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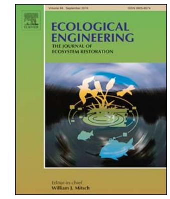

Spontaneous establishment of woodland during succession in a variety of central European disturbed sites

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A B S T R A C T

The aim of this work was to answer the question wheather woodland can be established spontaneously in a variety of disturbed sites. We analyzed 10 successional series lasting at least 80 years which were located across the Czech Republic, central Europe. The woody species were classified into early and late successional species. Species typical for the respective potential natural vegetation described for Czech woodland were considered as late successional while all the other species were classed as early successional. Data were processed using multivariate analyses and GLM. Cover and the number of woody species gradually increased during succession, and woodland established spontaneously in all series. The relative cover of early successional species reached its peak on average after 40–50 years of succession or gradually decreased in the model since the first year of site abandonment while that of late successional species gradually increased. However, the series largely differed and some of them did not follow the trends. *Betula* spp. (early) appeared to be by far the most frequent colonizer followed by *Pinus sylvestris* (late). Spontaneous establishment of woodland can be an effective method for ecosystem restoration in a range of disturbed sites within central Europe. Proportion of alien species was mostly low.

1. Introduction

The establishment of potential natural vegetation may represent a theoretical goal of restoration efforts in disturbed sites (Siles et al., 2010). Closed woodland represents the expected potential natural vegetation in sufficiently wet (usually over 400 mm of annual precipitation) temperate zones of the world (Archibold, 1995). If we adopt spontaneous succession as a convenient restoration measure (Prach and Pyšek, 2001; Walker et al., 2007), successful establishment of woody species in disturbed sites is a crucial step indicating gradual woodland recovery (Prach and Pyšek, 1994; Wright and Fridley, 2010). Shrubs and trees markedly change not only the physiognomy but also many ecological functions and services as well as aesthetic aspects of a colonized site (Walker et al., 2007). However, colonization of disturbed sites by woodland species through natural processes should not always be considered as a restoration target. Formation of a closed canopy of woody species may reduce the presence of rare heliophilous species in the understory. Moreover, the establishment and spread of not every woody species indicate establishment of a desirable woodland, for example in the case of site infestation by invasive alien woody species usually spreading from the close surroundings (Řehounková and Prach 2008). Woodlands dominated by alien species often exhibit low species diversity, low understory cover, and support generalists (Richardson and Rejmánek 2011). Some native, competitive strong early successional woody species may exhibit analogous effects (Dovciak et al., 2005). Despite these limitations, spontaneous restoration of woodland in disturbed sites may provide a cost-effective alternative to artificial afforestation, which is usually preferred especially in human-disturbed sites (Tischew and Lorentz, 2005). Such afforestation mostly consists of monocultures of woody trees which exhibit low natural value (Woziwoda and Kopeć, 2014; Šebelíková et al.,2015). Afforestation, for example, of spoil heaps from brown-coal mining in the Czech Republic costs up to 80,000 USD per hectare (Starý et al., 2014), which is in contrast to the virtually zero expense if the site is left to natural regeneration.

Although the establishment of woody species in succession has been studied many times in various series (Walker and del Moral, 2003), broader quantitative analyses comparing a higher number of series are still rare (Prach, 1994; Prach and Pyšek 1994; Wright and Fridley, 2010). The previous studies usually did not distinguish between early and late successional woody species (Fridley and Wright, 2012) except Smit and Olff (1998) Tischew and Lorentz (2005). The two groups of woody species may play a different role in succession (Walker and del Moral, 2003) and only the late successional woody species indicate

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restoration of the respective potential natural vegetation which best corresponds to the environmental site conditions (Somodi et al., 2012). Some authors question the concept of potential natural vegetation arguing that its delineation is vague and the species composition of vegetation itself, i.e. the whole community, has always been changing under a changing environment, including the present global change (Carrión, 2010). Moreover, the usefulness of potential natural vegetation as a surrogate for the endpoint of succession has also been questioned (Chiarucci et al., 2010). To overcome these limitations, in this study we considered not the whole community, i.e. the type of potential natural vegetation, but the participation of particular woody species which characterize it.

In this paper, we advanced further than in our previous studies (Prach, 1994; Prach and Pyšek, 1994) by including more series sampled for a longer time, and considering early and late successional species. This much more robust analysis enabled us to ask the following particular questions: (a) How do the number and cover of woody species change over the course of succession? (b) How do early and late successional woody species differ in their participation during succession? (c) Which woody species are the most successful in colonizing disturbed sites?

2. Methods

We analyzed 10 different successional series which lasted at least 80 years. These included successions running in sand and gravel-sand pits, extracted peatlands, burnt forests, artificial fishponds islands and barriers, acidic, basalt and limestone quarries, different types of spoil heaps from black coal mining and abandoned fields (see Table 1 for characteristics and references). The series occurred over nearly the whole Czech Republic (latitude 49°38′38"- 50°06′0", longitude 12°16′0–18°26′11"). A total of 2359 samples recorded in differently aged stages were available. The particular series differed in the number of samples, the number of sampled sites, the geographical area in which they occurred and successional age (Table 1, Prach et al., 2014). The differences in these characteristics resulted from the availability of successional stages and our capacity to sample them.

Phytosociological relevés of 16–450 m^2 in size were placed in the centre of each homogeneous stage. All vascular plants present in each sample plot were identified and their percentage cover was estimated visually (Kent and Coker, 1992). The cover and number of woody species was not dependent on the area of the vegetation records (corr. coef. 0.21, resp. 0.26, p-values = 0.34, resp. 0.41), therefore the differences in sizes of vegetation records were not further considered. All of the series occurred in places directly disturbed by humans, mainly by mining activities. All the series started on bare ground. Some series were sampled by the authors, while others were extracted from published or unpublished sources (see Table 1 and Prach et al., 2014). The age of the successional stages was determined, because the year of each site creation was known. The full data set was used in the ordination analysis (see below).

We are aware several limitations (Johnson and Miyanishi 2008) using the space-for time substitution, i.e. chronosequences (Pickett,1989; Walker et al., 2010). In our study, it was not feasible to establish and long-term monitor hundreds of permanents plots (Table 1) across the country, thus the space-for-time approach was the only one possible. This approach was further justified by selection of broad structural parameters such as total species richness and plant cover providing similar trends both in permanent and chronosequenced plots as documented by Myster and Malahy (2008).

The whole dataset was geographically stratified (within a grid of 0.37.5′ × 0.625′ or 0.7 × 0.65 km), thus obtaining the total number of grid cells (n = 469) with particular samples present in a given cell. From each grid cell only two samples were randomly selected using generator of chance numbers and selected altogether 938 samples from the whole datasets, i.e. 2359 samples. In this way, the effect of replicated occurrence of species in permanent plots or at closely located sites was restricted.

Woody species were extracted from the data set and divided into early and late successional woody species in the following way: We identified the potential natural vegetation corresponding to each of the sampling sites, i.e. each sampling site was located in the map of potential natural vegetation (Neuhäuslová, 2001) in the Geoportal application: https://geoportal.gov.cz/web/guest/wms/. Then, we extracted all species listed as diagnostic, constant or typical for the respective potential natural vegetation described in the complete survey of woodland vegetation in the country (Chytrý, 2013). These species were considered as late successional while all the other species were classed as early successional. For this study, two common species, i.e. *Betula pendula* and *B. pubescens*, were combined due to their hybridization and difficult identification at the seedling stage. The same was done for *Crataegus* species, *Rubus fruticosus* agg., and for *Populus nigra* and its hybrid (*P.* × *canadensis*). For each woody species, we calculated the percentage cover reached in all sampled plots.

Table 1
Main characteristics of the successional series under study. Each series is referred to by its number (1–10) in the text and the figures. The numbers in parentheses refer to database before stratification.

Sere	Location in the Czech Republic	Number of samples	Number of localities	Age of stages [years]	Data sources and References
1. Extracted peatlands	SW	84 (267)	18	1–100	Konvalinková and Prach, 2010; Bastl et al., 2009
2. Burnt forests	NW	41 (52)	35	1–168	Adámek et al. (2015)
3. Artificial fishponds islands and barriers	S	46 (108)	23	1–126	Prach, unpublished; Študent, unpublished; Rejmánek and Rejmánková (2002)
4. Spoil heaps from black coal mining I	Central	30 (88)	9	1–100	Dvořáková, unpublished; Prach et al. (2013)
5. Sand and gravel-sand pits	Various parts	106 (233)	36	1–80	Řehounková and Prach (2006); Řehounková and Prach (2008); Řehounková and Prach (2010)
6. Acidic stone quarries	Central	85 (135)	39	1–86	Trnková et al. (2010)
7. Spoil heaps from black coal mining II	NE	49 (182)	30	1 − 80	Koutecký, Prach, unpublished
8. Limestone quarries	E	102 (120)	45	1–89	Tichý, Sádlo, Bartošová, unpublished
9. Abandoned fields	Various parts	173 (288)	164	1–91	Prach et al. (2007); Osbornová et al. (1990); Jírová et al. (2012)
10. Basalt quarries	NW	152 (http://10.10.23.110:8080/TDXPSLIVELATEX02/gateway/elsevierjournal/index.jsp#441)	67	1–80	Novák and Prach (2003)