Improved space-for-time substitution for hypothesis generation: secondary grasslands with documented site history in SE-Hungary

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with 5 figures and 6 tables

Abstract. Space-for-time substitution (SFT) is a common method to study vegetation dynamics; yet, different site histories make it often unreliable. We studied the first 38-yr succession on abandoned fields in a Hungarian steppe landscape, controlling for present and past abiotic conditions, landscape context and disturbance regime. The sites chosen in the landscape appear suitable for a historically improved SFT.

The results of the SFT show that the most characteristic features of the local succession are: 1. the very limited colonization of specialist species, though this landscape was expected to be a good propagule source for colonization since there are many species-rich loess grassland patches scattered in the landscape surrounding the old-fields, 2. the development of a closed, low diversity grassland dominated by perennial generalists, 3. the sharply decreasing rate of succession in 25–38-yr-old fields. The old-fields converged in floristic composition with succession. Convergence may be determined by the following factors: 1. low chances for woody species colonization (as a consequence of a poor propagule source for woody species and regular grazing), 2. dominance of Festuca and other generalists that may prevent further colonization and 3. regular sheep and cattle grazing as a homogenizing factor.

Hypotheses were generated based on these results that can be used to plan local long-term experiments or observations e.g. to decide whether dispersal limitation or recruitment limitation determines the low colonization rate of specialist species observed in this landscape.

Since the 25–38-yr-old fields have a very “characterless” species composition (and lack the distinctive features of loess grasslands), future restoration works will need to focus on the artificial diversification of these secondary grasslands, if the goal is a species-rich grassland that resembles the region’s ancient loess grasslands.

Improved space-for-time substitution seems to be a useful tool to study local vegetation dynamics. Detailed historical reconstruction could improve the reliability of SFT studies; unfortunately, reconstruction of the history is not an easy task and the site choice is never perfect. The challenge of historical reconstruction may be one reason why SFT studies of sites with documented history are rare. Improved space-for-time substitution may also be an appropriate tool to design restoration projects.

Keywords: colonization, dispersal and recruitment limitation, landscape and land use history, loess steppes, old-fields, propagule source, restoration, specialist species.
Introduction

It is generally accepted that the dynamics of vegetation is best studied by long-term observations and experiments (Lιkens 1989; Gosz 1996). Both well planned observations (the tracking of “natural experiments”, e.g. by permanent plots (Herren 1996; Barker et al. 1996) or by photographs (Hart & Laycock 1996) and experiments testing the mechanisms of succession need well defined questions. One way to generate hypothesis about the studied local succession is to study different aged sites of the same landscape and to infer features of the succession from these sites. This approach is called space-for-time substitution (SFT), the result of which is the chronosequence (Pickett 1989). Besides hypothesis generation, appropriate SFT can aid planning of observations and experiments and site selection for further study.

Space-for-time substitution can be successfully used when general local or regional trends or regional variations are sought. The procedure, however, has several key assumptions and if these are not fulfilled, SFT can be unreliable. SFT assumes that abiotic condition, landscape context, and disturbance regime are the same across sites, that is “the past is everywhere the same” (Pickett 1989). This critical assumption is the functional equivalent of the statistical condition of stationarity used in analyses of time series and spatial patterns. Accordingly, improved determination of past abiotic conditions, past landscape and land use changes, and minimization of variation between site histories should all greatly improve the robustness of SFT. Some SFT studies have controlled for abiotic conditions, e.g. climate, elevation, soil, (Aber 1979; Driscoll et al. 1988); while many others have not. Controlling for past disturbance regime, however, has been rare. An example is Bard’s study on abandoned fields in Illinois (Bard 1952) where only sites unfertilized, unburnt, unmown, and ungrazed following abandonment were used in the SFT.

The purpose of this paper is to demonstrate SFT improved by a detailed historical reconstruction of the sites and their landscape context. Hypotheses are generated concerning the dynamics of grasslands on abandoned agricultural fields, the constraints of colonization, and the development of species richness. Abiotic and historical factors are controlled for and variation between sites is kept at a minimum.

Study area

Site selection

For the study a landscape was chosen which met the following requirements:
- abiotic condition of differently aged sites is similar,
- landscape context of the sites is similar, and
- land use history of the sites is similar.

Space-for-time substitution for hypothesis generation

The length of the chronosequence (youngest and oldest site, the time intervals between samples) and the size of the sites were also taken into consideration. Size of the “abandoned” patches was also an important factor: fine-scale disturbances regenerate relatively quickly in this grassland type (Virág 1989) but disturbances across large extents may regenerate only very slowly (Peterken & Game 1984: personal observations in other steppe areas). The chosen landscape is a semi-natural short-grass steppe, where old-field vegetation on chernozem (black earth) soils and loess steppe grasslands as propagule sources have been studied.

The landscape

The Blaskovich steppe, the landscape chosen, lies in SE-Hungary on the western edge of the Békés-Csanád alluvial fan of the river Maros (Fig. 1). Extensive arable fields on dry chernozem soils, alkali steppes and temporal wetlands are the dominant features of the wider surroundings. The rainfall is 550 mm with a maximum in June and an extended dry period in July and August (Pécsei 1989). The Blaskovich steppe itself (Fig. 2) is a fine-scale mosaic of loess, alkali and wet areas (Molnár 1992). The mosaic pattern of the steppe is determined by surface water erosion, the depths of the soil water, and the salt content of the B horizon. Loess grasslands and old-fields are confined to the higher areas (0.5–2 metres above the alkali surfaces).

Fig. 1. The studied landscape (the Blaskovics steppe, shown as a filled square) lies in the Great Hungarian Plain, in the southern part of the region Tisztántúl (dotted line). The other areas on the map show those sites where the data about the regional behaviour of species were collected from.
The vegetation

Up to the present 553 vascular plant species have been recorded in the area (Jankó 1886; Thaissz 1905; Molnár 1992 and others), 205 from them occur in loess grasslands or old-fields (Molnár 1992 and observation since).


Loess steppe grasslands that are in a more or less natural condition can be classified as Salvio nemorosae-nutantis – Festucetum repicolae tibiscense Zólyomi 1962, the more degraded sites as Cynodonto-Poetum angustifolii Rapae sx Soó 1957 (Molnár 1992).

The matrix (the vegetation among the loess grasslands and old-fields) is an ancient alkali steppe of Boreal origin (Molnár 1996), dominated by the following communities: Artemisia alkali-steppe (Artemisio-Festucetum pseudovinace Soó in Mathé 1933), alkali meadows (Agrostio-Alopecuretum pratensis Soó (1933) 1947), highly salt – tolerant communities of alkali bottoms (Camphorosmetum annuae Rapae sx Soó 1933, Puccinellietum limosaec Rapae sx Soó 1933, and Pholiuro-Plantaginetum Wendelb. 1943).

Methods

Reconstruction of landscape and land use history

The necessary first step of the historical reconstruction was the detailed floristic and coenological survey and mapping of present vegetation (Molnár 1992). Historical botanical data (e.g. the early 19th century travel diary of Kitaibel in Gombóc 1945 and Radics 1970; Jankó 1886; Thaissz 1905) provided direct information about past vegetation states. Present vegetation together with these historical botanical data
provide the first reference from which the past environment can be reconstructed in detail.

The most important sources were the different maps, since the vegetation of this lowland region can be studied in detail by maps (cf. Molnár 1997): 1st military survey (1783), 2nd military survey (1861–1866), 3rd military survey (1884), the map of out-fields of the city Mako (made by István Védres in 1805 (Védres in Tóth 1992), and the cadastral map from 1854 (in Tóth 1992). Aerial photos from 1950, 1953, 1964, 1981 and 1996 were available for the historical reconstruction of the surrounding landscape and for the precise determination of historical old-field boundaries, as well as for approximate dating of old-field age.

Historical geographic and local settlement historical studies and essays about past agricultural practices provided data about past grazing regimes, and cultivated crops. Geographic studies helped reconstruct changes in the abiotic cultivated environment, e.g., soils, water regime, climate, etc., (for a detailed reference list, see Molnár 1996). Detailed reconstruction of past land use and precise determination of field age could only be done based on the living memories of local elder inhabitants. Since data from interpersonal communication often involves the risk of subjectivity (cf. Molnár 1997), the more important data was cross-validated.

Vegetation survey

The main steps of vegetation survey were the followings: since 1986 a detailed floristic survey of the whole landscape with abundance estimation of certain species, 345 coenological relevés from different associations, a 1 : 10 000 vegetation map about the loess steppe grasslands, old-fields, and the matrix in 1995 (helped with an aerial photo).

Mapping of the propagule source took place in 1994–1995. We assume (but can not be really sure) that the loess grasslands, arable fields and old-fields around the abandoned fields serve as a propagule source for the old-fields, since the other habitats of this landscape (alkali grasslands or wetlands) have very different species composition (only species with very wide tolerances may be able to colonize from these habitats). All species of these patches that were identifiable and countable in May and June were surveyed, and population sizes were estimated. A detailed floristic survey was conducted in three 11-yr-old fields in 1996 (estimation of population sizes).

For the SFT 25 plots of 4x4 metres were surveyed in May and June 1996. In each of the age classes 5 plots were surveyed: 2 fields of 1-yr-old, 1 field of 4-yr-old, 3 fields of 11-yr-old, 1 field of 25-yr-old and 3 fields of 38-yr-old. None of the former relevés available from these sites were used to minimize variation caused by climate and plot size. Percent cover of each species in the plots was visually estimated.

Space-for-time substitution for hypothesis generation

Vegetation analysis

Reference grasslands

End points of succession as a reference for old-field vegetation is often used in space-for-time substitution. Generally "old, natural, climax" communities were chosen (e.g. Aber 1979). This approach is, however, not acceptable here since these "reference" stands may not have the same abiotic condition, landscape context and history than the much younger old-fields. The difficulties of reference choice has been discussed in detail by Cairns (1987). Since we could not find any site much older than 38 years having the same history, the only pseudo-reference used is the grassland of the propagule source with the same present land use, similar abiotic conditions, but a completely different earlier history. The only goal of this pseudo-reference was to show how far the old-field grasslands are from the features of the propagule source. (This is an important information for restoration plans to recreate loess grasslands on former agricultural fields.)

Species groups

To follow changes with succession we grouped plant species based on their coenological and site condition preferences. Although this analysis ignores patterns at the species level, it serves several useful purposes (simplification, recognition of general patterns and consistent changes with field age). Both the preference maximum and its width were determined for each species. Though the indicator values of the Hungarian plant species (coenological preference, life-for categories, ecological indicator values for humidity, nitrogen and salt tolerance and for many others) are readily available in a digital database (Horváth et al. 1995), only the behaviours of species in the Tiszántúl region were considered. Literature data (e.g. Jankó 1886; Thaissz 1905; Zölyomi & Jankó 1962; Tóth 1985), and personal observations were used from sites shown on Fig. 1. Since the behaviour of species can change profoundly between regions (Ellenberg et al. 1991), this regional classification must be more precise than the Hungarian "average". (Even at its finer scale not all species were unanimously classifiable.)

The species groups used:
- species occurring exclusively in loess grasslands (specialist I)
- species occurring mainly in loess grasslands (specialist II)
- species of all sorts of dry grasslands (generalists)
- species of dry grasslands and wet meadows in common (generalist-m)
- species of dry grasslands and alkaline grasslands in common (generalist-a)
- species of dry grasslands and arable fields in common (generalists-w)
- species of arable and old-fields and ruderal sites (weeds) (these species occur only in heavily disturbed sites in loess grasslands).

Nomenclature follows Horváth et al. (1995). Festuca rapoica and Festuca pseudovina were indistinguishable in the field, thus "Festuca" includes both species. Similarly Thymus includes both Thymus glabrescens and Thb.
marchallianus. Dominant species are those having larger cover values than 5% at least in two plots.

Plant species diversity was calculated from each plot from the cover values using the Shannon-Wiener index. Evenness was calculated from the formulation E = H/ln S, where H is the Shannon-Wiener diversity, and S is the number of species in the plot (Piepoli 1975). Data were calculated for plots and for ages (average of plots of the same age). Heterotopy (variation of plots of the same age) was calculated from the formulation suggested by Dahl (1960):

\[ \alpha = \frac{S-S_a}{\ln n} \]

where
- \( a \) = heterotopy
- \( S_a \) = average species richness of plots
- \( S \) = species richness of ages
- \( n \) = number of plots.

Comparison of plots was based on species lists, cover values and standardized cover values. Types of transformations and similarity indexes can be found in Table 1. Dissimilarity matrices were analyzed by non-metric multidimensional scaling (NMDS) (Podani 1994). Separation of different aged plots was tested by probability ellipses (Feoli & Lagonegro 1991). All other statistical tests used the Wilcoxon test (Reimann & Tóth 1991).

Tab. 1. Types of transformations and similarity indexes used in the ordinations.

<table>
<thead>
<tr>
<th>Data type</th>
<th>Transformation</th>
<th>Dissimilarity function</th>
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<td>Sorensen</td>
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<td>cover</td>
<td>-</td>
<td>similarity ratio</td>
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<tr>
<td>standardized cover</td>
<td>standardization by range</td>
<td>similarity ratio</td>
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Results

Landscape history

1. History of the wider surroundings before the 20th century

The history of the Pitvaros-Makó region from the Middle Ages was reconstructed by Molnár (1996). In the 16th century seven settlements with developed agricultural practices flourished in this region (Blazovich 1985). Archaeological evidence suggests (cf. Blazovich 1985), that during the Middle Ages most of the loess steppe grasslands may have been ploughed at least temporarily. During the Turkish Occupation (16–17th centuries) all of these settlements (except Makó) had been ruined, cultivated fields turned into secondary steppes. The vast grasslands were used for nomadic-like gray cattle grazing (Gaál 1895; Bohdaneczky 1940). During the second half of the 18th and in the 19th century, grazing was gradually replaced by plant cultivation (see the decreasing grassland area on the 1st, 2nd and 3rd military survey maps). In the 18th century shifting agriculture, later the three-field system, and in the 19th century the small-farm system was the characteristic form of land use (5–15 farms per square kilometre). The main crops were wheat and corn (Palugyay 1855; Bohdaneczky 1940). From the late 18th century sheep-farming increased and cattle-farming decreased (Gaál 1895).

2. History of the old-fields and their surroundings

The area of the extant old-fields has been a pasture since at least the 17th century (Palugyay 1855). Most of the fields became cultivated between 1860 and 1884 (Martonyi et al. 1970, II. and III. military survey maps), though some only after the Second World War (Fig. 3). Fertilizer use was low (Martonyi et al. 1970). The main crops were barley, wheat, corn, sunflower and onion (pers. comm.). Some of the cultivated fields have been abandoned in the last 40 years, these are the subjects of our study.

The following historical summary aimed to reconstruct the hypothesized operational environment of the old-fields and the immediate surroundings and other details that may also be important (for a summary see Table 2).

Landscape context

Land use in the 18th century was fairly homogenous, since the land was a vast continuous pasture (Fig. 3) (1st military survey map; Bohdaneczky 1940; Palugyay 1855). By the late 19th century all land suitable for cultivation had been ploughed (this can be determined if we compare the 3rd military survey map from 1884 and the soil map by Sfk (1935)). The ploughing pressure (sensu Elek 1937) was very high, which resulted in a fairly stable landscape pattern since the late 19th century (Fig. 3): all of the large loess grasslands are ploughed, alkali grasslands (not suitable for cultivation) are grazed and meadows are mown. This was a common land use pattern in this region in the last 150 years (Frisnyák 1990; Molnár & Biró 1997). Only those loess grasslands embedded in pasture as small islands have persisted. The spatial pattern of these grasslands must have changed very little in the last 100 years. Up to 1945 the area belonged to the Blaskovics estate (pers. comm.). After 1945 some of the large loess grasslands of the former Blaskovics pasture were also ploughed (pers. comm.). The matrix, the alkali steppe, has also changed little (Molnár 1996). In the last decades drainage decreased the soil water table by 0.5–1 m and the extent of surface waters in the spring (Molnár 1996). These hydrologic changes may have little or no effect on the higher lying loess grassland fragments (cf. Szabolcs 1961).

Most of the habitats of the landscape can serve as a propagule source for the old-fields, though to differing degrees. Many generalist and specialist species can arrive from the neighboring loess grasslands: 83 relatively spe-
Tab. 2. Summary table of data of the individual old-fields. Abiotic conditions, landscape context and land use history of the sites are shown. For references see text. Data about fertilizer use, last crop, type of abandonment, land use since abandonment, dominating propagule source, mean distance of neighbouring propagule sources, and surrounding landscape come from personal communications with I. HERÉSZI, I. NEMES and I. KERESZTES (local inhabitants) and from personal observations since 1986.

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<td>ancient field, ancient grassland</td>
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Fig. 3. Pattern changes of the grassland-arable field mosaic in the Blaskovics steppe in the last 200 years (grasslands are indicated with the grass sign). Notice the fairly stable pattern in the last 100 years. Old-fields are shown as grasslands.

Species-rich loess steppe patches were found at a maximum distance of 1000 m. Very few species (only those with very wide tolerances) can colonize from the alkali grasslands and the wet meadows, while many weeds can arrive from the arable fields nearby, and weed and generalist species from the other old-fields.

The propagule source of specialist and generalist species must have changed little in the last 100 years, given the stable spatial land use pattern of the loess grasslands. Comparing the species list of JANKÓ (1886) and TRIÁSZ (1905) with the present one (MOLNÁR 1992), no major changes were detectable in the general species composition of the loess grasslands: non-native species are not spreading in the landscape, none of them is dominant in the present-day grasslands; the main generalist species are the same (e.g. Festuca, Poa angustifolia, Koeleria cristata, Salvia nemorosa, S. australis, Carduus nutans); specialist species did not become locally extinct except two species (Salvia nutans and Taraxacum serotinum). The persistence of
traditional grazing practices for sheep and cattle (Molnár 1996) and the similar vegetation composition of present day pastures (Molnár 1992) suggest that the species composition of loess grasslands may be fairly stable. The only exceptions are those patches that have borne heavy traffic: near wells, animal pens or small farms, or have been near to sheep pens and thus became overgrazed.

The propagule source of the weeds could have changed much more since the 1960s, as a consequence of changed use of herbicides in the surrounding agricultural lands. Thirty-eight dry habitat species (i.e. species of dry (but non-alkali) grasslands, road verges and fields) from an earlier flora list (Jankó 1886) could not be detected in the last 10 years, 29 of them being agricultural weeds (Molnár 1992).

Dispersal agents in this landscape are expected to be abundant, since the insect, bird, and mammal communities are rich (pers. comm. and pers. observ.) and because the wind can freely blow across the open landscape. All of these fields are surrounded by many small loess grasslands patches, some of these are contiguous with the old-fields. These landscape features suggest that colonization in this landscape is not limited by distance or by the spatial pattern of the propagule source (McClanahan 1986; Baudry & Merriam 1988; van der Valk 1992; Bullock & Webb 1995; Gustafson & Gardner 1996).

Abiotic conditions
The old-fields have very similar abiotic conditions: the elevation is 89.5–91.0 m asl; the soil surface is levelled; and the soil water table lies below 2 m even in the spring (pers. observation in wells). Differences in microclimatic conditions are not expected. Macro-climate, however, has changed in the last 15 years, the precipitation decreased by 16% (Zoltomyi et al. 1994). The soil of the fields is also very similar (see the data of Sík 1935 and Sík & Schmidt 1938). The genetic soil type is chernozem with meadow character (black earth) with very little spatial variation. According to the soil map (Sík 1935) all the fields belong to category 77 or 77a (the latter being a variant of 77 with shallower humus layer). The upper 0.8 m of the soil profile has 10–18% Ca-carbonate, pH 8–8.5 increasing downwards, the base rock is loess. The humus layer is 1.2 m deep (humus content in the upper 0.2 m is 3.6%). Soluble salt can only be detected below 0.7 m (0.11–0.18%), below this depth the soil is alkali silts. Since this soil type changes very little through time (Szabolcs 1961) we presume that the soil conditions of the extant fields is still fairly similar.

Disturbance regime
The main source of disturbance to the vegetation is grazing. Conservation management has not affected the disturbance regime, nor could we find data about grassland fertilization or overseeding (methods used in this region for grassland improvements). Field mice and moles are, however, not rare, and must have some unquantified effect on grassland dynamics. Hares and roe deer are the native larger herbivores with an unknown but presum-

ably minor impact on the vegetation relative to the domestic grazers. We could not find any detectable spatial variation in the intensity of grazing of native herbivores. Buildings for animal husbandry has caused local disturbance to some of the grassland patches. The exact spatio-temporal pattern of grazing intensity in the last 50 years is unknown and unreconstructable, but sheep and cattle grazing practices have changed little during this period. The northern part of the area has been used mainly for cattle grazing in the last 15 years with occasional over- and undergrazing. Since the early 1990s, stock is decreasing as a consequence of social changes, but grazing management has changed little.

Initial conditions
The time of abandonment could be determined relatively accurately (+/- 0-2 years; by personal communication). The last crop is largely unknown, but was barley in the younger fields. The 4- and 11-yr-old fields were abandoned as a newly sown Festucapsaturna swarth. This species became extinct in a few years time, as it is a wet meadow species. In the 8-yr-old fields Bromus inermis may have been initially sown (since this species is still common in the grassland though is rare in the ancient patches). Macroclimatic conditions in the first years of abandonment are moderately variable between ages.

Conclulsions
The minimization of variation in land use history, landscape context and abiotic conditions was aided by the fairly stable local landscape and the close arrangement of the fields. In spite of the fairly stable and homogeneous conditions of the sites, the story of the individual fields is not identical (e.g. the last crop and the history of the grazing regime), but appears similar enough for an adequate and correct space-for-time substitution (cf. Pickett 1989).

Vegetation: The chronosequence
1. Cover, species richness and diversity
Cover increases sharply in the first years, but remains more or less the same later though with decreasing variance (Fig. 4a). Species richness per plot does not show a clear trend with succession, but is significantly less than in the propagule source grasslands (Fig. 4b). Species richness per age and diversity per plot show a temporary increase in yr 4 and 11, but decrease later (Fig. 4b, c).

Dominance-diversity curves neither show a clear progressive increase in evenness and richness with succession (Fig. 4c). The curves for the 25- and 38-yr fields are much steeper than that for the younger fields. Evenness and diversity is highly correlated, i.e. diversity changes are connected to changes in evenness and not to species richness. Evenness and diversity
values approach the values of the propagule source grasslands in the first 11 years, but decrease rapidly later with succession (Fig. 4d).

2. Trends of the species groups (Tab. 3)
The dominance of weed species of arable and old-fields and ruderal sites decreases rapidly after a significant peak in the 4th year (cover values of fields > 4-yr-old do not differ significantly), in 25-yr fields their cover is generally less than 1%, though 5-15% of the species still belong to this category (Fig. 5c, d). Cardaria only persists with higher dominance from the earlier species.

Five to twenty % (compared to 27-38% in the propagule source) of the species in 25-38-yr fields are species occurring mainly in loess grasslands (specialists II), but none of the specialist I species appears by yr 38 (Fig. 5c, d). The average proportional cover of specialist I species increases significantly between yr 1 and 11, and between yr 25 and 38, but is significantly lower than in the propagule source. After yr 11 only very few specialist species colonize (e.g. Salvia austriaca), thus specialist species not arrived in the first 11 years of succession, are generally absent later on as well.

Generalist species, i.e. species of all sorts of dry grasslands in the Tiszántúl region dominate the fields > 4-yr-old, and reach 84-98 proportional cover in 25-38-yr-old fields (Fig. 5c, d).

The dominance of perennial species develops rapidly, significantly increases in the first 11 years of succession (Fig. 5a, b), which results in a closed grassland which is in physiognomy similar to the ancient grazed loess grasslands of the propagule source. Number of perennials changes significantly only between yr 4 and 11.

3. Behaviour of selected species
Dominant species of the propagule source grasslands
All of the dominant species of the 11-, 25-, 38-yr fields are also common and dominant in the propagule source (Fig. 5c). Festuca appears initially in the 4-yr fields, and becomes dominant by yr 25. Koeleria cristata appears one age later, and though is constant in the plots, becomes really dominant only in one 38-yr-old plot. Achillea collina appears similarly as Festuca but remains sub-dominant in the remainder of the sere. Galium verum is only dominant in the 25-yr fields. Thalictrum minus, Phlomis tuberosa, Agropyron intermedium, Carex praeox, and Ornithogalum orthophyllum do

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Fig. 4. Changes of some features with succession. a: cover (average, maximum and minimum), b: number of species per plot (average, maximum, minimum) (1), number of species per age (2), and heterotony (3), c: species-cover diversity (average, maximum, minimum), d: average diversity and evenness, e: dominance-diversity curves. For explanations see text.
not appear in the old-fields. Behaviour of Salvia austriaca, Salvia nemorosa, and Thymus is described below.

Specialist species Astragalus austriacus appears relatively early with its usual cover in the propague source grasslands (Fig. 5f). Thymus also appears in the 11-yr fields, but does not reach its normal value in the next 37 years. Salvia nemorosa colonizes later, again with low cover values. Bromus inermis is dominant in 38-yr fields only, but since this species is very rare in the propague source, it is suspected to be the remnant of former sowing. Salvia austriaca, Taraxacum laevigatum and Verbascum phoeniceum are rare and do not show trends with succession.

Dominant species of the fields
The number of dominant species per age has a temporary maximum in yr 4 and 11.

1-yr fields: Fallopia convolvulus (arable weed, annual), Matricaria chamomilla (generalist-a, annual), Lamium amplexicaule (generalist-w, annual)

4-yr fields: Bromus tectorum (arable weed, annual), Festuca (generalist, perennial), Asperugo procumbens (arable weed, annual), Festuca pratensis (weed because sown, perennial)

11-yr fields: Festuca (generalist, perennial), Cardaria draba (generalist-w, perennial), Achillea collina (generalist, perennial), Cardus nutans (generalist, perennial)

25-yr fields: Festuca (generalist, perennial), Poa angustifolia (generalist, perennial)

38-yr fields: Festuca (generalist, perennial), Koeleria cristata (generalist, perennial)

4. Spatial variation
Spatial pattern of vegetation is scale dependent, and is best studied at different spatial scales (e.g. Greig-Smith 1952; Juhasz-Nagy & Podani 1983). But even if only one spatial scale is studied, differences between plots are important since averages may obscure important dissimilarities. Differences between plots may suggest convergence or divergence of the successional feature studied.

Plot-to-plot variation: Heterotony has a maximum in the 4-yr-old fields and decreases later (Fig. 4b). The ordination of plots also show the variation of plots of the same age. Probability ellipses are the biggest in the 4-yr-old fields, and decreases sharply later with succession (Fig. 6). This implies divergence in the first years and convergence after yr 11.
Great variation between plots of the same age was found e.g. in the following features: proportional cover of weeds in yr 1, 4, and 11, proportion of weed species in the species list through the whole sere, proportional cover and species richness of generalists in 1- and 4-yr fields, the proportional cover and species richness of specialists in all but the 1-yr-old fields, absolute cover in yr 4, 11, and 38, the dominance of Festuca.

Little variance was found e.g. in species richness, the occurrence of specialist I species, the proportional cover of weeds in yr 25 and 38, proportional cover and species richness of generalists in 11-, 25-, and 38-yr fields, and the proportional cover of perennial species in 11–38-yr fields.

5. Direction and rate of succession

Centroids of different aged plots in the ordination space moves along the axes or along an arc which suggest that the dynamics is directed (and not only a fluctuation), unidirectional and convergent (Fig. 6). Differences in displacement distances are more or less the same with binary data, in the other two cases distances shorten. Even in the binary case same distances with increasing time spans suggest that the rate of succession is sharply decreasing (Table 4).

With binary data all ages differ significantly (Table 5). With cover values (when dominant species weigh more) the 25- and 38-yr-old fields do not differ significantly from the propagule source grasslands. Using standardized cover values (when all species have the same value) these ages again differ significantly which suggest that the cover values of dominant species similar between ages, but the subdominant and rare species differ highly between ages.

Discussion

Characteristics of local vegetation dynamics

There are many features that show changes and/or high variance with succession. Some of these differences may be the outcome of slightly different site histories of the individual fields, others may be the characteristic features of the local vegetation dynamics. The adequate separation of the two is presently not feasible. The following section summarizes and discusses

Fig. 5. Changes of species groups and selected species with succession. a: average number of annual and perennial species, b: average cover of annual and perennial species, c: average number species of species groups (1. weeds; 2. generalist-w; 3. generalist, generalist-m, generalist-s; 4. specialist I; 5. specialist II), d: average cover of species groups (signs as before), e: cover of four dominant species (average, minimum, maximum), f: cover of four specialist species (average, minimum, maximum). For explanations see text, and for statistical tests Table 3.
Space-for-time substitution for hypothesis generation

those aspects of the local succession inferred from space-for-time substitution that seem to be the general characteristics of the local old-field succession on chernozem soils and thus can form the basis for hypothesis generation.

Tab. 4. Rate of succession in the old-fields. Movement of centroids of groups in the ordination space were calculated. Notice the sharply decreasing rate if ordination is based on cover or standardized cover values.

<table>
<thead>
<tr>
<th>From</th>
<th>To</th>
<th>species list</th>
<th>cover</th>
<th>standardized cover</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 yr</td>
<td>4 yr</td>
<td>0.139</td>
<td>0.265</td>
<td>0.301</td>
</tr>
<tr>
<td>4 yr</td>
<td>11 yr</td>
<td>0.239</td>
<td>0.17</td>
<td>0.219</td>
</tr>
<tr>
<td>25 yr</td>
<td>38 yr</td>
<td>0.132</td>
<td>0.048</td>
<td>0.076</td>
</tr>
<tr>
<td>38 yr</td>
<td>propague source</td>
<td>0.16</td>
<td>0.006</td>
<td>0.063</td>
</tr>
</tbody>
</table>

Tab. 5. Test of separation of groups in the ordination space by t-statistics. Significant differences are shown by asterisks. *P < .05, **P < .01, ***P < .001.

<table>
<thead>
<tr>
<th>Compared ages</th>
<th>d.f</th>
<th>species list</th>
<th>cover</th>
<th>standardized cover</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 yr -- 4 yr</td>
<td>5</td>
<td>3.143</td>
<td>4.269</td>
<td>4.597</td>
</tr>
<tr>
<td>1 yr -- 11 yr</td>
<td>6</td>
<td>12.4***</td>
<td>11.59***</td>
<td>13.28***</td>
</tr>
<tr>
<td>1 yr -- 25 yr</td>
<td>6</td>
<td>14.66**</td>
<td>13.79***</td>
<td>17.08***</td>
</tr>
<tr>
<td>1 yr -- 38 yr</td>
<td>6</td>
<td>16.72**</td>
<td>13.44**</td>
<td>19.02**</td>
</tr>
<tr>
<td>1 yr -- propague source</td>
<td>7</td>
<td>15.26***</td>
<td>12.82***</td>
<td>17.96***</td>
</tr>
<tr>
<td>4 yr -- 11 yr</td>
<td>5</td>
<td>6.252**</td>
<td>3.555**</td>
<td>5.567****</td>
</tr>
<tr>
<td>4 yr -- 25 yr</td>
<td>5</td>
<td>8.76**</td>
<td>4.287**</td>
<td>7.921****</td>
</tr>
<tr>
<td>4 yr -- 38 yr</td>
<td>5</td>
<td>9.066***</td>
<td>4.332***</td>
<td>8.408***</td>
</tr>
<tr>
<td>4 yr -- propague source</td>
<td>6</td>
<td>9.148***</td>
<td>4.542***</td>
<td>9.83***</td>
</tr>
<tr>
<td>11 yr -- 25 yr</td>
<td>6</td>
<td>8.491***</td>
<td>3.98***</td>
<td>4.636***</td>
</tr>
<tr>
<td>11 yr -- 38 yr</td>
<td>6</td>
<td>6.499**</td>
<td>3.362**</td>
<td>5.582***</td>
</tr>
<tr>
<td>11 yr -- propague source</td>
<td>7</td>
<td>5.565**</td>
<td>2.711**</td>
<td>9.207***</td>
</tr>
<tr>
<td>25 yr -- 38 yr</td>
<td>6</td>
<td>10.51***</td>
<td>0.9165</td>
<td>6.154***</td>
</tr>
<tr>
<td>25 yr -- propague source</td>
<td>7</td>
<td>3.562**</td>
<td>1.36</td>
<td>7.62***</td>
</tr>
<tr>
<td>38 yr -- propague source</td>
<td>7</td>
<td>5.233***</td>
<td>1.144</td>
<td>13.03***</td>
</tr>
</tbody>
</table>

Earlier species are replaced by later species with succession, but neither species richness per plot nor the dominance-diversity curves show a clear trend with succession as was expected (cf. Bazzaz 1975). Species richness per age and diversity per plot show a temporary increase in yr 4 and 11, respectively, which will be explained below. Diversity changes are connected to changes in evenness and not to species richness, since the latter does not change significantly with succession.
There are clear recognizable trends and profound differences in the performance of species groups: number and cover of weed species decrease by yr 4, generalist and perennial species increase from the beginning, and the colonization of specialist species is low. Dominance changes of species could be easily explained by species characteristics (cf. NOBLE & SLATTERY 1980), though some species behave exceptionally, e.g. the early appearance of *Taraxacum laevigatum* and the low dominance and frequency of the generalist *Euphorbia cyparissias*, which is very common in the propagule source. This "misbehaviour" of species was emphasized by BROWN (1992) when discussing a long-term primary successional series. Species behaviour, however, can change regionally, and thus local "misbehaviour" can be caused by wrong determination of species characteristics. If, however, an identical species according to their preferences in Hungary, much more misbehaviour would have been found than with regional classification. Time of colonization and dominance changes of species seem to be species specific. It is generally accepted that species performance is individualistic in many dynamic situations (GLENN-LEVIN 1980; MISTRY & PICKETT 1988 and HANSSON 1988).

Weed species (except *Cardaria*) diminish by yr 25, unlike to other observations in old-fields where early species survived till later stages (BAZZAZ 1968; PICKETT 1982). Rapid extinction of early (mainly annual) species may be caused by the strong dominance of *Festuca* and other perennial generalists by yr 11, since they form a more or less closed canopy. Suppression by a closed vegetation cover has often been cited as the major factor reducing the probability of successful recruitment or invasion (e.g. REJMANEK 1989; TILMAN 1993; BURKE & GRIME 1996).

Species richness and dominance of specialist species increase much more slowly than expected. Even specialists common in the propagule source do not colonize in the first 38 years (e.g. *Potentilla arenaria*, *Filipendula vulgaris*, *Fragaria viridis*, *Thalictrum minus*). Species which occur only in loess steppe grasslands in the Tiszántúl region do not appear at all, thus, with the former ones they can be considered as ancient grassland indicators in this landscape and at this time scale (cf. PETERKEN & GAME 1984). Though WELLS (1990) mentioned secondary grasslands which became rich in specialist species, generally even older secondary grasslands and woodlands are poor in specialist and/or "climax" species (BAZZAZ 1968; PETERKEN & GAME 1984; DWONKO & LOSTER 1992). The landscape of this study was expected to be a good source for colonization since there are many species rich loess grassland patches scattered in the landscape surrounding the old-fields, and some are even contiguous with them. These features are considered as favouring immigration into new territories (BAUDRY & MERRIAM 1988; MCCLANAHAN 1986; VAN DER VALK 1992; BULLOCK & WEBB 1995; GUSTAFSON & GARDNER 1996). Limited dispersal of specialist species has often been reported. PETERKEN & GAME (1984) and DWONKO (1993) for example found that 1000 and 2–300 metres, respectively, prevented the colonization of woodland species. In our landscape distance alone can not be the major factor preventing colonization since most of the specialist species occur in the immediate surroundings of the old-fields, and as PORTNOY & WILLSON (1993) emphasize, the tail of the dispersal curve may be very long.

Most of the specialists that are able to colonize in these old-fields appear relatively early (by yr 11), and very few specialist species colonize after this age. This suggests that there are mobile and less mobile specialists. Similarly large differences in colonization ability were found by PETERKEN & GAME (1984) in English woods at a time scale of 130 years. Limited seed production besides poor dispersal ability could explain the immobility, together with low establishment after arrival (GROSS 1987). In this landscape often seeds near the soil surface can only be produced as a consequence of grazing (pers. observation) which may strongly hinder dispersal to old-fields.

Besides dispersal limitation, recruitment limitation may be another reason for low performance of later species, and for the lower species richness in older fields (cf. FACELLI et al. 1987; BURKE & GRIME 1996; TILMAN 1997). The high dominance of *Festuca*, a perennial, generalist grass species may prevent germination and establishment of new immigrants. The high availability of nutrients in the chernozem soils (SZABOLCS 1961) may facilitate competitive exclusion, as was suggested by HUSTON (1978). Closing of the invasion window in old-fields was found to be connected to increased vegetation cover and decreased gap availability (GROSS 1980). Litter also decreases the availability of gaps for colonization (FACELLI & PICKETT 1991). Thus dominant species can limit further immigration and this can result in decreasing diversity and increasing evenness, as was found also by FACELLI et al. (1987). In their case the dominance of the annual grass *Lotium multiforme* resulted in the above-mentioned changes but in a much shorter time than in our case where the dominant is a perennial grass becoming dominant only by yr 11. Disturbances caused by soil dwelling animals could increase the probability of colonization (PEART 1989) but in our old-fields field mice and moles may not be abundant enough.

Limited colonization results in decreasing rate of succession (if measured by compositional change) after yr 11. This seems to be a general feature of old-field successions (SHUGART & HEET 1973; MISTRY & PICKETT 1994) though in our case successional change between yr 11–25 and 25–38 is extremely low.

The old-fields converged in floristic composition with succession and the number of dominant species decreased in the 25- and 38-yr-old fields. These later dominant species are a subset of the dominants of the loess grasslands of the propagule source. This may be an important factor in determining the pathway of the local succession. Convergence seems to be the general trend in old-field successions (MISTRY & PICKETT 1990), though there are also exceptions (e.g. INOUE et al. 1987). Convergence in our landscape may be determined by the following factors: 1. low chances for woody species colonization (as a consequence of a poor propagule source for woody species and of regular grazing), 2. dominance of *Festuca* and other generalists and 3. regular sheep and cattle grazing as a homogenizing factor.
Hypotheses for further studies

The results of the SFT show that the most characteristic features of the local succession are the very limited colonization of later species, the relatively rapid development of a characterless grassland dominated by generalists, and the sharply decreasing rate of succession in 25–38-year-old fields.

The following hypotheses are suggested for long-term studies to study the mechanisms behind these phenomena:

End points: Smaller differences in grazing regime do not effect the end points of individual old-field successions, i.e., there are no highly divergent pathways in this landscape. Smaller differences mean the normal variation of the traditional grazing regime: moderate over- or undergrazing by sheep or cattle. The end point is a characterless Festuca-Poa-Koeleria-Achillea grassland even in a longer term.

Dispersal limitation: Species not colonizing the old-fields in the first 38 years do not have a viable seed bank in the soil of the old-fields. If they had, then recruitment limitation would be the major cause that prevents the colonization of later species (cf. Tilman 1997). Species not colonizing the old-fields in the first 38 years have very low seed production in the propagule source under the present way of land use. This would also contribute to dispersal limitation. Species added by seed to older secondary grasslands germinate and become established in the subsequent years. This would also mean dispersal limitation of local succession (cf. Burke & Grime 1996; Tilman 1997).

Recruitment limitation: Spatially highly heterogeneous grazing increases the colonization of specialist species. Partial over- and undergrazing could create a wide variety of safe sites for immigration or open new invasion windows, and thus could decrease recruitment limitation (cf. Burke & Grime 1996). Increased field mouse and mole activity or artificial disturbance to the Festuca-Poa-Koeleria-Achillea grassland increases colonization of specialist species by creating gaps in the closed vegetation.

Conclusions

Space-for-time substitution is a useful tool to study local or regional vegetation dynamics. Though to overcome the numerous shortcomings of SFT is not an easy task, Pickett (1989) emphasizes that SFT, long-term study, experiments, and observations should be used together in various combinations to understand the dynamics of ecological systems.

It is important to emphasize that, even adequately conducted SFT studies are unable to predict the exact dynamics of other local successions not studied, as was often expected (cf. Pickett 1989). Inadequate generalizations are not rare in ecology (cf. the critique by Murphy 1989). Ecological phenomena are often idiosyncratic, regionalizations and generalization are therefore difficult to make (Murphy 1989). An important goal to use SFT prior more intensive field studies would be to be prepared for oncoming changes on that site, and not to exactly predict changes in other sites.

Minimization of variation in a particular chronosequence and "maximization" of variation between chronosequences could improve further the information gained from SFT studies, as was suggested by Pickett (1989). Unfortunately it is rare to find suitable landscapes for such parallel chronosequences where abiotic conditions, landscape context and land use can be controlled for adequately. This is a major limitation to parallel SFT studies.

Another possibility to improve the applicability of SFT studies is to use the knowledge about species attributes and species behaviour collected in a wider landscape or in a region. Indicator values, species preferences have proved to be useful in vegetation analysis (Ellenberg et al. 1991). Some of the uncertainties of SFT could be overcome by this sort of expert knowledge. For example "misbehaviour" of species during succession could be interpreted, or species could be grouped in many ways, which could help recognizing trends or the absence of trends.

Directing succession to achieve vegetation qualities sought by nature conservationists when conducting restorations is still a difficult and often unfeasible task. Therefore preliminary information on passive regeneration of areas to be restored are very useful. 1. for selecting sites for restoration, and 2. for choosing between different land use alternatives on sites being restored. SFT may be an appropriate tool to design restoration projects.

Adequately conducted space-for-time substitution is much more useful, than the "general average" SFT, where often present vegetation features provided the main or only information for creating the chronosequence. Unfortunately the detailed reconstruction of the history of the studied site is not an easy task. The site choice is never perfect; there is often the detailed reconstructed history which expose the formerly not expected differences in field histories. Difficulties of historical reconstruction may be one reason why SFT studies of sites with documented history are rare.

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References

Palugyay, I. (1855): Békés-Csanád, Csongrád és Honfő vármege r leírása. (Description of the counties Békés-Csanád, Csongrád and Honf.) - Pest.
Thaiss, L. (cca. 1905): Csnád megye flórákatológusa. (Flora list of Csnád county.) - Manuscript, TTM Növénytár, Tudománytörténeti Gyűjtemény.