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

supervisor
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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?

Prach, K. & Řehounková, K. (2006)
Preslia 78: 469–480

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

Chapter II

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

Řehounková, K. & Prach, K. (2006)
Journal of Vegetation Science 17: 583–590

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)

Chapter III

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

Řehounková, K. & Prach, K. (2007)
Restoration Ecology [in press]

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

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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

Řehounková, K. & Prach, K.
[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

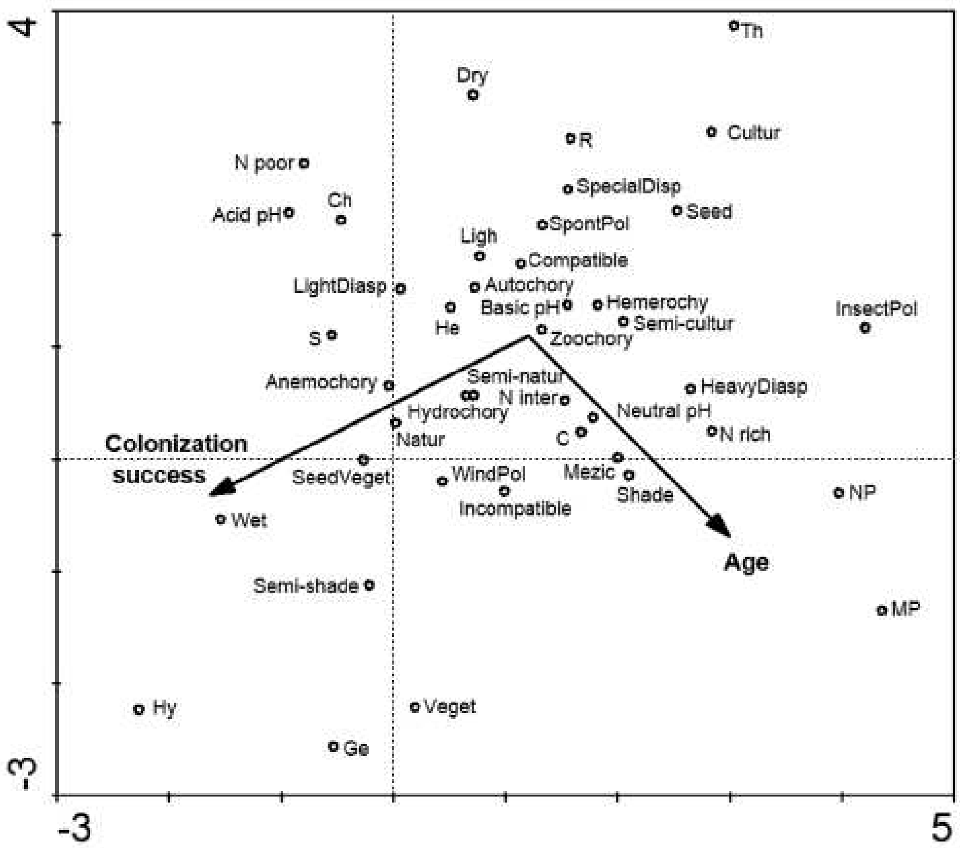


Fig. 1. DCA ordination based on life-history traits and habitat preferences of species. Variables (Age, Colonization success) were fitted *ex post* as passive variables, for details see the text. For abbreviations see Table 1.

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).

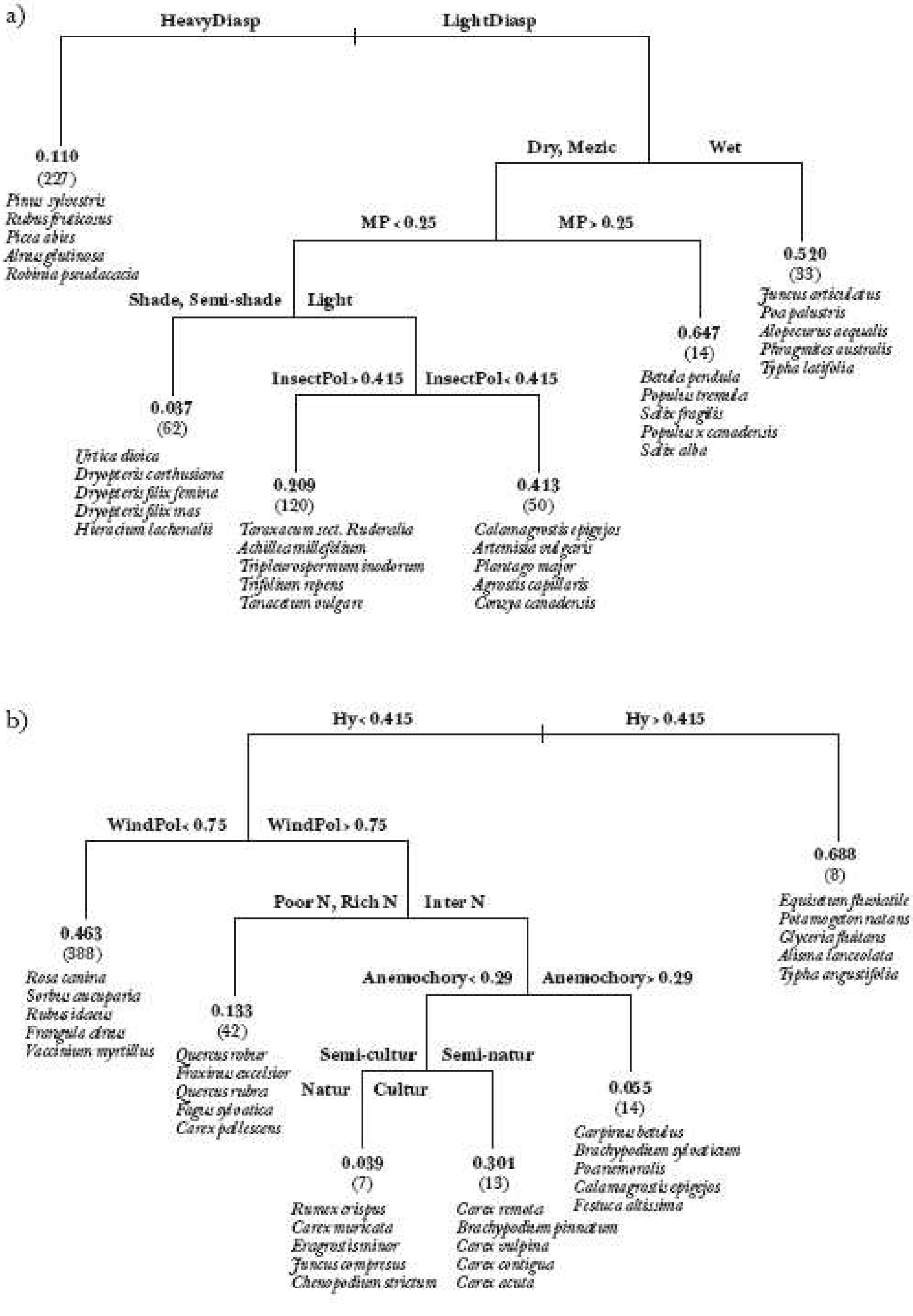
Results

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.


a)
HeavyDiasp
LightDiasp
0.110
(227)
Pinus sylvestris
Rubus fruticosus
Picea abies
Alnus glutinosa
Robinia pseudacacia
Dry, Mezic
Wet
MP < 0.25
MP > 0.25
0.520
(33)
Juncus articulatus
Poa palustris
Alopecurus aequalis
Phragmites australis
Typha latifolia
Shade, Semi-shade
Light
0.647
(14)
Betula pendula
Populus tremula
Salix fragilis
Populus x canadensis
Salix alba
InsectPol > 0.415
InsectPol < 0.415
0.037
(62)
Urtica dioica
Dryopteris carthusiana
Dryopteris filix femina
Dryopteris filix mas
Hieracium lachenalii
0.209
(120)
Taraxacum sect. Ruderalia
Achillea millefolium
Tripleurospermum inodorum
Trifolium repens
Tanacetum vulgare
0.413
(50)
Calamagrostis epigejos
Artemisia vulgaris
Plantago major
Agrostis capillaris
Conyza canadensis
b)
Hy < 0.415
Hy > 0.415
WindPol < 0.75
WindPol > 0.75
0.688
(8)
Equisetum fluviatile
Potamogeton natans
Glyceria fluitans
Alisma lanceolata
Typha angustifolia
Poor N, Rich N
Inter N
0.463
(388)
Rosa canina
Sorbus aucuparia
Rubus idaeus
Frangula alnus
Vaccinium myrtillus
Anemochory < 0.29
Anemochory > 0.29
0.133
(42)
Quercus robur
Fraxinus excelsior
Quercus rubra
Fagus sylvatica
Carex pallescens
Semi-cultur
Semi-natur
Natur
Cultur
0.055
(14)
Carpinus betulus
Brachypodium sylvaticum
Poa nemoralis
Calamagrostis epigejos
Festuca altissima
0.039
(7)
Rumex crispus
Carex muricata
Eragrostis minor
Juncus compressus
Chenopodium strictum
0.301
(13)
Carex remota
Brachypodium pinnatum
Carex vulpina
Carex contigua
Carex acuta

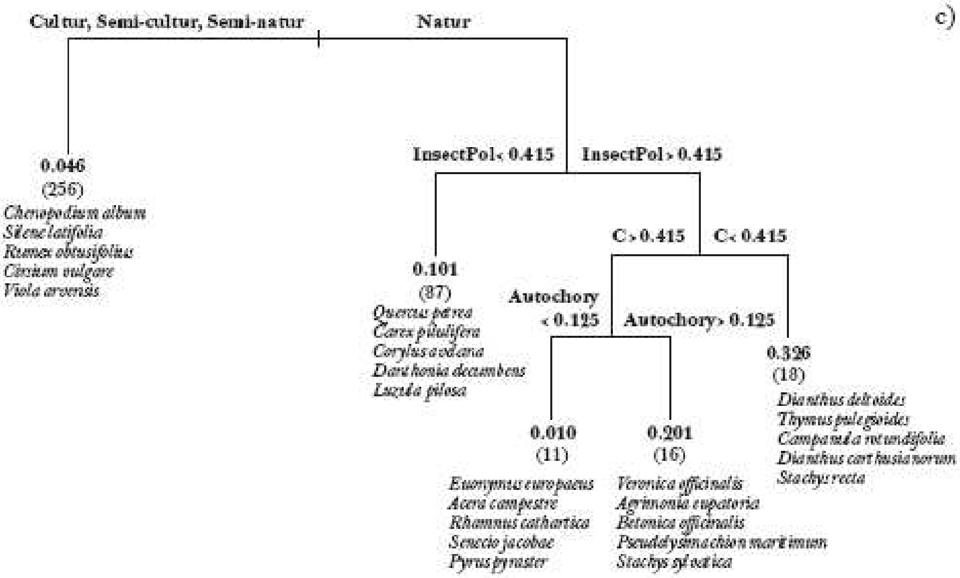


Fig. 2. Hierarchical predictions of colonization success of species in three successional stages based on plant-history traits and habitat preference using regression tree analyses. The pruned tree is shown for each successional stage: (a) young, 1-10 years; (b) middle, 11-20 years; and (c) late, 21-75 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 (Dickman & 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.

Acknowledgements

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Chapter V

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

Řehounková, K. & Prach, K.
[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 nated 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	Partial r	Partial %-explained	Partial F	Partial P	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	**

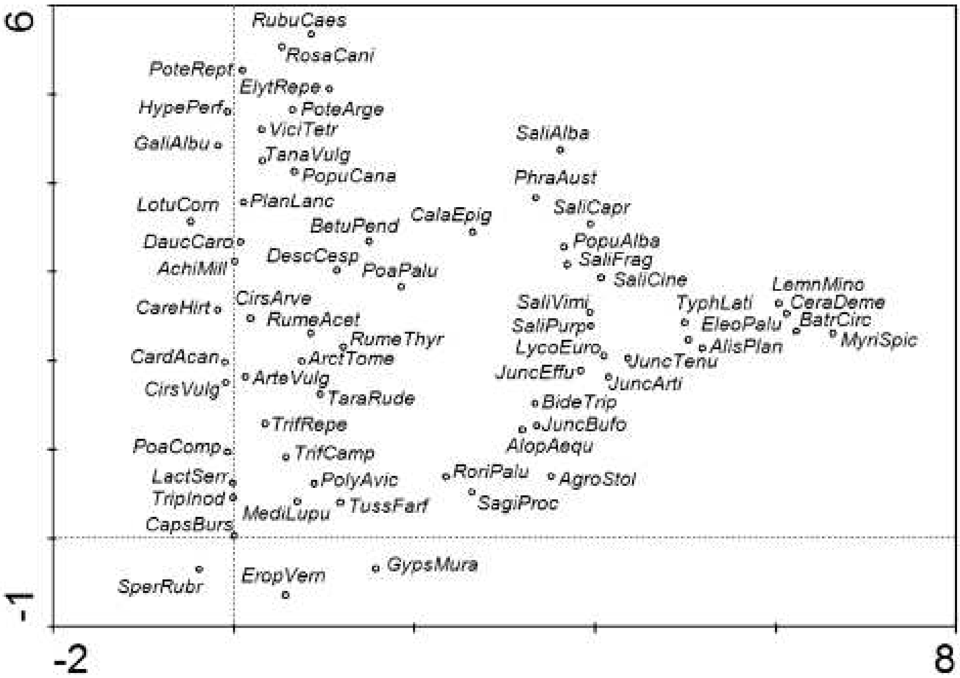

Fig. 1a. DCA species ordination. The inset figure shows the DCA ordination of significant environmental factors (P<0.05, Table 1) fitted *ex post* as passive variables. The species with weight >5% were considered. Species abbreviations used are composed of the first four letters of the generic and species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

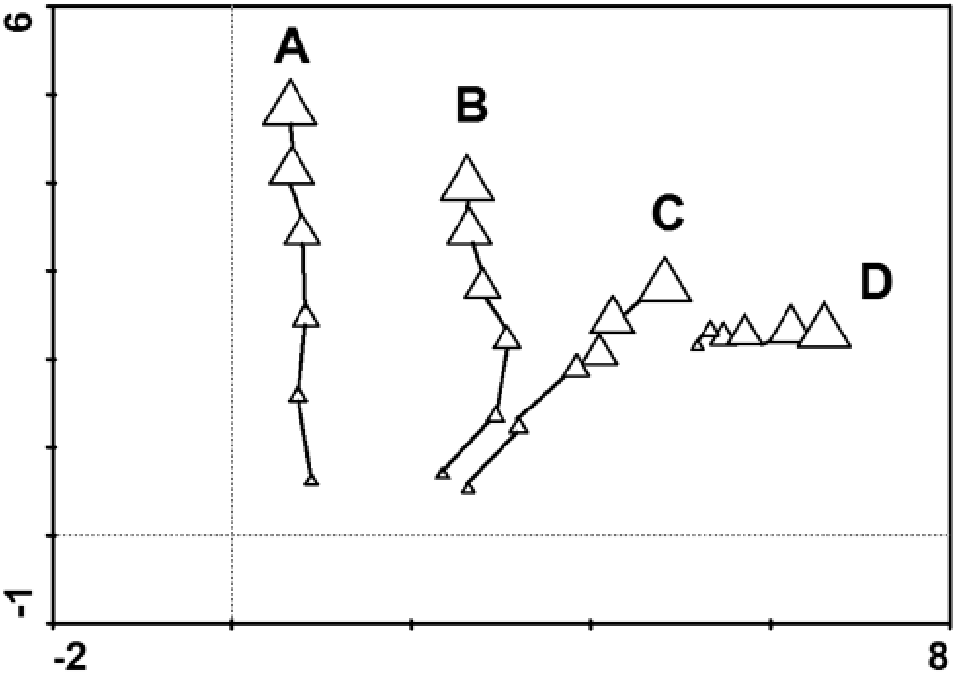

Fig. 1b. The directions of succession in particular seres are shown using centroids (triangle) for each group of seral stages. Increasing size of the symbols corresponds to increasing age (years): 1998 (1 year), 1999 (2 years), 2000 (3 years), 2001 (4 years), 2002 (5 years), 2005 (8 years). Seres are 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 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, *Salix* 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.