

Vegetation succession in basalt quarries: Pattern on a landscape scale

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Abstract. A spatio-temporal variation of vegetation during spontaneous succession was studied in 56 basalt quarries spread over 1800 km² in the České středohoří Hills (NW Czech Republic, Central Europe). Differences in the particular habitats inside a quarry, i.e. steep rocky slopes, bottoms and levels; dumps; and screes were considered. The habitats ranged in age from 1 to 78 yr since abandonment. Macroclimate (mean annual temperature and precipitation) significantly influenced the course of succession, which led to a formation of shrubby grassland, shrubby woodland or tall woodland. Participation of target species typical of steppe-like communities significantly depended on the occurrence of the communities in the vicinity, up to a distance of 30 m from a quarry. Disused quarries may become refugia for rare plant species. Spontaneous successional processes led in the reasonable time of ca. 20 yr to semi-natural vegetation. Thus, they can be successfully exploited in restoration programs scheduled for the disused quarries.

Keywords: Climatic gradient; Restoration; Species pool; Spontaneous succession; Target species.

Nomenclature: Hennekens (1995) for taxa; Oberdorfer (1992) for syntaxa.

Introduction

Despite the large number of studies on vegetation succession, there are not many of them investigating the variability of succession over a larger geographical area, except for Rydin & Borgegård (1991); Osbornová et al. (1990); Prach (1994); Csetcserits & Rédey (2001); Verhagen et al. (2001); and for limestone quarries Ursic et al. (1997) and Wheeler & Cullen (1997). Investigating the variability provides possibilities which are not able to be achieved by even very detailed analyses of a limited number of sites. Seeking to answer questions such as those on divergence vs. convergence of succession on a broader spatial scale (Lepš & Rejmánek 1991), influence of different climate (Prach 1994), and the role of different species pools in the course of succession (Strykstra et al. 1998) is not possible without a broader

geographical analysis of one type of succession. Moreover, an analysis of a large number of sites can produce insights that can better be applied in restoration ecology than those from only one or a few sites. It has been argued repeatedly that spontaneous succession is a suitable tool for restoration of various disturbed sites (Parker 1997; Harker et al. 1999; Prach et al. 2001), including stone quarries (Cullen et al. 1998).

We had an opportunity to study spontaneous succession in 56 basalt quarries spread over ca. 1800 km², in an old volcanic hilly area in central Europe, where a distinct climatic gradient is known.

We asked: 1. How does the vegetation succession differ among the quarries located in climatically different situations? 2. What are the differences in succession in particular habitats inside the quarries? 3. How is the participation of target species, typical for species-rich grasslands, influenced by the surrounding vegetation?

Study area

The area, named the České středohoří Hills, is located in the northwestern part of the Czech Republic, Central Europe, 50°34' - 50°48' N, 13°41' - 14°32' E (Fig. 1). The altitudinal range is from 123 m a.s.l. at the bank of the River Elbe, up to 837 m a.s.l. at the top of the highest volcanic hill. The studied quarries are located between 160 and 610 m a.s.l. The area forms an elongated shape, running about 90 km from the southwest to the northeast, and was declared as a Protected Landscape Area by national law in 1976.

Three regions can be distinguished in a SW-NE direction (Kubát 1970); they show differences both in climate and the occurrence of species belonging to different range types (Meusel & Jäger 1992).

The climate in the SW part (Region 1) shows continental features with only sporadic snow cover in winter and rather dry summers, with the lowest annual precipitation in the country. The region is characterized by the

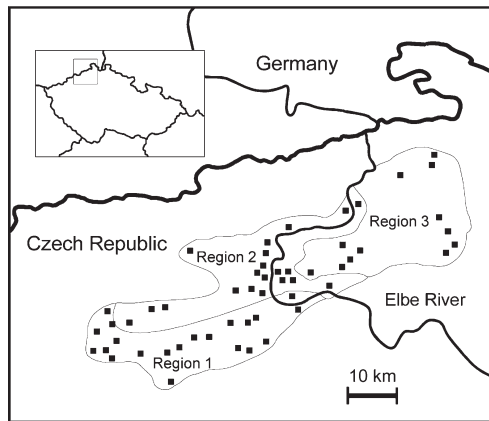


Fig. 1. Location of the studied basalt quarries. Three climatically different regions were delimited according to climatic characteristics (based on Kubát 1970).

occurrence of species belonging to the Euro-Asian, and European meridional-submeridional-continental range types (Kubát 1970), e.g. *Stipa pulcherrima*, *Helictotrichon desertorum*, *Astragalus excapus* and *Artemisia pontica*. They occur in extensive vegetation patches of *Festucetalia valesiaceae*. The occurrence of *Quercetalia pubescenti-petraeae* vegetation is only sporadic and woodlands of *Fagetalia sylvaticae* do not occur there.

The central part (Region 2) is equally warm, but wetter than Region 1. Thermophilous oak forests (*Quercetalia pubescenti-petraeae*) are typical natural vegetation. Patches of *Festucetalia valesiaceae* are numerous but smaller than in Region 1. Species with a submediterranean-(pontic) range, e.g. *Cornus mas*, *Quercus pubescens*, *Geranium sanguineum* are more abundant there.

The northeastern part (Region 3) is wetter and colder than the previous parts. There is an absence of plants of the continental range type. Species belonging to the submediterranean-(pontic) range type are sporadic. Species of the Central-European range type e.g. *Quercus petraea*, *Corylus avellana*, *Galium odoratum* and *Brachypodium sylvaticum* are typical here. *Carpinion*, *Tilio-Acerion*, *Fagion* and *Arrhenatherion* prevail, while *Festucetalia valesiaceae* vegetation is rare. Charac-

teristics are summarized in Table 1.

Quarrying in the area started before World War II and culminated in the 1980s. Some quarries are still in use.

Methods

All available basalt quarries were considered if spontaneously re-vegetated sites occurred in a quarry. The history of each quarry was reconstructed on the basis of official records from the agencies exploiting the quarries or from the Administration of a Protected Landscape Area. Moreover, local people were consulted. The following particular habitats inside each quarry were considered: (1) steep rocky slopes (walls); (2) flat rocky and stony bottoms and levels; (3) dumps of various spoil material (disintegrated, fine-structured bedrock; low soil horizons); and (4) screes and debris at the foot of the walls. The habitats ranged in age from 1 to 78 yr since abandonment. Because exact dating was not possible in all cases, age categories were defined before data analyses started: Age 1: 1-3 yr old; Age 2: 4 - 10 yr; Age 3: 11-25 yr; Age 4: 26-40 yr; Age 5: > 40 yr.

Phytosociological relevés of 5 m × 5 m were recorded in representative sites in each quarry, avoiding additionally disturbed sites, sites of unclear history or those being very fragmented and heterogeneous. We used the seven degree Braun-Blanquet scale (van der Maarel 1979) to estimate the cover of all species present (427 species together). The type of habitat (see above) was recorded. In total, 386 relevés were recorded with a mean number of seven relevés per quarry. The presence of natural xerotherm grasslands in the vicinity of a quarry (up to 30 m from the margin of a quarry) was recorded.

Mean annual temperature was obtained from Moravec & Votýpka (1997). 50-yr averages of mean annual precipitation and mean winter (X-III) precipitation were taken from the nearest meteorological station (Vesecký et al. 1960).

The vegetation data were analysed by multivariate methods in CANOCO version 4 (ter Braak & Šmilauer 1998) and were not transformed. We expected unimodal relationships between species occurrence and time and therefore used DCA (length of the gradient of 5.9 SD)

Table 1. Characteristics of the climatic regions. The altitude ranges concern the studied quarries.

Region	Mean annual precipitation (mm)	Mean annual temperature (°C)	Typical natural vegetation	Frequent floristic elements	Altitude (m)	Number of quarries
1	460 - 500	8.1-9.0	<i>Festucetalia valesiaceae</i>	Eurasian, continental	190-380	21
2	501 - 600	7.6-9.0	<i>Quercetalia pubescenti-petraeae</i>	Submediterranean - (Pontic)	160-550	21
3	601 - 820	6.1-7.5	<i>Fagetalia sylvaticae</i>	Central European	290-610	14

and CCA ordinations. For DCA, detrending by segments was used, and species with a weight from 5% were considered. For CCA, inter-sample distance by Hill scaling and unrestricted permutations (999) were used without forward selection, and *p*-values and *F*-ratio were calculated (ter Braak & Šmilauer 1998).

Results

Changes in species composition

Except for steep walls, the succession of vascular plants starts in the studied quarries immediately after habitat creation. There are annual species which usually occur in the initial stages (Age 1) as dominants in most quarries disregarding the climatic region: *Arenaria serpyllifolia*, *Senecio vernalis*, *Lactuca serriola* and *Tripleurospermum inodorum*.

The initial stages are followed after 4 yr (Age 2) by annual and biennial species such as *Bromus tectorum*, *B. sterilis*, *Daucus carota*, *Trifolium arvense*, *Medicago lupulina*, and *Echium vulgare*, often accompanied by perennials such as *Poa compressa* and *Picris hieracifolia*. Several species occur only in the warmest Region 1, e.g. *Oxytropis pilosa*. On very rocky sites, such as the bottoms and levels, *Sedum album*, *Erysimum crepidifolium*, and *Verbascum lychnitis* occur also. *Tussilago farfara* appears early as a dominant on dumps with a higher proportion of fine-structured subsoil.

Gradually, after 10 yr (Age 3) perennial grasses and hemicryptophytes expand. *Arrhenatherum elatius* is a major dominant in all mesic habitats. *Dactylis glomerata*, *Lotus corniculatus*, *Hypericum perforatum*, *Inula conyza*, *Hieracium bauhinii*, *Echinops sphaerocephalus*, *Melilotus albus* and *Potentilla argentea* are also frequent. *Calamagrostis epigejos* is common on substrates with a higher content of clay. *Anthemis tinctoria*, *Convolvulus arvensis*, *Euphorbia cyparissias*, *Melica transsilvanica* and *Sanguisorba minor* are common on unstabilized debris and screes. Region 1 is characterized by the typical occurrence of 'steppe' species, e.g. *Koeleria macrantha*, *Artemisia campestris*, *Centaurea stoebe* and *Stachys recta*. Mesophilous species, e.g. *Poa nemoralis*, *Rubus idaeus* and young trees and shrubs of *Salix caprea*, *Betula pendula*, *Corylus avellana* and *Sambucus nigra*, are common in Region 3.

Trees, shrubs, sciophytes and nitrophytes expand after 25 yr (Age 4) in Regions 2 and 3, while heliophilous species decrease. Typical dominants for Region 2 are *Rosa canina*, *Sambucus nigra* and *Cornus sanguinea*, and young trees are becoming frequent, e.g. *Fraxinus excelsior*, *Acer campestre* and *Prunus avium*. *Betula pendula*, *Corylus avellana* and *Salix caprea* are very

common in Region 3. The course of succession in the dry Region 1 is rather different. Grasses, such as *Festuca valesiaca* and *Bromus erectus*, and perennial herbs, e.g. *Thymus pannonicus*, *Salvia nemorosa* and *Scabiosa ochroleuca*, are typical for this age.

The oldest successional stages (Age 5) in Regions 2 and 3 are characterized by the gradual formation of a tree layer. *Fraxinus excelsior*, *Acer campestre*, *Crataegus* spp. are typical for Region 2 with the tree layer less closed. Heliophilous species such as *Fragaria viridis* and *Geranium sanguineum* are abundant. In the wettest Region 3, *Quercus petraea* and *Fraxinus excelsior* form the tree layer besides the already present *Betula pendula*. In the herb layer, nitrophilous and mesophilous species, such as *Geum urbanum*, *Impatiens parviflora*, *Campanula rapunculoides* and *Geranium robertianum* are common. In Region 1, the oldest stage resembles a 'shrubby steppe' with a higher occurrence of shrubs, especially *Prunus spinosa*, in wetter sites of the respective quarries. 'Steppe' species are represented especially by *Festuca valesiaca*, *Festuca rupicola*, *Elymus hispidus*, *Poa angustifolia*, *Bromus erectus*, *Dianthus carthusianorum* and *Scabiosa ochroleuca*. The oldest successional stages seem to be rather stabilized, so we expect further successional changes to be slow and mostly of a quantitative character.

Differences between habitats

Differences in the course of succession in the considered habitats are clearly evident from the results of the DCA ordination presented in Fig. 2 (eigenvalue of axis 1 = 0.648, axis 2 = 0.459). Generally, the course of succession seems to be divergent both among the regions and inside quarries within each region. The lowest within-quarry differences were found in Region 3., where the high humidity probably makes the habitats more uniform due to a higher participation of woody species in all the habitats. The differences among the particular habitats are more profound in the warmer and drier regions. Here, the dumps seem to be the most mesic sites, while the walls are most xeric. Quarry walls in Region 2 even appeared to be more xeric than dumps from Region 1. Succession on dumps is most rapid and slowest on steep walls (the two youngest stages of walls are not represented here because there is no vegetation in that age). The positions of the centroids in Fig. 2 suggest that the early successional stages on walls lag ca. 10 yr behind: the 11 - 25 yr old stages are close to those of the 4-10 yr stages of other habitats, and later the delay can be even greater.

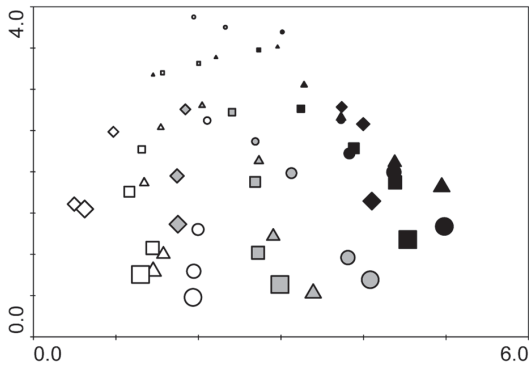


Fig. 2. DCA ordination of phytosociological relevés, grouped per habitat type, successional stage and region. ▲ = flat bottoms, ● = dumps, ■ = screes and debris at the foot of walls, ◆ - walls. The increasing size of symbols corresponds to 5 classes of successional age (1-3 yr; 4 - 10 yr; 11 - 25 yr; 26 - 40 years; > 40 yr). Region 1 - empty symbols; Region 2 - grey symbols; Region 3 - black symbols.

Influence of climate

The quarries were clearly arranged along the considered climatic gradients, i.e. mean annual temperature, mean annual precipitation, and mean winter precipitation, in the CCA ordination (Fig. 3). The quarries from the three regions were clearly separated ($p < 0.001$, $F = 11.054$). The eigenvalues of the first and second CCA axes were 0.497 and 0.186, respectively.

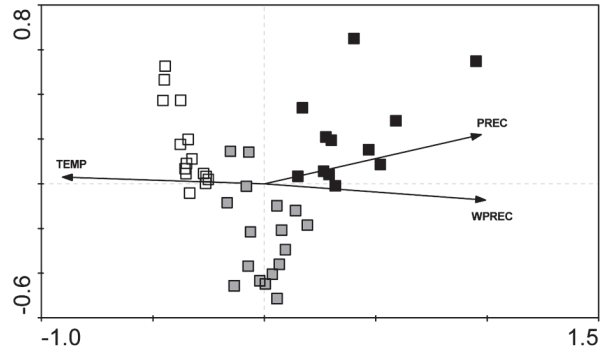


Fig. 3. CCA ordination biplot of quarries and climatic conditions. TEMP = Mean annual temperature; PREC = Mean annual precipitation; WPREC = Mean winter precipitation. Region 1 - empty symbols; Region 2 - grey symbols; Region 3 - black symbols.

Influence of surrounding vegetation

The presence of natural or semi-natural xerotherm grasslands in the vicinity of a quarry has a significant (CCA, $p < 0.001$; $F = 10.331$) effect on the course of succession (Fig. 4). The eigenvalues CCA axes 1 and 2 were 0.474 and 0.436 respectively. The differences are relatively small in the early stages of succession (Ages 1 and 2) when common ruderal species are typical of all grasslands. However, with increasing successional age, the differences between quarries with and without xerotherm grasslands in their vicinity increase.

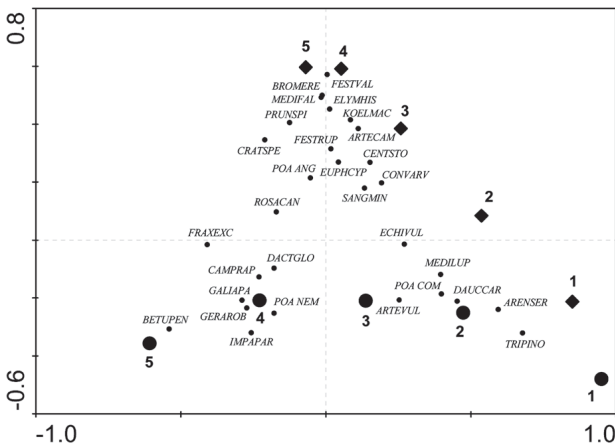


Fig. 4. CCA ordination of species and quarries, sorted according to the presence (◆) and absence (●) of xerotherm grasslands at a distance of up to 30 m from the margin of a quarry. Numbers 1-5 correspond to age categories. Species – represented with four letters from the genus and three from the species name – are mentioned in the text.

Age [years]			
1-3	Annual species		
4-10	Annual, biennial + first perennial species		
11-25	Perennial grasses	Perennial grasses + young trees	
26-40	Grassland	Shrubs	Trees
>40	Shrubby grassland	Shrubby woodland	Woodland
	Region 1	Region 2	Region 3

Fig. 5. Generalized scheme of succession in the basalt quarries in the three regions, based on the dominance of life forms and physiognomy of vegetation.

Discussion

Successional patterns

Studies on vegetation succession on a broader geographical scale can provide results which cannot be attained by any detailed study in one or a few sites: e.g. influences of macro-climate, and differences in species pool in the course of succession. Moreover, analysing a high number of sites, despite using rather robust methods, we obtained a much broader view on a particular type of succession, which can be used practically in restoration ecology. Unfortunately, there is still a lack of such studies (Burrows 1990; Luken 1990; Glenn-Lewin et al. 1992). We had a great advantage in our study that both the substratum (basalt) and the system of quarrying were similar in all studied sites. This enabled us to better recognize the effects of other factors in the course of succession.

The succession appears to be divergent both within and among quarries. Divergent succession trends on larger geographical scales have been reported several times earlier (Lepš & Rejmánek 1991; Prach 1994; Ursic et al. 1997) but at smaller scales, i.e. inside localities, succession tends to be convergent (Lepš & Rejmánek 1991). The opposite trend in the case of the studied quarries is probably caused by the fact that during the initial stages all habitats are colonized by a common set of ruderal species with a broad ecological amplitude (generalists). Later, more specialized species appear.

Despite the differences and the divergent status of succession among the habitats, the direction of succession inside a quarry is principally the same if life forms and dominant species are considered. There are more differences in the rate of succession, with a great delay of vegetation development on steep walls.

Successional divergence is also apparent in the physiognomy of vegetation in the three regions. The earlier stages are dominated everywhere by annual, biennial or perennial herbs whereas the late successional stages are dominated either by grasses, shrubs or trees (summarized in Fig. 5). The proportion of woody species is generally higher in less extreme habitats, i.e. more humid in this case (Olsson 1987; Prach & Pyšek 1994).

Our study has shown that the course of succession is also dependent on the type of vegetation in the close vicinity. Even if the role of the surrounding vegetation in the process of colonization of disturbed sites has been repeatedly emphasized, there are only very few quantitative studies focusing on this topic (Zobel et al. 1998; Strykstra et al. 1998). It is known that species forming xerotherm grasslands are mostly dispersed over a short distance (Grime et al. 1988; Poschlod et al. 1996) and it is, therefore, not surprising that they are able to colonize

the quarries only if they occur in their close proximity (Davis 1982). Recently, we conducted sowing experiments with dominant species from xerotherm grasslands and showed that these species are able to establish and grow in suitable habitats in any of the quarries, including those in Region 3 (J. Novák unpubl.). Their occurrence seems indeed to be limited mainly by dispersability (van der Valk 1992).

Implications for restoration practice

The results presented here demonstrate that spontaneous succession from bare quarries to semi-natural vegetation takes on average ca. 20 yr. Under certain conditions, i.e. if xerotherm grasslands are present in close vicinity to a quarry, even highly valuable communities may develop inside a quarry. These sites resemble natural steppe-like grasslands in species composition and physiognomy (Kubát 1970) and harbour rare and endangered species (see also Jefferson 1984). Several of such species find refugia even in younger stages (e.g., *Oxytropis pilosa* and *Erysimum crepidifolium*). Typical species from natural steppe-like grasslands that fail to establish naturally could be sown into suitable quarry habitats during restoration programs, thus accelerating and directing the succession (Luken 1990).

The intensity of quarrying in the region is decreasing but there are still several quarries operating. We recommend to include the preservation of at least some remnants of (semi-)natural grasslands into the extraction schemes (if they still occur in the locality). We recommend also to eliminate the invasive *Robinia pseudacacia* from the surroundings in order to protect a quarry against invasion which we observed in several sites.

Generally, stone extraction is not appreciated in a Protected Landscape Area. However, under some future compromises, quarrying can be accepted if it respects the recommendations of ecologists. Our study showed that spontaneous succession can be a suitable, effective tool to restore quarries. This was found also in other studies on quarries (Davis et al. 1985; Ursic et al. 1997; Wheather & Cullen 1997) and does agree with general recommendations (Parker 1997; Harker et al. 1999; Prach et al. 2001; Perrow & Davy 2002).

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References

- Burrows, C.J. 1990. *Processes of vegetation change*. Unwin Hyman, London.
- Csetcserits, A. & Rédey, T. 2001. Secondary succession on sandy old-fields in Hungary. *Appl. Veg. Sci.* 4: 63-74.
- Cullen, W.R., Wheeler, P.C. & Dunleavy, P.J. 1998. Establishment of species-rich vegetation on reclaimed limestone quarry faces in Derbyshire, UK. *Biol. Conserv.* 84: 25-33.
- Davis, B.N.K. (ed.) 1982. *Ecology of quarries*. Institute of Terrestrial Ecology, Cambridge, UK.
- Davis, B.N.K., Lakhani, K.H., Brown, M.C. & Park, D.G. 1985. Early seral communities in a limestone quarry: an experimental study of treatment effects on cover and richness of vegetation. *J. Appl. Ecol.* 22: 473-490.
- Glenn-Lewin, D.C., Peet, R.K. & Veblen, T.T. (eds.) 1992. *Plant succession. Theory and prediction*. Chapman & Hall, London, UK.
- Grime, J.P., Hodgson, J.G. & Hunt, R.J. 1988. *Comparative plant ecology. A functional approach to common British species*. Unwin Hyman, London, UK.
- Harker, D., Libby, G., Harker, K., Evans, S. & Evans, M. 1999. *Landscape restoration handbook*. 2nd. ed. Lewis, Boca Raton, FL, US.
- Hennekens, S.M. 1995. *TURBO(VEG). Software package for input, processing, and presentation of phytosociological data*. IBN-DLO, Wageningen, NL.
- Jefferson, R.G. 1984. Quarries and wildlife conservation in Yorkshire Wolds, England. *Biol. Conserv.* 29: 363-380.
- Kubát, K. 1970. *Rozšíření některých druhů rostlin v Českém středohoří. Fytogeografická studie [Occurrence of plant species in the České středohoří Hills. Phytogeographical study]*. Okresní museum, Litoměřice, CZ. (In Czech with German summary.)
- Lepš, J. & Rejmánek, M. 1991. Convergence or divergence: what should we expect from vegetation succession? *Oikos* 62: 261-264.
- Luken, J.O. 1990. *Directing ecological succession*. Chapman and Hall, London, UK.
- Meusel, H. & Jäger, E. (eds.) 1992. *Vergleichende Chorologie der zentraleuropäischen Flora. Band III*. G. Fischer, Jena DE.
- Moravec, D. & Votýpka, J. 1997. *Klimatická regionalizace České republiky [Climatic regions of the Czech Republic]*. Karolinum, Praha, CZ. (In Czech.)
- Oberdorfer, E. 1992. *Süddeutsche Pflanzengesellschaften*. G. Fischer, Jena, DE.
- Olsson, G. 1987. Effects of dispersal mechanisms on the initial pattern of old-field succession. *Acta Oecol.* 8: 379-390.
- Osbornová, J., Kovářová, M., Lepš, J. & Prach, K. (eds.) 1990. *Succession in abandoned fields. Studies in Central Bohemia, Czechoslovakia*. Kluwer, Dordrecht, NL.
- Parker, V.T. 1997. The scale of successional models and restoration objectives. *Restor. Ecol.* 5: 301-306.
- Perrow, M.R. & Davy, A.J. (eds.) 2002. *Handbook of ecological restoration. Vol. 2: Restoration in practice*, pp. 466-485. Cambridge University Press, Cambridge, UK.
- Poschlod, P., Bakker, J., Bonn, S. & Fischer, S. 1996. Dispersal of plants in fragmented landscapes. In: Settele, J., Margules, C.R., Poschlod, P. & Henle, K. (eds.) *Species survival in fragmented landscapes*, pp. 123-127. Kluwer, Dordrecht, NL.
- Prach, K. 1994. Vegetation succession on river gravel bars across the Northwestern Himalayas, India. *Arct. Alp. Res.* 26: 349-353.
- Prach, K. & Pyšek, P. 1994. Spontaneous establishment of woody plants in Central European derelict sites and their potential for reclamation. *Restor. Ecol.* 2: 190-197.
- Prach, K., Bartha, S., Joyce C.B., Pyšek, P., van Diggelen R. & Wiegleb, G. 2001. Possibilities of using spontaneous succession in ecosystem restoration: a perspective. *Appl. Veg. Sci.* 4: 111-114.
- Rydin, H. & Borgegård, S.-O. 1991. Plant characteristics over a century of primary succession on islands: Lake Hjälmaren. *Ecology* 72: 1089-1101.
- Strykstra, R.J., Bekker, R.M. & Bakker, J.P. 1998. Assessment of dispersule availability: its practical use in restoration management. *Acta Bot. Neerl.* 47: 57-70.
- ter Braak, C.J.F. & Šmilauer, P. 1998. *CANOCO Release 4. Reference manual and user's guide to Canoco for Windows: Software for Canonical Community Ordination*. Microcomputer Power, Ithaca, NY, US.
- Ursic, K.A., Kenkel, N.C. & Larson, D.W. 1997. Revegetation dynamics of cliff faces in abandoned limestone quarries. *J. Appl. Ecol.* 34: 289-303.
- van der Maarel, E. 1979. Transformation of cover-abundance values in phytosociology and its effects on community similarity. *Vegetatio* 38: 85-96.
- van der Valk, A.G. 1992. Establishment, colonization and persistence. In: Glenn-Lewin, D.C., Peet, R.K. & Veblen, T.T. (eds.) *Plant succession. Theory and prediction*, pp. 60-102. Chapman & Hall, London, UK.
- Verhagen, E., Klooker, J., Bakker, J.P. & van Diggelen, R. 2001. Restoration success of low-production plant communities on former agricultural soils after top-soil removal. *Appl. Veg. Sci.* 4: 75-82.
- Vesecký, A., Briedoň, V., Karský, V. & Petrovič, S. 1960. *Podnebí Československé republiky. Tabulky [Climate of Czechoslovakia. Tables]*. Academia, Praha, CZ.
- Wheeler, P.C. & Cullen, W.R. 1997. The flora and invertebrate fauna of abandoned limestone quarries in Derbyshire, United Kingdom. *Restor. Ecol.* 5: 77-84.
- Zobel, M., van der Maarel, E. & Dupré, C. 1998. Species pool: the concept, its determination and significance for community restoration. *Appl. Veg. Sci.* 1: 55-66.

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