Variability of spontaneous vegetation succession in disused gravel-sand pits: importance of environmental factors and surrounding vegetation

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Cover picture (back site):
Old succesional stages (>41 years)
1. Shrubby grasland – dry sere in lowlands
2. Deciduous woodland – dry sere in uplands
3. *Alnus* & *Salix* carrs – wet sere
4. Tall sedges, reed & *Typha* beds – shallow water sere

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PhD. Thesis

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Annotation

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Spontaneous vegetation succession in disused gravel-sand pits in various regions of the Czech Republic was studied using mostly the space-for-time substitution approach. The main objectives were focused on the variability of vegetation succession in different habitats inside gravel-sand pits over a larger geographical area, the relative importance of local site vs. landscape factors in determining spontaneous vegetation succession, the role of the local species pool, participation of target and undesirable species in the course of spontaneous vegetation succession, and how life-history traits and habitat preferences help predict the establishment of species. In addition, the variability of vegetation development and the relative importance of abiotic site factors influencing spontaneous vegetation succession during early successional stages were studied in a disused gravel-sand pit in the eastern part of the Czech Republic (central Moravia) using permanent plots.

The results demonstrate that vegetation development and differences in abiotic site factors described from one gravel-sand pit, showed similar trends as those from a broad-scale and multi-site study of gravel-sand pits throughout the Czech Republic. The ratio of approximately 1:2:3:4 (time, local site factors, undisclosed and random factors, and landscape factors) express the proportion of environmental factor effects influencing the course of vegetation succession.

Restoration of target vegetation in disused gravel-sand pits by the processes of spontaneous vegetation succession can be an effective and economic alternative to the still prevailing and expensive technical reclamation.

Declaration

I hereby declare that this thesis has been fully worked out by myself and the named co-authors with the use of cited reference.

Klára Řehounková

České Budějovice, 24th June 2007

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Introduction

Introduction

Primary succession is defined as species turnover on barren substrates where severe disturbances have removed most biological activity (Walker & del Moral 2003). Disused pits, where sand and gravel were extracted down to a depth of several metres, provide all of these conditions and represent suitable sites for research on succession, as processes of primary succession hardly ever can be observed elsewhere in the European cultural landscape, except for mining sites (Glenn-Lewin et al. 1992). Despite the fact that such sites are quite frequent in various landscapes, detailed or long-term studies on spontaneous vegetation succession in disused gravel-sand pits are very rare (Borgegård 1990) in contrast to other sites disturbed by extraction, including stone quarries (Ursic et al. 1997, Cullen et al. 1998, Novák & Prach 2003) or dumps and wastes (e.g., Skousen et al. 1994, Kirmer & Mahn 2001, Wiegleb & Felinks 2001, Kovář et al. 2004).

Distinguishing which environmental factors most influence the development of vegetation in disturbed sites is crucial for successful ecosystem restoration. Local site factors and landscape factors act as selective filters of species possessing different traits (Bazzaz 1996, Zobel et al. 1998). Physical and chemical deficiencies or habitat extremes, manifested through texture, stability, temperature, water retention, severe nutrient deficiency, extreme pH values and metal toxicity, are common handicaps of many sites disturbed by mining activities (Marrs & Bradshaw 1993, Bradshaw 2000). However, low water retention, related to texture, and slight nutrient deficiency can be considered as the only limiting abiotic factors of gravel-sand substrates (Lubke et al. 1996). Vegetation change is related to local species pool and governed by both dispersal limitation, and the ability of species to establish and persist (Bakker et al. 1996, Díaz et al. 1998, Pywell et al. 2003, Ozinga et al. 2005).

Spontaneous succession often provides desirable target ecosystems and has a large potential as a suitable tool for restoration of many sites disturbed by mining (Prach 2007). Besides its potential contribution to successional theory, an understanding of spontaneous vegetation succession over a landscape scale may be important for promoting natural recovery of degraded ecosystems (Luken 1990, Klötzli and Grootjans 2001, Prach et al. 2006). Using a broad-scale experience with succession, we can tentatively predict the rate and direction of succession if we rely upon spontaneous succession or expect to manipulate the spontaneous development in a disturbed site (Glenn-Lewin et al. 1992, Walker & del Moral 2003).

Aims and contents of this study

The main aims of this thesis were: (1) to analyze the spatial-temporal pattern of spontaneous vegetation succession in disused gravel-sand pits over a large geographical scale throughout the Czech Republic, (2) to quantify the effects of environmental factors influencing the course of succession, and (3) to evaluate the potential of spontaneous vegetation succession in restoration programs for particular pits. The following main questions were asked: (1) Does succession run towards (semi-)natural vegetation within a reasonable time? (2) Is succession divergent or convergent inside and among the pits? (3) Are local site or landscape factors more important for the course of succession? (4) Which species traits are correlated with the colonization success of particular species?

For this purpose, the study of disused gravel-sand pits (36) was conducted in various regions of the Czech Republic. The gravel-sand pits comprised stages of different ages, from 1 to 75 years since abandonment, and three habitat types: dry, wet and shallow water. Together, 224 vegetation relevés were recorded with species cover (%) visually estimated using the space-for-time substitution approach (Chapter II–IV).

In Chapter I, the question, which environmental variables determine the course of various successions on broad geographical scales, is answered based on review of 30 studies on vegetation succession, which deal with at least six sites which were spread at least over 10 km^2. Only seres started on bare ground were considered, i.e. various mining sites, old fields, plantages and pastures, and others (e.g. islands, sand dunes, glaciers). The chapter provides a broader background of the study.

Chapter II presents the results about variability of a particular vegetation succession, i.e. in gravel-sand pits, over a large geographical area. Detailed data about the relative importance of local site (such as water table and soil characteristics) and landscape factors, namely climatic parameters, presence of nearby (semi-) natural plant communities and main land cover categories in the broader surroundings, were evaluated.

In Chapter III, change in the importance of particular ecological groups of species during spontaneous vegetation succession in disused gravel-sand pits is shown. The role of the local species pool, and the participation of target (i.e. grassland, woodland, wetland) and undesirable (i.e. ruderal, alien) species in succession, is evaluated and the implications for spontaneous vegetation succession of disused gravel-sand pits in restoration programs are outlined.

Chapter IV demonstrates that certain life-history traits and habitat preferences are linked with the colonization success of species, occurring in the surrounding vegetation. The colonization success was evaluated separately for different successional stages, i.e. young, middle, late.

Chapter V presents the results of an eight-year monitoring study of spontaneous vegetation succession in 32 permanent research plots in a disused and later restored gravel-sand pit in the eastern part of the Czech Republic (central Moravia). The variability of vegetation development in four different habitats (mesic, wet, shallow water and aquatic), and the relative importance of abiotic factors, such as water table and soil physical and chemical characteristics, were analysed to determine how they influence spontaneous vegetation succession. This study can be seen as a pilot.

The main results of the thesis are summarized in the Conclusions.

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Chapter I

Vegetation succession over broad geographical scales: which factors determine the patterns?

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Vegetation succession over broad geographical scales: which factors determine the patterns?

Abstract

We reviewed 37 studies on vegetation succession in which the succession started on bare ground, was followed in at least six sites, and where these sites were spatially separated over at least 10 km^2. The effect of environmental factors, which were explored in at least five studies, on the course of succession was assessed, based on the proportion of significant and non-significant results. Surrounding vegetation, macroclimate, soil moisture, amount of nitrogen and soil texture appeared to have the highest influence on the course of succession. Less influential were the size of a disturbed site, pH, organic matter and phosphorus content. Surrounding vegetation exhibited a significant effect in all cases where this was considered. These results imply that succession cannot be studied without the landscape context. The large-scale approach to succession has the potential to contribute substantially to both the theory of succession and practical applications, especially in restoration ecology.

Keywords: environmental factors, landscape context, restoration ecology, species pool, vegetation succession

Introduction

An enormous number of published studies on succession deal with one or several, more or less comparable sites (e. g., Burrows 1990, Glenn-Lewin et al. 1992, Walker & del Moral 2003). In these studies, succession was often described in remarkable detail, often using experimental manipulation of environmental factors or vegetation itself, thus testing various hypotheses on mechanisms of vegetation change (Tilman 1988, van der Maarel 2005). However, there are not many studies that evaluate succession over broad, i. e. landscape, regional or even continental, scales (van Andel et al. 1993, Walker & del Moral 2003). Those attempts that have been made at this scale are often based on intuitive, not quantitative, comparisons of a high number of seral stages. It is obvious that quantitative studies on succession on a broad geographical scale cannot easily test hypotheses on mechanisms, but they do provide a good opportunity to test hypotheses on pattern. For various reasons, this opportunity has not been appropriately exploited sofar. Studying vegetation dynamics broader geographical scales can provide a useful framework to our detailed studies, supporting well-balanced interpretations of results. Using the broader approach, we can generate hypotheses which can be subsequently tested at small scales. Obviously, small-scale experimental studies and large-scale studies can be seen as complementary approaches.

Among the first attempts to describe successional changes in vegetation over larger scales were the studies of early generations of European phytosociologists. By the traditional descriptive approach (using phytosociological relevés) they often analysed many particular sites and then tried to depict intuitively general successional trajectories using formally described plant communities (associations) or dominant species (Ellenberg 1988). These studies provided a usefull, though limited overview over vegetation dynamics especially in the case of rapidly changing vegetation such as that on various ruderal sites in urban or industrial habitats (Pyšek & Pyšek 1988). Resulting general schemes were often helpful in urban or landscape planning (Laurie 1979).

Advances in computer technology and multivariate techniques enabled researchers to elaborate a large number of vegetation records (Jongman et al. 1987), including those from seral stages. Thus, it seems the number of studies dealing with succession on broad scales has been increasing. Here we review these studies and address the question: Which environmental variables determine the course of succession over broad geographical scales?

Which seres have been studied?

We have found 37 studies which match the following arbitrarily selected criteria: they deal with at least 6 sites, usually representing different particular seral stages, which were spread over at least 10 km^2 (Table 1). We considered only seres which started on bare ground in which the succession was followed from the very start. Old fields and various mining sites were the most frequently investigated, similarly as among other studies disregarding the scale (Walker & del Moral 2003). Environmental factors considered in the particular studies are listed in Table 1. Those factors, whose influence on the course of succession (defined here as changes in vascular plant species composition) was statistically tested in paticular studies, are indicated in the Table 1.

We are aware of the limitations of the data set extracted from the heterogenous studies which can be hardly mutually compared in a detail. Thus, we concentrate only on the most robust patterns. Causal influences of the environmental factors on the course of succession are differently dealt with in the studies not enabling us to make clear and undoubted generalizations. Tferefore only selected aspects are tentatively discussed further.

The studies differed in the number of the sampling plots and in the area covered. It must be mentioned that the same number of sampling plots spread over the same area need not be equally representative in different situations. For example, within a homogenous landscape a small local study can be representative for the whole area, but not so in a heterogenous landscape. Most studies on succession are scaled a priori by human-caused or natural disturbances and sampling follows the pattern. This introduced another component of heterogenity into the data set. Whether a factor exhibited statistically significant influence on the course of succession (Table 2) depended largely on the range of values dealt with in the particular studies. Generally, there is obviously higher probability of significant influence if the range is broad (Jongman et al. 1987). The studies differed considerably in this regard, thus further weakening the strength of our conclusions. Despite this limitation, the importance of the particular environmental factors is clearly seen from Tables 1 and 2.

Important environmental factors

The frequencies in which the factors were reported as having significant or non-significant influence on the course of succession are listed in Table 2, together with the total numbers of studies in which the factors were considered, regardless of whether or not statistics were employed (see Table 1). Time, i. e. successional age, was naturally the most frequent variable to which the course of succession was related, and this factor nearly always exhibited a significant influence on the vegetation pattern. In some studies, the temporal patterns were suppressed by the influence of some abiotic factors if these had a large amplitude (Vaňková & Kovář 2004, Prach et al. 2006). However, the successional age is a major but not only aspect of the temporal dimension. For example, the effect of starting date can also be important. Surrounding vegetation, expressed either as the occurrence of particular vegetation types, land use categories, occurrence of particular species, or dispersal categories around a considered site, had significant influence in all studies where it was considered. Nearly the same is true for macroclimate (temperature, precipitation, altitude and latitude), and for site moisture and nitrogen content among the edaphic factors. Soil structure was also highly influential, especially the content of soil particles such as clay or sand. Organic content, pH and phosphorus had significant influence only in some cases. At least some edaphic factors played a statistically significant role in nearly 80 % of studies in which these factors were tested.

Macroclimate and surrounding vegetation can be considered as landscape factors. Edaphic factors, represented mostly by substratum quality, and size of a site represent local site factors. The proportional influence of both groups of factors on the course of succession was only rarely evaluated in a quantitative way. In our study on succession in disused gravel-sand pits, the landscape factors together were responsible for vegetation variability in about 44 %, and the local site factors in 23 % in a CCA analysis. Time contributed about 10 % and the rest was unexplained variability. Soil moisture was the most important of the edafic factors (Řehounková & Prach 2006).

Surrounding vegetation and the role of the area of site

The fact that surrounding vegetation had a significant effect in all cases when it was tested implies that succession is a highly stochastic process if we consider only a particular site without considering the landscape context. Influence of the surrounding vegetation on succession is clearly manifested in species pool, which is determined by macroclimate, vegetation history, and land-use history (Zobel et al. 1998, Settele et al. 1996). Various studies demonstrated the decisive role of sources of diaspores

Table 1 – Studies on vegetation succession at broad geographical scales and environmental factors considered. In those studies which used rigorous statistics, the factors which appeared to be significantly correlated with successional pattern are given in bold. For those studies which did not use statistics, only factors which were reported to obviously influence the course of succession are listed (in italics).

Type of succession	Geographical area	Factors	References
1. Mining sites			
Gravel-sand pits	Czech Republic (36 pits; 78 000 km^2)	**age, proportion of arable land, urban land,** dry grasslands, pastures, **wet grasslands and woodland up to the distance of 1 km from a pit; presence of dry grassland, wet grasslands,** pastures, forest fringes **and woods up to 100 m from sampling site; altitude; mean annual precipitation; mean annual temperature; pH; water table proportion of gravel,** sand, clay **and silt**	Řehounková & Prach (2006)
Gravel pits	Sweden (68 pits, 700 000 km^2)	*age, surrounding vegetation type up to 100 m wide zone around the pit, area, macroclimate, pH, total N, C/N, P, K, texture*	Borgegård (1990)
Basalt quarries	Czech Republic (56 quaries; 1 800 km^2)	**age, presence of dry grasslands in the surroundings, mean annual precipitation, mean annual temperature**	Novák & Prach (2003), Novák & Konvička (2006)
Limestone quarries	Canada: S Ontario (18 quaries; 70 000 km^2)	**age, density of tree adjacent to the quarry, latitude, inclination, quarry size, substrate instability, habitat type (wall, floor, top)**	Ursic et al. (1997)
Open-cast mining	Germany: Lower Lusatia (50 sites; 5 000 km^2)	*age, dispersal, locality, pH, conductivity, maximum water capacity, amount of nitrate-nitrogen, total N, phosphate, organic C, P, sulphate, total sulphur*	Wiegleb & Felinks (2001a, Schulz & Wiegleb (2000)
Colliery waste heaps	England: S Lancashire (86 sites; 56 km^2)	*age, pH, texture, hill/hollow topography*	Molyneux (1963)
Coal strip mines	USA: Oklahoma (49 coal strip mines; 21 000 km^2)	**age, soil moisture,** pH, **total N,** total P, **K, Ca, Fe, Mn, Cu,** Zn, texture (gravel, sand, **silt,** clay)	Johnson et al. (1982)
Surface coal mine	USA: N Dacota (6 sites; 26 km^2)	*age, aspect, slope, pH, water saturation, conductivity, total N, P, Ca, Mg, K, Mn, Na,* SO_4^{2-}*, clay, silt, sand, bulk density*	Wali (1999)
Harvested peatland	Finland: central part (8 sites; 25 000 km^2)	**age, surrounding vegetation, conductivity, ash content, ammonium nitrogen content, nitrate nitrogen content, soluble P, mean particle size of surface peat, thickness of peat layer**	Salonen (1994)
2. Old fields and plantations			
Old fields	Canary Islands: Tenerife (11 fields; 100 km^2)	**age, surrounding vegetation, mean annual precipitation, moisture**	Otto et al. (2006)
Old fields	USA: New York (21 sites; 600 km^2)	*age, dispersal, previous land use, moisture*	Stover & Marks (1998)
Old fields	The Netherlands: E part (80 sites; 10 000 km^2)	**age, soil types**	Smit & Olff (1998)
Old fields after topsoil removal	the Netherlands (9 fields; 30 000 km^2)	*age, surrounding vegetation, field area, organic matter*	Verhagen et al. (2001)
Old fields	Romania: Transylvanian Lowland (40 old fields; 12 km^2)	**age, relative area of propagule sources (grasslands), propagule availability (grasslands)**, dispersal mode, field area, slope, exposure	Ruprecht (2005, 2006)
Old fields	Czech Republic (108 sites; 250 km^2)	*age, distance to propagule sources, moisture*	Osbornová et al. (1990)
Old fields	Finland (130 sites; 300 000 km^2)	*age, character of the surrounding landscape, previous cultivation of the field, latitude, site moisture*	Prach (1985)
Old fields	Spain: SE part (96 plots; 16 km^2)	**age, dispersal**	Bonet & Pausas (2004)
Old fields	Denmark (20 sites; 300 km^2)	**age, temperature, pH, moisture, nitrogen, light**	Ejrnæs et al. (2003)
Old fields	USA: Mississippi (40 sites; 1000 km^2)	**age, pH, organic matter, humus type, total C, total N, P, K, Ca, Mg, bulk density**	Switzer et al. (1979)
Abandoned ploughed pastures	Brazil: E Amazonia (15 sites; 2500 km^2)	**age, pasture-use history**, pH, organic matter, N, P, Ca, Mg, K, soil bulk density	Buschbacher et al. (1988)
Abandoned farmlands	Sweden: island in west coast (26 sites; 10 km^2)	**age, seed sources, dispersal mechanism, landuse**	Olsson (1987)
Abandoned culture lands	Spain: S part (137 sites; 100 km^2)	**type of human disturbance (agriculture/fire), inclination, altitude, slope, pH,** conductivity, water field capacity, organic matter content, **clay, sand,** silt	Gallego Fernández et al. (2004)
Abandoned coffee plantations and pastures	Puerto Rico (28 sites; 150 km^2)	**age, land use, altitude**, degree of slope, slope aspect, percentage of soil clay	Marcano-Vega et al. (2002)
3. Others			
Islands	Sweden: lake Hjälmaren (30 islands; 670 km^2)	**age, dispersal, distance to mainland or to a large island, number of islands within 200 m distance from the studied island,** habitat diversity on an island, **perimeter of the island,** island shape	Rydin & Borgegård (1988)
Islands	USA: Louisiana, Atchafalaya Delta (6 sites – transects; 110 plots, 20 km^2)	**age**, **hydrologic regime (degree of inundation),** *grazing*	Shaffer et al (1992)
Artificial islands	Czech Republic: Třeboň Basin (71 islands; 300 km^2)	**age, isolation, area, elevation**	Rejmánek & Rejmánková (2002)
Sand dunes	USA: Kreton (48 plots; 240 km along Oregon coast)	**age,** macroclimate, **microclimate, stabilization**	Kumler (1969)
Sand dunes	USA: Michigan (72 dune ridges; 20 km^2)	**age, wind velocity, evapotranspiration, sand movement, soil moisture,** pH, **total N, P, C, Ca,** Mg, K, **light availability**, sand burial, erosion, soil drying	Lichter (1998)
Wet dune slacks	Belgian and NW French coast (83 dune slacks; 1000 km^2)	**age, dispersal, isolation, area, moisture, pH, nitrogen, light**	Bossuyt et al. (2003)
Gravel bars	India: NW Himalayas (23 sites; 20 000 km^2)	*age, regional climax vegetation, elevation above the river, stand height, macroclimate*	Prach (1994)

Type of succession	Geographical area	Factors	References
Glaciers	USA: Alaska, Glacier Bay (10 sites; 1 000 km^2)	**age, distance to seed source**, soil texture	Fastie (1995)
Landslides	Puerto Rico (46 sites; 44 km^2)	**age, particle size distribution, slopes,** pH, **organic N, C,** total P, available P, Mg, Ca, K	Guariguata (1990)
Clearcuts and burned forests	Canada (386 sites; 300 000 km^2)	**age, type of disturbance, soil moisture, soil parent material, soil texture**	Schroeder & Perera (2002)
Ombrotrophic mires	Canada: Québec (16 sites; 60 km^2)	*age, climate, human drainage, fire*	Pellerin & Lavoie (2003)
Sedimentation basins	Czech Republic (18 sedimentation basins; 20 000 km^2)	age, **plant species in surroundings up to 100 m distance,** pH, altitude, **origin of the deposits (ore-washery/ash-slag),** length of perimeter of homogeneous sedimentary plots, content of chlorides/sulphates	Vaňková & Kovář (2004)
Volcano	USA: Washington, St.Helens (103 plots; 254 km^2)	*age, dispersal ability, proximity of propagule sources, seed rain, isolation, substrate moisture, microtopography, nutrient conditions, herbivory, deposit thickness, subsequent physical conditions*	Dale et al. (2005)
Post-fire sites	Canada: Quebéc (31 033 sites; 10 000 km^2)	*age, area, moisture, soil types, secondary disturbance*	Harper et al. (2002)

Table 2 – Frequency of significant and non-significant influence of the environmental factors on the course of succession as reported in the references listed in Table 1, and the total number of studies out of 37 listed in Table 1, in which the factor was considered regardless of whether its significance was tested. Results of both univariate and multivariate statistics were considered. Only those factors, which were evaluated at least in 5 studies, were included. The factor was considered as significant if at least one its parameter was significant (e. g., edaphic factors – together were considered as significant if at least one of a group of analysed factors was significant).

Factor	**Number of studies**	**Significant**	**Non-significant**
Age	36	23	1
Surrounding vegetation (incl. seed sources, dispersal, land use)	20	13	0
Size of a site	9	4	2
Macroclimate (incl. altitude)	12	7	2
Edaphic factors – together	30	14	4
pH	14	5	5
Moisture	17	8	1
Organic matter	9	4	2
Nitrogen (various forms)	12	7	1
Phosphorus (various forms)	9	3	3
Soil structure (incl. soil types)	19	11	3

in the vicinity of a disturbed site and intensity of transport of the diaspores (Fastie 1995, Ursic et al. 1997, Verhagen et al. 2001, Vaňková & Kovář 2004, Dale et al. 2005, Řehounková & Prach 2006). Because sites where succession proceeds can be seen as habitat islands, the theory of island biogeography can be applied to some extent (Bossuyt et al. 2003). The smaller the area of a site the easier, usually, is its colonization from close surroundings, and succession usually occurs faster and often directly towards restoration of a previous vegetation than in large sites (Dovčiak et al. 2005). In large disturbed site, more ruderals have a chance to establish and eventually may arrest or divert succession. In some cases, succession on real islands, either natural or human-made, was studied (Rydin & Borgegård 1988, Rejmánek & Rejmánková 2002). In all those cases, area and isolation were the most important factors, determining especially the number of present species.

It seems that the propagule sources in close vicinity are usually decisive for the establishment of late successional, often target and mostly rather specialized groups of species with lower dispersal ability (Poulin et al. 1999, Novák & Prach 2003). Generalists, which are often present among early successional species, often belong to easily dispersed species, which can colonize a site from a longer distance (Grime 2002). Late successional, dry grassland species colonized basalt quarries with a high probability if they occurred up to the distance of 50 m (Novák & Konvička 2006). Detailed studies of the unique post-eruption landscape of Mt St. Helens revealed the important role of refugia and the distance to the untouched vegetation for re-colonisation, but only up to about 100 m (del Moral et al. 2005). However, in the study conducted in chalk quarries in N England by Jefferson (1984) transport of diaspores of some target species was recorded up to the distance of several kilometers.

Macroclimate

The assumption that climate influences succession is trivial (Box 1981). It is, however, difficult to test because of the lack of directly comparable data and conclusions remain largely speculative (Walker & del Moral 2003: 262–266). Increasing precipitation increased stand height and biomass but also participation of alien species in an old-field succession in Tenerife island (Otto et al. 2006). In dry seres, species diversity increased permanently during succession, while it peaked early and then declined in wet seres (Otto et al. 2006). It seems to be a general pattern for extreme vs. moderate site conditions (Peet 1978, Osbornová et al. 1990). Macroclimate determined physiognomy of vegetation and participation of life forms in some studies (Prach 1994, Otto et al. 2006). A study of vegetation succession in 56 disused basalt quarries over a distance of 90 km, where mean annual precipitation varied between 460 and 820 mm, and mean annual temperature between 6.1 and 9.0 °C, found both these variables to be significantly correlated with vegetation pattern (Novák & Prach 2003). Besides the expected direct effects on species establishment, macroclimate influences vegetation succession through the regional species pool (Settele et al. 1996).

Substratum quality

The type of substratum is often reported to determine the course of succession; soil type is important in abandoned fields (Smit & Olff 1998; Gallego Fernández et al. 2004) and substratum texture in industrial and mining deposits (Molyneux 1963; Vaňková & Kovář 2004). Soil moisture (partly influenced by climatic factors), soil nutrients (especially nitrogen), and soil pH are often related to the type of substratum. These factors play a decisive role in driving succession at the local scale (Wilson & Tilman 2002) and often create gradients over large geographical scales (Ellenberg 1988). However, their influence on succession was not often investigated in these scales.

Soil moisture is probably the most important site factor driving succession, but it is difficult to measure it in a comparative way over a large geographical area due to local differences in actual precipitation. Moreover, precipitation itself cannot be always used as a surrogate for site moisture due to topography (but see Otto et al. 2006). Thus, simple categories evaluating site moisture can be used, such as dry, mesic, and wet (Osbornová et al. 1990, Prach et al. 2006). This robust approach may be sufficient even in tentative predictions of succession in landscape or regional scales (Prach et al. 1999). Site moisture often determines participation of different life forms and thus physiognomy of seral stages (Walker & del Moral 2003). This is evident in the participation of woody species, which is usually high in mesic sites but restricted at dry or wet extremes of the moisture gradient (Osbornová et al. 1990, Lichter 1998, Řehounková & Prach 2006)

Substratum pH exhibited significant influence in a half of the cases listed in Table 2, mostly in those that included a broad range of this factor. Both low (Schulz &Wiegleb 2000) and high (Vaňková & Kovář 2004) pH decreased species diversity and slowed down the rate of succession in various industrial and mining deposits. Low pH about 3.5 inhibited colonization by plants in some spoil heaps from brown-coal mining (Schulz &Wiegleb 2000). In an analyses of 15 successional seres on a national scale in the Czech Republic, soil pH was the only significant predictor of successional pattern among 10 soil characteristics tested (K. Prach et al., unpulished).

Amount of nitrogen exhibited significant influence in nearly all studies in which was tested. High levels of nitrogen usually support competitive herb and grass species (Tilman 1988) which often retard the establishment of woody species (Prach & Pyšek 1994; Smit & Olff 1998).

A study comparing seres running in various habitats: a promising approach

Most of the above-mentioned studies dealt with one type of succession. We have recently developed an approach comparing a number of seres running in various human-disturbed sites over a large region (Prach et al. 2001). Sampling the 15 seres included in the same way enabled a direct robust comparison using rigorous statistics. Multivariate methods revealed that (i) species number and rate of species turnover were positively correlated with soil pH and mean annual temperature, while negatively with altitude and precipitation, and (ii) cover of woody species increased with altitude and precipitation. Thus, soil pH and macroclimate were the most important driving variables in this study (K. Prach et al., unpublished).

Future perspectives

A rigorous comparison of exact data on the course of succession, obtained in many particular sites spread over a broader geographical scale, can help to distinguish between specific and general patterns. It can thus improve successional theory which concerns broad-scale phenomena mostly on intuitive basis only (Walker & del Moral 2003, van der Maarel 2005). The broad-scale approach can help to answer some questions better than detailed local studies. The questions concern especially the differences in the course of succession along large environmental gradients, including climatic ones, divergence vs. convergence, and the influence of different land use and vegetation history. The broad-scale approach may be helpful in studying the expected influence of global change on vegetation pattern (Morecroft et al. 2004).

Because it is practically impossible, in a broad-scale study, to ensure comparativness among distant sampling sites, this must be at least partly compensated by a high number of such sites, similarly as in traditional phytosociology. The most suitable for such broad-scale studies are abandoned fields that occur in various longitude, latitude and altitudes, and are less heterogeneous than, for example, various mining sites. Thus, using a standardized sampling seems to be easier. Combination of permanent plots and space-for-time substitution (Pickett 1989) is a reasonable approach. As promising, we see the approach when the same local experiments are repeated on a large geographical scale as have been already conducted in some EU projects (van der Putten et al. 2000).

Beside potential contribution to successional theory, knowledge on variability of spontaneous succession over a landscape scale can provide a useful framework to particular restoration projects, if they rely upon spontaneous succession or expect to manipulate the spontaneous development (Luken 1990, Klötzli & Grootjans 2001). For detailed predictions of participation of particular species in succession in a disturbed site we usually need at least a pilot study conducted just in a site, because the high stochasticity and thus often low predictability of species composition in a concrete site (Glenn–Lewin et al. 1992). Very important for restoration practice is to consider the landscape context, regarding especially sources of diaspores of desirable (target), and undesirable (e. g. invasive aliens) species and their chance to establish. Using a broad-scale experience with succession, we can tentatively predict the rate and directions of succession unless a detailed study is conducted usually due to the lack of time or money or both. Various expert systems, which can combine exact detailed data with experiential, often only qualitative knowledge, may be useful in such predictions. The model TELSA was developed to predict vegetation changes in large landscape units (Kurz et al. 2000). By the expert system SUCCESS we can tentatively predict succession in various disturbed sites in the territory of the Czech Republic (Prach et al. 1999). The large-scale approach may be practically exploited in landscape planning strategy. Because of both theoretical and practical contributions, the large-scale approach will probably receive more attention in the future studies on succession.

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Chapter II

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

Řehounková, K. & Prach, K. (2006)
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Spontaneous vegetation succession in disused gravel-sand pits: Role of local site and landscape factors

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* & *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 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 5 400 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 (altitude 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 re-vegetated 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 arbitrary 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 x 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 a 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 grass-

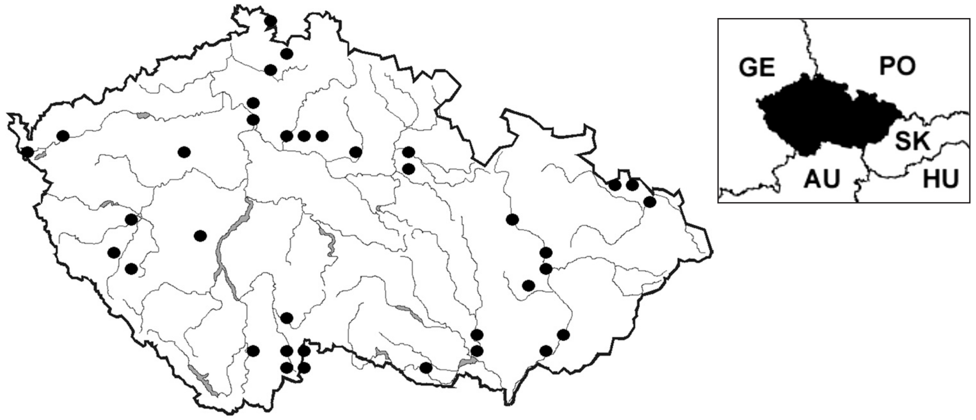

Fig. 1. Locations of the disused gravel-sand pits (black circles) within the Czech Republic. AU = Austria; GE = Germany; HU = Hungary; PO = Poland; SK = Slovakia.

land, pastures and woodland according to the Fundamental Base of Geographic Data (ZABAGED®) operated by the Czech Office for Surveying, Mapping and Cadastre.

Climatic data (mean annual temperature, mean annual precipitation) were obtained from the nearest meteorological station operated by the Czech Hydrometeorological Institute (CHI). 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 the beginning of August during 2002–2004. The following sites were arbitrary distinguished in the pits according to site moisture prior to the next analyses: dry (water table > 1 m), 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 from 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 (°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 (Fig. 2a). 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).

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			
	DRY			
Sere	(A1)	(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 & 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	Trees & shrubs (*Alnus* & *Salix* carrs)	Perennial graminoids and *Typha* beds

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 for 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 be 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. 2b). 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 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 occured 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 Mt. St. Helens, while site factors explained more of the variance in understorey vegetation in riparian forests (Holl & Crone 2004). It is obvious that the role of the two basic groups of factors depend on the scales and the system 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

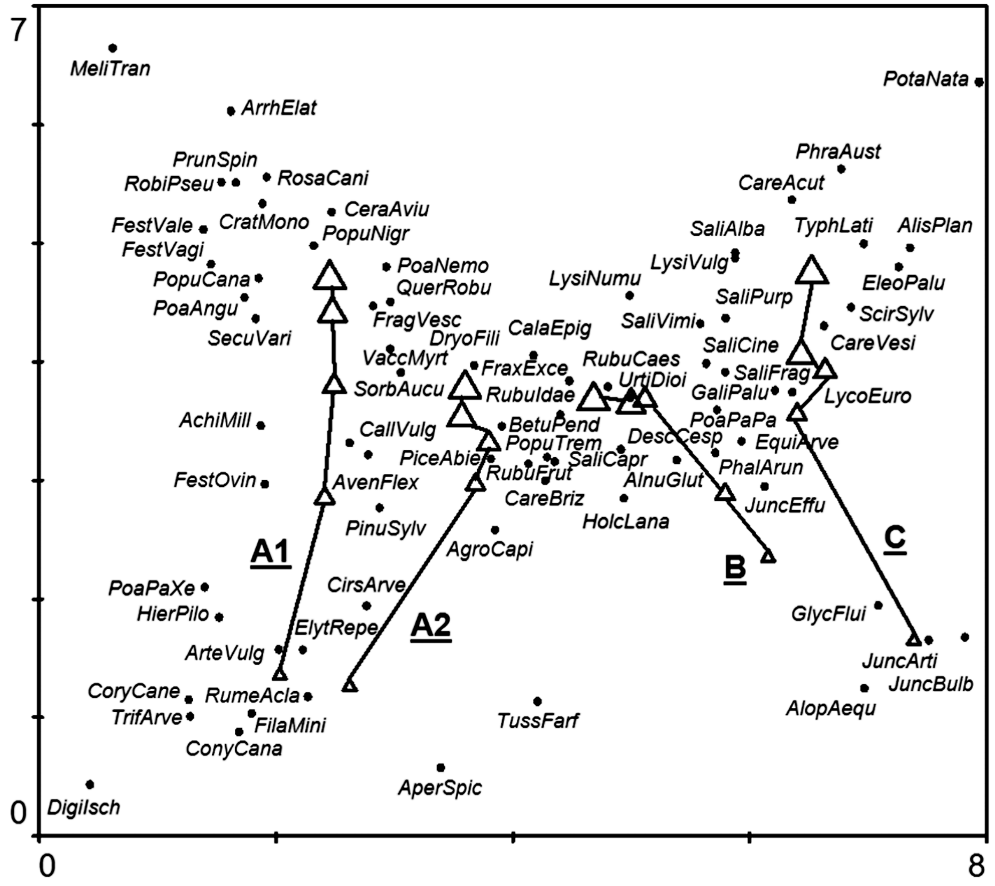

Fig. 2a. DCA ordination of species and samples. The direction of succession in particular seres are shown using centroids (triangle) for each age group. Increasing size of the symbols corresponds to increasing age: initial (1–3 yr), young (4–10 yr), middle (11–25 yr), late (26–40 yr), old (>40 yr). Seres are indicated with underlined letters: A1 – dry sere in dry and warm regions, A2 – dry sere in wet and cold regions, B – wet sere in both regions, C – shallow water sere in both region. The species with weight >5 % were considered. Species abbreviations used are composed of the first four letters of the generic and species names.

AchiMill – *Achillea millefolium*, AgroCapi – *Agrostis capillaris*, AlisPlan – *Alisma plantago-aquatica*, AlnuGlut – *Alnus glutinosa*, AlopAequ – *Alopecurus aequalis*, AperSpic – *Apera spica-venti*, ArrhElat – *Arrhenatherum elatius*, ArteVulg – *Artemisia vulgaris*, AvenFlex – *Avenella flexuosa*, BetuPend – *Betula pendula*, CalaEpig – *Calamagrostis epigejos*, CallVulg – *Calluna vulgaris*, CareAcut – *Carex acuta*, CareBriz – *Carex brizoides*, CareVesi – *Carex vesicaria*, CirsArve – *Cirsium arvense*, ConyCana – *Conyza canadensis*, CoroVari – *Coronilla varia*, CoryCane – *Corynephorus canescens*, DescCesp – *Deschampsia cespitosa*, DigiIsch – *Digitaria ischaemum*, DryoFili – *Dryopteris filix-mas*, EleoPalu – *Eleocharis palustris*, ElytRepe – *Elytrigia repens*, EquiArve – *Equisetum arvense*, FestOvin – *Festuca ovina*, FestVagi – *Festuca vaginata*, FestVale – *Festuca valesiaca*, FilaMini – *Filago minima*, FragVesc – *Fragaria vesca*, FraxExce – Fraxinus excelsior, GaliPalu – *Galium palustre*, GlycFlui – *Glyceria fluitans*, HierPilo – *Hieracium pilosella*, HolcLana – *Holcus lanatus*, JuncArti – *Juncus articulatus*, JuncBulb – *Juncus bulbosus*, JuncEffu – *Juncus effusus*, LycoEuro – *Lycopus europaeus*, LysiVulg – *Lysimachia vulgaris*, MelaTran – *Melica transsilvanicea*, PhalArun – *Phalaris arundinacea*, PhraAust – *Phragmites australis*, PiceAbie – *Picea abies*, PinuSylv – *Pinus sylvestris*, PoaAngu – *Poa angustifolia*, PoaNemo – *Poa nemoralis*, PoaPaPa – *Poa palustris* subsp. *palustris*, PoaPaXe – *Poa palustris* subsp. *xerotica*, PopuCana – *Populus x canadensis*, PopuNigr – *Populus nigra*, PopuTrem – *Populus tremula*, PotaNata – *Potamogeton natans*, PrunAviu –*Prunus avium*, PrunSpin – *Prunus spinosa*, QuerRobu – *Quercus robur*, RobiPseu – *Robinia pseudacacia*, RosaCani – *Rosa canina*, RubuCaes – *Rubus caesius*, RubuFrut – *Rubus fruticosus*, RubuIdae – *Rubus idaeus*, RumeAcet – *Rumex acetosella*, SaliAlba – *Salix alba*, SaliCapr – *Salix caprea*, SaliCine – *Salix cinerea*, SaliFrag – *Salix fragilis*, SaliPurp – *Salix purpurea*, SaliVimi – *Salix viminalis*, ScirSylv – *Scirpus sylvaticus*, SorbAucu – *Sorbus aucuparia*, TrifArve – *Trifolium arvense*, TussFarf – *Tussilago farfara*, TyphLati – *Typha latifolia*, UrtiDioi – *Urtica dioica*.

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 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 acidophillous 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 & Pets 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 influencial on the course of succession. The vegetation pattern was farther 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 1 km from a pit. The landscape factors combined were more influential (44 %) than local site factors (23 %) in affecting the course of vegetation succession.

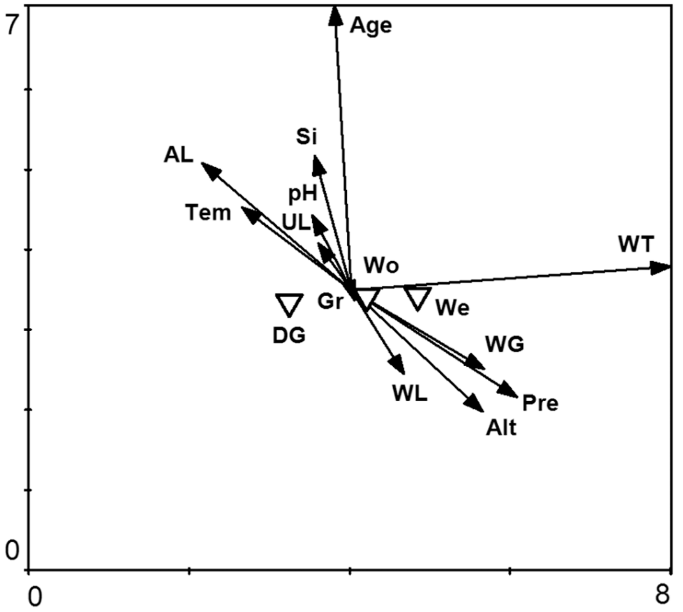

Fig. 2b. DCA ordination of significant environmental factors (P< 0,05, Table 1) fitted *ex post* as passive variables.

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Chapter III

Spontaneous vegetation succession in gravel-sand pits: a potential for restoration

Řehounková, K. & Prach, K. (2007)
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Spontaneous vegetation succession in gravel-sand pits: a potential for restoration

Abstract

Vegetation variability, the participation of target and undesirable species and the role of local species pool were studied in the course of spontaneous succession in disused gravel-sand pits. The study was conducted in various regions of the Czech Republic, Central Europe. The regions represented either agrarian lowlands with a relatively warm and dry climate, or mostly woodland uplands with a relatively cold and wet climate. The gravel-sand pits (36) comprised stages of different age from 1 to 75 years since abandonment. Three types of environments were distinguished: dry, wet, and hydric in shallow flooded sites. Altogether, 224 vegetation samples were recorded with species cover (%) visually estimated. Species affinity to different vegetation types was assessed in each sample based on the species cover. 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 landcover categories in the broader surroundings, were evaluated as well as the participation of target (grassland, woodland, and wetland) and undesirable (ruderal, alien) species. Ordination analyses showed that vegetation succession led to target grassland, wetland, or woodland vegetation depending on local site factors and the presence of (semi-) natural vegetation in the surroundings (local species pool). Restoration of target vegetation in disused gravel-sand pits by processes of spontaneous succession can be possible and successful in about 20 yr, especially if (semi-) natural vegetation exists in the surroundings. The invasion of the alien tree *Robinia pseudacacia* must be taken into consideration within the dry sites in lowlands.

Keywords: gravel-sand pits, restoration, spontaneous succession, vegetation, species pool, target species, alien species.

Nomenclature: Kubát et al. (2002)

Introduction

The restoration of land damaged by gravel-sand mining is increasingly considered in various countries. It has appeared as an important problem also in the Czech

Republic, where this study was conducted. In this country, about 5 400 ha have been affected by gravel-sand mining. Production of gravel-sand reaches 3.5 t per capita, which is slightly less than the production of the largest European producer, i. e. Germany, which produces 4.8 t per capita (Kavina 2004). The Czech land reclamation policies require that disused mining sites must be reclaimed to their previous use, i. e. to forests or agricultural use. Forest use is often interpreted as planting with conifers, mostly Scots pine (*Pinus sylvestris*). State forest agencies are often required to create plantations that generate economic benefit through timber production. Agrarian use is interpreted mostly as conversion to arable land. Reclamation to a water body is performed in sites where the gravel-sand was mined to below the groundwater table. The estimated average costs for reclamation of 1 ha is about 1.5 million Czech crowns (i. e. about US $ 60 000) depending on the type of reclamation (Kavina 2004). Thus, gravel-sand pit restoration is often a good business for reclamation companies, disregarding real necessity.

This paper contributes to the neglected topic of using spontaneous vegetation succession in ecological restoration of disused gravel-sand pits. At present, spontaneous succession is not considered as a regular rehabilitation method for post-mining landscapes; current thinking is still technocratic. We assumed that the minimum intervention inherent in spontaneous succession in the case of suitable site conditions, especially if the site is surrounded by (semi-) natural vegetation, could be an effective and economical option for establishing vegetation as found in other disused mining sites (Prach & Pyšek 2000, Wiegleb & Felinks 2001). In a previous study (Řehounková & Prach 2006) four particular seres were distinguished based on species data. Besides species, this study included ecological groups of species that are often sufficient for restoration practice (Voigt & Perner 2004). The groups were defined by affinity of species to distinct vegetation types, using the fidelity concept (Chytrý & Tichý 2003).

The questions addressed in this paper are: How does the participation of ecological groups of species change during spontaneous succession? What is the influence of the surrounding (semi-) natural vegetation on the course of vegetation succession? How successful were target and undesirable species, especially in relation to their presence in the surroundings? Is spontaneous succession really a suitable option for restoration of disused gravel-sand pits?

Methods

Study area

The study was conducted in 36 sand-gravel pits across the Czech Republic, Central Europe (48° 30´–51° N, 12°–18° 50'E). 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 in either (a) lowlands (altitude 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, or (b) uplands (altitude 255–540 m a. s. l.) having 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 pits were established on sand and gravel deposits originated from aeolian and fluvial processes during the Quarternary period (Kavina 2004). The area of the individual pits ranged from 1 to 95 ha.

Sampling

The gravel-sand pits were surveyed from 2002 to 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 re-vegetated sites, (2) the year of abandonment was known, (3) no evidence of allochthonous substrates, and (4) no evident additional disturbance. The period since abandonment (age) ranged from 1 to 75 yr. The following successional stages were arbitrarily designated: initial (1–3 yr), young (4–10 yr), middle (11–25 yr), late (26–40 yr) and old (> 41 yr). All sufficiently large and homogenous sites were sampled, avoiding those of unclear history. Phytosociological relevés 5 m x 5 m were recorded in the centre of each of the sites. In this way, 224 relevés were obtained with a mean number of six relevés per pit. Percent cover for vascular plant species and total cover of bryophytes and lichens were estimated in each relevé. The inclination of all sites where the relevés were recorded was only 0°–5°. Thus, inclination was not considered further as an explanatory variable. The presence of (semi-) natural vegetation, namely dry grasslands, forest fringes, pastures, wetlands, and woods was recorded up to 100 m from a relevé. The total list of species present in these vegetation types was made. The percentage of the main land cover categories was estimated up to 1 km from the margin of a pit. The following categories were considered: arable land, urban land, dry grasslands, wet grasslands, pastures and woodland according to the Fundamental Base of Geographic Data (ZABAGED®) operated by the Czech Office for Surveying, Mapping and Cadastre.

Climate data (mean annual temperature and 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 top soil layer were taken from each relevé and mixed into one pooled sample. Based on preliminary results of soil analyses from a pilot study on vegetation succession in disused gravel-sand 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 for determination of particles smaller than 0.05 mm. Percent weight of particular soil fractions followed the United States Department of Agriculture 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 the beginning of August in all three study years. The following sites were arbitrarily distinguished in the pits according to site moisture prior to data analysis: dry (water table deeper than 1 m), wet (water table 0–1 m below the surface) and hydric in shallow flooded sites (0.05–0.2 m above the surface).

Data analyses

Vegetation and environmental data were analyzed using multivariate methods in CANOCO version 4.5 (ter Braak & Šmilauer 2002). Determination of alien species follows Pyšek et al. (2002). Species were classified according to their affinity, called fidelity, to grassland, ruderal, woodland and wetland vegetation according to Chytrý & Tichý (2003) and then, by the same approach, to particular vegetation type listed in Fig. 1. Total species cover, representing each vegetation type, was calculated for each relevé. In this way, data were obtained on vegetation types used in a DCA as 'species' data (ter Braak & Šmilauer 2002).

A unimodal relationship between species occurrence and time was expected, therefore DCA (length of the gradient of 4.9 SD) and 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-sample distance and Hill scaling were used, because of data with long composition gradients. Environmental data were fitted *ex post* to the DCA ordination axes as passive variables (ter Braak & Šmilauer 2002). To separate the effect of locality (i. e. pit), the identification of relevés situated in the same sites within the same pit was used as a covariable in the analyses. Besides successional age, the following environmental factors were used (Table 1): pH, texture determined by percent weight of soil fractions, water table, mean annual temperature, mean annual precipitation, altitude, presence of (semi-) natural vegetation, and percentage of land cover categories in the surroundings. Forward selection was conducted with all environmental factors using the Monte-Carlo permutation test with 999 permutations.

DCA species response curves of target and undesirable species groups were performed using Canodraw (ter Braak & Šmilauer 2002). The effect of fertile black locust (*Robinia pseudacacia*), present up to a distance of 100 m from a sampling site, on particular successional stages (initial, young, middle, late, old) in disused gravel-sand pits in lowlands (A1), was tested by CCA using the Monte-Carlo permutation test with 999 permutations. The occurrence of *R. pseudacacia* in other seres (A2, B, C) and in their surroundings was very rare, thus it was not tested.

Results

Vegetation pattern and environmental factors

The ordination analyses distinguished four particular seres: dry in lowlands (A1), dry in uplands (A2), wet (B) and flooded (C), with the latter two disregarding the regions. The groups of species belonging to different vegetation types, i. e. grassland, woodland, wetland and ruderal, used in the ordination are given in Fig. 1. Site moisture was the main factor delimiting the seres, while macroclimate separated sub-seres only in the case of dry sites.

The dry sere in lowlands (A1) started with annual and perennial thermophilous ruderal species. Some species typical of late successional, open herbaceous, open sand, and dry grassland vegetation on shallow soils, e. g. grey hair-grass (*Corynephorus canescens*), occurred already in the initial stages. The course of succession in the dry sites in lowlands ran towards two different vegetation types: dry shrubby grasslands or *Robinia* groves.

The initial stages (1–3 yrs) of the dry sub-sere in uplands (A2) were dominated by perennial mesophilous ruderal and grassland species. There was a gradual transition from grassland to woodland in this sub-sere. Broad-leaved deciduous forests are the most distinguished vegetation type of late stages (>41 yrs) in these dry sites in uplands.

The wet sere (B) started with nonruderal wet grassland species. This sere changed over time from wet grassland to wet woodland. The old stages (>41 yrs) were represented by alder and willow carrs.

The initial stages (1–3 yrs) of the hydric sere in shallow flooded sites (C) were dominated by the nonruderal annual species of wet eutrophic soils. Species typical of reed and tall-sedge beds dominated in the old stages (>41 yrs).

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

	Age	age from abandonment	yr
Local site factors (LSF)	Cl	proportion of clay	%
	Gr	proportion of gravel	%
	pH	pH	1–14
	Sa	proportion of sand	%
	Si	proportion of silt	%
	WT	water table	m
Landscape factors (LF)	**AL**	proportion of arable land up to 1 km from a pit	%
	Alt	altitude	m a. s. l.
	DG	presence of dry grasslands up to 100 m from sampling site	yes/no
	DL	proportion of dry grasslands up to 1 km from a pit	%
	Ff	presence of forest fringes up to 100 m from sampling site	yes/no
	Pa	presence of pastures up to 100 m from sampling site	yes/no
	PL	proportion of pastures up to 1 km from a pit	%
	Pre	mean annual precipitation	mm
	Tem	mean annual temperature	^{0}C
	UL	proportion of urban land up to 1 km from a pit	%
	Wo	presence of woods up to 100 m from sampling site	yes/no
	WG	proportion of wet grasslands up to 1 km from a pit	%
	We	presence of wet grasslands up to 100 m from sampling site	yes/no
	WL	proportion of woodland up to 1 km	%

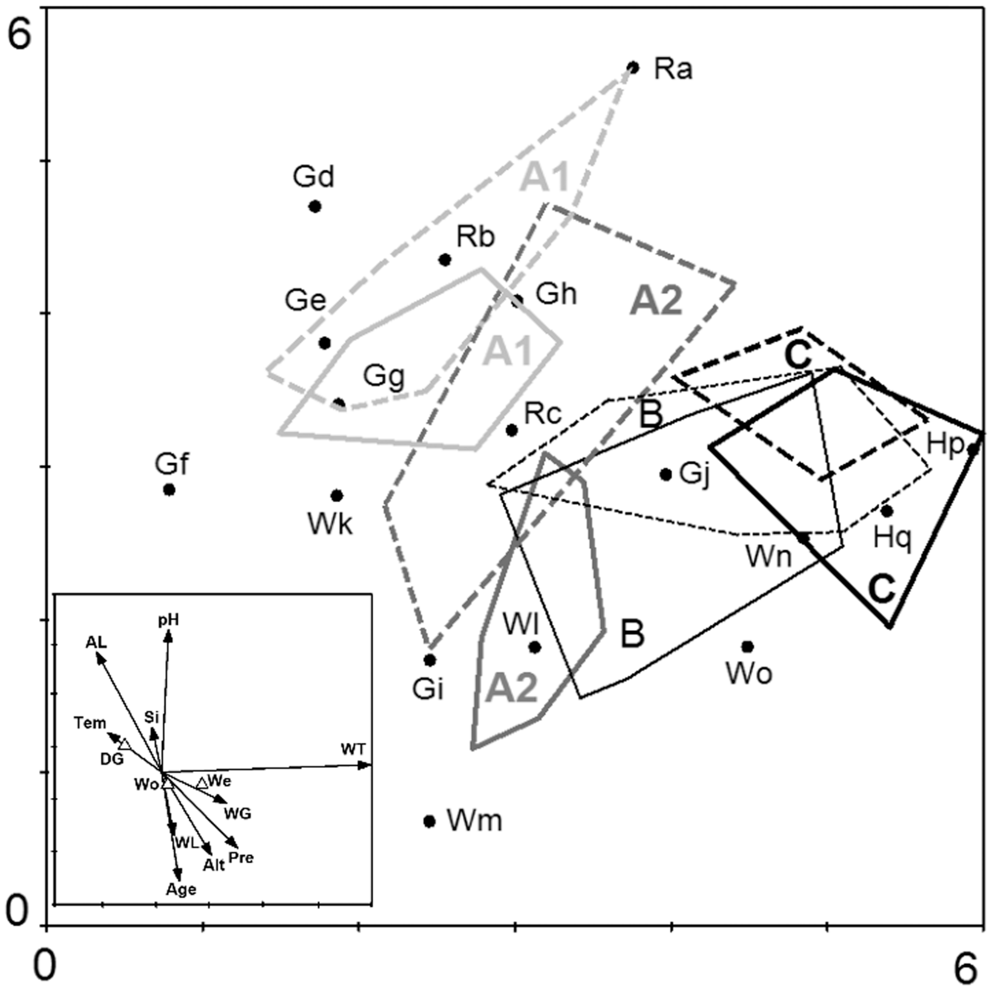

Fig. 1. DCA ordination of species groups and samples.

Polygons enclose the vegetation records of initial (1–3 yrs, dashed line) and old (> 41 yr, solid line) stages of each sere. Seres: A1 – dry in lowlands, A2 – dry in uplands, B – wet, C – shallow flooded. The inset diagram shows significant environmental variables ($P < 0.001$, see Table 1) fitted *ex post* as passive variables. The vegetation types with weight > 5 % were considered:

Grassland: Gd – open herbaceous grassland on shallow soils, Ge – close dry grassland, Gf – dry shrubby grassland, Gg – open sand grassland with *Corynephorus canescens*, Gh – mesic grassland, Gi – *Nardus* grassland & heathland, Gj – wet grassland

Woodland: Wk – *Robinia* grove, Wl – coniferous forest, Wm – broad-leaved deciduous forest, Wn – riverine willow scrub and willow-poplar forest, Wo – alder and willow carrs

Wetland: Hp – annual vegetation of wet eutrophic soils, Hq – reed and tall-sedge bed

Ruderal vegetation: Ra – with prevailing annuals, Rb – with prevailing perennials on drier sites, Rc – with prevailing perennials on mesic and wet sites

Because the DCA (λ_1: 0.788, λ_2: 0.667) and CCA (λ_1: 0.654, λ_2: 0.562) showed basically the same pattern, only DCA graphical outputs are displayed (Fig. 1). The environmental factors, which were significantly correlated with the ordination axes, are indicated in bold in Tab. 1. The occurrence of dry grassland, wet grassland, and woodland species in disused gravel-sand pits was clearly associated with the presence of respective vegetation types in the surroundings of a sampling site (Table 1).

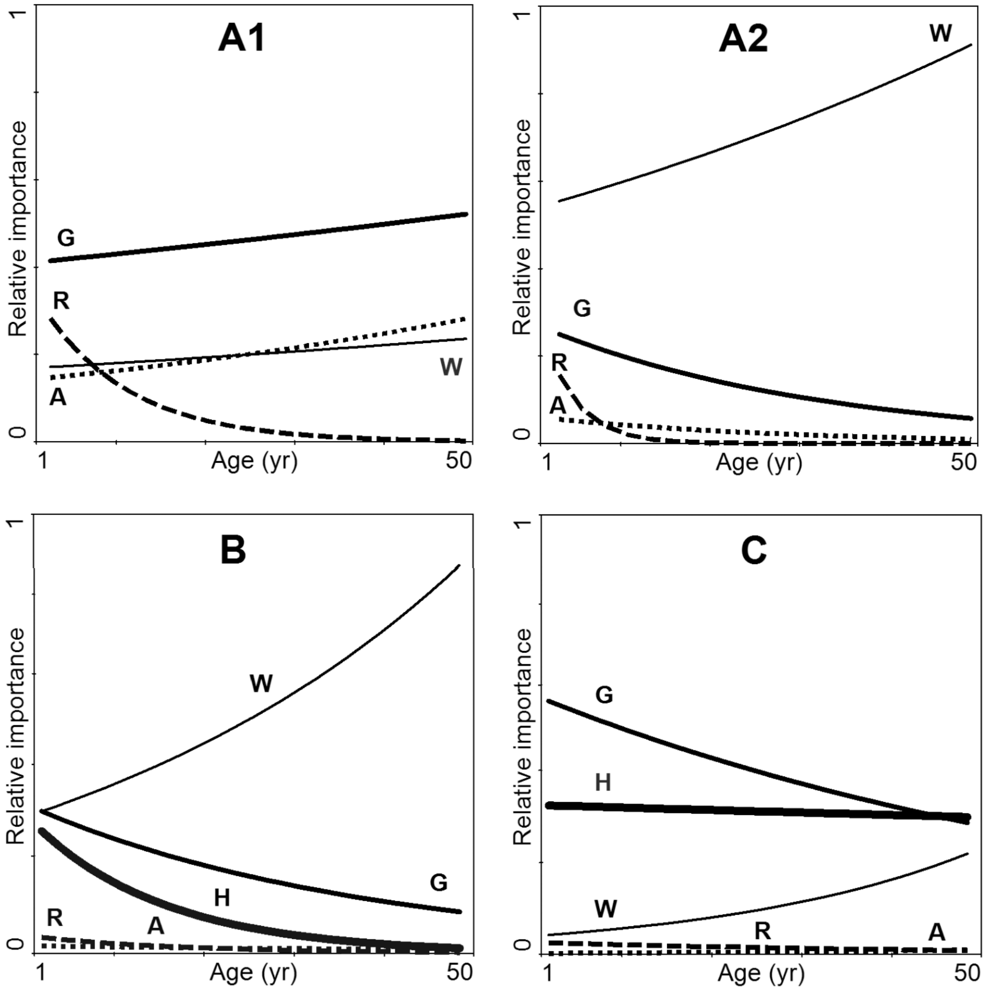

Fig. 2. DCA responses curves of target and undesirable groups of species.
Seres: A1 – dry in lowlands, A2 – dry in uplands, B – wet, C – shallow flooded. Target groups of species: G – grassland, H – wetland, W – woodland. Undesirable groups of species: A – aliens, R – ruderals. Relative importance of particular groups of species was calculated from species cover.

Target and undesirable groups of species

Changes in the proportion of target (grassland, woodland and wetland) and undesirable (ruderals and aliens) groups of species during succession in each sere are shown in Fig. 2. The importance of grassland species decreased in most sites, except dry sites in lowlands, during succession, while woodland species increased. The importance of wetland species in shallow flooded sites remained stable for 50 years, in wet sites they decreased rapidly in the course of succession due to the expansion of woodland species (Fig. 2). The importance of undesirable species groups (ruderals, aliens) decreased in the majority of sites, except the alien group of species in dry sites in lowlands; this reflects the expansion of *Robinia pseudacacia* in some sites. The participation of ruderal and alien species was much lower in wet than in dry sites.

Nearly three-quarters of target grassland and woodland species, occurring in the surroundings, appeared in the pits (Fig. 3). Wetland species were the most successful group of target species, because nearly 90% expanded into the pits from the surroundings, and some others migrated even from a longer distance. Only about 50% of ruderal species expanded from the surroundings. However, the least desirable alien species were rather successful and about three-quarters expanded from the surroundings into the pits.

The presence of mature *R. pseudacacia* trees in the surroundings (up to 100 m from a sampling site) had a significant effect (CCA, F=2.012, $P<0.05$, λ_1: 0.571, λ_2: 0.456) on the course of succession in dry sites in lowlands (Fig. 4). The direction of succession was very similar only in the initial and young stages (1–10 yrs) irrespective of the presence of fertile *R. pseudacacia* in the surroundings. However, the differences between sites with and without *R. pseudacacia* in the surroundings increased with increasing successional age. In the former sites, the old stages were formed by *Robinia* groves accompanied by nitrophilous species such as small balsam (*Impatiens parviflora*), greater celandine (*Chelidonium majus*), herb bennet (*Geum urbanum*) and herb robert (*Geranium robertianum*). The old stages in sites without *R. pseudacacia* in the surroundings were formed by a (semi-) natural wooded grassland.

Discussion

Analyses based on species groups, representing different vegetation types, showed a similar pattern of vegetation succession as those based on particular species. Similar conclusions were found also for the role of environmental factors (see details in Řehounková & Prach 2006). This indicates that the groups of species can be used instead of particular species for an outline of succession in restoration programs (Voigt & Perner 2004). However, the scientific basis should be at the species level, because of the assignation of species to groups.

Undesirable ruderal and alien plants can be expected to be of larger importance if a disturbed site is located in heavily altered landscapes such as those composed mostly of intensively used agrarian or urban land (Roy et al. 1999, Prach et al. 2001). The occurrence of ruderals and especially aliens was lower in pits located in less human altered landscapes, which have a higher proportion of forests and are located in wetter and colder regions (see the sub-sere A2); this seems to be a general pattern. The lower importance of ruderals and aliens in uplands and wet sites (seres B and C) corresponds with the fact that more Central European ruderal and alien species require drier and warmer sites than those in the local flora (Pyšek et al. 1995).

Although it has been noted that the surrounding vegetation generally influence succession in post-mining sites (e.g. Roche et. al. 1998, Ninot et al. 2001, Martínez-Ruiz et al. 2001), few quantitative studies have focused on this topic (Borgegård 1990, Brändle et al. 2003). The restoration potential of the surrounding vegetation, in influencing the processes of spontaneous vegetation succession in disused pits, is quite high (Fig. 3). A comparably high number of species were found in both the pits and surrounding (semi-) natural vegetation in the case of woodland, grassland and especially wetland species. Alien species were also successful in colonizing the pits. The low proportion of ruderal species was surprising because many are easily dispersed generalists (Grime 2002). It seems that the nutrient-poor environment of the gravel-sand pits is not very favorable for them.

Borgegård (1990) studied the effect of surrounding vegetation represented by different forest types in 68 abandoned gravel pits, ranging in age from 1 to 100 years throughout Sweden, and found that, on average, only about one third (35%) of spe-

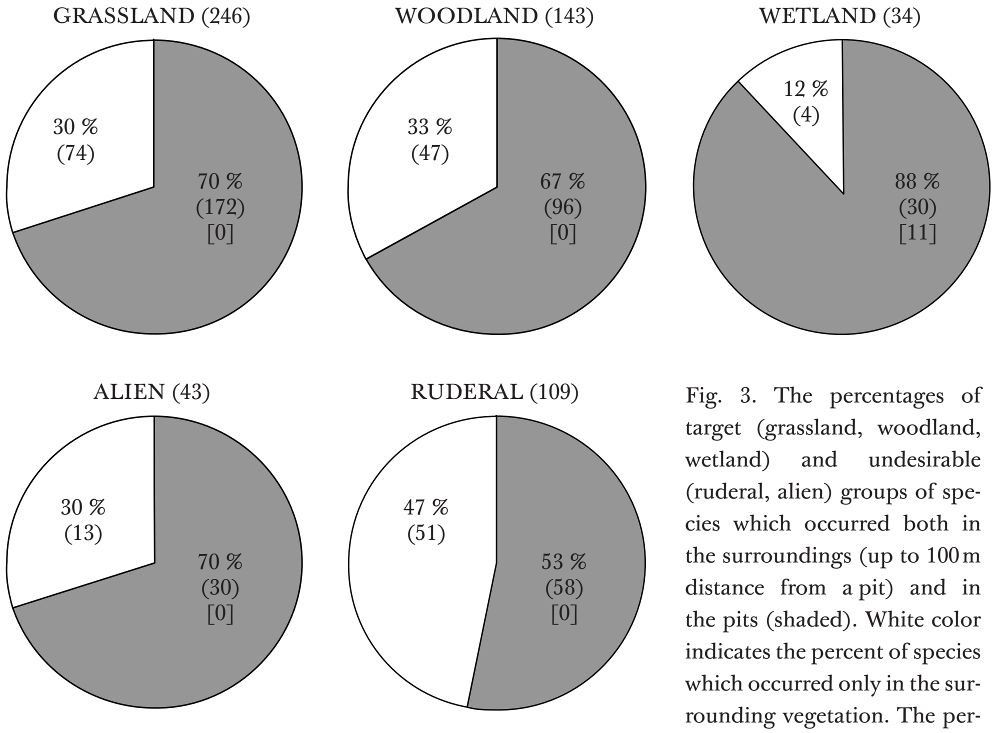

Fig. 3. The percentages of target (grassland, woodland, wetland) and undesirable (ruderal, alien) groups of species which occurred both in the surroundings (up to 100 m distance from a pit) and in the pits (shaded). White color indicates the percent of species which occurred only in the surrounding vegetation. The percentages of target and undesirable groups of species were calculated based on the number of species in each group (given in parentheses). The number of species occurring only in pits and not in the surroundings is given in square brackets.

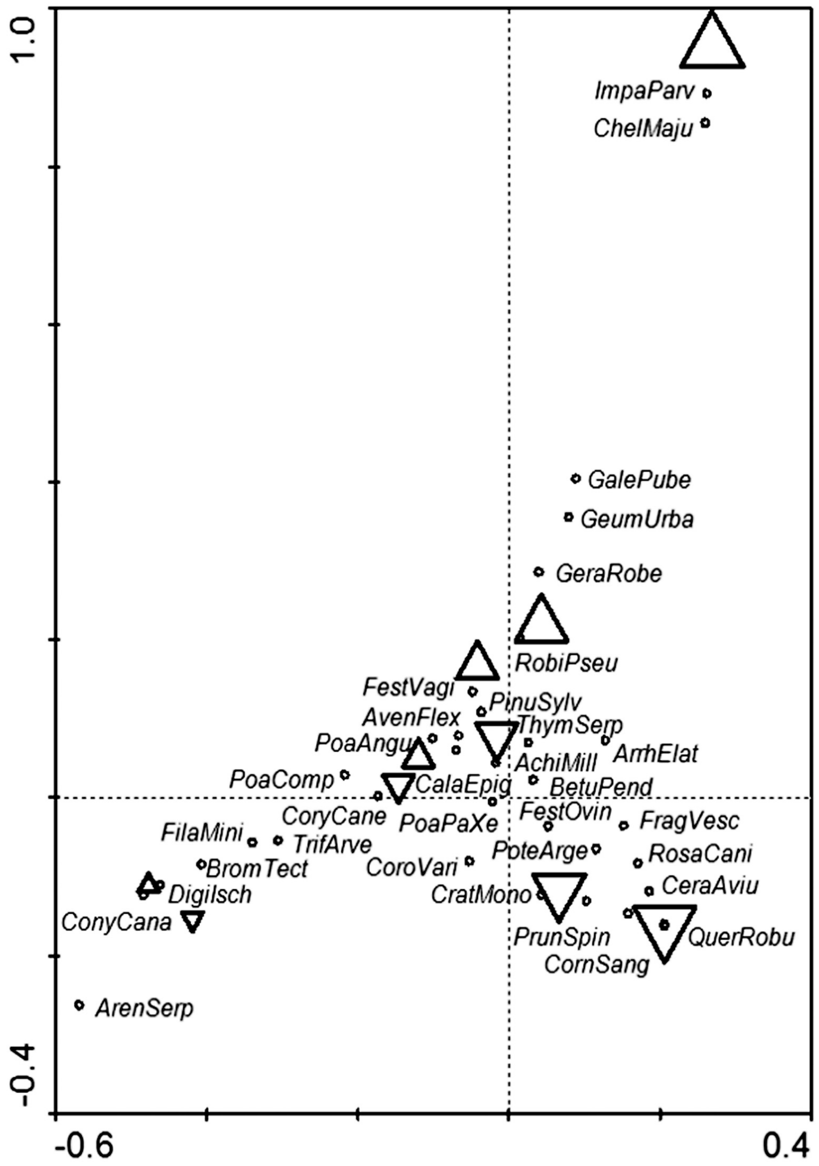

Fig. 4. CCA ordination of species and successional stages in dry regions, sorted according to the presence (△) and absence (▽) of generative *Robinia pseudacacia* in the surrounding vegetation (up to 100 m from a sampling site – sere A1, $P < 0.05$). The direction of succession is shown using centroids (triangle) for each age group. Increasing size of the symbols corresponds to increasing age: initial (1–3 yr), young (4–10 yr), middle (11–25 yr), late (26–40 yr), old (>41 yr). Species with weight >5 % were considered. Species abbreviations used are composed from the first four letters of generic and species names.

AchiMill – *Achillea millefolium*, ArenSerp – *Arenaria serpyllifolia*, ArrhElat – *Arrhenatherum elatius*, AvenFlex – *Avenella flexuosa*, BetuPend – *Betula pendula*, BromTect – *Bromus tectorum*, CalaEpig – *Calamagrostis epigejos*, CeraAviu – *Cerasus avium*, ChelMaju – *Chelidonium majus*, ConyCana – *Conyza canadensis*, CornSang – *Cornus sanguinea*, CoroVari – *Coronilla varia*, CoryCane – *Corynephorus canescens*, CratMono – *Crataegus monogyna*, DigiIsch – *Digitaria ischaemum*, FestOvin – *Festuca ovina*, FestVagi – *Festuca vaginata*, FilaMini – *Filago minima*, FragVesc – *Fragaria vesca*, GalePube – *Galeopsis pubecens*, GeraRobe – *Geranium robertianum*, GeumUrba – *Geum urbanum*, ImpaParv – *Impatiens parviflora*, PinuSylv – *Pinus sylvestris*, PoaAngu – *Poa angustifolia*, PoaComp – *Poa compressa*, PoaPaXe – *Poa palustris* subsp. *xerotica*, PoteArge – *Potentilla argentea*, PrunSpin – *Prunus spinosa*, QuerRobu – *Quercus robur*, RobiPseu – *Robinia pseudacacia*, RosaCani – *Rosa canina*, ThymSerp – *Thymus serpyllum*, TrifArve – *Trifolium arvense*.

cies were shared by gravel pits and their surroundings. About half of the local species pool was found within non-reclaimed lignite mining sites in Germany (Brändle et al. 2003). Recently established forest fragments in Belgium contained 47 % of the flora found within a 100 m radius in the neighbouring old forest (i. e. local species pool) (Butaye et al. 2002). It is likely that the target vegetation may be well restored via natural colonization in those disused gravel-sand pits that are adjacent to (semi) natural vegetation, which can act as seed sources for many target species. Long-distance dispersal mostly by epizoochory, besides seed sources in the surroundings, may also be important for the establishment of wetland vegetation (Krahulec & Lepš 1994). If the pit is flooded, it is highly likely that water birds will help the expansion of wetland species into the pit because of bird migration among water bodies across the landscape. In this study, 11 wetland species were found to occur only in the pits and were not observed in the close surroundings; there were no such species among the other groups. If wetlands, including shallow water bodies, occurred in the close vicinity, there was a high probability that the respective species occurred in a pit. This is also related to the frequent short-distance migration of waterfowl (Figuerola et al. 2005).

Alien species may be able to colonize early after a disturbance, interfering with restoration efforts or altering successional processes that would otherwise lead to a native assemblage (D'Antonio & Meyerson 2002). In this study, this situation was associated with the dry sere in lowlands, which provided suitable conditions for the alien *R. pseudacacia*. This species can form compact cover and change the course of vegetation succession from the target of shrubby grassland to undesirable *Robinia* groves. The same was observed in the case of disused stone quarries by Novák & Prach (2003) and by Cleveland & Kjelgren (1994) in deep-tilled minesoil. *Robinia pseudacacia* is easily dispersed vegetatively and by seeds over a short distance (Halassy 2004, Török & Lohász 2004, Dzwonko & Loster 1997), and it is, therefore, not surprising that it is able to colonize the sites in gravel-sand pits only if it occurs in their close proximity. The role of *R. pseudacacia* in succession may be complex, since it also affects litter decomposition, nitrogen fixation and the mineralization rate of other nutrients (White et al. 1988). The effect of *R. pseudacacia* on species composition of the field layer through nitrogen fixation is likely to be strongest on poor sandy soils where nitrogen is the main limiting soil resource, resulting in a considerable rise in the number and cover of nitrophilous and ruderal herb species (see also Dzwonko & Loster 1997, Török & Lohász 2004).

Table 2. Survey of old vegetation stages in the disused gravel-sand pits in relation to the main environmental factors.

	Increasing site moisture			
Sere	(A1) **DRY**	(A2)	**WET** (B)	**SHALLOW WATER** (C)
Climatic region	Warm & Dry	Cold & Wet	Any	
Altitude	Lowlands	Uplands	Any	
Landscape	Agrarian (arable land) & Urban	Woodland & Agrarian (grassland)	Any	
Target vegetation	**SHRUBBY GRASSLAND**	**DECIDUOUS WOODS**	**ALDER & WILLOW CARRS**	**TALL SEDGE, REED & CATTAIL BEDS**
Undesirable vegetation	*Robinia pseudacacia* **groves**	**None**	**None**	**None**

Differences in nitrogen and light availability are expected to contribute to the strong divergence in the successional development of older stages of the dry sub-sere in lowlands (see also Peloquin & Hiebert 1999). Despite the fact that there are some studies which documented slow colonization of *Robinia* groves by native tree and woodland herb species in Europe (Hruška 1991, Dzwonko & Loster 1992), no signs of succession from *Robinia* groves to woods dominated by native tree species were observed in the gravel-sand pits, as well as in other disturbed sites, in the Czech Republic.

The successional trends are summarized and generalized in Table 2, in regards to site moisture and geographical location (being related to macroclimate). It is obvious from the table that site moisture is the main factor determining the physiognomy of the vegetation and participation of ecological groups of species. Macroclimate is a second predictor only in the case of dry sites, where low soil moisture may be a limiting factor. Naturally, this is not the case in wet and flooded sites where other factors are more important. The potential of spontaneous vegetation succession for restoration of disused gravel-sand pits is also seen from the table, which may be used as a rough guide of succession in restoration programs for particular pits.

Implications for practice

- Restoration of target vegetation (i. e. grassland, woodland or wetland) in the stu-died disused gravel sand pits by processes of spontaneous vegetation succession can be successfully achieved in about 20 years. Thus, no technical restoration is needed.
- The presence of (semi-)natural vegetation in the close surroundings facilitates this process; thus it is important to preserve at least some remnants of the vegetation during mining and postmining operations.
- However, the invasion of alien species, such as black locust (*Robinia pseudacacia*) in dry sites in lowlands in this study, must be taken into consideration. Such species should be eradicated in the vicinity of a pit before the onset of succession.

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Chapter IV

Life-history traits and habitat preferences of species in relation to their colonization success in disused gravel-sand pits

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[manuscript]

Life-history traits and habitat preferences of species in relation to their colonization success in disused gravel-sand pits

Abstract

We used plant life-history traits and habitat preferences by species to find which of the characteristics predict establishment of species in different successional stages inside the disused gravel-sand pits.

Data were collected in 36 abandoned gravel-sand pits in various regions of the Czech Republic. Seral stages in the gravel-sand pits ranged in age from 1–75 years. Together 224 phytosociological relevés were recorded in 5 m x 5 m plots in representative parts of all available seral stages. Complete lists of species occurring in (semi-) natural habitats were surveyed up to the distance of 100 m from each relevé. Colonization success of each species was expressed by an index between 0–1 which was obtained as the ratio: the number of relevés with species present/the number of relevés with the species occurrence in the surroundings. Data were elaborated by the ordination analysis and the regression tree analysis.

Results showed that certain traits were linked with colonization success in three main stages of vegetation succession: young, middle, and late. Generally, the most successful colonisers of disused gravel-sand pits were hydrophytes with ability to vegetative reproduction. At the beginning of succession, the most important role played anemochorous, stress tolerant species, possessing light diaspores, being typical for nitrogen poor and acid habitats. Later, the importance increased of sciophylous and nitrophilous species of mesic habitats, with heavier diaspores, mostly phanerophytes or geophytes, often with ability to vegetative reproduction and higher demands for pH. Probability of species occurring in the surroundings to colonize gravel-sand pits is decreasing in succession: young stages – 41 %, middle stages – 30 %, late stages – 15 %.

Synthesis and application

Plant functional traits were recognized as powerful tools to predict colonization success of plants available in the local species pool. It may help in prediction of vegetation succession in various human-disturbed sites and thus be used in various restoration programmes.

Keywords: regression trees, plant traits, habitat preferences, gravel-sand pits
Nomenclature: Kubát et. al. (2002)

Introduction

There is an increasing interest in using species' traits, and the grouping of species by their traits into functional types, to predict vegetation responses to environmental factors or human activities, such as climate (Díaz & Cabido 1997), disturbance (McIntyre et al.1999; Lavorel et al. 1997), land-use (Lloret & Montserrat 2003; Verheyen et al. 2003), ecological restoration (Pywell et al. 2003) or grazing (de Bello et al. 2005). The concept of ecological succession often underpins the studies (Walker & del Moral 2003). Relatively little is known how successfully established species on newly created sites differ in their biological and ecological traits from those which do not play an important role in vegetation succession (Rydin & Borgegård 1991; Prach & Pyšek 1999).

Dispersal of diaspores into newly created habitats, especially if a viable seed bank is lacking, may be considered as a key process for the establishment of vegetation (Bakker et al. 1996). How many and which species ultimately will be able to reach such habitats by their diaspores depends on characteristics of the diaspores, availability and behaviour of the transporting vectors, and the composition, abundance and proximity of the local seed sources (Díaz et al. 1998; Yao et al. 1999; Nathan & Muller-Landau 2000; Ozinga et al. 2005). Beside dispersal itself, other reproductive characteristics, such as germination and vegetative spread, and ecological demands of species are usually considered to determine colonization success of species during succession (van der Valk 1992). Integral categories such as life-forms and life-history strategies may be good predictors of species colonization success (Grime 2001). Local site factors act as selective filters of the species possessing different traits (Bazzaz 1996). Thus, a joint analysis of species and habitat characteristics may increase prediction of species success which may have, besides theoretical, also practical implications especially in restoration ecology (van Andel & Aronson 2006).

In previous studies, we analysed role of local site and landscape factors in the course of spontaneous vegetation succession in disused gravel-sand pits over a broader geographical scale (Řehounková & Prach 2006; Řehounková & Prach 2007). In the present paper, we attempted to define trait-based groups of plant species occurring in the close surrounding of disused gravel-sand pits in relation to their colonization success inside the pits. We considered in our study a short-distance dispersal, which was arbitrarily defined as dispersal up to 100 m distance following Cain et al. (2000). Considering dispersal may allow prediction and generalization of vegetation changes in disturbed sites in a landscape scale (Verheyen et al. 2003).

The ordination and regression tree analyses were used to express relationships between species traits and habitat preferences and the colonization success of the species. The following main questions were asked: Species of what traits and ecological demands are successful/unsuccessful colonizers of disused gravel-sand pits? How do the traits differ among species successful in differently aged successional stages?

Methods

Study area

The study was conducted in gravel-sand pits spread over the Czech Republic, Central Europe (48° 30´–51° 00´ N, 12° 00´–18° 50' E) in 2002–2004. The altitude of the studied pits ranged from 170 to 540 m a. s. l. The history of each pit was reconstructed on the basis of official records from mining companies and county authorities and by interviewing local administrators. The pits and representative disused sites in each of them were selected using the following criteria: (1) the existence of sufficiently large, spontaneously re-vegetated sites, (2) the year of abandonment was known, (3) no evidence of allochtonous substrates, (4) no evident additional disturbance. 36 pits in the entire country were those which matched the criteria. The period since abandonment (age) ranged from 1 to 75 years among the particular sites. Three main successional stages were distinguished according to age: young (1–10 yr), middle (11–20 yr) and late (21–75 yr).

The pits were classified according to their location in either (a) lowlands (altitude 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, or (ii) uplands (altitude 255–540 m a. s. l.) having a relatively cold and wet climate (mean annual temperature 6.8–7.9 °C, mean annual precipitation 551–780 mm) and dominaned by woodland. All of the sites developed on sandy and gravelly deposits originated from eolic and fluvial processes in the Quartenary period. The pit area ranged from 1 to 95 ha.

Sampling

Differently aged successional stages were distinguished in each pit and phytosociological relevés (5 x 5 m) were recorded in the centre of each of the stages (for details see Řehounková & Prach 2006). For the purpose of this study, a species list was considered for all relevés of the respective successinal stage, i. e. young, middle, and late. Species which attained dominance at least 1% at least in one relevé were considered as successfully established in the respective successional stage. The surrounding (semi-) natural vegetation, i. e. not influenced by mining and reclamation activities – woodland, grassland, wetland, occurring up to 100 m from each relevé was surveyed and all vascular plant species were recorded. We considered only species occurring in (semi-) natural vegetation which was expected to exist before mining started and which is the most relevant from the point of view of restoration of a site. Thus, we neglected species often of the same seral stage which would bias the next calculations.

Data elaboration

Colonization success was expressed as an index between 0–1. It was calculated for each species separately and expressed as the ratio: number of relevés in which the species was present/number of relevés with the species occurrence in (semi-)natural vegetation in the surroundings.

Altogether seven basic life-history traits and five habitat preference characteristics based on the Ellenberg indicator values for light, moisture, nitrogen and soil reaction (Ellenberg et al. 1992) were considered (see Table 1). The information was compiled from available databases and other relevant sources: Klotz et al. (2004), Grime et al. (1988), Ellenberg et al. (1992), Bonn et al. (2000), Jackel et al. (2006), and Tackenberg et al. (unpublished).

The habitat preferences were grouped each into three categories as evident from Table 1. The degree of hemeroby was grouped into the category of habitats (Klotz et al. 2004). Habitat type: Natural – species of very weakly utilized woodlands, near-natural dry grasslands or wetlands; (Semi-)natural – species of utilized forest with well developed shrub and herb layer, slightly utilized pastures and meadows; (Semi-)cultural – species of intensely used pastures, meadows or forest with little developed shrub and herb layer; Cultural – species of arable fields with typical weed communities, ruderal sites (e. g. landfills). Traits and habitat preference characteristics were categorized by means of fuzzy coding, i. e. the species can belong to several classes of one trait at the same time. For example, species, which can disperse by anemochory and zoochory would have a score 0.5 as anemochorous and 0.5 as zoochorous with the total sum 1 for the trait dispersal.

Table 1. Numbers of vascular plant species, relevés and gravel-sand pits representing the particular successional stages.

Number of species in surroundings: Total – number of vascular plant species in the surroundings; NE – remaining species in the surroundings not yet successfully established in the previous stages, a species was considered as successfully established if obtained at least 1 % of cover in any relevé of the respective successional stage. Only surroundings – number of species occurred only in the surroundings and not spread into the gravel-sand pits; species with cover ≥ 1 % occurred already in the previous stage/stages in the gravel-sand pits were not counted.

Number of species in gravel-sand pits: Total – the number of vascular plant species which occurred in the respective stages in the disused gravel-sand pits, the species with cover ≥ 1 % occurred already in the previous stage/stages in the gravel-sand pits were not counted. Cover < 1 % – number of vascular plant species with cover < 1 % first occurred in the particular stages in disused gravel-sand pits. Cover ≥ 1 % – number of vascular plant species with cover > 1 % first occurred in the particular stages in disused gravel-sand pits.

Stage	**Number of species in surroundings**			**Number of species in gravel-sand pits**			**Number of relevés**	**Number of gravel-sand pits**
	Total	**NE**	**Only surroundings**	**Total**	**Cover > 1 %**	**Cover < 1 %**		
Young (1–10 years)	507	507 (100 %)	252 (50 %)	145 (50 %)	107	107	70	25
Middle (11–20 years)	544	472 (86 %)	309 (65 %)	163 (35 %)	85	78	67	25
Late (21–75 years)	545	388 (71 %)	252 (65 %)	136 (35 %)	62	74	87	27

Table 2. Summary of life-history traits and habitat preferences of species used in the analyses.

	Groups	**Categories**	**Description**	**Remarks**
Life - history traits	1. Strategy	C strategist	C	Klotz S., Kühn I. & Durka W. (2004)
		S strategist	S	
		R strategist	R	
	2. Life forms	Therophyte	Th	Klotz S., Kühn I. & Durka W. (2004)
		Chamaephyte	Ch	
		Geophyte	Ge	
		Hemicryptophyte	He	
		Hydrophyte	Hy	
		Nanophanerophyte	NP	
		Macrophanerophyte	MP	
	3. Reproduction	Seed	Seed	Klotz S., Kühn I. & Durka W. (2004)
		Seed & Vegetative	SeedVeget	
		Vegetative	Veget	
	4. Self-sterility	Self-compatibel	Compatibel	Klotz S., Kühn I. & Durka W. (2004)
		Self-incompatibel	Incompatibel	
	5. Pollen vector	Insect	InsectPol	Klotz S., Kühn I. & Durka W. (2004)
		Spontaneous	SpontPol	
		Wind	WindPol	
	6. Dispersal	Anemochory	Anemochory	Bonn et al. (2000), Jackel et al. (2006), Tackenberg et al. (unpublished)
		Autochory	Autochory	
		Hemerochory	Hemerochory	
		Hydrochory	Hydrochory	
		Special disp. mechanisms	SpecialDisp	Ballochory, blastochory, herpochory, bolechory. Ombrochory in sense of Bonn et al. (2000), Jackel et al. (2006), Tackenberg et al. (unpublished)
		Zoochory	Zoochory	Diaspore weight < 1 mg Klotz S., Kühn I. & Durka W. (2004)
	7. Diaspore weight	Light diaspore	LightDiasp	Diaspore weight < 1 mg Biolflor
		Heavy dispore	HeavyDiasp	Diaspore weight ≥ 1 mg Klotz S., Kühn I. & Durka W. (2004)
Habitat preferences	8. Habitat naturalisness	Natural	Natur	Klotz S., Kühn I. & Durka W. (2004)
		(Semi-)natural	Semi-natur	
		(Semi-)cultural	Semi-cultur	
		Cultural	Cultur	
	9. Light	Light	Light	Indicator values 7–9: Ellenberg et al. (1992)
		Semi-shade	Semi-shade	Indicator values 4–6: Ellenberg et al. (1992)
		Shade	Shade	Indicator values 1–3: Ellenberg et al. (1992)
	10. Moisture	Dry	Dry	Indicator values 1–4: Ellenberg et al. (1992)
		Mesic	Mesic	Indicators values 5–8: Ellenberg et al. (1992)
		Wet	Wet	Indicator values 9–11: Ellenberg et al. (1992)
	11. Nitrogen	Poor	Poor N	Indicator values 1–3: Ellenberg et al. (1992)
		ntermediate	Inter N	Indicators values 4–6: Ellenberg et al. (1992)
		Rich	Rich N	Indicators values 7–9: Ellenberg et al. (1992)
	12. Reaction (pH)	Acid	Acid pH	Indicator values 1–5: Ellenberg et al. (1992)
		Neutral	Neutral pH	Indicator values 6–7: Ellenberg et al. (1992)
		Basic	Basic pH	Indicator values 8–9: Ellenberg et al. (1992)

Two approaches were applied to evaluate which species characteristics are related to the colonization success of species in the course of succession: the ordination analysis (CANOCO, ter Braak & Šmilauer 2002) and the regression tree analysis (R software, R Development Core Team 2004). In ordination, the Canonical Correspondence Analysis (CCA) was carried out with the only significant explanatory variable, i. e. age (years since the site abandonment). The score of species on the ordination axis was used as the species response to the age of site. In the second step, the Detrended Correspondence Analysis (DCA) was performed. The traits and habitat characteristics were used as a "species" data. The species response to the successional age, obtained by CCA, and the colonization success of species were fitted *ex post* as passive variables (Lepš & Šmilauer 2003).

The regression trees provide an alternative to regression techniques (Vayssières et al. 2000). The tree is built by repeatedly splitting the data, defined by a simple rule based on a single explanatory variable. At each split, the data are partitioned into two exclusive groups, each of which is a homogeneous as possible. The length of the tree was controlled by choosing the best trade-off between explained deviance and tree size through cross-validation procedure. Pruning the trees was applied (Venables & Riplay 2002; Thuiller et al. 2003). The regression trees are used as a suited tool for analyses of rather robust ecological data, but only rarely used to predict vegetation succession (e.g., de Bello et al. 2005). The regression tree approach allows the visualization of hierarchical trait combinations and the effects are usually non-additive (De Patta & Sosinski 2003).

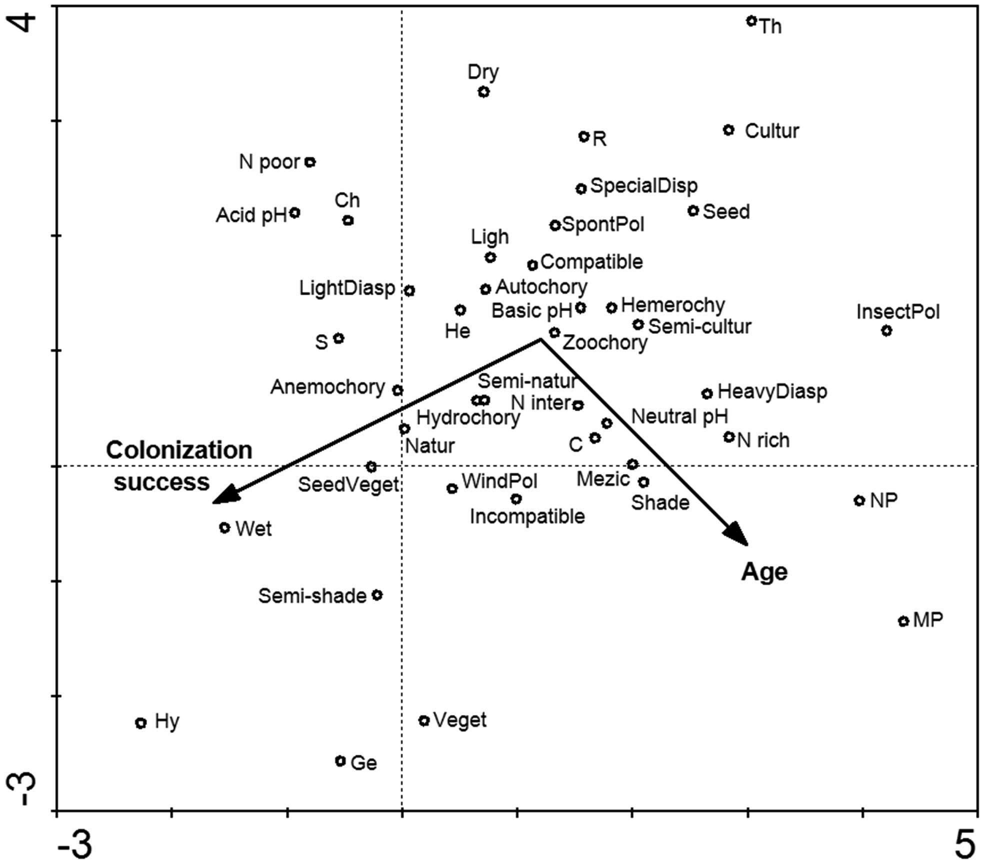


Fig. 1. DCA ordination based on life-history traits and habitat preferences of species. Variables (Age, Colonization success) were fitted *ex post* as passive variables, for details see the text. For abbreviations see Table 1.

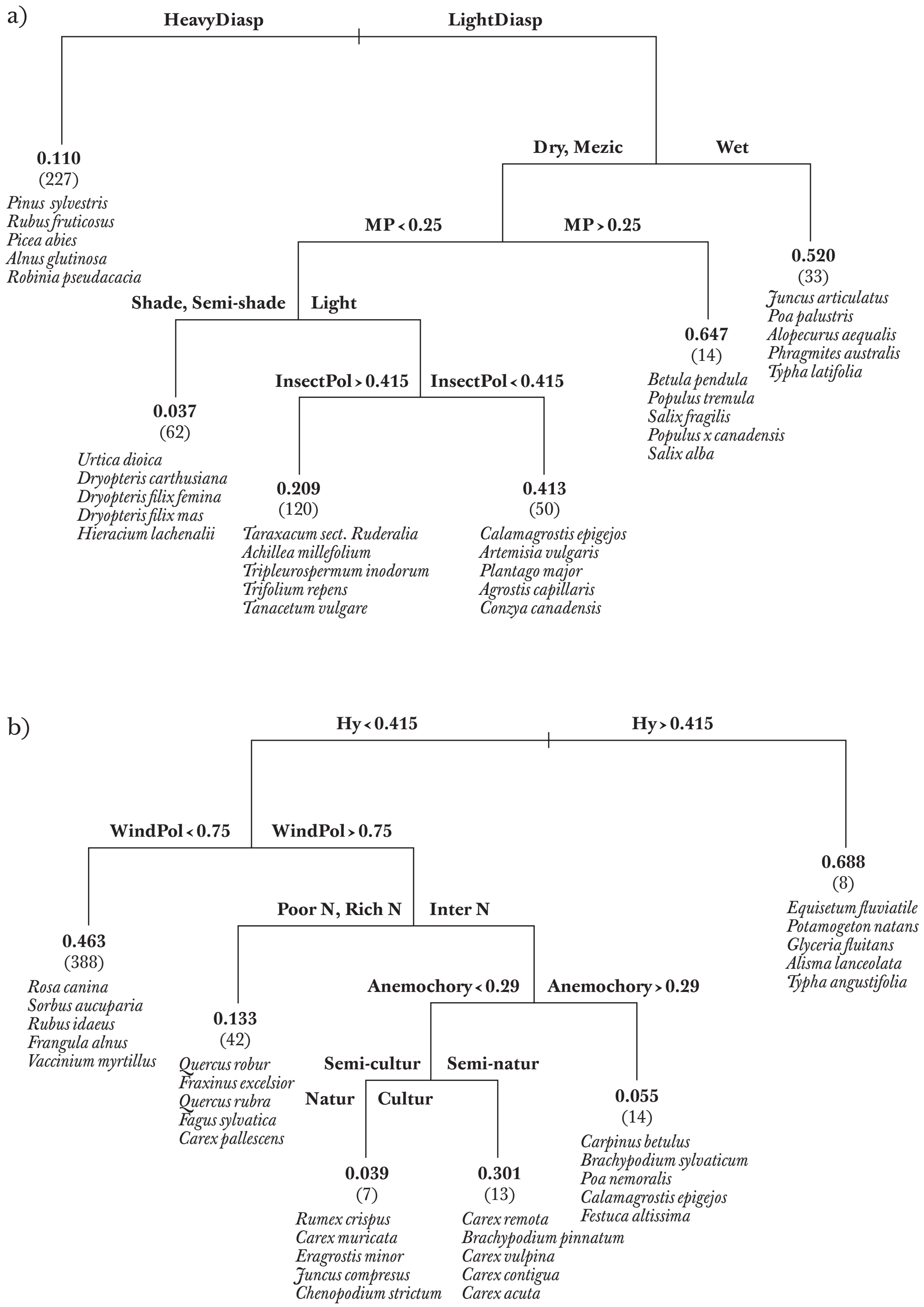
Results

In total, 624 vascular species were recorded in the gravel-sand pits and their surroundings. Eight species occurred only in pits while 194 only in the surroundings. That means, about two-thirds of the species occurring in the surroundings appeared in the course of succession also inside the pits. The proportion of newly established species decreased with successional age (Table 2). The proportion of remaining species not yet established in the previous stages, calculated from the total number of species in the surrounding for each stage, decreases about one-third during the succession (Table 2). Probability to colonize gravel-sand pits by species from the surroundings decreased during succession: young stages – 41 %, middle stages – 30 %, late stages – 15 %.

The indirect ordination analyses showed which life-history traits and habitat characteristics are important for successful colonization of disused gravel-sand pit in the course of succession (Fig. 1). The eigenvalues of the first and second axis were 0.6 and 0.49 respectively. In general, the most successful colonizers were hydrophytes possessing ability to vegetative reproduction. In the young stages, the most successful colonizers were anemochorous stress tolerant species, growing on nitrogen poor and acid sites. The unsuccessful colonizers of these stages are characterized as disturbance tolerant species (R-strategists) typical of arable fields and ruderal sites reproducted exclusively by seeds, mostly therophytes. In the late stages, competitive, sciophilous and wind pollinated species typical of (semi-)natural habitats possessing vegetative reproduction, mostly hydrophytes or geophytes of mesic and wet sites are favoured. The unsuccessful colonizers of late stages are predominantly insect pollinated, nitrophylous phanerophytes typical for sites intensively altered by humans.

Results of the regression tree analyses basically corresponded to DCA ordination. In the regression trees we visualized also the combination of particular life-history traits and habitat preference characteristics in three different successional stages – young, middle and late (Fig. 2).

The most successful colonizers in the young stages (1–10 years) were either moisture demanding species with light diaspores (colonization success – 52 %) or if not moisture demanding species than macrophanerophytes with light seeds (65 %) and if not macrophanerophytes than non-insect pollinated heliophilous species with light diaspores (41 %). The least successful colonizers of the young stages are sciophilous non-macrophanerophytes, with light diaspores growing on dry or mesic sites (4 %) – Fig. 2a.



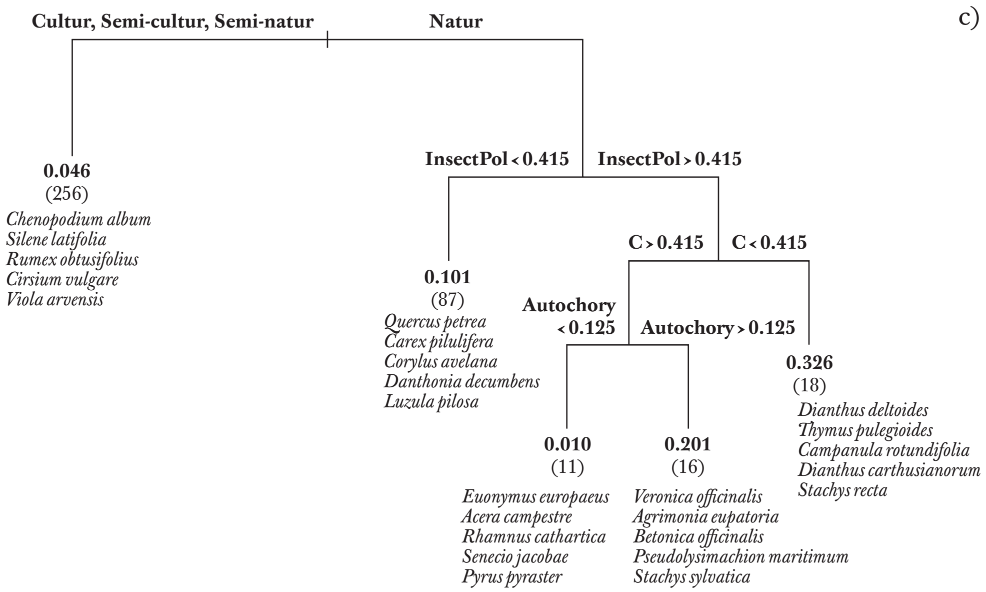


Fig. 2. Hierarchical predictions of colonization success of species in three successional stages based on plant-history traits and habitat preference using regression tree analyses. The pruned tree is shown for each successional stage: (a) young, 1–10 years; (b) middle, 11–20 years; and (c) late, 21–75 years. Each of the splitting node is labeled with the variable that determine the split. The number of species sharing these characteristics/traits is indicated in parentheses. The average colonization success together with five most frequently occurred species (arranged in decreasing order) are shown for each terminal node. For explanation of the explanatory traits see Table 1.

The most successful colonizers in the middle stages (11–20 years) are either hydrophytes (69 %) or if not hydrophytes than wind pollinated species typical of (semi-) natural habitats with intermediate demand for nitrogen (30 %). The unsuccessful colonizers of these stages are either wind pollinated anemochorous species with intermediate demand for nitrogen (6 %) or if not anemochorous species than species typical of habitats with either very high or rather low level of naturalness (4 %) – Fig. 2b.

The most successful colonizers in the late stages (> 21 years) are either insect pollinated species of natural habitats less exhibiting C-strategy (33 %) and if competitive species, than there are autochorous (20 %). The unsuccessful colonizers of these stages are either species typical of human-altered habitats (5 %) or if not than insect pollinated not competitive and not autochorous species of natural habitats – Fig. 2c.

Discussion

Vegetation changes at all scales are governed by both dispersal limitation, and the ability of species to establish and persist (Pywell et al. 2003). Life-history traits adaptive to different conditions are likely to be inversely correlated (Duckworth et al. 2000). Therefore, those that are important in early succession are less likely to be important in late successional stages and *vice versa*. Our results were mostly consistent with this pattern.

The DCA ordination provided non-hierarchical combinations of species related to colonization success of species and successional time, while the regression trees considered hierarchy of traits (Thuiller et al. 2003). This may cause some differences obtained by both methods. For example, autochory appeared to be important in late stages only in the case of insect-pollinated, C-strategists being typical for natural habitats, while in the DCA ordination diagram autochory appeared to be negatively correlated with time and neutral to the colonization success. Similarly, insect pollination, though related to late successional stages and being negatively related to species success in the ordination, appeared an important trait in early successional stages but only in the case of heliophillous species of dry and mesic sites possessing light diaspores. This justifies using both methods.

Species colonizing particular successional stages (young, middle, late) of disused gravel-sand pits exhibited different combinations of traits in terms of life-history traits and habitat preferences. Initial success was related to traits which determine colonization ability of the species, such as anemochory and production of light diaspores, whereas persistence-related traits, such as vegetative reproduction and high competitive ability, increased in importance in time (Pakeman 2004). Our results are mostly consistent with theoretical expectations (Glenn-Lewin et al. 1992; Grime 2001), however, there are some trends which differ. Progressive replacement of therophytes by hemicryptophytes, chamaephytes, and phanerophytes during succession on man-made sites has been repeatedly reported (Prach et al. 1997; Vile et al. 2006). We found chamaephytes to be often successful in the young stages while therophytes were unsuccessful in general. It may be attributed to the nutrient poor, acid site conditions on bare sand or gravel for which species from the families Ericaceae and Vacciniaceae are typical (Grime et al. 1988, Ellenberg et al. 1992). The bare sand and gravel seem to provide rather adverse conditions for fast growing ruderals. Similarly, the transition from R-strategists to C- and S- strategists is usually prevailing during succession (Grime 2001; Osbornová et al. 1990), however in our case S-strategists belonged to the species with the highest colonization success in the young stages. R-strategists also spread into the gravel-sand pits mostly at the beginning of succession but they usually did not expand too much. It is obviouse, the succession on nutrient poor and acid sites has some specific features (Tilman 1988). The increase of the former ones can be explained by the fact that many species typical of initial stages of succession do not posses specific modes of dispersal.

There is usually expected a shift from high prevalence of wind dispersal of light seeds in the early successional stages to the high prevalence of zoochory and autochory in mature stages of succession (Rydin & Borgegård 1991; Wiegmann & Waller 2006) as small seeds are generally advantageous for long-distance dispersal, whereas larger seeds have a greater possibility of germinating and establishing in closed vegetation (Schippers et al. 2001; Verheyen et al. 2003). In our case, both anemochory and zoochory, and also hydrochory, were more or less neutral to the successional age (Fig. 1). It may be explained by some earlier findings that first colonizers posses heavier seeds, less dispersed by wind but often by animals, to overcome severe environmental conditions than next species typical of early but not initial stages of succession (Fenner 1985; Prach et al. 1997). This may counterbalance the expected increase of zoochory and decrease of anemochory in the late stages. In the distance of 100 m, considered in the study, advantages or disadvantages for long- or short-distance dispersal by the respective vectors were not probably manifested enough. Hydrophytes with a limited terrestrial dispersal capacity may largely extend their colonization range by hydrochory and epizoochory by water fowls disregarding successional age (Boedeltje et al. 2003). Capability for vegetative reproduction increased colonization success of species especially in later successional stages (Grime 2001, Brown 1992).

Prach & Pyšek (1999) studied vegetation succession on various human-made habitats in the Czech Republic and characterized the "average ideal successional colonizer" as a tall, wind pollinated plant, often a geophyte capable of intensive lateral spread, requiring high nutrient supply and sufficient site moisture. They concluded that life forms and life strategies are among the characteristics best correlated with species success in succession. Most of these conclusions fit to our description of species with high colonization success despite sand and gravel are less fertile habitats than most of those studied by the authors. Beside the characteristics already discussed, wind pollination was the best correlated in our study with colonization success among all pollination vectors (Fig. 1) which is typical for various successional stages (Fenner & Thompson 2005). From the point of view of ecological restoration of the disused gravel-sand pits there is very positive conclusion that weedy and ruderal species exhibit a low colonization success (Fig. 1) and those typical of natural habitats increase during succession (Fig. 2, see also Řehounková & Prach 2006). The former probably results from the low site productivity (Grime 2001), the latter corresponds with the prevailing trends in most successional seres (Walker & del Moral 2003).

The change in the predictive value of colonization success determined by preferred functional traits of species in each successional stage indicates filtering effects of changing conditions in disused gravel-sand pits on the local species pool (Zobel et al. 1998). Environmental filters can be regarded in low probability to colonize the sites by species that lack the respective traits. If we arbitrary set the low probability to establish less than 5%, the respective species traits combinations are seen in Fig. 2.

The non-additivity and hierarchical structure of the traits in the case of the regression trees method (Vayssières et al. 2000) makes possible to predict a species response to environmental gradients, such as time in our case, if the species possesses a certain hierarchical set of traits (Diekman & Falkengren-Grerup 2002, de Bello et al. 2005). Thus the use of plant functional types instead of species provides possibility to predict a colonization success of species present in the local species pool (Díaz et al. 1998, Temperton et al. 2004). This has a potential to be used in practical restoration ecology when species lists can be made in the surroundings of a disturbed site in the time of its creation, and then try to predict the course of succession. A similar approach can be applied to other successional seres.

Conclusions and aplications

1. The most successful colonizers of the disused gravel-sand pits are hydrophytes with ability to vegetative reproduction. The least successful are annual weeds and ruderals.
2. Species typical of natural vegetation are largely successful, most in the late stages.
3. In young stages, the most important role play the anemochorous, stress tolerant perennial species with light diaspores, typical for nitrogen poor and acidic habitats
4. The importance of scio- and nitrophilous species of mesic habitats, with heavier diaspores, mostly phanerophytes or geophytes, often with ability to vegetative reproduction and preferring less acidic sites increase with age.
5. Probability of species to colonize gravel-sand pits from the surroundings is decreasing in succession: young stages – 41 %, middle stages – 30 %, late stages – 15 %.
6. Plant functional types can be a useful tools in predicting colonization success of species occurring in the surrounding (semi-)natural vegetation into disused gravel-sand pits and this may be potentially exploited in various restoration programmes.

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Chapter V

Spontaneous vegetation succession and the effect of abiotic factors in a disused gravel-sand pit

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[manuscript]

Spontaneous vegetation succession and the effect of abiotic factors in a disused gravel-sand pit

Abstract

Variability of vegetation development and the relative importance of abiotic factors influencing spontaneous vegetation succession were studied in a disused gravel-sand pit in the eastern part of the Czech Republic (central Moravia). The study site was 2 ha and gravel and sand extraction was stopped in 1982. Four types of sites habitats were distinguished: mesic, wet, shallow flooded and aquatic. Vegetation relevés were recorded in 34 permanent plots (4 m x 1 m). Semiquantitative cover of all vascular species and bryophytes was estimated by the seven point Braun-Blanquet scale. The vegetation samples were repeated between 1997 and 2005, that is 1, 2, 3, 4, 5 and 8 years since the extraction was stopped. Abiotic factors, such as water table and soil physical and chemical characteristics, were evaluated. Ordination analysis showed that, after eight years, vegetation development led to the formation either of mesic grassland with scattered shrubs, *Salix* carrs accompanied by *Phragmites australis*, *Typha latifolia* and *P. australis* or macrophyte vegetation in pools depending predominantly on site moisture conditions. Water table was the factor most influencing spontaneous vegetation development. Vegetation succession was further significantly influenced by other abiotic factors, namely soil texture and pH.

The vegetation development and changes in abiotic factors, though observed for only the first 8 years of succession, showed similar trends as those resulting from a broad-scaled and multi-site study of gravel-sand pits throughout the Czech Republic.

Keywords: CCA, Czech Republic, DCA, permanent plots, soil factors, species pattern

Nomenclature: Kubát et al. (2002)

Introduction

The excavation of gravel and sand in large pits, necessitating the removal of topsoil, has created large areas completely devoid of vegetation and diaspores (Borgegård

1990). In spite of the fact that such sites are quite frequent in various landscapes, detailed or long-term studies on spontaneous vegetation succession in disused gravel-sand pits are very rare (Borgegård 1990, Řehounková & Prach 2006). Unfortunately, these sites are often technically reclaimed to large water bodies or planted with conifers, eventually reclaimed for agrarian use. For ecologists, the disused gravel-sand pits represent suitable sites for research on succession as processes of primary succession hardly ever can be observed elsewhere in the European cultural landscape except mining sites (Glenn-Lewin, Peet & Veblen 1992). Moreover, such sites provide a challenge for conservation biology, providing refugia for rare and retreating species or wetland formation (Řehounková & Prach 2007).

Restoration ecology involves the development of structural or functional characteristics of ecosystems that have been lost (van Andel & Aronson 2006). It includes habitat creation that may aim to establish plant communities that are representative of the original, undamaged state. Many restoration projects are implemented as mitigation for the loss of natural wetlands resulting from the development of cultural ecosystems. However, spontaneous succession often provides desirable target ecosystems better than technical reclamation (Prach 2003). Distinguishing which factors most influence the development of a plant community is crucial for successful ecosystem restoration. The use of permanent plots is the best method to study long-term changes in vegetation (Bakker et al. 1996).

The main objective of this study was to relate the course of spontaneous vegetation succession in the restored part of a gravel-sand pit to abiotic factors during the first eight years after site creation. The questions addressed in this paper are: What is the variability of spontaneous vegetation succession in a disused gravel-sand pit? Which abiotic and environmental factors potentially influence vegetation succession?

Study area

The Nature Reserve Chomoutov lake (4 km north from the town of Olomouc – 49° 40’ N, 17° 15’ E) is part of a Protected Landscape Area situated in the eastern part of the Czech Republic (central Moravia). The southern part of the studied gravel-sand pit was used as sludge ponds and a waste site for topsoil and tailings during gravel and sand extraction. In 1997, 15 years after finishing mining activities, a restoration project was begun, including topsoil extraction down to the depth of 0.5 m. The creation of a 2 ha wetland area, including peripheral water ditch with several pools separated from inside the larger water body by habitats with water table 0–2 m below the surface, was established and let to spontaneous vegetation establishment. The altitude of the site ranges from 213.5 to 216 m a. s. l. Mean annual temperature is 8.4 °C, and mean annual precipitation 520 mm (Czech Hydrometeorological Institute in Olomouc). The geology, hydrogeology and hydrology of the studied site were influenced by the gravel and sand mining. The pit was established on gravel and sand deposits originating from fluvial processes during the Quarternary period (Havlíček et al. 1996).

Methods

Sampling

The gravel-sand pit was surveyed from 1998 to 2005. The following habitats were arbitrarily distinguished in the pit according to site moisture prior to the following analyses: mesic (water table 1–2 m below the surface), wet (water table 0–1 m below the surface), shallowly flooded sites (0.05–0.2 m above the surface) and aquatic (more than 0.2 m above the surface). A total of 34 permanent plots was established in the site with topsoil removed in 1998 in all habitat types (dry, wet, shallow flooded and aquatic). The plots were fixed by an inserted metal square plate with a spike in each corner. A wooden peg (height 1 m above the surface) was inserted near each metal plate to find the plot easier. Horáková (1999) recorded the vegetation in 1 m x 4 m permanent plots in the first year of succession (1998) in a water ditch, habitats with water table 0–2 m below the surface and in the larger water body. Therefore, the methodology used by Horáková (1999) was respected to describe the vegetation succession from the beginning. Phytosociological relevés were recorded in each of the permanent plots at the end of July and beginning of August during the 1st, 2nd, 3rd, 4th, 5th and 8th year after site restoration. In this way, 204 relevés were obtained. Semiquantitative cover, defined by the seven point Braun-Blanquet scale, was estimated for vascular plants in each relevé (Kent & Coker 1992).

Water table depth was measured in a bore hole on the margin of each relevé. In total, 20 measurements were conducted during the six studied vegetation seasons from 1997 to 2005. The inclination of all sites where the relevés were recorded was 0°–5°. Therefore, inclination was not considered further as an explanatory variable.

Soil samples were collected in all studied years, i. e. 1998, 1999, 2000, 2001, 2002 and 2005. Four subsamples of the first 0.3 m below the organic layer of the top soil were taken from margins of each relevé and mixed into one pooled sample. The samples were analysed for pH, texture, total nitrogen, organic carbon (Zbíral 1997), phosphorus, potassium, calcium, magnesium and electric conductivity (Antanasopoulos 1990). Soil texture was determined by wet sieving and a Fritsch Scanning-Foto-Sedimentograf 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).

Data analysis

Vegetation and abiotic data were analysed using multivariate methods in CANOCO version 5.4. (ter Braak & Šmilauer 2002). A unimodal relationship between species occurrence and time was expected, thus Detrended Correspondence Analysis (DCA) and Cannonical Correspondence Analysis (CCA) were used. The length of the DCA gradient was 6.63 SD. Species data were not transformed. In DCA, detrending by segments was used and species with a weight of at least 5 % were shown. In CCA, inter-sample distance and Hill scaling were used. Abiotic data were fitted *ex post* to the

DCA ordination axes as passive variables (ter Braak & Šmilauer 2002). To show the effect of successional changes, the identifier of relevés (coded as several dummy variables) was used as a covariable in the analyses. Besides successional age, the following abiotic factors were used (Table 1): water table, texture expressed as the percentage of of soil fraction weights, pH, total nitrogen, organic carbon, phosphorus, calcium, magnesium, potassium and electric conductivity.

Forward selection was conducted with all abiotic factors (Table 1). Variance Inflation Factors (VIFs) were below 3, 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 the Monte Carlo permutation test (i. e. 999 permutations), allowed for the testing of the partial effect (denotes the variability explained by a given environmental variable considering the effects of other environmental factors, i. e. covariables) of abiotic factors. Marginal effects (denotes the variability explained by given environmental variables without considering other environmental factors) in CCA were also calculated with CANOCO and tested for significance with the Monte Carlo permutation test (i. e. 999 permutations).

Results

Species pattern

Altogether, 130 species were recorded in the permanent plots during the eight years. Vegetation development differed depending on the habitat type, resulting in four successional seres: A) mesic, B) wet, C) shallow flooded and D) aquatic (Fig. 1b). Species turnover is clearly seen in all successional seres, except the aquatic one (Fig. 1a). Aquatic species, such as *Myriophyllum spicatum*, *Ceratophyllum demersum* and *Lemna minor*, dominated in the aquatic sere in each year of the eight year succession. Because no significant species turnover appeared, the aquatic sere was not further described in details as the other seres (Fig. 1a)

A sparse cover of annual species was characteristic for the dry habitats in the first year of succession. The typical species were *Capsella bursa-pastoris*, *Erophila verna*, *Lactuca serriola, Medicago lupulina*, *Spergularia rubra*, and *Tripleurospermum inodorum* in the mesic habitats, while *Sagina procumbens* or *Rorippa palustris* dominated in the wet and shallow flooded habitats. *Tussilago farfara* also occurred in the mesic habitats and *Agrostis stolonifera* in wet habitats in the first year.

In the second year, perennials (e.g. *Poa compressa, Trifolium repens, Tussilago farfara*) in the mesic habitats, *Agrostis stolonifera*, *Alopecurus aequalis*, *Juncus bufonius* and *Bidens tripartita* in the wet and shallow flooded habitats, grew along with the annuals (see above). Ruderal species (e.g. *Taraxacum* sect. *Ruderalia*, *Artemisia vulgaris*) and biennials (e.g. *Carduus acanthoides, Cirsium* vulgare) also occurred in mesic habitats.

Ruderal perennial species and graminoids dominated in the third year of site succession. The typical species in the mesic habitats were *Carex hirta*, *Cirsium arvense*, *Rumex acetosa* and *Rumex thyrsiflorus*, while *Juncus effusus*, *Juncus tenuis* and *Juncus articulatus* were frequent in wet and shallow flooded habitats.

Table 1. Abiotic factors considered. The significant factors (CCA) are marked in bold.

Age	age from abandonment	yr
WT	water table	m
Gr	proportion of gravel	%
Cl	proportion of clay	%
Si	proportion of silt	%
Sa	proportion of sand	%
pH	pH	1–12
N	Total nitrogen	(mg/kg of soil)
P	Phosphorus	(mg/kg dry matter)
C	Organic carbon	%
Mg	Magnesium	(mg/kg dry matter)
Ca	Calcium	(mg/kg dry matter.)
K	Potassium	(mg/kg dry matter)
EC	Electric conductivity	mS/cm

Table 2. Summary results of the ordination analyses, covariables (plot identifier).

T – type of analysis, EV – significant environmental variables (15 variables), r – species-environment correlation, λ_1, λ_2 – eigenvalues corresponding to the first or second axis, % 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	0.828	0.866	0.493	–	–	–
2	CCA	all	0.853	0.528	0.293	74. 7	14.871	***

The proportion of perennial grassland herbs and graminoids increased and ruderal species decreased in the fourth year. Grassland species, such as *Lotus corniculatus*, *Achillea millefolium, Plantago lanceolata, Deschampsia cespitosa* and *Poa palustris*, were typical for mesic habitats, while wetland species, such as *Alisma plantago-aquatica*, *Eleocharis palustris, Phragmites australis* and *Typha latifolia*, occurred in shallow flooded habitats. The first pioneer trees and shrubs appeared in dry (*Betula pendula*) and wet (*Salix purpurea*, *S. viminalis*, *S. cinerea*) habitats. *Calamagrostis epigejos* started to expand both in mesic and wet habitats.

In the following year (5), vegetation composition in all habitats reflected the successional trends from the previous year. Perennial species, such as *Galium album* and *Vicia tetrasperma*, were accompanied by scattered woody species (*Betula pendula*, *Populus* x *canadensis*) in mesic habitats. *Tanacetum vulgare* was the only ruderal species markedly presented in mesic habitats. Gradually, woody species (*Salix caprea*, *S. fragilis, Populus alba*) expanded into the wet habitats. Wetland species cover, especially *Typha latifolia*, increased in shallow flooded habitats.

After eight years, the mixture of perennial herbs and grasses, with the first scattered shrubs (*Rosa canina*, *Rubus caesius*) and trees (*Betula pendula*, *Populus* x *canadensis)*, dominated in the mesic habitats. The relatively closed herb layer was formed by grassland species (e.g. *Potentilla reptans*, *Potentilla argentea*, *Hypericum perforatum* and *Elytrigia repens*) in the mesic habitats. The woody species composition in wet habitats formed open willow carrs (e.g. *Salix alba*, *S. caprea*, *S. fragilis*, *S. cinerea*) accompanied by *Phragmites australis* in the understory. Wetland species (e.g. *Typha latifolia* and *Phragmites australis*) formed a relatively closed herb layer in shallow flooded habitats,.

Abiotic factors determining vegetation succession

Significant abiotic factors included water table level, all four particular soil fractions and pH, while seven factors were found not to significantly influence vegetation variability during the first eight years of vegetation succession (Table 1). Only the DCA graphical outputs are displayed (Fig. 1), because of the similarity with the CCA ordination results demonstrated by the high values of species-environment correlations on the first DCA and CCA axes (Table 2). The CCA analyses found that 74.7 % of variability was explained by seven environmental factors (Table 2). Both partial and marginal effects of each of the six abiotic factors and age were significant (Table 3).

The importance of abiotic factors and age, influencing the processes of spontaneous vegetation succession in the disused pit, is shown in Fig. 1a (inset diagram). Water table was positively correlated with the first axis and explained the largest amount of vegetation variability, i. e. 28.4 % (partial effect). The second axis was positively correlated to site age and explained 14.7 % (partial effect) of vegetation variability. Fine-grained substrates, with higher amounts of clay and silt particles, were related to wetter habitats and increased with time, while coarse-grained substrates formed by sand and gravel particles prevailed in mesic habitats. The pH increased with age.

Table 3. Results of CCA – partial and marginal effects, covariables (plot identifier).

F-value of the F-statistic, P (*** P < 0.001, ** P < 0.01, * P < 0.05) – probability level obtained by the Monte-Carlo test, 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). EV – significant environmental variables (see Table 1).

Analysis	EV	Partialr	Partial %-explained	PartialF	PartialP	Marginal r	Marginal %-explained	Marginal F	Marginal P
1	WT	0.820	28.4	14.055	***	0.820	27.0	14.098	***
2	Age	0.784	14.7	6.695	**	0.784	13.3	6.262	**
3	Gr	0.753	8.9	4.730	**	0.688	6.45	3.456	**
4	Cl	0.724	7.2	3.145	**	0.720	8.0	4.897	**
5	Si	0.698	5.0	2.218	**	0.693	7.26	3.840	**
6	Sa	0.682	4.7	2.093	**	0.656	5.5	3.140	**
7	pH	0.657	3.6	1.610	*	0.629	3.5	2.456	**

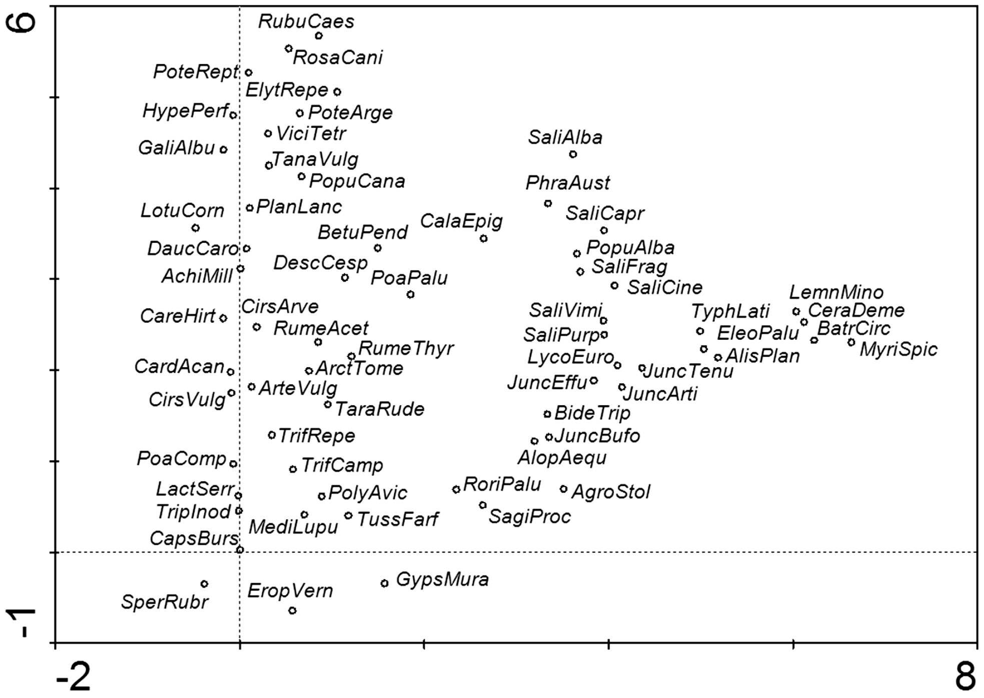

Fig. 1a. DCA species ordination. The inset figure shows the DCA ordination of significant environmental factors (P<0.05, Table 1) fitted *ex post* as passive variables. The species with weight >5% were considered. Species abbreviations used are composed of the first four letters of the generic and species names.

AchiMill – *Achillea millefolium*, AgroStol – *Agrostis stolonifera*, AlisPlan – *Alisma plantago-aquatica*, AlopAequ – *Alopecurus aequalis*, ArctTome – *Arctium tomentosum*, ArteVulg – *Artemisia vulgaris*, BatrCirc – *Batrachium circinatum*, BetuPend – *Betula pendula*, BideTrip – *Bidens tripartita*, CalaEpig – *Calamagrostis epigejos*, CapsBurs – *Capsella bursa-pastoris*, CardAcan – *Carduus acanthoides*, CareHirt – *Carex hirta*, CeraDeme – *Ceratophyllum demersum*, CirsArve – *Cirsium arvense*, CirsVulg – *Cirsium vulgare*, DaucCaro – *Daucus carota*, DescCesp – *Deschampsia cespitosa*, EleoPalu – *Eleocharis palustris*, ElytRepe – *Elytrigia repens*, EropVern – *Erophila verna*, GaliAlbu – *Galium album*, GypsMura – *Gypsophila muralis*, HypePerf – *Hypericum perforatum*, JuncArti – *Juncus articulatus*, JuncBufo – *Juncus bufonius*, JuncEffu – *Juncus effusus*, JuncTenu – *Juncus tenuis*, LactSerr – *Lactuca serriola*, LemnMino – *Lemna minor*, LotuCorn – *Lotus corniculatus*, LycoEuro – *Lycopus europaeus*, MediLupu – *Medicago lupulina*, MyriSpic – *Myriophyllum spicatum*, PhraAust – *Phragmites australis*, PlanLanc – *Plantago lanceolata*, PoaComp – *Poa compressa*, PoaPalu – *Poa palustris*, PolyAvic – *Polygonum aviculare*, PopuAlba – *Populus alba*, PopuCana – *Populus x canadensis*, PoteArge – *Potentilla argentea*, PoteRept – *Potentilla reptans*, RoriPalu – *Rorippa palustris*, RosaCani – *Rosa canina*, RubuCaes – *Rubus caesius*, RumeAcet – *Rumex acetosella*, RumeThyr – *Rumex thyrsiflorus*, SagiProc – *Sagina procumbens*, SaliAlba – *Salix alba*, SaliCapr – *Salix caprea*, SaliCine – *Salix cinerea*, SaliFrag – *Salix fragilis*, SaliPurp – *Salix purpurea*, SaliVimi – *Salix viminalis*, SperRubr – *Spergularia rubra*, TanaVulg – *Tanacetum vulgare*, TaraRude – *Taraxacum* sect. *Ruderalia*, TrifCamp – *Trifolium campestre*, TrifRepe – *Trifolium repens*, TripInod – *Tripleurospermum inodorum*, TussFarf – *Tussilago farfara*, TyphLati – *Typha latifolia*, ViciTetr – *Vicia tetrasperma*.

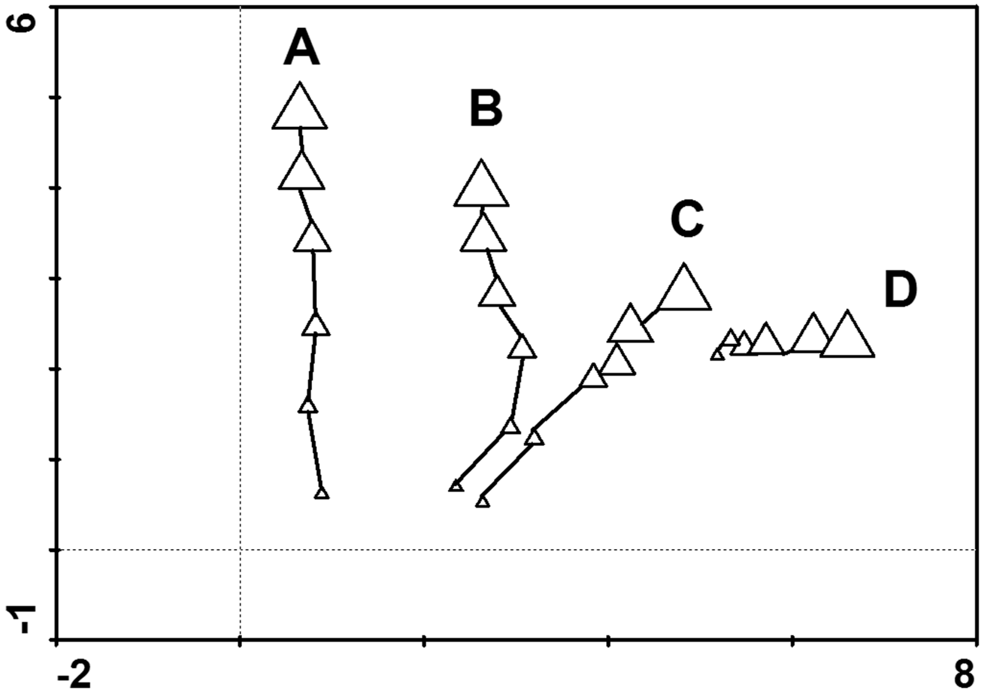

Fig. 1b. The directions of succession in particular seres are shown using centroids (triangle) for each group of seral stages. Increasing size of the symbols corresponds to increasing age (years): 1998 (1 year), 1999 (2 years), 2000 (3 years), 2001 (4 years), 2002 (5 years), 2005 (8 years). Seres are indicated with letters: A – mesic, B - wet sere, C – shallow flooded, D – aquatic.

Discussion

Vegetation succession in the studied gravel-sand pit followed the pathways of early primary succession documented from similar post-mining sites such as quarries (Novák & Prach 2003) or spoil heaps from open-cast brown mining (Wiegleb & Felinks 2001). Species composition changing during succession is influenced by local site factors, such as abiotic characteristics, disturbance and species interactions, and landscape factors such as macroclimate, the species pool and land-use history (Walker & del Moral 2003).

The course of spontaneous vegetation succession in the restored part of the gravel-sand pit differed due to variable moisture conditions. We found a diverse mosaic of vegetation on each four habitat types, while further vegetation development proceeded only in three of the habitats (mesic, wet and shallow flooded). The three major successional seres (i. e. mesic, wet, shallow water) clearly differed also within the broad-scaled study of gravel-sand pits (Řehounková & Prach 2006). On the other hand, it appears that the species composition of the aquatic habitat did not show any successional trends in species pattern. The aquatic plants present appeared as early as in the first year of succession being probably dispersed by water birds from various types of water bodies and wetlands occurring in the surroundings. Epizoochoric dispersal of water macrophytes is often easy and fast (Figuerola et al. 2005). Despite that only initial (1–3 years) and young (4–8 years) successional stages were analysed, the direction of vegetation succession is principally the same as the successional pattern within a broad-scaled and multi-site study of gravel-sand pits throughout the Czech Republic (Řehounková & Prach 2006). Also, the particular ecological group of species and dominant species in each succesional sere were similar (Řehounková & Prach 2007).

Ruderal species (mostly annuals) dominated in the dry and mesic habitats during the initial stages, while more specialized wetland species appear in wet and flooded habitats of the same age (Pietsch 1996). Later, the proportion of more specialized grassland species (perennial herbs and grasses) slowly increased in dry and mesic sites (Novák & Prach 2003). The first woody species appeared there, whereas the proportion of woody species in less extreme sites, i. e. wet sites in this case, increase much faster after as early as in the third year (Wiegleb & Felinks 2001). It is clear that on the other side of the moisture gradient, i. e. in flooded sites, woody species did not have a chance to established (Prach & Pyšek 1994). The competitive grass *Calamagrostis epigejos* can arrest further establishment of grassland species and shrubs by forming monodominant compact swards (Prach & Pyšek 2001) and change the course of vegetation succession in dry sites. Both anemochorous seed dispersal from the close surroundings and subsequent vegetative propagation are responsible for the expansion of *C. epigejos* in such sites (Rebele & Lehmann 2001). Wet and flooded sites are dominated mostly by specialists (Pietsch 1996), i. e. mostly graminoids, while also woody species in wet sites.

Hydrologic variables have been broadly found to be important abiotic factors influencing the pattern of vegetation (e. g. De Steven & Toner 2004, Ashworth et al. 2006). In this study, the moisture gradient was the most important of all environmental factors. Moreover, it probably masked the effect of time on vegetation development. Time explained only ca. 15% of the vegetation variability in the data set in contrast to moisture (i. e. water table), which was responsible for ca. 28 %. This corresponds to evidence from the broad-scaled study of gravel-sand pits throughout the Czech Republic, but the differences in variability explained by the factors was more marketable in the present study site (Řehounková & Prach 2006).

Geology and hydrogeology play important roles in the relationship between species pattern and abiotic factors (especially the hydrologic regime) in the studied site that was influenced by gravel-sand pits extraction and following site restoration. The proportion of the fine-grained and coarse-grained fractions is an important factor influencing availability of soil water, which is important during the whole vegetation season (Havlíček et al. 1996). The relationship between size of soil particles and site moisture was documented also from the broad scaled study of gravel-sand pits, where texture explained ca. 4 % of vegetation variability (Řehounková & Prach 2006). This is six times less than in our study. This is probably due to only two soil factions (i. e. gravel, silt) being significant in the broad scaled study.

The influence of pH on community development has been found in studies on created or restored sites (Borgegård, 1990, Ashworth et al. 2006). Soil pH increased with time and explained ca. 4 % of vegetation variability, which is similar to the 6 % found in the broad-scaled study of gravel-sand pits (Řehounková & Prach 2006).

The other soil characteristics, i. e. total nitrogen, phosphorus, organic carbon, magnesium, calcium, potassium and electric conductivity, did not show any significant influence on vegetation development during the eight years of succession, probably because of the small range of their absolute values (Jongman et al. 1987).

We are aware that the observation time (8 years) was short to analyse a full sequence of successional seres, but some succesional trends in young (1–3 years) and early (4–8 years) stages were recognized. This study showed that spontaneous vegetation succession proceeds relatively fast towards (semi-) natural vegetation shortly after abandonment of restored gravel-sand pits, i. e. to grasslands with scattered shrubs in mesic habitats, *Sali*x carrs accompanied by *Phragmites australis* in wet habitats, *Typha latifolia* and *P. australis* in shallow water habitats or macrophyte vegetation in pools. Site moisture was the most influential abiotic factor on the course of succession, but it was further influenced by other abiotic factors (i. e. texture, pH). However, a more detailed analysis of landscape factors and their role during early vegetation succession will be necessary to evaluate the restoration project.

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Conclusions

Conclusions

The review of 37 studies on vegetation succession over a broader geographical scale, started on bare ground in various disturbed sites over the globe, showed that environmental factors have a significant influence on vegetation development. Besides time, i.e. successional age, landscape factors, namely surrounding vegetation and macroclimate, and some local site factors, i.e. soil moisture, amount of nitrogen and soil texture, had the highest influence on the course of succession. Organic content, pH, phosphorus content and size of a disturbed site are local site factors, which have significant effects only in some cases. Surrounding vegetation exhibited a significant effect in all cases whenever this was considered. The results imply that spontaneous succession in various types of disturbed sites, including mining sites such as gravel-sand pits, cannot be studied without a broader landscape context (Chapter I).

At the country scale, spontaneous vegetation succession in gravel-sand pits led to the formation of either shrubby grassland in dry sites in lowlands, deciduous woodland in dry upland sites, alder and willow carrs in wet sites, regardless of region, and tall sedge or reed and cattail beds in shallow flooded sites disregarding the region (Chapter II and III). Except for some dry sites in lowlands, where the alien species *Robinia pseudacacia* may expand, succession proceeds towards (semi-)natural vegetation within approximately 20 years (Chapter III). 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, and altitude, mean annual temperature, mean annual precipitation, presence of some vegetation types up to 100 m from a sampling site, and predominant land cover up to 1 km from a pit. 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 %) (Chapter II).

Restoration of target vegetation, i.e. grassland, woodland or wetland, in the studied disused gravel-sand pits by processes of spontaneous vegetation succession can be successfully achieved in about 20 years. This means that no technical restoration is needed. The presence of (semi-) natural vegetation in the close surroundings facilitates this process; thus it is important to preserve at least some remnants of the vegetation during mining and postmining operations. However, the invasion of alien species, such as black locust (*Robinia pseudacacia*), in dry lowland sites in this study, must be taken into consideration. Such species should be eradicated in the vicinity of a pit before the onset of succession (Chapter III).

Plant functional types can be a powerful tool in predicting colonization success of species occurring in the surrounding (semi-)natural vegetation into disused gravel-sand pits. This may help in the prediction of spontaneous vegetation. It was documented that different traits were linked with colonization success in three main stages of vegetation succession: young, middle, and late. Generally, the most successful colonizers of disused gravel-sand pits were hydrophytes with the ability to vegetatively reproduce, while the least successful were annual weeds and ruderals. Moreover, species typical of natural vegetation are largely successful, mostly in the late stages. The anemochorous, stress tolerant species, with light diaspores typical for nitrogen poor and acid habitats, played the most important role at the beginning of succession. Later, the importance of sciophylous, nitrophilous species of mesic habitats with heavier diaspores, increased. These species are mostly phanerophytes or geophytes, often with the ability to reproduce vegetatively and higher demands on pH. The probability to colonize gravel-sand pits by species from the surroundings decreases during succession: young stages (41 % of species appeared in a pit), middle stages (30 %), late stages (15 %) (Chapter IV).

Vegetation development and changes in abiotic factors, though observed on permanent plots for only the first 8 years of succession in only one extensive pit, showed similar trends as those resulting from a broad-scaled and multi-site study of gravel-sand pits throughout the Czech Republic using the space-for-time substitution approach. Spontaneous vegetation succession proceeded relatively quickly towards (semi-) natural vegetation shortly after abandonment of the restored gravel-sand pit, i. e. to grasslands with scattered shrubs in mesic habitats, *willow* carrs accompanied by *Phragmites australis* in wet habitats, *Typha latifolia* and *P. australis* in shallow water habitats or macrophyte vegetation in pools over the eight years. Site moisture was the most influential abiotic factor on the course of succession, but succession was further significantly influenced by other abiotic factors, such as texture and pH (Chapter V).

It can be concluded that in many restoration projects potentially scheduled for disused gravel-sand pits, we can completely rely upon spontaneous vegetation succession. Moreover, the disturbed sites provide a challenge for conservation biology, providing valuable biotopes, such as wetlands or open sand grasslands. On the other hand, the negative effects of intensive gravel-sand mining cannot be neglected, such as the destruction of valuable habitats or the presence of monotonous coniferous monocultures resulting from traditional technical reclamation of the pits.