

Spontaneous succession of vegetation on acidic bedrock in quarries in the Czech Republic

Spontánní sukcese vegetace v kyselých kamenolomech v České republice

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Variability in vegetation, participation of target and non-target species and the role of the local species pool in the spontaneous succession on acidic bedrock were studied in quarries. The study was conducted in the Českomoravská vrchovina uplands (central Czech Republic). A total of 135 relevés, 5 × 5 m in size, were used to sample 41 quarries that were abandoned from 1 to 92 years ago. Three types of sites were distinguished: mesic, wet and periodically flooded. Species cover (seven point Braun-Blanquet scale) was visually estimated. The following characteristics were noted: steep rocky slopes, bottoms and levels, dumps and screes as habitat types; age; proportion of the main land-cover categories (arable land, ruderal and urban, grassland, woodland and wetland) in the surroundings up to 100 m and 1 km from each quarry; and the occurrence of target (grassland, woodland, wetland) and non-target (ruderal, alien) species up to 100 m from each quarry. Ordination indicates that the spontaneous succession of vegetation results in the formation of mixed woodland, *Alnus* and *Salix* carrs, or tall sedge and *Typha* beds with scattered *Salix*, depending on the wetness of a site, surrounding vegetation and land cover. Restoration of target vegetation in the quarries by spontaneous succession is possible and can occur within about 25 years, especially if the target species are present close by.

Key words: Czech Republic, ordination, restoration, species pool, stone quarries, target species, vegetation succession

Introduction

Mining can cause irreversible changes to the landscape, but the disturbed sites might provide valuable habitats, such as wetlands or dry grasslands (Bradshaw et al. 1982, Jefferson 1984, Davis et al. 1985, Novák & Prach 2003). Therefore, abandoned quarries may be converted into important biodiversity centres if spontaneous succession is allowed to occur and appropriate restoration methods are taken (Novák & Prach 2003, Novák & Konvička 2006). Unfortunately, spontaneous succession in quarries is only rarely prescribed in restoration projects (Prach et al. 2010). In the countryside, they usually consist of technical reclamation when surface is levelled, organic material rich in nutrients is spread and commercial seed mixtures sown or trees densely planted in rows. Such reclaimed sites have a much lower diversity of plants and animals and support competitive species with broad ecological niches at the expense of specialists typical of nutrient poor spontaneously developed sites (Tropek et al. 2010).

Quarries located in the area of the Českomoravská vrchovina uplands are surrounded both by woodland and agrarian landscapes, which are inhabited by species that potentially could colonize habitats within the quarries. Microclimate and geomorphological conditions, structure and texture of the substratum and differences in the water retention of the different substrates contribute to the large habitat diversity within quarries and usually distinguish such sites from the surrounding landscape (Sádlo & Tichý 2003).

It is obvious that the diversity of plants occurring in quarries can be related to many factors, including random effects (Finegan & Harvey 1981). The presence of (semi-)natural vegetation next to a site disturbed by mining is considered to be a key factor in the successful colonization of an abandoned site by target species (Borgegård 1990, Novák & Prach 2003, Řehounková & Prach 2008) although some species can disperse over great distances (Kirmer et al. 2008). Understanding the relationships between the surrounding vegetation and the course of succession at a disturbed site may lead to better designed restoration programs and help explain the variability in successional trajectories.

The questions addressed in this paper are: (i) What is the course of the spontaneous succession of vegetation on acidic bedrock in quarries in the area studied? (ii) How do the proportions of the different ecological groups of species change during succession? (iii) What is the influence of the surrounding vegetation on the course of succession? (iv) How successful are target and non-target species at colonizing a site, especially if present in adjacent habitats?

Materials and methods

Study sites

This study was done in the centre of the Czech Republic, in the Českomoravská vrchovina uplands, between 49°16' and 49°50' N, 15°38' and 16°10' E. The altitude of the studied sites is about 500 m a.s.l. The distance between the northernmost and the southernmost quarries is ca 60 km, and the distance between the easternmost and westernmost ca 40 km. Mean annual precipitation is about 700 mm and mean annual temperature about 6.7 °C (Czech Hydrometeorological Institute 2009). All of the quarries have an acidic bedrock (gneiss, granite, hornblende schist; Czech Geological Survey 2003). A total of 41 quarries were surveyed in 2004–2007. The size of the quarries ranged from 0.05–15 ha. Period since abandonment (age) ranged from 1 to 92 years (see Electronic Appendix 1). The history of each quarry was reconstructed based on the official records of the mining companies, county authorities or by interviewing local administrators. The quarries and the study sites were selected using the following criteria: (i) known year of abandonment; (ii) existence of sufficiently large, spontaneously revegetated sites; (iii) no evidence of allochthonous substrates and (iv) no evident additional disturbance.

Sampling

The vegetation in the following habitats in the quarries was analyzed: steep rocky slopes, bottoms and levels, dumps and screes. Moreover, the wetness of these sites was categorized prior to the analysis of the vegetation as mesic, wet but not flooded and periodically flooded. The successional stages of the seres were distinguished as initial (1–3 years), young (4–10 years), middle (11–25 years), old (26–40 years) or late (> 40 years). The oldest periodically flooded site was only 35 years. All sufficiently large and homogenous sites were sampled, excluding those whose previous history was uncertain.

Phytosociological relevés (5 × 5 m) at the centres of each of the sites yielded a total of 135 relevés. The number of relevés per quarry varied from two to six. Semiquantitative cover, expressed in terms of the Braun-Blanquet scale, was estimated for the vascular plants in each relevé (Kent & Coker 1992). The slopes of sites where the relevés were recorded ranged from 0–60°. The percentage cover of the main categories of land cover (arable land; grassland; woodland; ruderal and urban; wetland) up to 100 m and 1 km from the margin of a quarry were estimated from satellite images (www.mapy.cz) and surface surveys. For each quarry lists of species occurring within it and within 100 m from the margin of the quarry were made. Species on these lists were characterized using a five point abundance scale (1 – very rare, 2 – rare, 3 – scattered, 4 – abundant, 5 – very abundant). Nomenclature of plant species follows Kubát et al. (2002)

Data analysis

Vegetation (relevés) and environmental data were analysed using the following multivariate methods, Detrended Correspondence Analysis (DCA) and Canonical Correspondence Analysis (CCA) in CANOCO version 4.5 (ter Braak & Šmilauer 2002). A unimodal relationship between species occurrence and time was expected and confirmed by DCA (length of the gradient of 5.3 SD). In the DCA detrending by segments was used. Environmental data were fitted to the DCA ordination axis as passive variables. In the CCA, inter-sample distance and Hill scaling were used, because of data with long composition gradients. To separate the effect of locality (i.e. quarry), the identifier of relevés situated in sites within the same quarry was used as a covariable in these analyses. The environmental factors considered are listed in Table 1. Forward selection was conducted with all environmental factors using the Monte-Carlo permutation test with 999 permutations. DCA species response curves enabled to express the changes in the target and non-target species groups on the gradient representing the age of site to be described by using generalized linear models in CanoDraw (ter Braak & Šmilauer 2002). Species were classified into ecological groups according to their phytosociological affinities: grassland, woodland and wetland species were considered following Ellenberg et al. (1991) to be the target species, and ruderal (Ellenberg et al. 1991) and aliens (following Pyšek et al. 2002) the non-target species.

Results

Species pattern and environmental factors

In total, 241 vascular species were recorded in the phytosociological relevés, 313 in the quarries and 362 in the surroundings up to 100 m from the quarries. Moreover, 10 species found in the quarries were threatened or endangered according to the Czech Red List (Holub & Procházka 2000): *Carex hostiana*, *Eleocharis ovata*, *Filago arvensis*, *Abies alba*, *Centaurea cyanus*, *Epipactis helleborine* subsp. *helleborine*, *Galium boreale*, *Lilium martagon*, *Schoenoplectus lacustris*, *Thymus praecox*. Most of them occurred within 100 m of the quarries, except *Schoenoplectus lacustris*, *Carex hostiana* and *Centaurea cyanus*. On the other hand, *Centaureum erythraea* was the only species on the Czech Red List that did not colonize the quarries although present in the area within a radius of 100 m from the quarries.

Table 1. – Environmental factors considered. Significant factors in CCA are marked in bold ($P < 0.05$, forward selection). Abbreviations used in Fig. 1 are given.

	Environmental variables	
	up to 100 m from a quarry	up to 1 km from a quarry
Land cover (%)	Arable land (Ar), Grassland (Gr), Woodland (Wo), Ruderal & Urban (Ur), Wetland	Arable land, Grassland (GL), Woodland (WL), Ruderal & Urban (UL), Wetland
Site characteristics	Age, Site moisture (ST)	

Differences in species composition of the vegetation in the various environments, i.e. steep rocky slopes, bottoms and levels, dumps and screes, were not significant (CCA, $P = 0.054$, forward selection). However, three a priori defined successional seres, i.e. mesic (A), wet (B) and periodically flooded (C), were clearly different in terms of their trajectories in the unconstrained DCA ordination (Fig. 1). Thus, site wetness was the main factor delimiting the seres. The results indicate that species turnover occurred in all the seres. As the DCA ($\lambda_1 = 0.59$, $\lambda_2 = 0.51$) and CCA ($\lambda_1 = 0.73$, $\lambda_2 = 0.6$) gave similar results, only the graphical outputs of the DCA are displayed (Fig. 1).

The initial stages of succession (1–3 years) had an average number of species of 5.6 ± 2.4 (mean \pm S.D.). The typical annual species were *Tripleurospermum inodorum* and *Poa annua* at mesic sites and *Rorippa palustris* at wet and periodically flooded sites. Several perennials, e.g. *Rumex acetosella* at mesic sites, *Ranunculus repens* and *Potentilla anserina* at wet sites and *Juncus articulatus* and *J. tenuis* at periodically flooded sites, grew along with the annuals.

In all young stages (4–10 years), perennial graminoids were the dominant plants and the average number of species was 12.1 ± 7.5 . Typical species at mesic sites were *Agrostis capillaris* and *Avenella flexuosa*, accompanied by *Deschampsia cespitosa*, while at wet sites *Poa palustris* and *Agrostis stolonifera* prevailed. Graminoids, such as *Juncus effusus*, were frequent at shallow flooded sites. Trees first appeared at mesic (*Betula pendula*, *Populus tremula*) and wet (*Alnus glutinosa*, *Salix cinerea*) sites. Semi-shrubs (*Rubus idaeus*, *Rubus fruticosus*) were found at mesic sites. *Calamagrostis epigejos* colonized both mesic and wet sites.

In the middle stage of succession (11–25 years) the composition of the vegetation at all sites continued from that in the previous stage. The average number of species was 14.1 ± 6.5 . Gradually, woody species colonized the mesic (*Acer pseudoplatanus*, *Fraxinus excelsior*) and wet (*Salix* sp. div.) sites. The cover of wetland species, especially *Typha latifolia*, increased at the periodically flooded sites.

After more than 25 years (late stage) the average number of species was 13.3 ± 5.6 and trees and shrubs were dominant at mesic and wet sites. The proportion of woody species also increased at periodically flooded sites. Typical woody species were *Quercus robur* and *Acer platanoides* at mesic, *Salix caprea* at wet and *Salix cinerea* at periodically flooded sites.

At the oldest stages (> 40 years) the average number of species was 12.0 ± 5.9 and they were mainly trees and shrubs at mesic and wet sites. A relatively rich mixture of woody species was present, including *Abies alba*, *Picea abies*, *Sorbus aucuparia*, *Fagus sylvatica* and other woody species already present at the previous stage. Also present were *Dryopteris filix-femina*, *Athyrium filix-mas* and *Vaccinium myrtillus*, i.e. typical herbaceous

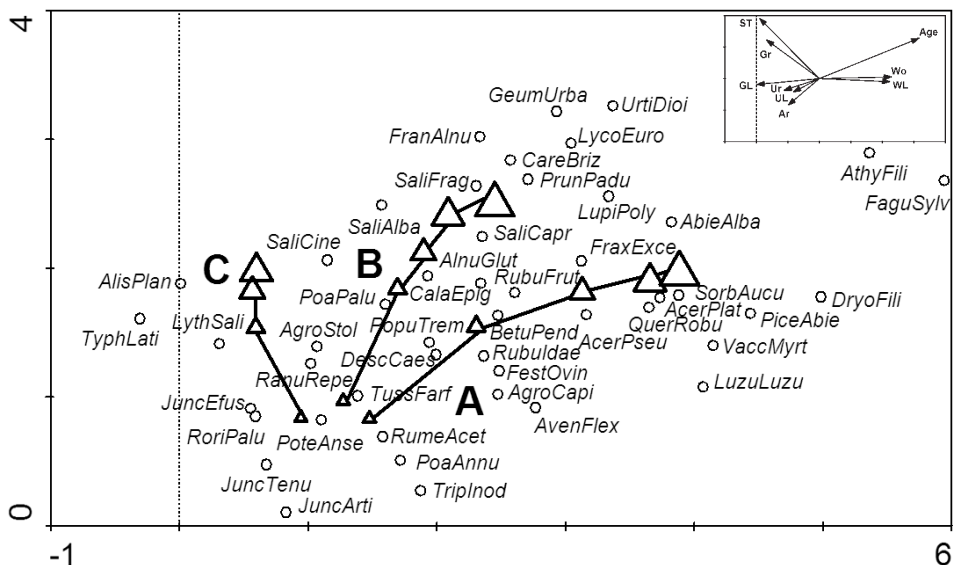


Fig. 1. – DCA ordination of species and samples. The direction of succession in particular seres is indicated by means of centroids (triangles) for each age group. Increasing size of the symbols corresponds to increasing age: initial (1–3 years), young (4–10), middle (11–25 yr), late (26–40), old (> 40). Seres are indicated by letters: A – mesic, B – wet, C – periodically flooded. Species with weight > 5% were considered. Species abbreviations used consist of the first four letters of the generic and species names. The inset diagram shows environmental variables, which appeared significant in the CCA (see Table 1), fitted ex post as passive variables. AcerPlat – *Acer platanoides*, AcerPseu – *Acer pseudoplatanus*, AgroCapi – *Agrostis capillaris*, AgroStol – *Agrostis stolonifera*, AlisPlan – *Alisma plantago-aquatica*, AlnuGlut – *Alnus glutinosa*, AthyFili – *Athyrium filix-femina*, AvenFlex – *Avenella flexuosa*, BetuPend – *Betula pendula*, CalaEpig – *Calamagrostis epigejos*, CareBriz – *Carex brizoides*, DescCaes – *Deschampsia cespitosa*, DryoFili – *Dryopteris filix-mas*, FaguSylv – *Fagus sylvatica*, FranAlnu – *Frangula alnus*, FraxExce – *Fraxinus excelsior*, FestOvin – *Festuca ovina*, GeumUrba – *Geum urbanum*, JuncArti – *Juncus articulatus*, JuncEffu – *Juncus effusus*, JuncTenu – *Juncus tenuis*, LupiPoly – *Lupinus polyphyllus*, LuzuLuzu – *Luzula luzuloides*, LycoEuro – *Lycopus europaeus*, LythSali – *Lythrum salicaria*, PoaAnnu – *Poa annua*, PoaPalu – *Poa palustris*, PoteAnse – *Potentilla anserina*, PiceAbie – *Picea abies*, PopuTrem – *Populus tremula*, PrunPadu – *Prunus padus*, QuerRobu – *Quercus robur*, RanuRepe – *Ranunculus repens*, Rubuldae – *Rubus idaeus*, RoriPalu – *Rorippa palustris*, RumeAcet – *Rumex acetosella*, SaliAlba – *Salix alba*, SaliCapr – *Salix caprea*, SaliCine – *Salix cinerea*, SorbAucu – *Sorbus aucuparia*, Triplnod – *Tripleurospermum inodorum*, TussFarf – *Tussilago farfara*, TyphLati – *Typha latifolia*, UrtiDioi – *Urtica dioica*, VaccMyrt – *Vaccinium myrtillus*.

plants of woodlands. The woody species at wet sites were *Alnus glutinosa* and several species of willows (e.g. *Salix fragilis*, *S. caprea*, *S. cinerea*) and other woody species like *Frangula alnus* and *Prunus padus*. Characteristic herbaceous plants were *Carex brizoides*, *Urtica dioica* and *Lycopus europaeus*. The neophyte *Lupinus polyphyllus* was also found at old stages of succession at both mesic and wet sites. Species typical of *Typha* beds with scattered *Salix cinerea* were dominant at periodically flooded sites. The pattern of succession is summarized in Table 2.

The environmental factors that were significantly correlated with the ordination axes in CCA are indicated in bold in Table 1. The importance of site characteristics, surrounding vegetation and character of the surrounding landscape (land cover) influenced the spontaneous succession of vegetation in the quarries. The occurrence of grassland, wetland and

Table 2. Generalized scheme of spontaneous succession in the quarries studied (41). The three main successional seres distinguished were (A) mesic, (B) wet and (C) periodically flooded sites. Prevailing life forms are indicated.

Sere	Increasing site moisture		
	MESIC (A)	WET (B)	PERIODICALLY FLOODED (C)
Flooded	Never	Rarely	Periodically
Initial stage [1–3 yr]	Annuals, perennial herbaceous plants, grasses		Annuals, perennial graminoids
Young stage [4–10 yr]	Perennial graminoids		
Middle stage [11–25 yr]	Trees, shrubs, perennial graminoids		Perennial graminoids
Late stage [26–40 yr]	Trees, shrubs, perennial graminoids		Perennial graminoids
Old stage [>40 yr]	Trees		(Perennial graminoids – expected)

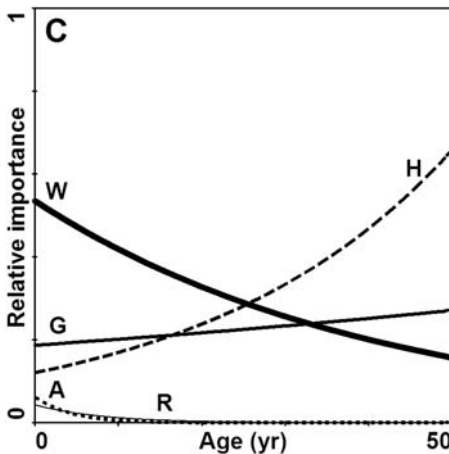
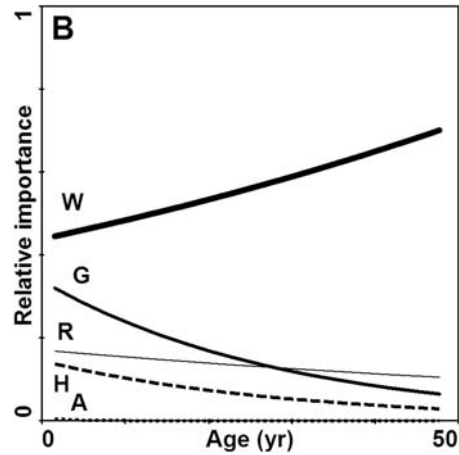
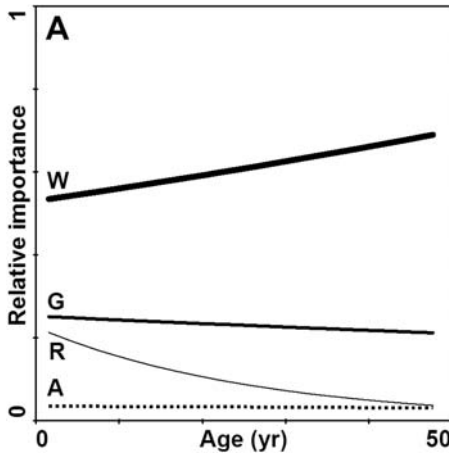


Fig. 2. – DCA response curves of target (G – grassland, H – wetland, W – woodland) and non-target (A – aliens, R – ruderals) groups of species. Seres: A – dry, B – wet, C – periodically flooded. Relative importance of particular groups of species was calculated using species cover.

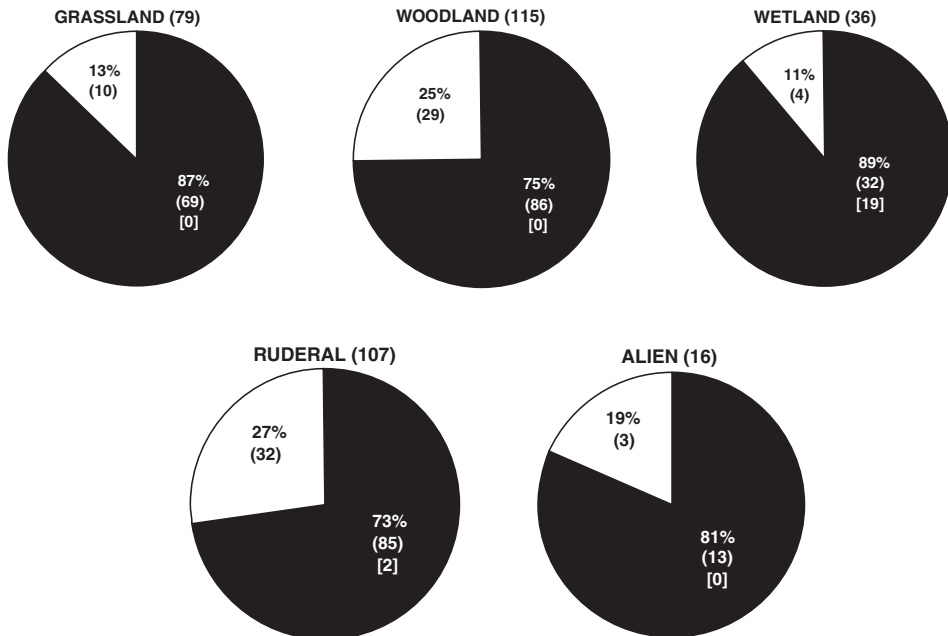


Fig. 3. – Percentage of target (grassland, woodland, wetland) and non-target (ruderal, alien) groups of species that occurred both in the surroundings (up to a distance of 100 m from quarries) and in the quarries (black). White colour indicates the percentage of species that occurred only in the surrounding vegetation. The percentages of target and non-target groups of species were calculated based on the number of species in each group (given in parentheses). The number of species occurring only in the quarries and not in the surroundings is given in square brackets. Twenty eight species were not classified because of their ambiguous rank.

woodland species in the quarries was associated with wetness, age, and the percentage cover of particular categories of land cover, namely grassland and woodland, both up to 100 m and 1 km from a quarry. The occurrence of ruderal and alien species was associated with the percentage cover of ruderal and urban land and that at young stages of succession (Fig. 1, inset diagram).

Target and non-target groups of species

Changes in the proportion of target (grassland, wetland and woodland) and non-target (alien and ruderal) groups of species during succession in the three major seres, i.e. those on mesic, wet and periodically flooded sites, are shown in Fig. 2. The importance of grassland species decreased at mesic and wet sites during succession, while woodland species increased. At periodically flooded sites, the importance of grassland species increased while woodland species did not, mainly due to fluctuations in waterlevel. The importance of wetland species increased rapidly at periodically flooded sites and decreased at wet sites in the course of succession due to the increase in cover of woodland species. The importance of non-target species (aliens and ruderals) decreased in all seres. However, the number of non native plants was generally low (Fig. 2).

Nearly three-quarters of the target woodland species that occurred in the surroundings colonized the quarries (Fig. 3). Grassland species, especially wetland species, were the most successful group of target species, because nearly 90% colonized the quarries. Some wetland species obviously came from localities at distances greater than 100 m from a quarry. The non-target groups of species were also successful as about three-quarters of ruderals (two ruderal species, *Sagina procumbens* and *Ballota nigra*, arrived from even greater distances) and 81% of the non-native plants came from the surroundings of the quarries.

Discussion

Generally, succession in the quarries resulted in mixed woodland often with an admixture of wetland, which is also documented for some other post-mining sites in Central Europe (Řehouňková & Prach 2006, Vojar 2006). The climax vegetation in this area is woodland. A similar succession is reported for quarries situated close to the study area in the northern part of the Českomoravská vrchovina uplands (Chuman 2006). The old stages of succession in abandoned quarries in drier and warmer parts of the country consist of either woodland or shrubby grasslands (Novák & Prach, 2003). Periodically flooded sites were not included in their study. The effect of topography, i.e. steep rocky slopes, bottoms and levels, and dumps and screes, was not significant unlike in some other studies where more diverse vegetation developed on such sites (Ursic et al. 1997, Khater et al. 2003, Novák & Prach 2003). It is possible that the rather humid climate in the study area partly masked the role of habitats. However, succession is possibly slower on steep rocky slopes (field observation, see also Novák & Prach 2003) where soil develops slowly and only in small patches compared to the other habitats.

In spite of the fact that acidic substrates are usually poorer in species than basic ones (Hodgson 1981), a relatively large number of species (313) colonized the 41 acidic quarries, i.e. 12% of Czech flora (Kubát et al. 2002). J. Novák (personal communication) found about 430 species (16%) in a similar study of 56 basalt quarries in the České středohoří hills (Novák & Prach 2003). The average number of species per relevé increased up to the middle successional stages and then decreased slightly, which is similar to that recorded for most seres (Peet 1992).

The significant effect of time, i.e. successional age or time since the quarry was abandoned, is also reported in other studies in which environmental factors determined the trajectory of spontaneous succession of vegetation at disturbed and abandoned sites (e.g. Osbornová et al. 1990, Ursic et al. 1997, Novák & Prach 2003, Řehouňková & Prach 2006, del Moral 2007). Site wetness seems to be the environmental factor driving the succession, because it influences the respective community species pool and participation of woody species. A similar conclusion is reported for gravel-sand pits (Řehouňková & Prach 2006).

The surrounding vegetation appeared to be an important factor affecting the process of colonization of mining-disturbed sites (see also Borgegård 1990, Novák & Konvička 2006, Řehouňková & Prach 2006). Sources of seed from (semi-)natural vegetation within a 100 m radius are usually decisive for the establishment of target vegetation (e.g. Cain et al. 2000, del Moral & Erin 2004, Novák & Konvička 2006). In this study, a high percentage of the woodland, wetland and grassland species in the quarries also occurred in the surrounding (semi-)natural vegetation. However, ruderal and alien species also successfully

colonized the quarries if they occurred in the surroundings. But the total number of alien species colonizing the quarries was low due to their low presence in the landscape (Chytrý et al. 2009). Moreover, the abundance of alien species decreased during succession with the exception of *Lupinus polyphyllus* at some sites. Altogether, 21 mostly wetland species occurred only in the quarries. It is likely that water birds, moving among water bodies across the landscape, helped disperse the wetland species by epizoochory (Řehouňková & Prach 2008). Two ruderal species were probably accidentally introduced.

Continuous vegetation cover in the studied quarries was usually formed in about 10 to 15 years after quarry abandonment, which is similar to that recorded for other sites disturbed by mining (Prach & Pyšek 2001, Holl 2002). Spontaneous succession in the abandoned quarries proceeded relatively quickly to the (semi-)natural vegetation typical of the area i.e. woodland and wetland, reaching that stage after approximately 25 years. This result is also consistent with that of some other studies conducted at mining sites in Central Europe (Novák & Prach 2003, Frouz et al. 2008, Řehouňková & Prach 2008).

Disturbed open sites, including quarries, may provide valuable habitats and serve as refugia for threatened and rare species unless they are reclaimed using technical methods (Novák & Prach 2003, Sádlo & Tichý 2002, Tropek et al. 2010). Such species are usually poor competitors and are unlikely to become established where there is closed vegetation. Thus, they preferably occur in young or arrested successional stages. However, the woodland vegetation that spontaneously developed in the quarries, despite being denser than at some drier and warmer sites in Central Europe, provides a sufficient area of open sites for species to become established, even at the late stages of succession. Wetlands in these quarries are especially valuable habitats, which provide sites for other organisms (e.g. Vojar 2006). Based on these results it is concluded that spontaneous succession is a reasonable means of restoring the vegetation in areas that have been quarried.

See <http://www.preslia.cz> for Electronic Appendix 1.

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Souhrn

Během spontánní sukcese v kyselých kamenolomech byla studována variabilita vegetace, podíl cílových a nežádoucích druhů a role lokálního „species pool“. Studie byla provedena na Českomoravské vrchovině. Zahrnuje 41 lomů s celkem 135 stadii odlišného stáří, od 1 do 92 let od ukončení těžby. Celkem bylo zaznamenáno 135 vegetačních snímků (5 × 5 m), v nichž byla pokryvnost druhů odhadnuta pomocí sedmičlenné Braun-Blanquetovy stupnice. Byly rozlišeny tři typy stanovišť: mírně vlhká, vlhká a periodicky zaplavovaná. Sledovány dále byly následující charakteristiky prostředí: skalní stěny, dna a etáže, odvaly, sutě; hlavní kategorie půdního pokryvu v okolí do vzdálenosti 100 m a 1 km od každého lomu; podíl cílových (lučních, lesních, mokřadních) a nežádoucích (ruderalních, invazních) druhů do vzdálenosti 100 m od okraje každého lomu. Ordinační analýzy ukázaly, že spontánní sukcese vegetace vedla k vytvoření smíšeného lesního porostu, vrbo-olšovým křovinám nebo k porostům vysokých ostřic a orobince s roztroušenými vrbami. Průběh sukcese závisel především na vlhkosti stanoviště, vliv měla i okolní vegetace. Sukcesní vývoj se na všech stanovištích uvnitř lomu jevil velmi podobně a rozdíl v jejich druhovém složení byl statisticky neprůkazný. Jen na skalních stěnách byl vývoj pomalejší. Obnova cílové vegetace v lomech pomocí spontánní sukcese je možná a může být úspěšná už během 25 let, zvláště pokud se v okolí vyskytují cílové druhy.

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