Vegetation succession in restoration of disturbed sites in Central Europe: the direction of succession and species richness across 19 seres

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Abstract

Questions: (1) How do seres differ with respect to vegetation changes? (2) What are the directions of succession? (3) How do species numbers change? (4) How do target species, i.e. those typical of natural and semi-natural vegetation, participate in succession? (5) Are spontaneously developed successional stages acceptable from the point of view of ecosystem restoration?

Location: Extracted peatlands, bulldozed sites in forests destroyed by air pollution, an emerged bottom of a water reservoir, corridors of former Iron Curtain, artificial fishpond islands and barriers, sedimentary basins, spoil heaps from mining, stone quarries, forest clearings, road verges, sand and gravel-sand pits, ruderal urban sites, river gravel bars and abandoned arable fields, located in various parts of the Czech Republic in Central Europe.

Methods: Phytosociological relevés were recorded in 10–25 m² plots located in the centre of representative successional stages defined by their age, ranging from 1 to 100 yrs. In total, we obtained 2392 vegetation samples containing 951 species. We performed DCA ordination to compare 19 seres. Desirable target species were considered as those representing (semi)-natural vegetation and all Red List species.

Results: The seres studied are more similar in their species composition in the initial and early stages, in which synathropic species prevail, than in the later stages when the vegetation differentiates. This divergence is driven mainly by local moisture conditions. In most cases, succession led to woodland, which usually established after ca. 20 yrs. In very dry or wet places (with limited presence of woody species) open vegetation developed, often highly valuable from the restoration and conservation point of view. The total number of species and the number of target species increased in the majority of seres with successional age.

Conclusions: The vegetation in the sites studied formed a continuum along a moisture gradient and by successional age. The individual seres largely overlapped in their species composition; the sere identity was not significant. Spontaneous succession usually proceeded towards woodland, except at very dry or wet sites, and generally appeared to be an ecologically suitable way of ecosystem restoration of disturbed sites because target species became dominant over time.

Introduction

Numerous different seres have been described from various parts of the world, often in remarkable detail (Walker & del Moral 2003). There is, nevertheless, still a lack of studies that compare a number of seres over a broad geographic scale in a rigorous, quantitative way (Prach et al. 1993, 2001, 2007, 2013; Anderson 2007; Prévosto
et al. 2011), largely because the use of different methods makes cross-study comparisons difficult (Prach & Rehounková 2006). This limitation can be overcome by sampling different seres in the same way, using a comparable size of plots and compatible methods of vegetation sampling. Data that match these criteria can also be extracted from different published and unpublished sources. Such comparable data make it possible to identify common and general trends in successional development among seres in a meta-analysis (Stewart et al. 2008). Quantitative comparisons across various seres, such as those presented in this paper, provide an overview of processes taking place in developing vegetation in a broader context. This knowledge is useful in both theory and practice. The theoretical side mainly includes general questions about successional development towards potential vegetation, convergence or divergence of succession, the rate of succession or changes in species diversity and species traits during succession (Walker & del Moral 2003). Practical aspects concern potential insights for ecological restoration (Walker et al. 2007; Prach & Walker 2011).

In the Central European country of the Czech Republic it has been estimated that, in past decades, about 2% of its area (about 1800 km²) was at least temporarily exposed to spontaneous succession that started on bare ground. About 0.8% originated from recent mining activities conducted in the second half of the 20th century (Prach et al. 2011), and about 0.6% is abandoned arable land (Hrázský 2006). The rest includes mostly habitats disturbed by construction activities. Restoration may be desirable at some of these sites.

We have two contrasting options when it comes to restoring disturbed land: (1) to rely on spontaneous succession, or (2) to adopt technical measures. The latter approach has prevailed in post-mining sites in the Czech Republic (Stýs & Braniš 1999) and generally involves levelling of the surface, spreading of organic material rich in nutrients and sowing of commercial seed mixtures or planting trees in regular rows. Similarly, road banks, sedimentary basins and various sites disturbed by construction works are often reclaimed by technical means. But is this really needed in all situations? Can desirable vegetation be attained by spontaneous development within a reasonable time frame? Spontaneous succession can, to a certain extent, be manipulated to reach the target stage. A continuum thus exists between technical reclamation and spontaneous succession (Prach & Hobbs 2008). In this paper, we compare 19 spontaneous seres, each subjected to a different kind of disturbance (Table 1). We focus on similarities in vegetation of different seres, directions of succession and species richness. Special attention was paid to the role of target species (defined as representatives of natural and semi-natural vegetation in a given region; Van Andel & Aronson 2012); these species are desirable from the restoration point of view and their participation can be used to assess succession from the restoration perspective.

Our goal was to answer the following questions: (1) how do the seres under study differ with respect to vegetation changes over time; (2) what are the directions of succession, and can they be generalized across different environments; (3) how does species richness change over the course of succession, and are there any general trends; (4) how do target species participate; and (5) are spontaneously developed successional stages acceptable from the point of view of ecosystem restoration?

Methods

Study sites

The successional sites considered in this study are located in the Czech Republic, but the range of habitats makes them representative of Central Europe. We sampled 19 habitats in which it was possible to identify seres. Twelve of the seres have already been described, at least partly, in separate studies (see Table 1 for description and references) and used for partial analyses (Prach et al. 1993, 1999, 2001, 2007, 2013); seven are newly included into this study. The seres differed in the number of samples, the number of sampled sites, the geographic area in which they occurred, and successional age. The differences in these characteristics resulted from the availability of successional stages and our capacity to observe them. All but one of the seres (on a river gravel bar) were triggered by human disturbances and started mostly on bare ground; the only exceptions were forest clearings created in Norway spruce plantations, but even here the cover of herb layer at the beginning of succession was usually low. We identified successional stages that were homogeneous, with a known year of the site’s creation and left to undisturbed development since succession had started.

Analysis

Sample plots of 10–25 m² were placed in the centre of the above stages. We combined the space-for-time substitution approach and permanent plot research (Pickett 1989) because some sites were observed over multiple years whilst others were observed for only 1 yr (compare figures in the 3rd and 4th column in Table 1). We identified all vascular plants present in each sample plot and visually estimated their percentage cover (Kent & Coker 1992). In some cases, the cover was estimated using semi-quantitative scales (Braun-Blanquet, Domin) and then transformed into percentage cover according to Van der Maarel (1979). The following successional stages were delimited and used for calculation of centroids (see below):
Table 1. Main characteristics of seres under study, listed approximately according to decreasing site moisture following their order in Fig. 1. In the figure, each sere is referred to by its number (1–19).

<table>
<thead>
<tr>
<th>Sere</th>
<th>Location in the Czech Republic</th>
<th>No. of samples</th>
<th>No. of sampled sites</th>
<th>Age of stages [yrs]</th>
<th>Data sources and references</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Extracted peatlands</td>
<td>SW</td>
<td>267</td>
<td>267</td>
<td>1–100</td>
<td>Konvalinková &amp; Prach (2010); Bastl et al. (2009)</td>
</tr>
<tr>
<td>2. Bulldozed sites in forests destroyed by air pollution</td>
<td>W</td>
<td>14</td>
<td>12</td>
<td>1–20</td>
<td>Pyšek (1992), Prach et al. (2001)</td>
</tr>
<tr>
<td>3. Emerged reservoir bottom</td>
<td>W</td>
<td>12</td>
<td>1</td>
<td>1–12</td>
<td>K. Prach, unpublished data; Prach et al. (2001)</td>
</tr>
<tr>
<td>7. Spoil heaps from uranium mining</td>
<td>Central</td>
<td>85</td>
<td>85</td>
<td>7–32</td>
<td>Dudičková (2007)</td>
</tr>
<tr>
<td>8. Acidic stone quarries</td>
<td>Central</td>
<td>135</td>
<td>135</td>
<td>1–86</td>
<td>Trnková et al. (2010)</td>
</tr>
<tr>
<td>11. Spoil heaps from black coal mining</td>
<td>Central</td>
<td>88</td>
<td>88</td>
<td>10–100</td>
<td>H. Dvořáková, unpublished data; Prach et al. (2013)</td>
</tr>
<tr>
<td>12. Spoil heaps from brown coal mining</td>
<td>W</td>
<td>147</td>
<td>82</td>
<td>4–55</td>
<td>K. Prach, unpublished data; O. Mudrák, unpublished data; Frouz et al. (2008); Mudrák et al. (2010)</td>
</tr>
<tr>
<td>15. Urban ruderal sites</td>
<td>W</td>
<td>36</td>
<td>3</td>
<td>1–12</td>
<td>Pyšek (1978); Prach et al. (2001)</td>
</tr>
<tr>
<td>16. River bars</td>
<td>NE and S</td>
<td>70</td>
<td>41</td>
<td>1–150</td>
<td>K. Prach, unpublished data; Z. Vaněček, unpublished data</td>
</tr>
<tr>
<td>17. Abandoned fields</td>
<td>Various parts</td>
<td>288</td>
<td>181</td>
<td>0–91</td>
<td>Osbornová et al. (1990); Prach et al. (2007); Jirová et al. (2012)</td>
</tr>
<tr>
<td>18. Basalt quarries</td>
<td>NW</td>
<td>441</td>
<td>441</td>
<td>1–80</td>
<td>Novák &amp; Prach (2003); Novák &amp; Konvička (2006); Prach et al. (2013)</td>
</tr>
<tr>
<td>19. Limestone quarries</td>
<td>E</td>
<td>120</td>
<td>120</td>
<td>0–35</td>
<td>L. Tichý, unpublished data</td>
</tr>
</tbody>
</table>

*The corridors of the former Iron Curtain were created along the state border during the communist dictatorship. It was a fenced strip of land about 6 m in width, kept without vegetation by continuous mechanical disturbance and herbiciding. It was abolished in 1989.

(1) initial, 1–3 yrs; (2) early, 4–10 yrs; (3) middle, 11–25 yrs; (4) late, 26–40 yrs; (5) old, >40 yrs.

We carried out a detrended correspondence analysis (DCA) of these vegetation samples (phytosociological relevés) in the form of a matrix comprising 2392 samples and 951 species. Isolines, indicating the total number of species and the number of target species, were included into the resulting diagrams. They represent response surface fitted with a loess model (see Cleveland & Davlin 1988). Influence of the successional age as an explanatory variable of species composition was tested with a permutation test in canonical correspondence analysis (CCA), with 999 permutations. In the case of repeated sampling, plot identity and elsewhere the habitat type were used as covariables defining permutation blocks. Prior to the ordinations using the CANOCO application (Microcomputer Power, Ithaca, NY, USA), we logarithmically transformed the data and down-weighted rare species. The use of the unimodal methods was justified by the length of the gradient, which reached 8.96 SD units (see Lepš & Šmilauer 2003).

We classified target species according to Ellenberg et al. (1991) into the following categories representing: (1) dry open habitats (Festuco-Brometea, Trifolio-Geranietea, Sedo-Scleranthetea), (2) mesic and dump grasslands (Melio-Arphenatheretea, Nardo-Callunetea), (3) wetlands (Phragmitetalia, Oxyccoco-Sphagnetalia, Scheuchzerio-Caricetalia nigrae), (4) scrubs and woodlands (Rhamno-Prunetalia, Querco-Fagetalia, Quercteeta robori, Vaccinio-Piceetea). Target species included all Red List species (Prochážka 2001), including those affiliated with other habitats. Ruderals and weeds representing Bidentetea, Chenopodietea, Secalietea, Artemisietea, Agropyretea, Plantaginetea and Epilobietea (Ellenberg et al. 1991), and all alien species (Pyšek et al. 2012a,b), except Red List species (Danihelka et al. 2012; Grulich 2012), were considered as non-target, undesirable species.

Results

In the DCA ordination, individual seres are arranged along the first ordination axis ($\lambda = 0.727$), which approximately
reflects site moisture conditions (Fig. 1a). On the right side of the diagram are rather dry basalt and limestone quarries in relatively warm regions; on the left are wet peatlands, which are often found in mountainous areas. The second ordination axis ($k = 0.565$) reflects successional age, as is evident from the directions of the arrow in Fig. 1b. The correlation coefficient ($R$) between the successional age of samples and their score on the second ordination axis is $-0.839$ ($P < 0.001$). The successional age, as the only explanatory variable, explained 19.3% of variability of the vegetation data in the CCA ordination ($F = 22.25, P < 0.01$). The identity of the sere appeared non-significant in the CCA analysis ($F = 2.13, P = 0.072$).

Some of the envelopes, which enclose samples of a particular successional sere, spread broadly along the first ordination axis, thus comprising a wide range of dry to wet habitats (typically sand and gravel-sand pits, stone quarries or abandoned fields). Other envelopes were limited in their extent along the gradient, indicating rather homogeneous successional vegetation (typically bulldozed sites in forest destroyed by atmospheric pollution, emerged bottom of water reservoirs and urban ruderal sites, all represented only by one or a few localities). Most seres appeared in the centre of the first axis gradient. The fact that the envelopes largely overlap indicates that there are strong similarities among the seres, and the successional vegetation forms a continuum along the moisture gradient.

A comparison between Fig. 1a,b reveals that succession generally runs from stages composed predominantly of synanthropic species (i.e. ruderals and weeds, such as *Elytrigia repens*, *Cirsium arvense*, *Tussilago farfara*, *Artemisia vulgaris*, etc.), located in the upper part of the diagram in Fig. 1b, towards a woodland, represented by species in the bottom part of the diagram (e.g. *Quercus* spp., *Fraxinus*...
Species representing dry grasslands and other open and dry habitats (dry sandy or sunny rocky sites) appear on the right part of the diagram (e.g. Bromus erectus, Festuca rubra, Brachypodium pinnatum, and Sedum album), and species representing wetlands and wet grasslands are on the left (e.g. Eriophorum vaginatum, Molinia caerulea, Agrostis canina and Juncus effusus). Species representing mesic grasslands appeared in the centre of the diagram (e.g. Agrostis capillaris, Poa pratensis, Festuca rubra and Dactylis glomerata).

The total number of species exhibited a general tendency to increase or, in a few cases, remained more or less equal over the course of succession (Fig. 1c) or decreased (peatlands and forest clearings). The total number of species increased towards the dry end of the moisture gradient represented by the first ordination axis. High total numbers of species are typical of seres in dry and sunny habitats, namely alkaline stone quarries and the majority of the abandoned fields studied. The high numbers of target species were also present in stone quarries and abandoned fields (Fig. 1d). Seres started with the lowest number of target species in abandoned fields and at some of the mining sites. In peatlands the number of target species clearly decreased. At sites bulldozed following forest destruction by air pollution, in forest clearings and in corridors of the former Iron Curtain, the numbers of target species decreased only slightly. In all the other seres the numbers of target species increased. Comparing Fig. 1c,d, one can see that in the late stages the target species represent on average about three-quarters of the total number of species.

Discussion

The main direction of seres considered in this study is towards re-establishment of woodland, which is the typical potential vegetation in the study area (Neuhäuslová 2001; Chytrý 2012). Succession towards woodland is typical of areas with relatively humid climates (Walker & del Moral 2003), which includes Central Europe. Reed or sedge wetlands generally establish over the course of succession in the wettest sites, provided that the water table remains sufficiently high. These wet microhabitats are typically found in low areas of spoil heaps (Prach et al. 1999), sand and gravel-sand pits (Rehounková & Prach 2006), extracted peatlands (Konvalinková & Prach 2010), some stone quarries (Trnková et al. 2010), artificial fishpond islets (Rejmánek & Rejmánková 2002) and exceptionally in abandoned fields (Jírová et al. 2012). On the other hand, grassland or shrubby grassland usually develop at dry sites in stone quarries (Novák & Prach 2003; Tichý 2012), on spoil heaps (Prach 1987) or in abandoned fields (Jírová et al. 2012). Woody species also usually do not establish on shallow, rocky substrates in quarries (Novák & Prach 2003; Tichý 2012), on dry, sandy soils in certain sand and gravel-sand pits, depending on the climatic region (Rehounková & Prach 2006), or on sporadically toxic substrates (Kovář 2004). Both wetlands and grasslands are valuable from the point of view of nature conservation and restoration because many heliophilous species can establish and survive in such open habitats without being out-competed by taller woody species. The importance of such open habitats has been documented in detail – for plants, see papers cited in Table 1; for other organisms, mainly arthropods, see Beneš et al. (2003), Tropek et al. (2010), Rehounková et al. (2011) or Heneberg et al. (2013); Vojar (2006) reports that wetlands developed at former mining sites are crucial for the survival of amphibians in the Czech Republic.

The sites in this study formed a continuum along the moisture gradient, and site moisture appeared here to be more important for vegetation development than successional age. Unfortunately, it was technically impossible to measure site moisture over all the studied sites. Site moisture, temperature, nutrients, substrate structure and acidity are most frequently reported, beside successional age, as the most important environmental factors determining the course of succession (Walker & del Moral 2003). For Central European seres, including some of those considered in this study, the macro-climate and soil pH were identified as significantly influencing the development of vegetation (Prach et al. 2007). Regional and local species pools, in addition to site conditions, influence community species pools in general (Zobel et al. 1998) and the participation of species in succession in particular (Rehounková & Prach 2008).

The majority of the seres can be considered as primary succession, a few as secondary succession (abandoned fields, forest clearings) or exhibiting features of both (artiﬁcial fishpond islands and barriers). In a previous study (Prach et al. 2001) we showed that primary vs secondary status of seres did not have a signiﬁcant effect on the course of succession, thus, we did not consider this status as a factor in the present paper.

Our seres, representing a range of initial site conditions, exhibited mostly increasing trends in the total numbers of species and target species, a pattern usually found especially in primary seres (Walker & del Moral 2003). The number of target species is perhaps a more important characteristic in ecological restoration than the total number of species (Van Andel & Aronson 2012). From the restoration point of view, species numbers are a more relevant indicator in older stages than in more ephemeral initial stages. Between the initial and older stages, species richness usually fluctuates, with minima being reached when strong competitors dominate (Peet 1978). Competitive exclusion
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is typically more common in secondary rather than in primary seres (Glenn-Lewin et al. 1992). Our Fig. 1c,d only include general trends between the youngest and the oldest successional stages. Moreover, the seres differ in the time over which succession was recorded, and some seres were sampled in plots of somewhat different size, i.e. by 10–25 m². Plot size can influence the absolute number of species but is not likely to effect overall trends (Chytrý 2001). In our case, the regression of the number of species on the size of sampling plots was not significant ($R = 0.12$, $P > 0.05$, $n = 2392$). Extracted peatlands are an exception among our seres because they exhibited a clear decrease in both number of total and target species over time. This pattern is probably caused by competitive exclusion under a dense canopy of woody species, which forms gradually, and/or an expansion of a strong dominant in the herb layer in later successional stages, e.g. *Phragmites australis* or *Molinia caerulea* (Konvalinková & Prach 2010).

The establishment of a continuous vegetation cover occurred within 1–15 yrs in all seres (see also Prach & Pyšek 2001; Řehounková et al. 2011), with its fastest formation in secondary seres, especially in abandoned fields (Osbornová et al. 1990). Heavily eroded, stony, toxic or exposed sites represent exceptions (Řehounková et al. 2011), but such sites were not sampled in our study. In Central Europe it usually takes ca. 25 yrs of succession to reach (semi)-natural vegetation, usually woodland, which subsequently changes little in species composition (Prach 2003). Thus, the establishment of woodland does not necessarily need to be aided by planting trees, as is often practised in many disturbed sites subjected to technical reclamation. Quite the contrary: it is sometimes desirable from the ecological point of view to slow down the establishment of a woodland by grazing or by felling trees and removing shrubs because open habitats are often more valuable than wooded ones for biodiversity (Řehounková et al. 2011). Only a slightly manipulated natural succession (Lukén 1990) or completely spontaneous succession should therefore be preferred over technical reclamation in the habitats that we studied. Compared to technical reclamation, spontaneous succession results in the development of more diverse plant communities with species composition closer to that of (semi)-natural vegetation (Hodačová & Prach 2003), and represents a cheaper option (Řehounková et al. 2011).

Restoration ecologists are sometimes worried about invasions of alien species if a site is left to spontaneous development. This is certainly justified in some parts of the world (e.g. Lukén 1997; Flory & Clay 2010; Saccone et al. 2010). In our case, the only alien species that may become a serious invader during succession in disturbed habitats is the black locust (*Robinia pseudacacia*), especially in certain sand and gravel-sand pits and stone quarries in dry and warm regions. Even at these sites, it was only observed if an invasive population occurred within ca. 100 m (Řehounková & Prach 2008). This species usually forms dense, species-poor stands dominated by nitrophilous species in the herb layer, which is not acceptable from the restoration point of view (Kowarik 1992; Pyšek et al. 2012a,b).

We conclude that spontaneous vegetation succession appears to be a suitable means of ecosystem restoration for disturbed sites under Central European conditions.

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**Supporting Information**

Additional supporting information may be found in the online version of this article:

**Appendix S1.** List of species names used in Fig. 1b.