Journal of Vegetation Science 17: 583-590, 2006
© IAVS; Opulus Press Uppsala.

Spontaneous vegetation succession in disused gravel-sand pits: Role of local site and landscape factors

Řehounková, Klára[1*] & Prach, Karel[1,2]

[1]*Department of Botany, Faculty of Biological Sciences, University of South Bohemia, Na Zlaté stoce 1, CZ-370 05 České Budějovice, Czech Republic,* [2]*Institute of Botany, Academy of Sciences of the Czech Republic, Dukelská 143, CZ-37982 Třeboň, Czech Republic, E-mail prach@bf.jcu.cz;* [*]*Corresponding author; E-mail ms_cora@hotmail.com*

Abstract

Questions: What is the variability of succession over a large geographical area? What is the relative importance of (1) local site factors and (2) landscape factors in determining spontaneous vegetation succession?

Location: Various regions of the Czech Republic, Central Europe. The regions represent two categories characterized by agrarian lowlands, with a relatively warm and dry climate, and predominant woodland uplands with a relatively cold and wet climate.

Methods: Gravel-sand pits ranged in age from 1-75 years since abandonment. Three types of sites were distinguished: dry, wet and hydric in shallow flooded sites. Vegetation relevés were recorded with species cover (%) visually estimated using the space-for-time substitution approach. Local site factors, such as water table and soil characteristics, and landscape characteristics, namely climatic parameters, presence of nearby (semi-) natural plant communities and main land cover categories in the wider surroundings, were evaluated.

Results: Ordination analyses showed that water table was the most important local site factor influencing the course of spontaneous vegetation succession. Succession was further significantly influenced by soil texture, pH, macroclimate, the presence of some nearby (semi-) natural communities and some land cover categories in the wider surroundings. Spontaneous vegetation succession led to the formation of either shrubby grassland, deciduous woodland, *Alnus* and *Salix* carrs, and tall sedge or reed and *Typha* beds in later stages depending predominantly on the site moisture conditions.

Conclusions: Although the water table was the most influential on the course of vegetation succession, the landscape factors together explained more vegetation variability (44%) than local site factors (23%).

Keywords: CCA; Czech Republic; DCA; Environmental factor; Ordination; Space-for-time substitution; Water table.

Nomenclature: Kubát et al. (2002).

Introduction

In contrast to the innumerable papers that describe a particular successional sere in a particular site or several nearby sites, there are surprisingly few studies that have examined one type of spontaneous vegetation succession at large landscape or country scales. Successional studies have been conducted at these scales on sites disturbed by extraction including stone quarries (Ursic et al. 1997; Cullen et al. 1998; Novák & Prach 2003), gravel pits (Borgegård 1990) and dumps and wastes (Skousen et al. 1994; Wiegleb & Felinks 2001). The use of permanent plots is the best method to study long-term changes in vegetation (Bakker et al. 1996). However, the slow rate of the successional process is a difficulty with the large-scale analysis of primary succession on mining deposits (Prach & Pyšek 2001). The alternative space-for-time substitution approach can then be used, especially if a high number of comparable sites is available. This robust approach provides an opportunity for analysing successional pathways over a shorter time than by permanent plots (Foster & Tilman 2000). Moreover, the combination of a large number of habitats and the wide range of successional ages covered allows for long-term successional patterns to be distinguished and offers an opportunity to study spontaneous vegetation succession in the landscape context.

Disused pits, where sand and gravel were extracted to a depth of several m, often provide good opportunities to study spontaneous vegetation succession on a bare substratum, which exhibits the characteristics of primary succession (Bradshaw 2000). Distinct seral stages of varying ages are often present. Three main types of sites can usually be distinguished: dry, wet and hydric in shallow flooded sites (Kondolf 1994).

Sand and gravel extraction occurs on a large scale in the Czech Republic (present mining area 5400 ha, annual production 35 million tonnes). This production is nearly the same as that of the greatest producer of gravel and sand in Europe, i.e. Germany (400 million tonnes, Kavina 2004), when related to country area and number of inhabitants.

The main objective of this study was to define the course of spontaneous vegetation succession in disused gravel-sand pits throughout the Czech Republic in relation to local site factors and landscape factors. The following main questions were asked: 1. What is the variability of spontaneous vegetation succession in disused gravel-sand pits over a large geographical area? 2. What is the relative importance of local site factors vs landscape factors in determining the spontaneous vegetation succession?

Methods

Study area

The study was conducted in the Czech Republic (48°30'- 51° N, 12°-18°50' E) (Fig. 1). The altitude of the studied sites ranged from 170 to 540 m a.s.l. The distance between the northernmost and the southernmost sites was ca. 250 km, and the distance between the easternmost and westernmost sites was ca. 500 km. The pits can be classified according to their location:

1. Lowlands (170-250 m a.s.l.) having a relatively warm and dry climate (mean annual temperature 8.0-9.2 °C, precipitation 480-550 mm) and used mostly for agrarian purposes.
2. Uplands (255-540 m a.s.l.) with a relatively cold and wet climate (mean annual temperature 6.8-7.9 °C, mean annual precipitation 551-780 mm) and dominated by woodland. All of the sites developed on sandy and gravelly deposits originated from eolic and fluvial processes in the Quartenary period. Pit area ranged from 1 to 95 ha.

Sampling

A total of 36 abandoned gravel-sand pits were surveyed in 2002-2004. The history of each pit was reconstructed on the basis of official records from mining companies and county authorities or by interviewing local administrators. The pits and representative sites in each of them were selected using the following criteria: (1) the existence of sufficiently large, spontaneously revegetated sites; (2) the year of abandonment was known; (3) no evidence of allochthonous substrates; (4) no evident additional disturbance. The period since abandonment (age) ranged from 1 to 75 years. The successional age was determined based on official records and checked by the tree core analysis. The following successional stages were arbitrarily applied: initial (1-3 a), young (4-10 a), middle (11-25 a), late (26-40 a) and old (> 41 a). All sufficiently large and homogenous sites were sampled, avoiding those of unclear previous history. Phytosociological relevés (5 m × 5 m) were recorded in the centre of each of the sites. In this way, 224 reléves were obtained with a mean number of six relevés per pit. Percent cover for vascular species and total cover of bryophytes and lichens were estimated in each relevé. The inclination of all sites where the relevés were recorded was 0°-5°. Thus inclination was not further considered as an explained variable. The presence of (semi-) natural communities (dry grasslands, forest fringes, pastures, wetlands and woodland) up to 100 m from a relevé was recorded. The proportion (in %) of the main land cover categories up to 1 km from the margin of a pit was estimated. The following categories were considered: arable land, urban land, dry grassland, wet grassland, pastures and woodland according to the Fundamental Base of Geographic Data (ZABAGED®) operated by the Czech Office for Surveying, Mapping and Cadastre.

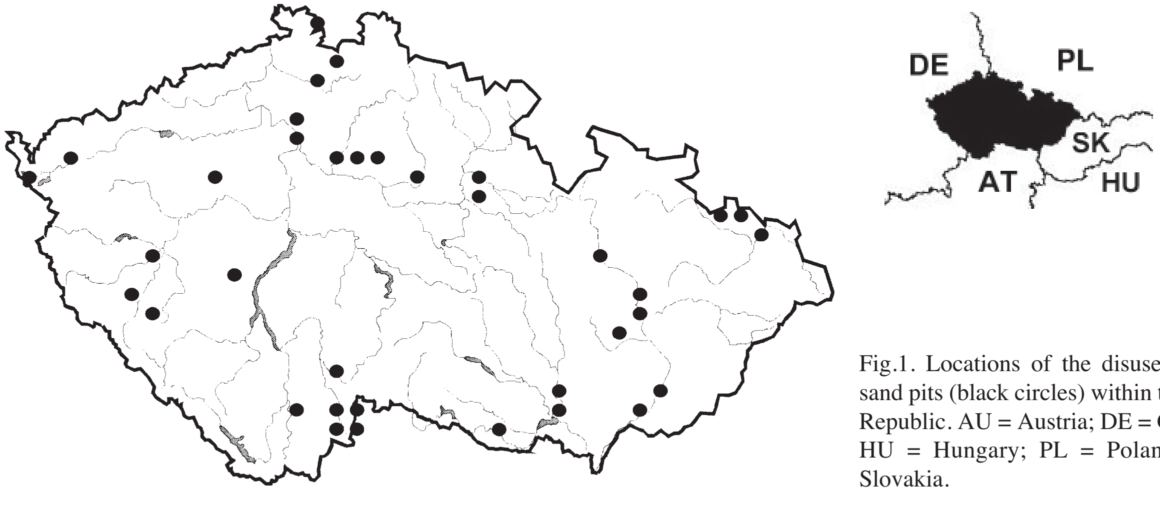

Fig.1. Locations of the disused gravel-sand pits (black circles) within the Czech Republic. AU = Austria; DE = Germany, HU = Hungary; PL = Poland; SK = Slovakia.

Climatic data (mean annual temperature, mean annual precipitation) were obtained from the nearest meteorological station operated by the Czech Hydrometeorological Institute. Site altitudes were derived from 1:50 000 maps. Soil samples were collected in 2004. Five subsamples of the first 0.3 m below the organic layer of the top soil layer were taken from margins of each relevé and mixed into one pooled sample. Following preliminary results of soil analyses from a pilot study on vegetation succession in disused gravel pits (Ryšavá 2001), the samples were analysed only for the most important characteristics of gravel-sand substrate, i.e. pH and texture (Zbíral 1997). Soil texture was determined by wet sieving and a Fritsch Scanning Foto-Sedimentograf (www.fritsch.de) for determination of particles smaller than 0.05 mm. Percentage weight of particular soil fractions followed the United States Department of Agriculture (USDA) standard method (gravel: particles > 2 mm, sand: 2-0.05 mm, silt: 0.05-0.002 mm and clay: < 0.002 mm). Water table depth was measured in bore holes on the border of each relevé. The results are based on three measurements conducted annually at the end of July and beginning of August during 2002-2004. The following sites were arbitrarily distinguished in the pits according to site moisture prior to the next analyses: dry (water table > 1 m deep), wet (water table 0-1 m below the surface) and hydric in shallow flooded sites (0.05- 0.2 m above the surface).

Table 1. Environmental factors considered. The significant factors (see Table 3) are marked in bold.

	Age	Age since abandonment (yr)
Local site factors (LSF)	Cl	Proportion of clay (%)
	Gr	Proportion of gravel (%)
	pH	pH
	Sa	Proportion of sand (%)
	Si	Proportion of silt (%)
	WT	Water table (m)
Landscape factors (LF)	**AL**	Proportion of arable land up to the distance of 1 km from a pit (%)
	Alt	Altitude (m a.s.l.)
	DG	Presence of dry grasslands up to 100 m from sampling site
	DL	Proportion of dry grasslands up to distance of 1 km from a pit (%)
	Ff	Presence of forest fringes up to 100 m from sampling site
	Pa	Presence of pastures up to 100 m from sampling site
	PL	Proportion of pastures up to distance of 1 km from a pit (%)
	Pre	Mean annual precipitation (mm)
	Tem	Mean annual temperature (^{0}C)
	UL	Proportion of urban land up to the distance of 1 km from a pit (%)
	Wo	Presence of woods up to 100 m from sampling site
	WG	Proportion of wet grasslands up to distance of 1 km from a pit (%)
	We	Presence of wet grasslands up to 100 m from sampling site
	WL	Proportion of woodland up to distance of 1 km (%)

Data analysis

Vegetation and environmental data were analysed using multivariate methods in CANOCO version 4.5 (ter Braak & Šmilauer 2002). Species data were logarithmically transformed. A unimodal relationship between species occurrence and time was expected, therefore Detrended Correspondence Analysis (DCA) (length of the gradient of 7.4 SD) and Canonical Correspondence Analysis (CCA) ordinations were used. In DCA analysis, detrending by segments was used and species with a weight of at least 5% were considered. In CCA analyses, inter-samples distance and Hill scaling were used because of data with very long composition gradients. Environmental data were fitted ex post to the DCA ordination axes as passive variables. To separate the effect of locality (i.e. pit), the identifier of relevés situated in sites within the same pit was used as a covariable in analyses. Besides successional age, the following environmental factors were used (Table 1): pH, texture expressed as percentage weight of soil fractions, water table, mean annual temperature, mean annual precipitation, altitude, presence of (semi-) natural communities and proportion of land cover categories.

Forward selection was conducted with all environmental factors (Table 1). Variance inflation factors were below 5, indicating a low correlation of variables (ter Braak & Šmilauer 2002). Subsequent analyses contained only the significant factors ($P < 0.05$). Within the CCA analyses, combining the factors and covariables followed by a Monte Carlo permutation test (i.e. 999 permutations), allowed for the testing of both the partial effect of environmental factors and the relative importance of local site factors and landscape factors. Marginal effects in CCA were also calculated with CANOCO and tested for significance with Monte Carlo permutation test (i.e. 999 permutations). The marginal effects of environmental factors denoted the variability explained by given environmental variables without considering other environmental factors, whereas partial effects denoted the variability explained by given environmental variable considering the effects of other environmental factors (covariables).

Results

Species pattern

Three major successional seres (dry (A), wet (B), and hydric in shallow flooded sites (C)) clearly differed as shown in the unconstrained ordination DCA (App. 1). The dry sere was further separated into two subseres: one in lowland (A1) and the other in upland (A2) regions. Obviously, site moisture was the main factor delimiting the seres, while macroclimate delimited subseres only in the case of the dry sites. Significant differences due to macroclimate also appeared only in the case of dry sites in the partial CCA analyses of each sere separately (not presented).

In total 452 vascular species were recorded, which is ca. 16% of the total Czech flora. A large group of annual species was typical for initial stages (1-3 a). The dominant species were *Conyza canadensis*, *Trifolium arvense*, *Digitaria ischaemum*, *Filago minima* and *Apera spica-venti* in dry sites, *Alopecurus aequalis* in wet sites and *Juncus bulbosus* in flooded sites.

Perennial species, such as *Poa palustris* ssp. *xerotica* and *Agrostis capillaris* in dry sites, *Juncus effusus* and *Phalaris arundinacea* in wet sites and *Glyceria fluitans* in shallow flooded sites, grew along with the annuals (see above) in young stages (4 -10 a). *Tussilago farfara* and *Elytrigia repens* dominated in early successional stages, especially on steeper slopes where the substrate was unstable. Open dry grasslands species (e.g. *Corynephorus canescens*, *Hieracium pilosella*) and ruderal species (e.g. *Artemisia vulgaris*) also occurred in dry sites in this stage.

Perennial grasses and forbs were major dominants in all middle aged stages (11-25 a). Typical species in dry sites were *Festuca ovina*, *Avenella flexuosa*, *Agrostis capillaris*, *Calamagrostis epigejos* and *Achillea millefolium*, while *Carex brizoides*, *Poa palustris* ssp. *palustris* and *Deschampsia cespitosa* were typical of wet sites. Sedges, such as *Carex vesicaria*, were frequent in shallow flooded sites. The first dwarf shrubs (e.g. *Calluna vulgaris*, *Rubus fruticosus*) appeared in all seres, except flooded sites, in this stage.

Gradually, trees and shrubs expanded into most of the sites after more than 25 a (late successional stages). The proportions of sciophytes and nitrophytes increased in the herb layer and species typical of open grasslands rapidly decreased. Typical woody species were *Betula pendula* and *Pinus sylvestris* in dry sites and *Populus tremula*, *Salix caprea*, *S. cinerea* and *Alnus glutinosa* in wet sites. Different successional trends occurred in relatively extreme sites, i.e. the dry or shallow flooded sites where dry grassland species (e.g. *Festuca valesiaca*, *F. vaginata* or *Poa angustifolia*) with scattered shrubs (e.g. *Rosa canina*) or, respectively, wetland species (e.g. *Carex vesicaria*) were common.

The oldest successional stages were dominated by trees and shrubs in dry sites located in uplands and wet sites irrespective of geographic area. A relatively rich mixture of woody species (*Quercus robur*, *Sorbus aucuparia* and other woody species already present in the previous stage) was typical of dry sites in uplands. They were accompanied by *Poa nemoralis*, *Dryopteris filix-mas* and *Vaccinium myrtillus* in the herb layer. The woody species composition in wet sites was relatively species-poor in comparison with the former, composed of *Alnus glutinosa* and some willows (e.g. *Salix alba*, *S. purpurea*, *S. viminalis*). A relatively closed herb layer was formed by wetland species in shallow flooded sites, e.g. *Carex acuta* and *C. vesicaria*, *Scirpus sylvaticus*, *Typha latifolia* or *Phragmites australis*. *Arrhenatherum elatius* was the major dominant in dry sites in lowlands. It was accompanied by other abundant grassland species such as *Securigera* (= *Coronilla*) *varia*, *Festuca vaginata* and *F. valesiaca* and by scattered shrubs represented by *Prunus spinosa*, *Crataegus monogyna* and *Rosa canina*. Woody species such as *Prunus avium* and *Robinia pseudacacia* were also found in these sites.

Environmental factors

Both the DCA and CCA ordinations showed the same general pattern. A high value of species-environment correlations on the first DCA and CCA axes revealed that the significant environmental factors were strong determinants of species variation in the data set (Table 2). Only the DCA graphical outputs are displayed because of the similarity. The CCA analysis showed that 76.3% of variability was explained by 15 significant environmental factors, while six factors were found not to significantly influence vegetation variability (Table 1). Both partial and marginal effects of each of the 15 environmental factors were significant (Table 3, analyses 1-15). The results of the CCA analyses (Table 3, analyses 16-17) showed that landscape factors combined were more influential on the course of vegetation succession (44%) than local site factors (23%). The landscape factors include macroclimate, accounting for 16.8% (partial effect) of variance, and factors related to propagule sources (23%, partial effect).

Water table explained the largest amount of vegetation variability (12.2%, partial effect) and was positively correlated with the first axis (Fig. 2). The second axis was positively related to site age, explaining nearly 10% (partial effect) of vegetation variability. The increasing site moisture (defined by water table depth) was related to the increasing proportion of wet grasslands and woods, and to the decreasing proportion of both

Table 2. Summary results of the ordination analyses: *T* = type of analysis, *EV* = significant environmental variables (15 variables), *r* = species-environment correlation on the first axis, λ_1, λ_2 = eigenvalues corresponding to the first or second axis, *r* = species-environment correlation, % explained = variance in species composition explained by significant environmental variables (see Table 1), *F*-value of the *F*-statistic, *P* (*** = $P < 0.001$) = probability level obtained by the Monte Carlo test.

	T	*EV*	*r*	λ_1	λ_2	% -explained	*F*	*P*
1	DCA	all	0.893	0.788	0.667	-	-	-
2	CCA	all	0.932	0.654	0.562	76. 3	4.205	***

Table 3. Results of CCA – partial and marginal effects (analyses 1 – 15) and variability partitioning (analyses 16 – 17). Covariables: analyses 1 – 17 (identifier of relevés situated in the sites within the same locality – i.e. pit), partial analyses 1 – 15 (all factors except the factor tested), analysis 16 (LF, Age), analysis 17 (LSF, Age). *F*-value of the *F*-statistic; *P* (*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$) = probability level obtained by the Monte Carlo test; nt = not tested; *r* = species-environment correlation; %-explained: marginal – variation attributed to environmental variables without considering other environmental variables, partial – variance attributed to variables with considering other environmental variables (covariables). LSF = local site factors; LF = landscape factors; EV = significant environmental variables (see Table 1).

Analysis		EV	Partial *r*	Partial %-explained	Partial *F*	Partial *P*	Marginal *r*	Marginal %-explained	Marginal *F*	Marginal *P*
1		Age	0.863	9.4	3.300	***	0.882	10.9	3.249	***
2	LSF	WT	0.882	12.2	4.103	***	0.909	13.2	4.188	***
3		pH	0.804	6.1	2.227	***	0.863	7.5	2.865	***
4		Si	0.757	2.9	1.467	***	0.774	3.9	1.722	***
5		Gr	0.725	1.3	1.227	*	0.741	1.7	1.556	***
6	LF	AL	0.825	8.1	3.044	***	0.854	9.9	3.002	***
7		Tem	0.816	7.2	2.933	***	0.853	8.8	2.860	***
8		Alt	0.801	5.5	1.932	***	0.834	6.1	2.695	***
9		Pre	0.768	4.1	1.776	***	0.815	5.0	2.664	***
10		Wo	0.764	3.5	1.671	***	0.842	5.4	2.262	***
11		WL	0.758	3.2	1.592	***	0.811	4.7	2.576	***
12		WG	0.754	2.6	1.312	**	0.804	3.3	2.137	***
13		DG	0.749	2.3	1.299	**	0.780	3.1	2.031	***
14		We	0.743	2.1	1.248	*	0.762	3.0	1.632	***
15		UL	0.723	1.2	1.192	*	0.696	1.6	1.398	*
16		LSF	0.876	23.2	2.954	***	nt	nt	nt	nt
17		LF	0.893	43.5	3.581	***	nt	nt	nt	nt

Table 4. Generalized scheme of spontaneous vegetation succession in the gravel-sand pits in two climatic regions within the Czech Republic. Three main succession seres are shown: dry (A), wet (B) and shallow water (C), with the dry sere further separated into two subseres: (A1) in lowland and (A2) in upland regions. Prevailing life forms are given.

→ → Increasing site moisture → →

Sere	(A1) DRY	(A2)	WET (B)	SHALLOW WATER (C)
Climatic region	Warm & Dry	Cold & Wet	Any	
Altitude	Lowlands	Uplands	Any	
Landuse	Agrarian (arable land) & Urban	Woodland & Agrarian (grassland)	Any	
Initial stage [1-3 yr]	Annual forbs & grasses		Annual graminoids	
Young stage [4-10 yr]	First perennial forbs & grasses		First perennial graminoids and forbs + first shrubs	First perennial graminoids
Middle stage [11-25 yr]	Perennial grasses & forbs	Perennial grasses & forbs + first shrubs & trees	Perennial graminoids & forbs, shrubs + first trees	Perennial graminoids
Late stage [26-40 yr]	Perennial grasses + first shrubs	Trees, perennial grasses & forbs	Shrubs & trees	Perennial graminoids
Old stage [>41 yr]	Perennial grasses & shrubs (Shrubby grassland)	Trees (Deciduous woodland)	Trees & shrubs (*Alnus* and *Salix* carrs)	Perennial graminoids (Tall sedge, Reed, *Typha* beds)

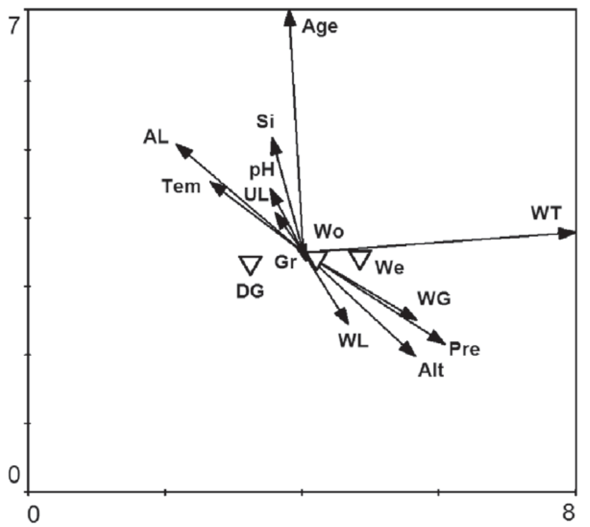

Fig. 2. DCA ordination of significant environmental factors ($P < 0.05$, Table 1) fitted *ex post* as passive variables. For abbreviations, see Table 1.

arable and urban land in the surrounding landscape. While coarse-grained substrates were related to wetter sites or those situated in humid, less altered uplands, fine-grained substrates prevailed in dry sites in agrarian lowlands. The pH was positively related to fine-grained (silty) substrates. Neighbouring (within 100 m of a site border) (semi-) natural dry grasslands were positively related to dry sites in lowlands, while (semi-) natural wood communities were associated with upland dry sites and all wet sites regardless of the region. (Semi-) natural wet grasslands were related to both wet and shallow flooded sites regardless of the region.

Discussion

General patterns of succession

Due to the broad moisture gradient, the dry, wet and shallow flooded sites are colonized by different ecological groups of species. Ruderal species with broad ecological amplitudes, which correspond to generalists, are typical for initial and young seral stages in dry sites, while more specialized wetland species occur in the wet and flooded sites of that age (Borgegård 1990, Pietsch 1996). This is also apparent in the vegetation physiognomy (summarized in Table 4). The final physiognomy of spontaneous successional vegetation is usually determined by the proportions of graminoids and woody species. However, some competitive grasses can arrest establishment of woody species for a long time by forming a dense, compact sward (Prach & Pyšek 2001). This is probably the case with *Arrhenatherum elatius*, which is dominant in some dry sites in agrarian lowlands. Flooded sites are usually colonized by specialists (mostly graminoids) forming monodominant stands (Pietsch 1996), which occurred in this study.

Numerous studies have focused on the relative role of site factors and external forces in driving succession (Tilman 1988; Pickett et al. 1987; Walker & del Moral 2003). It is important to know at least the relative importance of particular factors for predicting and possibly manipulating spontaneous successional processes (Walker & del Moral 2003). However, there is a lack of studies exactly evaluating the role of factors at wider geographical and environmental scales. Such studies require a high number of particular sites for a quantitative evaluation, where the same type of succession proceeds. Such sites are not always available. Some recent studies on succession at wider geographical scales provided different results. For example, del Moral et al. (2005) found much more importance of landscape factors, such as proximity of seed sources, than site factors in early primary succession on Mount St. Helens, while site factors explained more of the variance in understorey vegetation in riparian forests (Holl & Crone 2004). It is obvious that the roles of the two basic groups of factors depend on the scales and the systems studied. Salonen & Setälä (1992) transported substrate between two peatlands in Finland, allowed spontaneous succession to proceed on them and found that the surroundings, manifested in the local species pool, were much more responsible for the vegetation variability than substratum quality.

We expect that the relative importance of site factors and landscape factors are determined by the range of variability of both groups of factors. Obviously, the broader the gradients (such as site moisture), the greater is their responsibility for vegetation variability. The site moisture gradient was very broad in this study, while nutrients and texture were very similar (Řehounková unpubl.). The landscape factors were manifested in the large geographical area considered, and under diverse land cover. In spite of many limitations, the ratio of ca. 1:2:3:4 (time, local site factors, undisclosed and random factors, landscape factors) may be tentatively expected in other sets of seral stages of a similar character.

Surprisingly, time was responsible for only ca. 10% of the vegetation variability in our data set. This is less than in other studies covering such a range of successional ages (e.g. Holl 2002). It is likely that the broad environmental gradients covered in our study partly masked the role of time.

Particular environmental factors

In this study, the surrounding vegetation was a very important factor affecting the process of colonization of man-made sites. A similar conclusion has been reported from gravel-sand pits (Borgegård 1990), dumps (Ninot et al. 2001), stone quarries (Novák & Prach 2003), newly established wetlands (Reinartz & Warne 1993, Edwards & Proffitt 2003) and abandoned fields (Olsson 1987; Pickett et al. 2001). Climatic factors are also important for driving succession, because these influence the respective regional species pool and can physiologically constrain, among others, the participation of woody species in seral stages in central Europe (Novák & Prach 2003; Ruprecht 2006). The influence of altitude has been broadly referred to as an environmental factor modulating the general distribution pattern of vegetation through macroclimatic effects (Gallego Fernandéz et al. 2004). In this study, it seems that higher precipitation and lower evapotranspiration at the higher altitudes probably compensate for the lower water table of dry sites and, therefore, such sites provide suitable environmental conditions for the establishment of woody species. Woody species, which dominate the older stages within the dry sites in uplands and in all wet sites in the studied pits, started sooner and expanded faster under the moderate environmental conditions, while they were rare or absent in extreme (very dry or flooded) sites. This corresponds to evidence from other studies on the environmental factors determining the establishment of woody species in man-made sites (Christensen & Peet 1984; Prach & Pyšek 1994) besides the local species pool, competition for the herb layer and grazing (Olsson 1987; Pickett et al. 2001).

The mean water table depth of ca. 1 m seems to be critical for species requiring wet sites (Elgersma 1998). This agrees with studies in other excavated sites where soil moisture was considered to be the most important site factor determining the establishment and growth of vegetation (Brenner et al. 1984; Fierro et al. 1999).

Soil pH increased with age, which is different from a successional study in gravel-sand pits in Sweden (Borgegård 1990), and decreased with altitude. These trends are also reflected in the change in the vegetation pattern from the prevailing neutral species of dry grasslands in agrarian lowlands to the acidophilous woodland species in forested uplands participating in the succession (Ellenberg et al. 1991). This was probably due to the combined effect of different sedimentation in lowlands (Carling & Petts 1992) and macroclimate.

Decreasing grain size distribution from sites located in humid uplands towards the sites in dry lowlands probably reflects the general trend of decreasing size of river sediments downstream (Carling & Petts 1992).

Conclusions

At the country scale, spontaneous vegetation succession led to the formation of either (A1) shrubby grassland in dry sites in lowlands; (A2) deciduous woodland in dry sites in uplands; (B) *Alnus* and *Salix* carrs in wet sites, irrespective of region or (C) tall sedge or reed and *Typha* beds in shallow flooded sites irrespective of region (Table 4). Except for some dry sites in lowlands, where the alien species *Robinia pseudacacia* may expand, the succession proceeds towards stabilized, (semi-) natural vegetation within 40 years (Table 4). Site moisture was the most influential factor on the course of succession. The vegetation pattern was further significantly influenced by the following studied factors: pH and the proportions of silt and gravel among local site factors, altitude, mean annual temperature, mean annual precipitation, presence of some vegetation types up to 100 m from a sampling site and prevailing land cover up to 1km from a pit. The landscape factors combined were more influential (44%) than local site factors (23%) in affecting the course of vegetation succession.

Acknowledgements. The study was supported by the following grants: MSM 6007665801, AVOZ 6005908, GA CR 206/02/0617, Fund for Development of Universities 1839 and Foundation The Talent of Josef, Marie and Zdenka Hlávka. We thank Karen Holl, Anna Martha Elgersma and Sandor Bartha for their valuable comments on the manuscript, Jan Lepš for his advice on statistics and Keith Edwards for language revision.

References

Bakker, J.P., Olff, H., Willems, J.H. & Zobel, M. 1996. Why do we need permanent plots in the study of long-term vegetation dynamics? *J. Veg. Sci.* 7: 147-156.

Borgegård, S.O. 1990. Vegetation development in abandoned gravel pits: effects of surrounding vegetation, substrate and regionality. *J. Veg. Sci.* 1: 675-682.

Bradshaw, A. 2000. The use of natural processes in reclamation – advantages and difficulties. *Landscape Urban Plan.* 51: 89-100.

Brenner, F.J., Werner, M. & Pike, J. 1984. Ecosystem development and natural succession in surface coal mine reclamation. *Minerals Environ.* 6: 10-22.

Carling, P.A. & Petts, G.E. (eds.) 1992. *Lowland floodplain rivers. Geomorphological perspectives.* Wiley, Chichester, UK.

Christensen, N.L. & Peet, R.K. 1984. Convergence during secondary forest succession. *J. Ecol.* 72: 25-36.

Cullen, W.R., Wheater, C.P. & Dunleavy, P.J. 1998. Establishment of species-rich vegetation on reclaimed limestone quarry faces in Derbyshire, UK. *Biol. Conserv.* 84: 25-33.

del Moral, R., Wood, D.M. & Titus, J.H. 2005. Proximity, microsites and biotic interactions during early succession. In: Dale, V.H., Swanson, F.J. & Crisafulli, C.M. (eds.) *Ecological responses to the 1980 eruption of Mount St. Helens*, pp. 93-109. Springer, New York, NY, US.

Edwards, K.R. & Proffitt, C.E. 2003. Comparison of wetland structural characteristics between created and natural salt marshes in southwest Louisiana, USA. *Wetlands* 23: 344-356.

Elgersma, A.M. 1998. Primary forest succession on poor sandy soils as related to site factors. *Biodiv. Conserv.* 7: 193-206.

Ellenberg, H., Weber, H.E., Düll, R.,Wirth, V., Werner, W. & Paulißen, D. 1991. Zeigerwerte von Pflanzen in Mitteleuropa. *Scripta Geobot.* 18: 1-258.

Fierro, A., Angers, D.A. & Beauchamp, C.J. 1999. Restoration of ecosystem function in an abandoned sandpit: plant and soil responses to paper de-inking sludge. *J. Appl. Ecol.* 36: 244-253.

Foster, B.L. & Tilman, D. 2000. Dynamic and static views of succession: Testing the descriptive power of the chronosequence approach. *Plant Ecol.* 146: 1-10.

Gallego Fernandéz, J.B., García Mora, R. & García Novo, F. 2004. Vegetation dynamics of Mediterranean shrublands in former cultural landscape at Grazalema Mountains, South Spain. *Plant Ecol.* 172: 83-94.

Holl, K.D. 2002. Long-term vegetation recovery on reclaimed coal surface mines in the eastern USA. *J. Appl. Ecol.* 39: 960-970.

Holl, K.D. & Crone, E. 2004. Applicability of landscape and island biogeography theory to restoration of riparian understorey plants. *J. Appl. Ecol.* 41: 922-933.

Kavina, P. 2004. *Mineral commodity summaries of the Czech Republic*. Czech Geological Survey, Geofond, Praha, CZ.

Kondolf, M.G. 1994. Geomorphic and environmental effects of instream gravel mining. *Landscape Urban Plan.* 28: 225-243.

Kubát, K., Hrouda, L., Chrtek, J. jun., Kaplan, Z., Kirschner, J. & Štepánek, J. (eds.) 2002. *Key to the flora of the Czech Republic*. Academia, Praha, CZ. Academia, Praha. (In Czech.)

Ninot, J.M., Herrero, P., Ferré, A. & Guàrdia, R. 2001. Effects of reclamation measures on plant colonization on lignite waste in the eastern Pyrenees, Spain. *Appl. Veg. Sci.* 4: 29-34.

Novák, J. & Prach, K. 2003. Vegetation succession in basalt quarries: Pattern on a landscape scale. *Appl. Veg. Sci.* 6: 111-116.

Olsson, G. 1987. Effects of dispersal mechanisms on the initial pattern of old-field succession. *Acta Oecol.* 8: 379-390.

Pickett, S.T.A., Collins, S.L. & Armesto, J.J. 1987. A hierarchical consideration of causes and mechanisms of succession. *Vegetatio* 69: 109-114.

Pickett, S.T.A., Cadenasso, M.L. & Bartha, S. 2001. Implications from the Buell-Small Succession Study for vegetation restoration. *Appl. Veg. Sci.* 4: 41-52.

Pietsch, W. 1996. Recolonization and development of vegetation on mine spoils following brown coal mining in Lusatia. *Water Air Soil Pollut.* 91: 1-15.

Prach, K. & Pyšek, P. 1994. Spontaneous establishment of woody plants in Central European derelict sites and their potential for reclamation. *Restor. Ecol.* 2: 190-197.

Prach, K. & Pyšek, P. 2001. Using spontaneous succession for restoration of human-disturbed habitats: Experience from Central Europe. *Ecol. Engin.* 17:55-62.

Reinartz, J.A. & Warne, E.L. 1993. Development of vegetation in small created wetlands in southeastern Wisconsin. *Wetlands* 13: 153-164.

Ruprecht, E. 2006. Successfully recovered grassland: a promising example from Romanian old-fields. *Restor. Ecol.* 14:473-480.

Ryšavá, K. 2001. *Vegetation succession in the restored Nature Reserve of Chomoutovské jezero*. M.Sc. Thesis, Palacký University of Olomouc, Czech Republic (in Czech).

Salonen, V. & Setälä, H. 1992. Plant colonization of bare peat surface – relative importance of seed availability and soil. *Ecography* 15: 199-204.

Skousen, J.G., Johnson, C.D. & Garbutt, K. 1994. Natural revegetation of 15 abandoned mine land sites in West Virginia. *J. Environ. Qual.* 23: 1224-1230.

ter Braak, C.J.F. & Šmilauer, P. 2002. *CANOCO Reference Manual and CanoDraw for Windows User's Guide: Software for Canonical Community Ordination (version 4.5)*. Microcomputer Power, Ithaca NY, US.

Tilman, D. 1988. *Plant strategies and the dynamics and structure of plant communities*. Princeton University Press, Princeton, NJ, US.

Ursic, K.A., Kenkel, N.C. & Larson, D.W. 1997. Revegetation dynamics of cliff faces in abandoned limestone quarries. *J. Appl. Ecol.* 34: 289-303.

Walker, L.R. & del Moral, R. 2003. *Primary succession and ecosystem rehabilitation*. Cambridge University Press, Cambridge, UK.

Wiegleb, G. & Felinks, B. 2001. Primary succession in post-mining landscapes of Lower Lusatia – chance or necessity. *Ecol. Engin.* 17: 199-217.

Zbíral, J. 1997. *Soil analysis I*. Central Institute for Supervising and Testing in Agriculture, Brno. (In Czech.)

Received 20 January 2006;
Accepted 17 May 2006;
Co-ordinating Editor: N.C. Kenkel.

For App. 1, see JVS/AVS Electronic Archives;
www.opuluspress.se/