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Vegetation succession in old fields at broad landscape scales

Ph.D. Thesis

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Annotation

This thesis is focused on succession in old fields in Central Europe. Repeated sampling, analysis of surrounding vegetation and soil measurements were conducted in the Bohemian Karst Landscape protected area. Samples from the Doupovské hory Mountains and the rest of the Czech Republic were added to discover basic principles of old field succession at the larger scale of landscapes.

Declaration [in Czech]

Prohlašuji, že svoji disertační práci jsem vypracovala samostatně pouze s použitím pramenů a literatury uvedených v seznamu citované literatury.

Prohlašuji, že v souladu s § 47b zákona č. 111/1998 Sb. v platném znění souhlasím se zveřejněním své disertační práce, a to v úpravě vzniklé vypuštěním vyznačených částí archivovaných Přírodovědeckou fakultou elektronickou cestou ve veřejně přístupné části databáze STAG provozované Jihočeskou univerzitou v Českých Budějovicích na jejích internetových stránkách, a to se zachováním mého autorského práva k odevzdanému textu této kvalifikační práce. Souhlasím dále s tím, aby toutéž elektronickou cestou byly v souladu s uvedeným ustanovením zákona č. 111/1998 Sb. zveřejněny posudky školitele a oponentů práce i záznam o průběhu a výsledku obhajoby kvalifikační práce. Rovněž souhlasím s porovnáním textu mé kvalifikační práce s databází kvalifikačních prací Theses.cz provozovanou Národním registrem vysokoškolských kvalifikačních prací a systémem na odhalování plagiátů.

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List of papers and author's contribution

I Jírová, A., Klaudisová A., Prach K. 2012. Spontaneous restoration of target vegetation in old fields in a central European landscape: a repeated analysis after three decades. Applied Vegetation Science 15:245-252.

Alena Jírová collected data by repeated sampling, compiled and analysed all data, wrote the draft and edited the comments of Karel Prach. Alexandra Klaudisová collected the original data in 1975.

II Jírová A., Prach K. Importance of the surrounding vegetation and functional traits on species composition of old fields in Central Europe. (submitted)

Alena Jírová collected all data, performed data analysis, wrote a draft of the manuscript and edited the comments of the co-author.

III Prach K., Jírová A., Doležal J. Pattern of old-field vegetation succession on a country scale. (submitted)

Data were collected by A. Klaudisová. K. Prach and A. Jírová (only partly the same data as in paper I.). Alena Jírová compiled the data, analysed them and contributed to manuscript writing with Karel Prach. Jiří Doležal helped with statistical methods and improved them by regression trees.

Contents

Motto:

Left to herself, nature is always more or less civilized, and delights in a certain refinement (Thoreau 1906).

[*Ponechá-li se příroda bez zásahů, pak je vždy víceméně uhlazená a potrpí si na jistou vytříbenost.*]

1. Introduction

Succession

The common English word, succession, is derived from Latin and means coming after another in order or sequence. In ecology, it refers to an orderly process of change (Golley 1977). Description of changes in species composition represents a backbone of successional studies (Osbornová et al. 1990).

The first study on succession could be assumed to be the description of the development of Irish bog vegetation by King (1685), which actually reflects very old common human knowledge (Golley 1977, Glenn-Lewin et al. 1992). However, the first scientific studies on succession were made at the turn of the nineteenth and twentieth centuries (Glenn-Lewin et al. 1992), i.e. the case of primary successional seres such as sand dunes (Cowles 1911). Although Cowles made important contributions by pointing out the predictive power of succession as a concept, it was Clements (1904, 1916) who offered a comprehensive theory of plant succession. His scheme of the processes that drive succession contains the following basic phases: nudation, migration, ecesis, completion, reaction and stabilization (Glenn-Lewin et al. 1992). Important to the further development of successional theory were the first criticisms of the Clements theory by Tansley (1935), Gleason (1917, 1939) and Whittaker (1953). They highlighted especially variability in the process of succession which is influenced by differences among plant species behaviors (Gleason 1926, 1939), presence of chance events (Gleason 1926, 1939) and differences among geographical regions (Tansley 1935, Whittaker 1953).

Already by Clements (1916), succession was divided into two basic types based on how it begins. The first type occurs on new substrates that have not so far supported life is called primary succession. The second type, in which a community is disturbed or destroyed, but at least some soil and biotic legacy remains as a substrate for a new succession, is called secondary succession (Golley 1977).

That means that the primary succession usually follows some disturbance which destroys all life and creates a bare area and initiates a succession (nudation). New soil must be created during this type of succession. Such new substrates are usually poor in nitrogen, which implies that nitrogen-fixing organisms may be important in early stages (Glenn-Lewin et al. 1992). Primary succession is rarer in nature than secondary (Golley 1977). It has been studied in various habitats (Walker & del Moral 2003). Some of the succession initiating disturbances have natural origin, i.e. moving of sand dunes, retreating glaciers or volcanic deposits (Walker 2012). Other seres are induced by human activities, i.e. succession on spoil heaps, in abandoned quarries, on peat bogs etc. There is still a need for more, especially long-term studies to increase predictability just at the moment when succession starts.

Secondary sites differ from primary sites in that the sites were previously vegetated and therefore the seed or seedling bank and developed soil play an important role (Walker & del Moral 2003), especially at the beginning of revegetation, which is usually faster than in primary sites (Glenn-Lewin et al. 1992). Similarly to primary sites, the disturbances which initiate succession are caused by natural agents, such as fire, storm or insect attack, or after human impacts, such as burning, clearing or land abandonment. Hundreds of secondary succession studies have been done in old-fields (see Cramer & Hobbs 2007). Other studies include many reports of vegetation developed following fire (Veblen et al. 2003) or clear cuts (Walker & del Moral 2003).

However, like many others dichotomies in ecology, the concept of primary and secondary succession is a helpful way of organizing our observations of nature, but it is in some cases rather problematic and there are also transition types between primary and secondary succession (Glenn-Lewin et al. 1992, Walker & del Moral 2003). Nevertheless, the differences between primary and secondary succession are not as important in terms of the course of succession (Prach et al. 2001). Moreover, the course of primary succession on nutrient rich sites is more similar to secondary than to other primary successions (Tilman 1982).

Another dichotomy was that proposed by Tansley (1935), who divided succession into autogenic and allogenic. In autogenic succession, successive changes are brought about by the action of organisms themselves. This implies internal the importance of forces and mechanisms such as competition, shade generation and soil modification (Glenn-Lewin et al. 1992). In allogenic succession, the changes are brought about by external factors. Long-term vegetation responses to climatic change or river delta succession, which continuously receive sediments from upstream, could be examples (Glenn-Lewin et al. 1992). However, in the last case, the amount of sediment is influenced also by the vegetation of the river bank. Therefore, in such a case it is better to speak about autogenic and allogenic factors under the terms of one succession.

The first, and for a long time, accepted concept of the end of succession was that of the climax (Whittaker 1953). It was believed that succession is supposed to continue until the species combination was that best suited to the regional climate (Golley 1977), and through an orderly process of ecosystem stabilization (Forman & Godron 1986). The stabilized final stage is usually called the climax (Whittaker 1953). A new succession may start after any disturbance in the climax stage (Forman & Godron 1986). However, not every author considered the climax stage as relevant. Because succession is a continuous process of change responding to a dynamic background of disturbance across the landscape, some authors did not mean to imply that the end of succession is a closure to a Clemensian climax, but only a relative decrease in the rate of change of biotic and abiotic variables. Determining when the “climax” occurs was also critical in thinking about succession (Walker & Del Moral 2003). As ecological ideas developed, the climax state was seen to fluctuate, but it was generally regarded as being a stable or dynamic equilibrium state. It was realized that natural post-climax states exist. Both primary and secondary seres can proceed to a state of ecosystem retrogression (Walker et al. 2007). After a period of biomass build up (progressive succession), the vegetation biomass and the store of organic material in the surface soils decline (retrogressive succession). Retrogressive succession is typical for old-landscapes of the southern hemisphere (Walker et al. 2007), while the first successional studies were made in pedologically young landscapes prevailing in the northern hemisphere (Clements 1904, 1916; Gleason 1939; Whittaker 1953).

For a long time, there were more direct studies about early stages of succession while the late stages were studied more often indirectly by space-for-time substitution or short-term permanent plots. Recently, the total number of publications increased due to a higher amount of data from permanent plots. The application of several new multivariate methods increased also the number of publications on succession. The number of studies of late successional stages has recently increased (Dybzinski & Tilman 2012).

Century-long observation studies, such as those using long-term permanent plots, are not the only method for studying succession. Another popular method is chronosequence study (= space-for-time substitution). In chronosequence studies, it is assumed that measurements on several sites which represent different stages of one sere can provide enough data for an interpretation of the rate and direction of succession. However, weaknesses of chronosequence studies have been also amply addressed (Pickett 1989). A combination of chronosequence study with permanent plots research is a very effective methodological approach to study ecosystem changes, especially succession. Moreover, the short-term experimental results can be converted into long-term effects on successional rates and trajectories by modeling (Glenn-Lewin et al. 1992, Walker & del Moral 2003). Experimental manipulation of succession is another tool used for better understanding the process of succession. This includes, for example, removal experiments, sowing or planting of some species, manipulation with fitness, abiotic factors or using herbivores. Such manipulations of succession are popular with those who are concerned with the processes that drive succession, but weaknesses, such as investigator influence, often poor design or lack of protocols, can hinder data interpretation (Walker & del Moral 2003).

Because of a century of successional studies in many areas of the globe, these results can offer substantial contributions to restoration ecology (Walker et al. 2007). Restoration is fundamentally the manipulation of succession and frequently focuses on acceleration of species and substrate change to a desired endpoint. Restoration usually addresses similar time scales as successional studies, but is, nevertheless, dependent on the broader successional patterns of change for its success (Walker et al. 2007).

Land abandonment

There are two predominant ways of viewing land abandonment and subsequent activities: (a) the need for re-establishing a desired, previous type of management or (b) redevelopment of ecosystems present on a place before human impact (Cramer & Hobbs 2007). Both ways are topics of restoration ecology (Pickett et al. 2001).

The first view of abandonment (a) considers it to be more of a threat, resulting in the loss of specific ecosystem types that depended on ongoing agricultural management, i.e. fallows (Boatman et al. 2011) or semi-natural grasslands (Cramer & Hobbs 2007). Many plant species restricted to habitats such as grassland, meadow, heathland or dune grassland are dependent on traditional land use disturbance regimes (Prévosto et al. 2011). In this view, land abandonment is undesirable.

In the second view of abandonment (b), redevelopment of potential or any target vegetation could be used basically in three ways of restoration: (i) technical reclamation, (ii) manipulated succession, or (iii) spontaneous succession. This second view of abandonment includes studies on abandoned pastures in the tropics, old-fields (Cramer & Hobbs 2007), abandoned plantations (e.g. coffee plantations in Puerto Rico, Marcano-Vega et al. 2002) and natural revegetation of abandoned lands prairies (e.g. in Colorado, Costello 1944).

The presented dissertation is concerned with the second view of land abandonment and focused on spontaneous succession in old-fields with special attention to possible restoration of former potential vegetation in the area.

Old-fields

Nearly half (45%) of earth's terrestrial surface is devoted to agriculture, from which one third is in crops (Walker 2012). Between 1860 and 1990 there were abandoned over 200 million ha of croplands over the world and this amount is still rapidly increasing. The current emphasis on free trade and the removal of trade barriers has important implications for agriculture everywhere and will undoubtedly lead to the marginalization of agriculture in certain regions and, hence, increased land abandonment in some parts of the world (Cramer & Hobbs 2007). Old-field succession is a special case of secondary succession (Glenn-Lewin et al. 1992), and the study of old-field succession explains much of the local variation among ecosystems by describing the successional changes occurring over decades to centuries (Chapin III et al. 2002). The old-fields resulting from abandonment display a variety of dynamics and have been the subject of many ecological studies and considerations. They have played a pivotal role in the development of ideas and concepts of ecological succession (Cramer & Hobbs 2007). They occur abundantly in various landscapes all over the world and the results can be used for large-scale comparisons on country scales (Prach 1985, Ruprecht 2005, **paper III**) or in different regions (Cramer & Hobbs 2007, Prévosto et al. 2011).

Spontaneous succession in old-fields

The abandonment of traditional agricultural lands in some areas creates old-fields that require, according to site conditions and surrounding vegetation, limited or no restoration (Cramer et al. 2007). In those areas, the old-fields are suitable for spontaneous succession. The forest temperate zones of Europe and North America (Cramer & Hobbs 2007) are one of the typical areas where spontaneous succession can be used as a restoration tool for old-fields (Prach & Pyšek 2001). However, young stages of succession are valuable in some cases i.e. for butterflies. Therefore, continuing management, such as mowing or grazing, is desirable in such cases. Without any management, ecosystems do not always spontaneously return to the desired vegetation type, thus spontaneous succession is not a suitable means of restoration in all cases. For example, most old-fields in the Queets Valley of Olympic National Park (Washington, US) remain dominated by exotic herbs 60 years after abandonment although the fields are surrounded by temperate rain forest (Riege & del Moral 2004).

Basic successional stages in old-fields

Plant composition and species richness clearly change with age since abandonment (Cramer & Hobbs 2007). It is usually possible to distinguish several seral stages in the development of vegetation in abandoned fields through taxonomic identification and growth forms of dominants (Costello 1944; Keever 1979; Dubiel 1984; Prach 1985; Degn 2001; Feng et al. 2006, etc.). However, sometimes there is a gradual and continuous change in species composition and functional properties of the plant communities, and no objectively definable stages can be delimited (Mellinger & Mc Naughton 1975). In regions with forest climax, six stages of old field succession can be recognized: An initial dominance of annual and biennial weeds and ruderals (i) is followed by dominance of perennial weeds (ii), and then forbs and grasses (iii), which are followed by colonizing woody plants (iv). Under very wet or dry conditions, the late forbs and graminoids (v) may be the last stage for a long time, but more often the succession is terminated by late-successional tree species (vi) (Osbornová et al. 1990, Erjnǽs et al. 2002).

I. *Annual weeds.* This stage contains annual weed species for the first 2 (in some cases even 3) years after abandonment. It is typical for former arable land just shortly after its abandonment, and the seed bank plays a pivotal role in species development (Lepš 1987). The first stage lasted only one year in Pennsylvania (Keever 1979) as well as in the Transylvanian Lowland in Romania (Ruprecht 2005). This happens due to favorable soil conditions and a temperate climate supporting fast expansion of perennials. It may also depend on the previous agricultural management of the field; if expansive perennial weeds largely occur already during cultivation, they may expand fast after abandonment (e.g. *Elytrigia repens*).

II. *Perennial weeds*. For Europe, *Elytrigia repens* is a typical species of this stage (nomenclature is unified according to Kubát et al. 2001). It is an indigenous species in Europe, Asia and North Africa, but currently spreading over the entire world. Nearly monodominant growth (3-6 years after abandonment) of *E. repens* was recorded in Finland (Prach 1985), *E. repens* dominated fields for 12 years in Romania

(Rurecht 2005), 2-3 (-4) years of succession were dominated by a *Cirsium arvense* - *Elytrigia repens* species combination in Poland (Dubiel 1984) and this species dominated with other species for (1-) 2-6 year in fields in Denmark (Degn 2001). In the case of Denmark, a field was occupied already in the first year by *E. repens* and it persisted until the 6th year. This happened because, during the last years of cultivation of *Hordeum vulgare*, the field was fertilized and control of weeds was inefficient (Degn 2001). The occurrence of *Elytrigia* on reserved fields in Central Finland was very uneven: it appeared on relatively few fields, but was usually then very dominant (Hokkanen & Raatikainen 1977). In Colorado, *Agropyron smithii,* a species similar to *E. repens,* frequently appears instead of *E. repens* (= *Agropyron repens*) (Costello 1944). *E. repens* is the most important dominant of early successional stages in old-fields in most parts of Europe and some parts of North America (Cramer & Hobbs 2007).

III. *Successional perennial forbs or graminoids*. Succession in some areas proceeds just to this stage which often resembles a grassland, because the establishment of woody vegetation is hindered by grazing, mowing or by the scarcity of woodlands as seed sources in the surroundings (Ruprecht 2005). Establishment of woody species can also be limited by low soil moisture. The number of tree and shrub species may increase only slightly with the age of abandoned fields; the occurrence of parent plants in the near surroundings is essential to the presence of their seedlings in fields (Dubiel 1984).

IV. *Successional woody species* (usually more than 15 years after abandonment). Woody plant succession is characterized by increases in the emergence, density and richness of woody species over time and usually a shift from early dominance by wind-dispersed species to later dominance by bird dispersed species (Foster 2004). Early successional 'pioneer' woody species dispersed by wind have usually fewer difficulties in colonizing old-fields than late successional forest species (Smit & Olff 1997). Nevertheless, the wind dispersed species with small seeds sometimes have trouble with establishment in the dense ground cover of herbs (Fenner & Thompson 2005). Bird dispersed species are facilitated by the presence of perches (McDonell & Stiles 1983, Pausas et al. 2006). In restoration ecology, artificial perches have already been exploited as attractors for bird dispersal (Pickett at al. 2001). However, bird dispersed species occasionally occur despite the lack of perches (Osbornová et al. 1990).

V. *Late forbs or graminoids*. Colonization by woody species is crucial in all successional seres in temperate climates, and seems to be restricted only under extreme site conditions (Prach et al. 2007). This restriction was found, for example, in the Bohemian Karst (Czech Republic), where there are two types of late successional stages: oak-hornbeam forest or shrubby grassland. The shrubby grassland stage is possible to see also on a 91 year old field (**paper I, II, III**). In other studies, such grasslands also are reported to be an important mid- and late successional stage in drier seres in some parts of Central Europe (Ruprecht 2005).

VI. *Late woody species*. There is a general decrease in participation of woody species toward drier and warmer regions (Prach et al. 2007). The number of of tree and shrub species may increase only slightly with the age of abandoned fields (Dubiel 1984). Many herb species evidently colonized in early stages, but later disappeared when shade increased under the closing canopy. Only a very small proportion of the early successional species can survive in the ground layer of a mature woodland (Harmer et al. 2001). This means that the total species number is usually higher before canopy closure. The degree to which a typical forest species manages to colonize a post-agricultural forest depends, in addition to the site environmental conditions, on their dispersal and colonization traits and on forest habitat availability (species pool) in the landscape (De Frenne et al. 2011). In the United Kingdom, for example, natural succession changed abandoned fields into mixed deciduous woodland in one century (Harmer et al. 2001), while it was even earlier in the Bohemian Karst (**paper I**).

Spontaneous succession as a restoration tool

Other habitats besides old-fields may be suitable for spontaneous succession as a restoration tool. In the Czech Republic, spontaneous succession was studied also in quarries (Novák & Prach 2003, Novák & Konvička 2006, Trnková et al. 2010), gravel sand pits (Řehounková & Prach 2008), peat bogs (Konvalinková & Prach 2010), spoil heaps (Prach 1987, Frouz et al. 2008, Hodačová & Prach 2003, Mudrák et al. 2010), etc.

However, the ability of a site to repair itself depends also on the various biotic and abiotic legacies of previous cultivation, i.e. landscape fragmentation, environmental suitability for agriculture, soil properties, soil seed bank, type of agriculture, presence of invasive exotic species, and species facilitation (Cramer et al. 2007). Plant functional traits were recognized as a powerful tool for predicting the colonization success of plants available in the local species pool (Řehounková & Prach 2010, **paper II**). Therefore, the surrounding vegetation, as an important diaspore source for natural restoration by spontaneous succession, is also a highly important factor (Borgegård 1990, del Moral et al. 1995, Campbell et al. 2003, Dovčiak et al. 2005, Novák & Konvička 2006, Prach & Řehounková 2006, Kirmer et al. 2008, Řehounková & Prach 2008, Trnková et al. 2010, De Frenne et al. 2011, **paper II**).

Subjects of dissertation

The presented study is focused mainly on the late stages of old field succession in the Bohemian Karst Protected Landscape Area (**paper I**, **paper II**). Vegetation on old-fields in this area was already studied (see Osbornová et al. 1990). Some studies paid special attention to early weedy (Lepš 1987) or late shrubby stages (Lepš & Prach 1981, Prach 1981), or concentrated on soil moisture (Rambousková

1980, Rambousková 1981). Earlier and recent vegetation data provided an opportunity to elaborate them together and make some general conclusions. The first of the included papers (**paper I**) describes the development of old-fields in the Bohemian Karst Protected Landscape Area through repeated sampling after more than three decades (Klaudisová 1976) and found two types of late stages of old-fields, namely deciduous woodland and shrubby grassland. The second paper (**paper II**) deals with spontaneous succession in the same area, but in the broader, landscape context with special attention to the influence of the surrounding vegetation on the course of succession and comparing the traits of species present in the fields and their surroundings. It also deals with the difference between two types of late stages found in the previous paper. The third paper is a broader scale study in which samples from other parts of the Czech Republic were added (**paper III**), making altogether 282 samples. Past (Klaudisová 1976, Prach unpubl.) and recent (Jírová et al. 2012, Jírová unpubl., Prach unpubl.) samples were analyzed together and show some general trends in the course of succession at the larger scale of the country.

Aims

The following main questions were asked in the presented dissertation: What directions of succession are typical for old-fields in the Bohemian Karst (**paper I**, **paper II**) and for the Czech Republic (**paper III**)? Are the trends similar? Particularly, how do species richness and environmental characteristics change during succession (**paper I**)? What is the influence of surrounding vegetation on the species composition of old fields, and species of what traits and ecological demands are most successful in establishing and persisting in the old fields (**paper II**)? Which factors determine spontaneous succession in old-fields at landscape and country scales (**paper I, paper II, paper III**)? Do successional trends differ or are they the same if studied at landscape and country scales (**paper III**)? How can spontaneous succession be exploited in restoration and landscape management (**paper I, paper II, paper III**)?

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Paper I

Spontaneous restoration of target vegetation in old fields in a central European landscape: a repeated analysis after three decades.

A. Jírová, A. Klaudisová, K. Prach

Applied Vegetation Science 15:245-252, 2012

Abstract

Questions: (a) What are directions of spontaneous succession; in particular, do target stages (identified as shrubby grassland and semi-natural deciduous woodland) develop, and if so, which species are involved? (b) Are the target stages predictable? (c) How do species richness and environmental characteristics change during succession? (d) What are the consequences for restoration and landscape management?

Location: The Bohemian Karst Protected Landscape Area, SW of Prague, Czech Republic (49° 52' – 50° 00' N, 14° 03' – 14° 21' E, 251–488 m a.s.l.).

Methods: In a repeated analysis, phytosociological relevés recorded in 4 m × 4 m plots in 58 old-fields initially surveyed in 1975 were compared to those from 28 still existing fields in 2008–2009. Average Ellenberg indicator values were calculated for each relevé. Aspect and slope were measured and potential radiation calculated. pH was measured from soil samples. Species were grouped according to their affiliation to the phytosociological classes of *Querco-Fagetea*, *Festuco-Brometea*, *Trifolio-Geranietea*, *Molinio-Arrhenatheretea*, and weedy and ruderal vegetation. Those belonging to the first three classes were considered target species. The data were analysed using multivariate (ordination methods) and univariate statistics.

Results: The spontaneous succession in old-fields proceeded towards target communities, either deciduous woodlands or shrubby grasslands. Their establishment can be tentatively predicted by soil pH and early occurrence of grassland species. Except pH, all Ellenberg indicator values changed during succession. Both pH values (Ellenberg and measured) were higher in shrubby grasslands than in woodlands. The total number of species decreased during succession, the number of target woodland species increased, and that of target grassland species remained the same in the shrubby grassland stages but decreased in the woodland stages during the past 33 yr of succession.

Conclusions: Target shrubby grasslands, resembling natural steppe-like communities typical of the region and valuable from the conservation point of view, can be restored by spontaneous succession

within a few decades in about one third of the studied old-fields. Other fields developed into deciduous woodland. Restoration of well-developed target woodland will take a longer, but the trend is already obvious, although less desirable nitrophilous woodland might also alternatively develop. Repeating earlier chronosequence studies may provide valuable information useful in restoration ecology and landscape management.

Následující pasáž v rozsahu 20 stran obsahuje skutečnosti chráněné autorskými právy a je obsažena pouze v archivovaném opriginále disertační práce uloženém na Přírodovědecké fakultě Jihočeské university v Českých Budějovicích.
Publikace vyšla tiskem v časopise Applied Vegetation Science.

Paper II

Importance of the surrounding vegetation and functional traits on species composition of old fields in Central Europe.

A. Jírová, K. Prach

(submitted)

Abstract

Late successional stages of old fields (46) were studied in the Bohemian Karst Protected Landscape Area in the Czech Republic, central Europe. Two types of late spontaneous stages were distinguished: shrubby grassland and woodland. The first one developed on shallower soils. Land cover categories, occurring within 1 km of the broad surroundings and in the close surroundings up to the distance of 100 m from the field margins, were considered. Complete lists were compiled of species in each field and its close surroundings up to 100 m. The colonization success of each species was expressed by an index (CSI) between 0 and 1 which was obtained as the ratio between the number of old fields with a species present and the number of the species occurrence in their surroundings. Colonization success was also calculated separately for the two types of late successional stages. Life-history traits, affiliation to vegetation units and Ellenberg indicator values of colonizing species were considered (taken from databases). Vegetation data were analyzed using uni- and multivariate statistics. Various land cover categories in the surroundings, including participation of synantropic vegetation, woodlands and mesic meadows, exhibited significant relationships to the species composition of woodland old fields, while shrubland cover was related to the species composition of shrubby grassland old fields. Generally, target (*Querco-Fagetea, Festuco-Brometea* and *Trifolio-Geranietea*) species, perennials, phanerophytes, natives and species producing lower number of seeds were successful in the late successional stages. Species composing woodland and shrubby grassland target stages differed in their Ellenberg indicator

values. Obviously, there are important characteristics favoring which species colonize and participate in late successional stages.

Následující pasáž v rozsahu 40 stran obsahuje skutečnosti chráněné autorskými právy a je obsažena pouze v archivovaném opriginále disertační práce uloženém na Přírodovědecké fakultě Jihočeské university v Českých Budějovicích.
Publikace je ve fázi odeslání.

Paper III

Geographical pattern of old-field succession – a country scale analysis.

K. Prach, A. Jírová, J. Doležal

(submitted)

Abstract

Question: Which factors determine spontaneous succession in old-fields at a broad geographical scale? What are the directions of succession? How much do target species participate and on which factors is their participation dependent?

Location: Czech Republic (central Europe).

Methods: Altogether 282 phytosociological relevés ($25 m^2$) were recorded in old-fields located in various parts of the country. The old-fields were from 1 to 91 years old. The following environmental characteristics were determined for each old-field: altitude, phytogeographical region, soil moisture, and substratum acidity. Species were classified according to their endangerment, origin (natives, archeophytes, neophytes) and affiliation to vegetation units. Vegetation data were analyzed using multivariate statistics, generalized linear mixed models and regression trees.

Results: All the environmental characteristics had significant effects on species composition of seral stages. Vegetation succession was clearly divergent into three subseres reflecting soil moisture: dry, mesic and wet. The number of target species representing deciduous woodland (*Querco-Fagetea*), dry grasslands (*Festuco-Brometea*) and fringe communities (*Trifolio-Geranietea*) increased during succession. On the contrary, the number of archeophytes, neophytes and synanthropic species decreased with field age. More endangered and target species and fewer archeophytes, neophytes and synanthropic species occurred in warmer lowlands than in colder uplands. The number of endangered, target and the total number of species decreased with soil moisture, while the number of neophytes and synanthropic

species increased. The number of target species typical of dry grasslands decreased with altitude while that of synanthropic species increased.

Conclusions: The age of old-fields and soil moisture appeared as the most important drivers of succession considering the broad geographical scale. Besides, local site factors, climate, being represented by altitude and reflected also in biogeographical regions, modified the course of succession. Succession was clearly divergent on the country scale.

Následující pasáž v rozsahu 30 stran obsahuje skutečnosti chráněné autorskými právy a je obsažena pouze v archivovaném opriginále disertační práce uloženém na Přírodovědecké fakultě Jihočeské university v Českých Budějovicích.
Publikace je ve fázi odeslání.

2. Conclusions

Directions of succession

Succession in old-fields in the Bohemian Karst appeared as divergent. One fourth of old fields developed by spontaneous succession within three decades into shrubby grasslands, resembling natural steppe-like communities typical of dry sites in the region and valuable for conservation. Other fields developed into deciduous woodland (**paper I, paper II**). The shrubby grasslands developed on fields with lower soil depth. There were also differences in the Ellenberg indicator values between the two types of late successional stages. Shrubby grasslands possessed more light-demanding species and a lower number of moisture- and nutrient-demanding species than woodland stands. The pH values (Ellenberg and measured) were higher in shrubby grasslands than in woodlands (**paper II**).

Succession was clearly divergent also at the larger scale of the country following in principle the same trajectories as the previous analyses based on data sets taken in a particular landscape only. The most important drivers of succession appeared to be the age of the old-fields and soil moisture. Macroclimate and substrate acidity also exhibited some significant effects on vegetation pattern (**paper III**).

Species richness and endangered species during succession

Species diversity of old-fields usually reaches its minimum at the *Elytrigia* stages, if it is present, and maximum at the initial weedy stages (Prach 1985). Consequently, species richness in the fields usually rapidly decreases in the early stages of succession. Then repeated increases in species number are evident, especially during the transition from one stage to the consecutive one and species typical of these different successional stages temporarily coexist (Osbornová et al. 1990). In the presented study, species richness decreased with field age in the case of already established woodland and remained the same in the case of shrubby-grassland old-field succession (**paper I**, Table 1). Soil moisture appeared as an important factor influencing species richness: Dry old-fields were species richer than mesic and wet old-fields (**paper III**).

Species groups, species traits

Target (*Querco-Fagetea*, *Festuco-Brometea* and *Trifolio-Geranietea*) species, perennials, phanerophytes, natives and species producing a lower number of seeds were successful in the late successional stages, while the presence of annuals, therophytes, aliens and species with a high number of seeds occur more in the early stages (see also Cramer & Hobbs 2007, Walker & del Moral 2003). The success of target and indigenous species, and the low success of synanthrophic species, supports the idea of using spontaneous succession as a suitable tool to restore desirable semi-natural vegetation in old-fields in the study area (**paper II**).

Except for pH, all Ellenberg indicator values, which represent environmental characteristics, changed during succession. Generally, the number of light- and temperature-demanding species decreased during succession. The number of continentality-demanding species decreased, but only in the woodland stages. Nutrient- and moisture-demanding species increased, but again only in the woodland stages (**paper I**).

Role of the surrounding vegetation

Species composition in the old-fields was significantly related to the occurrence of synanthropic vegetation, and marginally also to the occurrence of woodlands within a 1km distance. The degree of synanthropisation and extent of semi-natural woodlands in the surroundings are probably responsible for the divergence of woodland old-fields into either stages dominated by *Fraxinus excelsior* with nitrofilous herb species, or stages more resembling a natural oak–hornbeam woodland (*Carpinion betuli)*, which is the potential vegetation in the area (Neuhäuslová 2001). The presence of dry grasslands in the surrounding was low, and there was no significant relationship to vegetation in the old-fields.

Lessons learned and future perspectives

Repeating earlier chronosequence studies, especially if conducted over large scales, is desirable and may provide valuable information improving successional theory. It is also useful in restoration ecology and landscape management (Glenn-Lewin et al. 1992, Walker & del Moral 2003). Large-scale comparative studies may test hypotheses about successional pattern, while small-scale experiments test hypotheses on the mechanisms of succession. Both approaches are important and complementary and should be more frequently used. In the Bohemian Karst, various experiments were conducted (see Osbornová et al. 1990), but controlled experiments over broad geographical scales are lacking, but are very desirable (Fridley & Wright 2012).

Comparative analyses across many different successional seres in the Czech Republic are under progress and **paper III** can be considered as a pivotal study. Future analyses of the set of old-fields investigated here after some two or three decades may provide a more precise view on the course of succession and verify the trends suggested here.

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