitoring carried out between 1998 and 2003 are shown in Figure 2 and Appendices B, C, and D. We found no decrease in species number in any of the species groups. In age-group 1, the number of perennials, high and low disturbance-tolerant species increased, as well as that of closed grassland, grassland generalist, sandy grassland, forest and plantation species. The mean species number of the other categories did not change. In age-group 2, only the number of annuals, woody species, grassland generalists and forest species increased. In age-group 3, species numbers in most groups increased, only the number of biennials, disturbance-requiring species, anthropogenic, forest and plantation species did not change. Age-group 4 showed a similar trend to age-group 3, with the difference being that the number of woody and closed grassland species did not change either. The number of disturbance-requiring and anthropogenic spe-

Table 3. Predictions based on the chronosequence analysis in 1998 (**a**) and the realised changes of species groups during the monitoring (**b**). Prediction; -: decreasing, 0: no change, +: increasing, (+), (-): predicted changes on the basis of space-for-time results of distant age-groups. The species number of the groups is found inside the parentheses. Realised changes; -: decreasing, 0: no change, +: increasing (Wilcoxon-test, $p < 0.05$), grey background: prediction was realised. Boldface values pertain to species groups without any expected or realised change.

	a. Prediction				b. Realised changes			
	Age-group 1	Age-group 2	Age-group 3	Age-group 4	Age-group 1	Age-group 2	Age-group 3	Age-group 4
Species number								
Life form								
Annual (90)	-	0	0	0	0	0	+	0
Biennial (23)	0	0	0	0	0	+	0	0
Perennial (126)	+	0	0	0	+	0	+	+
Woody (34)	0	0	0	0	0	+	+	0
Disturbance tolerance								
Requiring (71)	-	0	0	0	0	0	0	0
High (133)	0	0	0	0	+	0	+	+
Low (52)	+	0	0	0	+	0	+	+
Habitat preference								
Anthropogenic (50)	-	0	0	0	0	0	0	0
Grassland generalist(31)	+	0	0	0	+	+	+	+
Closed grassland (99)	0	0	0	0	+	0	+	0
Sandy grassland (50)	(+)	0	0	0	+	0	+	+
Forest (15)	+	0	0	0	+	0	0	0
Plantation (20)	0	0	0	0	+	0	0	0
Total (277)	0	0	0	0	+	+	+	0
Abundance								
Life form								
Annual	(-)	0	0	0	-	-	-	0
Biennial	0	0	0	0	0	0	0	-
Perennial	(+)	0	0	0	+	+	+	0
Woody	+	0	0	0	+	0	0	0
Disturbance- tolerance								
Requiring	(-)	(-)	0	0	-	-	-	-
High	0	0	0	0	+	+	0	0
Low	+	0	0	0	+	0	+	0
Habitat preference								
Anthropogenic	-	-	0	0	-	-	-	-
Grassland generalist	(+)	0	0	0	+	0	0	0
Closed grassland	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**
Sandy grassland	0	0	+	0	0	0	0	0
Forest	+	0	0	0	+	0	0	0
Plantation	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**

cies did not change during the studied 5 years in any of the age-groups.

Changes in abundance during monitoring can be seen in Figure 2 and Appendices B, C, and D. In age-group 1, the abundance of annuals, disturbance-requiring and anthropogenic species decreased, and the abundance of perennials, woody species, high and low disturbance-tolerant species, grassland generalist and forest species increased. In age-group 2, the abundance of annuals, disturbance-requiring and anthropogenic species decreased again. In this age-group the abundance of perennials and high disturbance-tolerant species increased. Age-group 3 behaved similarly to the other two; the abundance of annuals, disturbance-requiring and anthropogenic species decreased, the abundance of perennials and low disturbance-tolerant species increased and the others did not change. In age-group 4, the abundance of biennials decreased, while disturbance-requiring and anthropogenic species and the abundance of other species groups did not change. The abundance of disturbance-requiring and anthropogenic species decreased during the 5 years in every age-group, while their species number did not change.

Comparison of the chronosequence study and 5-year monitoring

The predictions made for the changes of each species group and the fulfilment of these predictions based on the results of the monitoring are shown in Table 3 and Appendices C and D. When we compared the species numbers, the predictions proved to be true in approximately half of the species groups (30 out of 52), which were mostly “no change” predictions. The “increase” predictions proved to be true in all five of the possible cases (perennials, low disturbance-tolerant species, grassland generalist, sandy grassland and forest species) in age-group 1. We expected species number to “decrease” in three cases (annuals, dis-

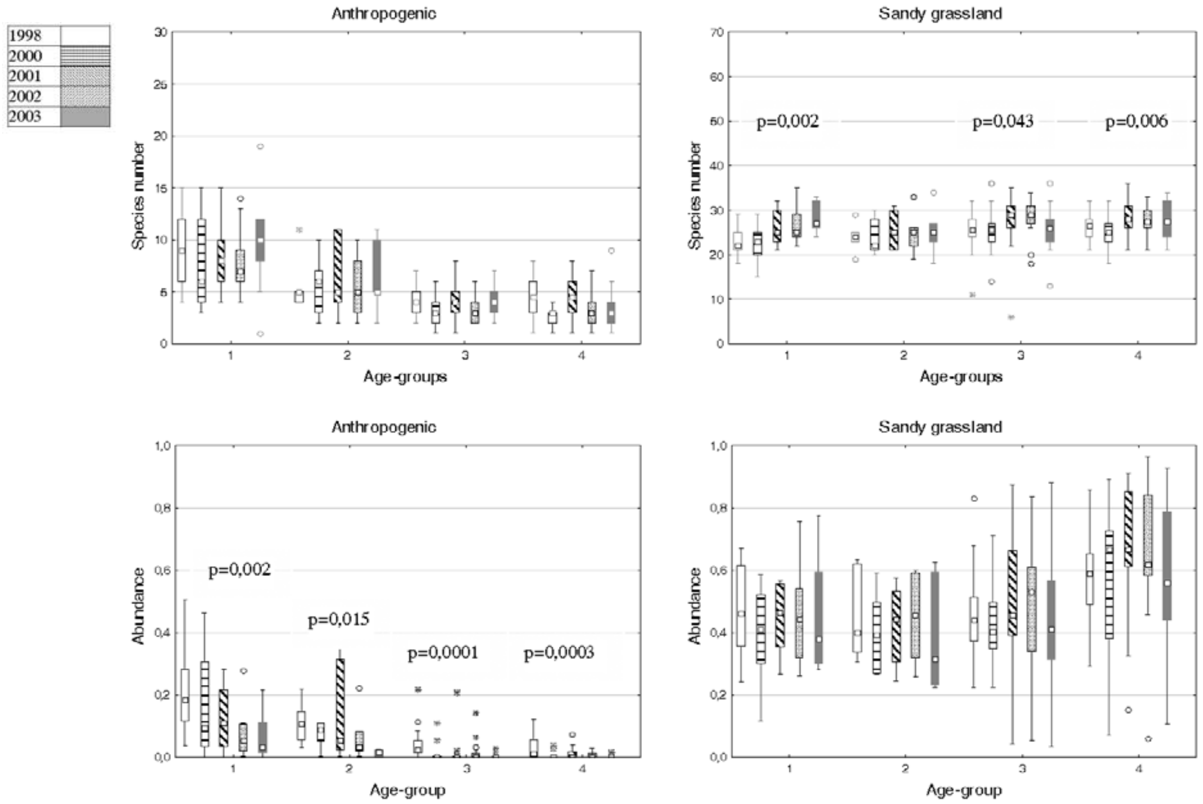

Figure 2. Changes of species number and the abundance of anthropogenic species and sandy grassland species between 1998 and 2003. The consecutive colums for each age group represent results for the studied years (1998, 2000, 2001, 2002, 2003). For the meaning of age-groups 1, 2, 3 and 4 see Table 1. Medians, 25% and 75% quartiles and ranges are indicated in addition to outliers (O), and extremes (*). In order to visualize small values, we used two different scale maxima on the 'species number' axis; 30 in case of anthropogenic species and 70 in case of sandy grassland species. Significant changes ($p < 0.05$) during the monitoring are indicated.

turbance-requiring and anthropogenic species, all in age-group 1), but none of them were found. Predictions proved to be false mostly when the "no change" prediction was not fulfilled; we found an increase in the species number instead.

Considering the abundance of changes among the species groups, two-thirds of our predictions were realised, mostly the "no change" predictions (39 out of 52). Similar to the changes in species number, the "increase" predictions always proved to be true, that is the abundance of perennials, low disturbance-tolerant, and grassland generalist species increased. In the case of abundance changes, there were more "decrease" predictions in the younger age-groups for the annuals, disturbance-requiring and anthropogenic species, and these predictions were all realised. When a prediction was not fulfilled, the change was mostly an increase instead of "no change", while in three cases (annuals, disturbance-requiring and anthropogenic species) a non-expected decrease was found in the older age-groups.

Discussion

Successional trends of sandy old-fields based on the chronosequence study

Several chronosequence studies have been carried out on abandoned fields (e.g., Bard 1952, Inouye 1987, Tatoni and Roche 1994, Ne'eman and Izhaki 1996, Bonet and Pausas 2004), but only a few took place in areas where the potential vegetation is forest-steppe (e.g., Molnár and Botta-Dukát 1998, Sendko 1999, Ruprecht 2005). In 1998, we used the chronosequence approach to describe the secondary succession of sandy abandoned fields in the forest-steppe biome (see Csecserits and Rédei 2001). The results of this study have shown that old-field succession in the study area is relatively fast, and that the abundance of annual and disturbance-requiring species decreases in the first 5-10 years. The perennial, low disturbance-tolerant species, or species typical of dry grasslands are already present in the first stages of succession and their number, and later their abundance, increase rapidly and remain at high levels permanently. Similarly rapid secondary succession was found by Ruprecht (2006) on Transylvanian abandoned fields and by Jongepierova et al. (2004) in the Czech Republic. The relatively quick regeneration after abandonment is most likely due to the presence of semi-natural grassland patches in the surroundings that serve as propagule sources. Fortunately, such remnants of the natural vegetation can be found in many parts of Eastern Europe. By contrast, these natural propagule sources are missing from large areas in Western Europe, thus there is a strong dispersal limitation to species recolonisation (Muller et al. 1998, Butaye et al. 2001). Extensive grazing can enhance colonisation of grassland species from the patches of natural vegetation to the abandoned fields (Gibson et al. 1987, Fischer et al. 1996, Ruprecht 2006). The other reason for the relatively rapid successional changes in the study area may be that the soil has not been drastically changed, no herbicides and only small amounts of fertilisers were used during the previous cultivation – unlike e.g., in the Netherlands (Van Diggelen et al. 1997, Verhagen et al. 2001) – therefore the nitrophilous weeds can be easily repressed by natural grassland species.

The temporal changes of vegetation and the applicability of species groups

The favourable trends (i.e., trends leading to the mature grassland) of secondary succession on sandy oldfields were confirmed by the 5 years of monitoring. The species richness and abundance of perennial, low disturbance-tolerant and dry grassland species have increased, while the abundance of species groups typical of early successional stages, such as annuals, disturbance-requiring and anthropogenic species have decreased. At the same time, some other species groups have also increased in species number or abundance.

The applied species groupings indicate different aspects of the successional changes. The directions of the changes were similar: abundances and species numbers in species groups indicating the initial stages of succession decreased, while those indicating the late stages of succession increased. This is not surprising since our groups are overlapping, because there are many common species among the annuals, disturbance-requiring and anthropogenic species groups; and the low disturbance-tolerant species are mostly perennials at the same time. But changes among each species group reflect different aspects of succession. Using the life form spectrum promotes the comparison between successional courses of distant areas (McIntyre et al. 1999). However, the important information for nature conservation management is the amount of rare or protected species rather than the abundance of annuals or perennials (Noss 1990). Creating categories based on the disturbance-tolerance of the species helps in this practical aspect, as species with low disturbance-tolerance are mostly rare and worth protecting. Additionally, the habitat requirement categories indicate the type of habitat that can regenerate in the given climatic and soil conditions. Of course, the establishment of one species from a particular habitat type does not necessarily lead to the establishment of that habitat. Some species are able to establish in different habitats other than their main habitat type. However, there are connections between species and habitats: if there are many species present typical for a habitat we could assume the development of that habitat also. By comparing the results of the three different species groupings we gained a more detailed description of successional processes.

Comparison of the results and the method of chronosequence study and monitoring

Studying succession with the chronosequence approach requires relatively short time, therefore it is a popular method, but may result in errors in the prediction of successional series. For example, a dune series at Lake Michigan suggested by Cowles in 1899 has been disproved by Olson (1958) and Jackson et al. (1988) or the traditionally accepted prairie succession path was later confuted by Collins and Adams (1983). In both cases, the critics pointed to the wrong selection of abandoned fields for the space-for-time study, namely the historical and environmental conditions of the constituents of the chronosequence were too different. There is a similar case in Hungary concerning the primary succession of sandy grassland. The formerly described theoretical series of sandy succession has not been confirmed by field studies and further field experience has shown that the first stage of primary succession is dominated by perennial grasses and not by annuals (Fekete et al. 1992, Bíró and Molnár 1998). A further problem can be that different researchers study the vegetation at different scales, therefore several successional pathways can be valid in the same vegetation type, but at different scales (Margóczi 1993, Bartha et al 1999-2000).

There are only a few studies where a chronosequence study was controlled by monitoring at the same location. Debussche et al. (1996) re-sampled the chronosequence survey once after 12-14 years and Foster and Tilman (2000) re-sampled after 14 years. Debussche et al (1996) found that changes in species richness and floristic composition during the succession of Mediterranean abandoned fields were consistent with their previous predictions. Foster and Tilman (2000) found that the result of the chronosequence study was a good predictor for changes in species abundance, but it was a poor predictor for species richness. The Buell-Small Succession study (BSS) in the USA was established to test the successional pathways described by a chronosequence study (Bard 1952). The main difference between the patterns in the BSS study and the chronosequence was the local uniqueness and not the random variation, and they found that the succession is slower and more variable than was expected (Pickett et al. 2001). In our research, we re-sampled the same areas as the chronosequence survey in four later years in order to get more detailed information about the successional process. Our results correspond with the above mentioned findings that the chronosequence approach predicts changes in abundance better than changes in species richness.

In our study, we investigated the species-pools of entire old-fields because we were interested in the succession of the entire field, including the field-scale heterogeneity. However, each old-field was of different size (between 0.13 and 1.30 ha), thus we could not calculate some generally used parameters such as Shannon diversity. In order to remove the effect of plot size we decided to calculate with Arrhenius' species-area relation (MacArthur and Wilson 1967), which is a good estimation for the connection between species number and area. This approach is widely used for removing effects of confounding factors.

Another limitation of our study is that the number of available old-fields was different in each age-group. We speculate that one reason for the scarcity of significant results in age-group 2 is that there were only seven abandoned fields in this group.

If the sampling had been repeated in only one year, less predictions would have been realised. With the yearly monitoring we could detect the moment when a certain species group showed significant changes and we could eliminate the effects of random short-term disturbances, like an extreme weather event (Appendix C, D). For example, we found that several species groups (closed grassland, grassland and sandy grassland species) did not change by the second year after the first survey (2000), but in the following years both their species number and abundance increased. Our hypothesis is that a drought in 2000 caused this result, as the death of many plant individuals created gaps for the establishment of other species in the following years.

As a result of our 5-year monitoring approach, more than half of the predictions have come true, with a larger proportion concerning the abundance than the species number (39 and 30, respectively, out of 52, Table 3). These were mostly "no change" predictions, but the "increase" predictions indicating fast vegetation regeneration have been also proved in all cases. In case of predictions not verified, we mostly found changes in species number or abundance instead of the expected "no change". There was only one case when a predicted change was not confirmed: the decrease of the species number of annuals did not occur. Consequently, the static view of older abandoned fields suggested by the chronosequence approach has not been confirmed by the results of the 5-year monitoring approach.

The chronosequence approach resulted in mostly similar changes in species numbers and in abundances. The results of the monitoring were more divergent. For instance, while the species number of disturbance-requiring species did not change, their abundance decreased (in the case of disturbance-requiring species in each age-group), and the species number of sandy grassland species increased in age-groups 1, 3, and 4, but their abundance did not change. We even found the opposite changes of species numbers and abundances, namely the species number of annuals increased in age-group 3, while their abundance decreased. The reason for this is probably that the chronosequence method is more robust; it compares the age-groups, while the monitoring detects more changes.

During the monitoring, we found surprisingly many changes also on the older abandoned fields. These changes occurred mainly in species numbers probably because of the faster and more accidental species establishment and extinction processes compared to the changes of the abundances of already established species. The increases of species numbers in the older age-groups – they were mostly non-expected changes – could also be caused by the gap formation after a disturbance (e.g., increasing grazing intensity) or a year with favourable weather. According to Gross' theory (1980), "windows" open up during the course of succession, which means that several factors have to be simultaneously favourable to enable species establishment. The year 2000 could be an example of this when many gaps developed due to the unusual drought (Bartha et al. 2003, Török and Lohász 2004), or where the increase in grazing intensity (personal observation) resulted in such regeneration windows.

We found a non-expected increase in abundance of perennials, high and low disturbance-tolerant species, and a non-expected decrease in abundance of annuals, disturbance-requiring, and anthropogenic species. These changes can be related: the place of repressed annuals is taken by the perennials which are mainly high or low disturbance-tolerant species. The species number of annuals increased while their abundance decreased in the age-group 3, because the "annual" category contains segetal weeds and grassland weeds also. Segetal weeds disappear during the course of succession, as they behave similarly to the anthropogenic species, namely their species number did not change while their abundance decreased. However, the species number of sandy grassland and grassland generalist species — containing also annuals – increased while their abundance did not change. Thus, the segetal weeds are generally repressed, but some individuals remain present for a long time; while the annuals associated with grasslands establish gradually and their abundance does not increase in a level that we can detect as significant. The behaviour of the annuals shows that not only the perennial grassland develops during the secondary succession, but also the annual community transforms, occupying the permanently existing gaps caused by the abiotic stress (Myster and Pickett 1988, Bartha et al. 2004).

In our study, the number and abundance of woody species increased only in the first age-group, and we did not expect changes based on the space-for-time survey. Although we also found some patches of woody vegetation in age-groups 3 and 4 of the old-fields, their areas were omitted from the sample plots because those woody stands consisted of alien species, such as *Robinia pseudoacacia* and *Ailanthus altissima* and therefore we did not consider them as part of the grasslands. Based on aerial photographs and our field observations, these stands originated from sprouts of groups of trees or alleys planted near the edge of the fields and they did not spread during the monitoring. On two fields, *Populus alba,* which is a natural dominant tree species in the region, spread from groves next to the field also by sprouting; we also omitted their closed stands.

Vegetation development is affected by many factors so it is a system with high noise levels. We can reduce the noise by using functional groups to describe vegetation, by enhancing the sample size or even with the chronosequence approach. However, the great advantage of long-term monitoring is that we get a more detailed and dynamic view about succession (Foster and Tilman 2000). At the same time, the generalisation of these results is more difficult because of the problems in separating trends and fluctuations (Pickett et al. 2001). In our case, monitoring of secondary succession of sandy old-fields showed similar trends to the ones predicted by the chronosequence study. There were more changes during monitoring which can be caused by weather fluctuations or local disturbances. In the chronosequence study, we compared the old-fields to one another, while in the case of 5-year monitoring, each field was compared to itself. According to general experience, vegetation development during the course of succession depends less and less on the elapsed time since abandonment, but becomes increasingly dependent upon the biotic and abiotic factors of the site (Lepš 1991). This can be a reason for the large variance and great changes found on the older abandoned fields which the chronosequence approach is worst at detecting. The monitoring shows that the vegetation development continues, primarily due to the environmental conditions of the site.

Conclusion

The regeneration capacity of sandy grasslands on abandoned fields proved to be good in the studied region based on the results of both the chronosequence study and the 5-year monitoring approach. The basic trends of spontaneous succession can be predicted well, therefore a chronosequence can be used for hypothesis generation, and nature conservation interventions can rely on the results of it. The vegetation that develops spontaneously during the course of secondary succession can provide a good example for nature conservation management regarding the possible stages that can be expected on newly abandoned fields.

According to our study, the advantages of the chronosequence approach are that it shows the general trends of successional change and it describes a process that has already occurred, but a disadvantage of this method is that it results in a more static view of the successional process. In comparison, the advantages of monitoring are that it shows a more dynamic, detailed view of succession and records finer details of variation, but the disadvantages of monitoring are that it is affected by local conditions, gives less information about the future and is difficult to discriminate between trends and fluctuations.

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Source of historical maps

Anon. I. Military survey of Hungary 1783, sheet XV/XXVI., Military History Museum, Budapest

Anon. II. Military survey of Hungary 1861-1866, sheet XXXIV/56. Military History Museum, Budapest

Anon. III. Military survey of Hungary 1883, 5263/1 Military History Museum, Budapest

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Appendix A. The list of species and their classification to species groups.

Appendix B. Changes of species number and abundance of species groups between 1998 and 2003.

Appendix C. Predictions, one year comparisons (comparison of the year 1998 with the years 2000, 2001, 2002 and 2003, respectively) and monitoring of species numbers.

Appendix D. Predictions, one year comparisons (comparison of the year 1998 with the years 2000, 2001, 2002 and 2003, respectively) and monitoring of abundances.

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