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Spontaneous vegetation succession in human-disturbed habitats: A pattern across seres

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Abstract. Vegetation samples from 15 successional seres in various disturbed habitats in the western part of the Czech Republic were analysed to detect possible trends. For particular seres, data on species cover were available from the onset to 10-76 yr of succession. All seres started on bare ground. Species which attained at least 1% cover in any sere in any year were used as input data for Canonical Correspondence Analysis, assessing the effect of time as the environmental variable, for Detrended Correspondence Analysis and TWINSPAN classification. Two distinct groups of seres were distinguished: '*ruderal*', occurring in agricultural, industrial or urban landscapes altered by men, usually on fertile sites; and '*non-ruderal*', occurring in less altered, mostly forested landscapes, usually on acid, nutrient-poor and wetter soils. The former type of succession starts with ruderal annuals, being followed by ruderal perennials. In the latter case non-ruderal clonal perennials prevail from the onset of succession. The landscape frame is emphasized, beside site environmental conditions, as influencing the type of succession. The character of species attaining dominance in succession, participation of dominant woody plants and the character of late successional stages, i.e. features important from the point of view of potential restoration of human-disturbed habitats, are discussed.

Keywords: Dominant; Landscape character; Restoration ecology; Ruderal plant; Site condition; Woody species.

Nomenclature: Rothmaler (1986).

Introduction

Spontaneous successional processes are an important aspect of ecological restoration because they often determine the type and timing of restoration measures used and affect the final success. Therefore, spontaneous succession should be taken into account in virtually any restoration program. Results of both spontaneous processes and restoration measures are usually intermingled and influence each other (Luken 1990). In some restoration programs we can completely rely on spontaneous succession. To recognize the role of spontaneous succession in particular restoration programs we need (1) respective case studies and (2) comparative studies providing information on general trends, limits, and possibilities of spontaneous processes (Prach et al. 2001).

Many individual successional seres have been described, often in great detail (e.g. Burrows 1990; Glenn-Lewin et al. 1992). However, little attention has been paid to quantitative analyses of the pattern of succession over more seres in a large region, the main reason for this being the lack of available data. We used this approach in our previous studies comparing 15 different seres in central-European man-made habitats with respect to various successional characteristics, such as the rate of succession (Prach et al. 1993), pattern of changes in species traits (Prach et al. 1997), role of woody plants (Prach & Pyšek 1994) and the pattern of achieving dominance in succession (Prach & Pyšek 1999). For practical applications, with the aim of restoration, a predictive expert system was built (Prach et al. 1999).

The present paper will (1) analyse the same data set, focusing on dominant species which determine the pattern of succession and hence are most relevant from the restoration viewpoint, (2) search for general patterns among of spontaneous succession seres and (3) discuss implications of such patterns for restoration of disturbed habitats by means of spontaneous processes.

Material and Methods

Study sites and sampling

All the seres started on bare ground immediately following a disturbance, and were all located in the western part of the Czech Republic. In some seres permanent plots (usually 5 m × 5 m) were established immediately after the creation of a site and sampled more or less annually, especially in the early stages of succession. In other seres, permanent plots were established in comparable stages but of different ages and the course of succession was inferred by comparison. These plots were also sampled at regular intervals and both approaches were later combined. Percentage values of species cover were estimated visually in the period of maximum vegetation development (between June and September). The period of time for which succession data were available ranged from 10 to 76 yr. A brief description of the studied seres (1 to 15) follows. Frequency of sampling in the particular seres is evident from App. 1. For more detailed information on particular seres see Prach et al. (1997), Prach & Pyšek (1999) and the data sources given below. The abbreviations of the seres are given (used hereafter in the paper) together with the age of the sere in years. The oldest stages are characterized by dominant species.

1 – 3. Old-fields in the Bohemian Karst area near Prague. Three seres were distinguished according to soil moisture conditions: xeric (**Ox**, 76), mesic (**Om**, 57), wet (**Ow**, 32). The oldest xeric stage was dominated by the grasses *Festuca rupicola* and *Poa angustifolia*, with few shrubs (*Crataegus* spp., *Rosa* spp.). In the mesic sere, *Crataegus* spp. formed a dense cover and *Fraxinus excelsior* started to form a viable population in the understorey. In the wet site, *Phragmites australis* expanded after 25 yr. Data source: Osbornová et al. (1990) and K. Prach (unpubl.).

4 – 6. Ruderal urban sites in the town of Plzeň. Three particular seres were distinguished according to the nutrient status of the substratum: nutrient poor, mineral (**Up**, 12) finally dominated by grasses (*Agropyron repens* and *Calamagrostis epigejos*); moderate in nutrients, mineral (**Um**, 12) later dominated by woody species (*Sambucus nigra, Salix caprea, Populus tremula, Betula pendula*) with *Artemisia vulgaris* and *Epilobium angustifolium* prevailing in the ground layer; and nutrient rich, organic (**Ur**, 12) with *Sambucus nigra, Aegopodium podagraria* and *Urtica dioica* in the ground layer. Data source: Pyšek (1978).

7 – 8. Large spoil heaps from open-cast brown coal mining in the Most region, NW Czech Republic. Two seres were distinguished: on tops and slopes of hills and in shallow depressions between them (**Sh**, 38) later dominated by *Calamagrostis epigejos* and *Arrhenatherum elatius* with scattered shrubs and trees (especially *Betula pendula* and *Sambucus nigra*) and in wet, deep depressions (**Shw**, 38) where *Phragmites australis* finally prevailed. Data source: Prach (1987 and unpubl.).

9. Exposed bottom of a destroyed water reservoir in the Most region, NW part of the country (**Eb**, 12). *Calamagrostis epigejos* expanded early and formed dense cover with scattered *Betula pendula*. Data source: T. Frantík, J. Osbornová & K. Prach (unpubl.)

10. Sand pit abandoned after sand and gravel extraction (**Sp**, 24), in the Třeboň Basin in the southern part of the country. *Pinus sylvestris* established very early, forming a compact woodland with forest herbs gradually expanding. Data source: P. Kořár & K. Prach (unpubl.).

11 – 12. Dumps around a newly constructed fishpond formed by sandy subsoil (**Ds**, 15) or organic, peaty topsoil (**Dp**, 15) in the Třeboň Basin in the southern part of the country. In the former site, a more or less closed woodland with *Pinus sylvestris* and *Betula pendula* gradually formed with a sparse herb layer, in the latter sere *Alnus glutinosa, Frangula alnus* and *Betula pendula* prevailed with *Phalaris arundinacea* in the understorey. Data source: K. Prach (unpubl.).

13. Peatland abandoned after peat extraction and drainage (**Pe**, 10) in the Třeboň Basin in the southern part of the country. Succession ran to an open woodland with *Betula pendula, Pinus sylvestris* and *Salix* spp. Data source: M. Bastl (unpubl.).

14 – 15. Bulldozed sites in areas of former *Picea abies* plantations deforested due to air pollution in the Krušné hory Mts on the NW border of the country. To make replanting easier the sites were scraped creating plots with no grass cover or topsoil (**Bp**, 20) and mounds formed by the dumped material (**Bm**, 20). In both sites, *Calamagrostis villosa* and *Deschampsia flexuosa* expanded with rare occurrence of *Betula pendula*. Data source: Pyšek (1992 and unpubl.).

Data analysis

Phytosociological relevés from each year of each sere were used as input data for ordination, yielding a matrix of 177 samples and 247 species (mean cover values were calculated from relevés taken in the same stage in the same year, and these 'pooled' relevés were used in the matrix). Species with cover less than 1 % in any relevé were excluded. Ordinations were performed using logarithmically transformed species percentage cover values. Each relevé was characterized by its age (determined by the year since the onset of succession in which the relevé was made) as an environmental variable. Because data for stages older than 20 yr were not available for all seres, relevés from stages > 20 yr old were considered 20 yr of age for the purpose of statistical analysis. This may be justified by the fact that beyond this age vegetation cover had usually stabilized and mostly only quantitative changes in species cover occurred after then, without replacement of dominant species. Data were analysed by Canonical Correspondence Analysis (CCA), Detrended Correspondence Analysis (DCA) and divisive numerical classification, using CANOCO for Windows software (ter Braak & Šmilauer 1998) and TWINSPAN (Hill 1979). Significance was tested by the distribution-free Monte Carlo test (1000 permutations). In the Monte Carlo test, the distribution of the test statistics under the null hypothesis is generated by random permutations of cases in the environmental data (for details see ter Braak & Šmilauer 1998).

Results

Results of the CCA ordination are presented in Fig. 1. The first axis ($\lambda_1 = 0.434$) reflects the development of particular seres in time, the only environmental variable included, and accounted for 3.3 % variance in the data set. Monte Carlo permutation test for the first axis was highly significant ($P = 0.001$, $F = 7.308$).

Arrows indicating the directions of succession in particular seres were fitted by connecting centroids of relevés from the years 1 to 5 with positions of relevés representing the oldest stage in the given sere. The centroids were considered to better represent the initial stages than year 1 because of high variability in species composition and fluctuations usually associated with low cover in the first years of succession. Positions of dominant species, disregarding the extent to which they fit the model, are indicated in the ordination diagram.

The seres were clearly arranged along the second axis ($\lambda_2 = 0.829$), forming two distinct groups. In the lower part of the ordination space there is a group of seres from urban, industrial or agricultural landscapes. They usually start with ruderal annuals or biennials (*Atriplex nitens*, *Arctium tomentosum*, *Carduus acanthoides*, *Chenopodium* spp., *Melilotus alba*, *Sisymbrium loeselii*) followed by perennial ruderals such as *Agropyron repens*, *Artemisia vulgaris*, *Cirsium arvense*, *Tanacetum vulgare* and *Urtica dioica*. These may be called **'ruderal successions'**.

The other group, located in the upper part of the diagram, is represented by seres which usually occur in less disturbed, mostly forested landscapes. These sites are characterized by higher soil moisture, lower nutrient levels and lower pH than the former group. Succession in these seres does not usually start with dominant ruderals but with clonal, moisture demanding species such as *Carex gracilis*, *Galium palustre*, *Glyceria fluitans* and *Juncus effusus* or, at drier sites, *Rumex acetosella* with occasional occurrence of annuals such as *Polygonum lapathifolium*, *P. persicaria* and *Rumex maritimus*. We called this group of seres **'non-ruderal successions'**. Seres from wet old-fields and wet sites on spoil heaps fell between these groups but we have considered them as ruderal by their character.

Later successional stages in both groups of seres are usually dominated by grasses and scattered trees or shrubs. *Agropyron repens* (Up), *Arrhenatherum elatius* (Sh, Om), *Festuca rupicola* (Ox) or *Holcus lanatus* (Sh) are typical of xeric or mesic sites. In wet sites, *Phragmites australis* often forms a dense cover (Shw, Ow) while *Calamagrostis villosa* and *Deschampsia flexuosa* dominate in mountainous regions (Bm, Bp).

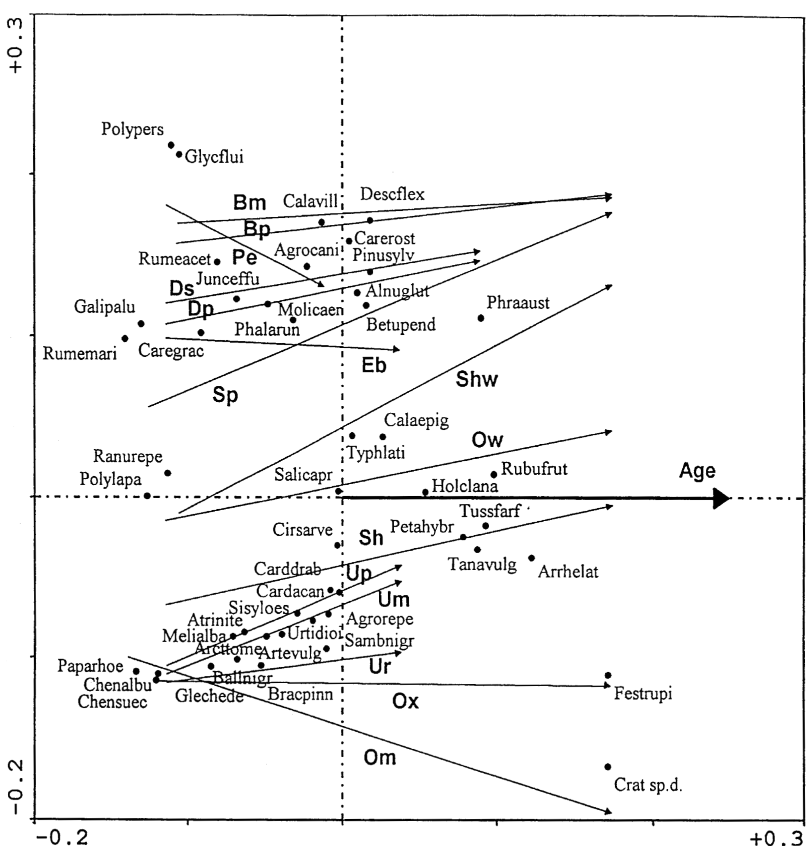

Fig. 1. Canonical Correspondence Analysis of relevés from all 15 successional seres taking the successional age (time from the onset of succession) as the only variable. Relevés from sites with succession running longer than 20 yr were considered 20 yr old. Dominant species (those that attained dominance in at least one sere in at least one year sampled) are displayed; arrows indicate successional direction of particular seres. Abbreviations of species names use the first four letters of the genus and species names. The species are listed in App. 1. Bm = bulldozed mounds; Bp = bulldozed plots; Dp = dumps peaty; Ds = dumps sandy; Eb = exposed bottom; Om = old-fields mesic; Ow = old-fields wet; Ox = old-fields xeric; Pe = peatland; Sh = spoil heaps; Shw = spoil heaps wet; Sp = sand pit; Um = urban moderate; Up = urban poor; Ur = urban rich.

However, the most common species in later successional stages is *Calamagrostis epigejos*, which forms a dense cover in several seres ranging from wet exposed bottom of the water reservoir to drier spoil heaps (Eb, Pe, Up, Sh) with some occurrence in most other seres. The most common woody species of late successional stages is *Betula pendula* (Pe, Ds, Eb, Sh, Um), followed by *Sambucus nigra* (Ur, Um, Om, Sh) and *Pinus sylvestris* (Sp, Ds, Pe) (see also Prach & Pyšek 1994). Woody species formed more or less a closed cover in the abandoned sand pit, extracted peatland, on dumps around the new pond (mostly *Pinus sylvestris* and *Betula pendula*) and in mesic old-fields (a specific case with dominating *Crataegus* spp.). Indirect gradient analysis (DCA) clearly arranged both samples and species along the first axis representing the two, clearly separated groups of seres described above, i.e. 'ruderal' and 'non-ruderal'. No other gradients, including successional age, were recognized which indicates that differences in species composition among the seres were much more important than differences within seres caused by successional change. As essentially the same information was obtained by CCA and DCA, graphical outputs of DCA are not presented.

Results of TWINSPAN classification are presented in Fig. 2, giving the clusters corresponding with the two groups of seres distinguished above. Species having the greatest significance in the clustering are presented in the figure. Within both main clusters we can tentatively distinguish clusters of seres running on more fertile sites with deeper soil, and clusters of seres on shallow and less fertile soils. Indicator species which can be considered as ruderals are present exclusively in the cluster of 'ruderal' seres. It is interesting to see the later successional stages on wet spoil heaps, and one late stage of wet abandoned fields falling into the cluster of 'non-ruderal' seres. This corresponds well with the intermediate position of the respective successions in the ordination diagram, as well as with our field experience according to which the seres apparently start with ruderals but later appear closer to the non-ruderal course.

The list of species which dominated in particular relevés, i.e. attained the highest cover value in the given seres and year, is presented in App. 1.

Discussion

The results presented here have implications for restoration ecology and management of disturbed sites. They demonstrate, as well as the anticipated role of site environmental conditions, the importance of the character of the landscape surrounding the site to be restored. Landscape character must be seriously considered in any restoration effort (Brand & Parker 1995; Bakker et al. 1998). If a site is located in heavily altered landscapes such as those with prevailing intensively used arable land and industrial or urban situations, ruderal plants can be expected to be of great importance. These species may even eventually arrest succession for a long time which is often the case with *Calamagrostis epigejos*, a species forming dense compact cover rarely outcompeted by other plants. In less altered landscapes with a higher representation of forests and especially in wetter regions, the aggressive ruderals generally occur with lower frequency and are less important in succession. Apparently, the regional species pool, i.e. sources of diaspores and colonization potential of species play a role in this respect (Van der Valk 1992; Strykstra et al. 1998; Zobel et al. 1998).

The environmental conditions of a site represent

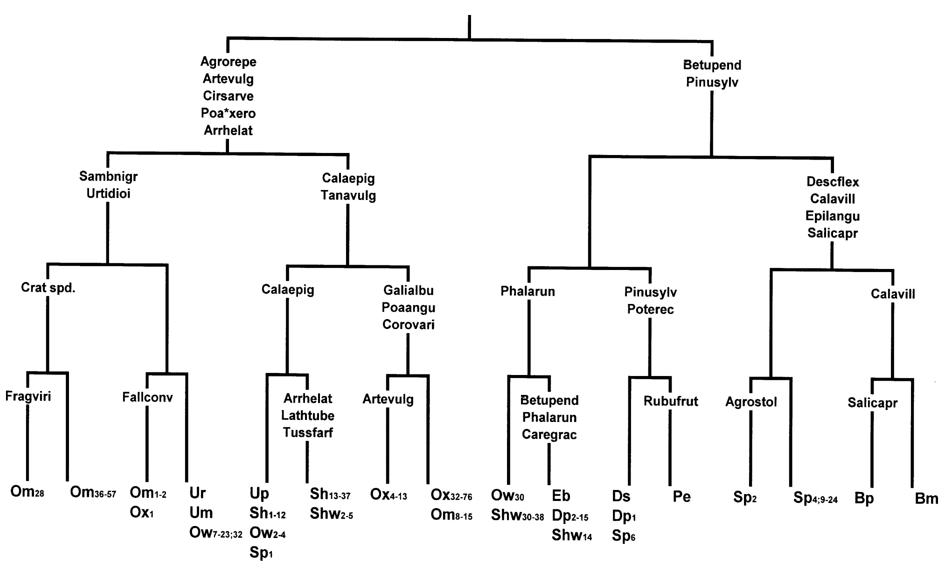

Fig. 2. Dendrogram based on a TWINSPAN analysis of the phytosociological relevés. Differential species are indicated. Numbers after the sere abbreviations (see Fig. 1) indicate the successional age of the respective samples. For full species names see App. 1. The differential species not listed as dominants in App. 1 are *Agrostis stolonifera, Coronilla varia, Epilobium angustifolium, Fallopia convolvulus, Fragaria viridis, Galium album, Lathyrus tuberosus, Poa angustifolia, Poa palustris* ssp. *xerotica, Potentilla erecta.*

other important variables determining the rate and directions of spontaneous succession, and must inevitably be considered in potential restoration programs. Of these, site moisture and nutrient availability are amongst the most important (Tilman 1988). However, there are many methodological obstacles to making comparisons of distant sites, especially when moisture conditions are concerned. Thus, we are still not able to analyse exactly the gradients in our data set. In our seres, participation of ruderal species is most apparent at sites which are nutrient-rich, less acidic and exhibit moderate to dry moisture conditions in accordance with general expectations (Grime 1979). By evaluating the expansion of woody species, which is often crucial for restoration, it appears that establishment tended to be easier under moderate environmental conditions and retarded in extreme habitats such as very dry, very wet or very acidic (Prach & Pyšek 1994).

Landscapes with prevailing nutrient-poor, acidic and often wet soils have been less intensively used for arable land, are less inhabited and remain more forested. Thus, both aspects considered here as decisive for the course of spontaneous succession, i.e. the character of surrounding landscape and environmental site conditions, are mutually linked.

Dominant species (see App. 1) exhibit a wide variation of life history traits and characteristics (Brown 1992; Rösch et al. 1997). However, a previous study of species capable of attaining dominance (Prach & Pyšek 1999) has shown that some characteristics favour dominance more than others. An 'ideal successional dominant' of disturbed habitats is a tall, wind-pollinated plant, often a geophyte capable of intensive lateral spread, requiring high nutrient supply and sufficient site moisture. However, the pattern of dominant species in the ordination diagram (Fig. 1) does not relate to these characteristics.

In this study, no recognizable differences in the pattern of succession and division of seres into 'ruderal' and 'non-ruderal' groups were found between seres that can be classified as primary or secondary succession. This corresponds to results of previous studies (Prach & Pyšek 1994; Prach et al. 1997) and indicates that primary or secondary status probably does not determine the course of succession (see also Glenn-Lewin et al. 1992; van Andel et al. 1993). Another trend seems to be apparent from Fig. 1, namely the prevailing divergence among the 'ruderal' seres and convergence among the 'non-ruderal' seres. However, we consider our data insufficient to make any firm conclusions.

It can be concluded that the comparative study of 15 successional seres in disturbed habitats within a larger region showed some general trends which might be considered useful when evaluating potential habitat restoration. It is evident that the 'non-ruderal' course of succession is generally more acceptable from the perspective of restoration ecology. It must be considered that the variability of succession in man-made habitats is very large (Walker & Chapin 1987; Pickett et al. 1987; Glenn-Lewin et al. 1992) and specific restoration programs must be based on detailed knowledge of the course of succession in particular habitats and ecological situations. However, the approach presented here can provide a framework in which spontaneous vegetation succession can operate as a part of the restoration process. Indeed, we expect that distinguishing 'ruderal' and 'non-ruderal' successional seres is, in principle, also applicable in other regions.

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App. 1. List of species which dominated in at least one sere in at least one year (the years when the species dominated are indicated by numbers following the abbreviation of the seres). Note that the years given reflect the years in which the vegetation was sampled.

Species	Sere abbreviation and year
Agrostis canina	Pe 10
Agropyron repens	Ox 6,8
Alnus glutinosa	Dp 15
Arctium tomentosum	Ow 7
Arrhenatherum elatius	Om 15; Ox 13,32; Sh 21,24,25, 26, 27, 28,29,30,31,32,33
Artemisia vulgaris	Ox 4; Sh 8,9,10,11; Um 4,5,6,7,8,9,10,11
*Atriplex nitens**	Sh 6,7
Ballota nigra	Ur 5,6
Betula pendula	Ds 11,12,13,14,15
Brachypodium pinnatum	Om 8
Calamagrostis epigejos	Ds 4,5,7,8,9,10; Eb 4,5,6,7,8,9, 10,11,12; Sh 12,18,19,37; Sp 1; Up 10,11,12
Calamagrostis villosa	Bm 1,4,5,6,10,15,20; Bp 1,4,5,6
Cardaria draba	Sh 3,4,5
Carduus acanthoides	Sh 12
Carex gracilis	Eb 2
Carex rostrata	Pe 10
Chenopodium album	Up 1,2,3; Ur 1,2,3
Chenopodium suecicum	Um 1,2,3
Cirsium arvense	Om 1; Ow 1
Crataegus spp.	Om 28,36,47,54,57
Deschampsia flexuosa	Bp 10,15,20; Sp 4
Festuca rupicola	Ox 55,67,74,76
Galium palustre	Dp 1,2
Glechoma hederacea	Om 2
Glyceria fluitans	Pe 2,4
Holcus lanatus	Sh 13,14
Juncus effusus	Eb 3; Pe 10
Melilotus alba	Up 6
Molinia caerulea	Ds 1,2,3; Pe 8
Papaver rhoeas	Ox 1
Petasites hybridus	Ow 13,23
Phalaris arundinacea	Dp 3,4,5,7,8,9,10,11,12,13,14
Phragmites australis	Ow 30,32; Pe 10; Shw 14,30,38
Pinus sylvestris	Sp 6,9,12,18,21,24
Polygonum lapathifolium	Sh 1,2
Polygonum persicaria	Pe 4
Ranunculus repens	Ow 2,4,5
Rubus fruticosus	Pe 6
Rumex acetosella	Pe 3; Sp 2
Rumex maritimus	Eb 1
Salix caprea	Um 12
Sambucus nigra	Ur 11,12
Sisymbrium loeselii	Up 4,5
Tanacetum vulgare	Sh 15,16; Up 7,8,9
Tussilago farfara	Shw 2
Typha latifolia	Shw 5
Urtica dioica	Ur 4,7,8,9,10

*(= *A. sagittata* Borkh.)