Spontaneous succession of vegetation in mined peatlands: a multi-site study

Spontánní sukcese vegetace na těžených rašeliništích v České republice

Petra Konvalinková[1,2,3] & Karel Prach[1,2]

[1]*Department of Botany, Faculty of Science, University of South Bohemia, Branišovská 31, CZ-370 05 České Budějovice, Czech Republic, email: konvalin@prf.jcu.cz, prach@prf.jcu.cz;* [2]*Institute of Botany, Academy of Sciences of the Czech Republic, Dukelská 143, CZ-379 82 Třeboň, Czech Republic;* [3]*DAPHNE – Institute of Applied Ecology, Husova 45, CZ-370 05 České Budějovice, Czech Republic*

Konvalinková P. & Prach K. (2010): Spontaneous succession of vegetation in mined peatlands: a multi-site study. – Preslia 82: 423–435.

This study was conducted at 17 peatlands in the Czech Republic mined either by the traditional block-cut method or industrially. Phytosociological reléves of 5 × 5 m were carried out in representative parts of successional stages in disturbed peatlands. Age and environmental characteristics were assessed for each relevé (position of water table, water pH, substratum chemistry, geographical area) or each locality (altitude, average annual temperature and precipitation). Phytosociological reléves recorded in natural vegetation, representing the respective target stages, were included into some analyses. Altogether, 210 relevés were analysed by the DCA ordination. Separately, relevés from milled and block-cut sites were elaborated by CCA with marginal and partial effects calculated. Despite the great variability in vegetation, especially among industrially harvested sites, there is a general tendency for peatland vegetation to recover spontaneously, especially at traditionally harvested sites, which all were, however, older than 50 years. The vegetation at the younger industrially harvested sites exhibited only a tendency to recover. All environmental variables investigated had at least some significant effect on the vegetation pattern, among them, soil pH, water table, nitrates, successional age and geographical location were most important. Abiotic site factors together and geographical location appeared to be more important in determining species composition than successional age.

Keywords: abiotic factors, bryophytes, mined peatland, ordination, restoration, successional age, vascular plants

Introduction

Although peat is not nowadays an important fuel, it is still used for various commercial or medical purposes in many parts of the World. The largest areas of peat currently being mined are in Russia, Ireland, Belarus, Finland, Germany, Latvia and Canada (Lappalainen 1996). In the Czech Republic (Central Europe), where this study was done, peatlands cover only 0.3% of the area (Bragg & Lindsay 2003, Montanarella et al. 2006). Peat was, and still is, mined almost exclusively from peatlands that are usually classified as raised bogs (Hochmoor), see Dierssen & Dierssen (2001). They are confined to rather isolated patches occurring mostly in humid and mountain regions (Neuhäusl 1972, Bastl et al. 2008). The patches can be seen as habitat islands (Spitzer 1994), some of which have continuously existed since the late Glacial or early Holocene, and these habitats have an azonal character with a high level of relictness (Jankovská 1980). Under natural conditions they are usually covered by bog pine (*Pinus rotundata*) at low altitudes (approximately below 700 m a.s.l.) or by its hybrids with dwarf pine (*Pinus mugo*) at high altitudes (Businský 1998, Bastl et al. 2008). There are about 200 well developed bogs in the Czech Republic. Traditionally, peat was mined for fuel by hand digging (block-cut). The water level remained high after digging because drainage was poor and the peat was usually dug down to the ground water level, leaving a thick layer of peat. Usually, peat was dug only in a part of a bog and bog vegetation survived in the surroundings. This type of mining was replaced by mining by machinery in the 1950s. The large-scale industrial mining (milling) that developed had profound effects on a whole locality, especially because of deep drainage and often the extraction of the whole peat layer. Drainage ditches were dug approximately 25 m apart and the area between them was given a moderately convex profile in order to facilitate water run off into the ditches.

The sites traditionally mined were usually left to regenerate naturally, while industrially mined sites were mostly afforested by monocultures of Scots Pine (*Pinus sylvestris*) with a few areas left to regenerate naturally (Bastl et al. 2009). Thus, it is now possible to study processes of spontaneous succession in areas where peat has been mined, which may provide information on how best to restore disturbed sites (Girard et al. 2002, Lavoie et al. 2003, Schrautzer et al. 2007). Most studies of peatland are limited to only one or a few sites and specific problems such as species composition, *Sphagnum* establishment, seed rain, effect of nursery plants, hydrology, carbon cycling and gas emission, and various restoration activities. Information from studies on spontaneous succession before 2003 is summarized by Lavoie et al. (2003). As far as we know, there are only a few studies of succession in large geographic areas: Poulin et al. (2005) and Graf et al. (2008) in Canada, Salonen (1994) in Finland and Orru & Ramst (2009) in Estonia. This study follows on some previous investigations of successional processes in disturbed peatlands in the Czech Republic (Horn & Bastl 2000, Lanta et al. 2004, Kučerová et al. 2008, Bastl et al. 2009), which were confined either to a specific region or only one or a few localities. The present multi-site study should provide an overview of the potential for spontaneous succession in disturbed peat bogs in a broader geographical context. The data may be used in restoration projects, especially for predicting the future development at sites left to spontaneous succession (Sliva & Pfadenhauer 1999, Vasander et al. 2003). The following questions were addressed: (i) Do the spontaneous successional processes vary among mined sites? (ii) Are there differences in the successional vegetation at traditionally and industrially mined sites? (iii) Which environmental factors determine the vegetation variability and is it possible to manipulate these factors in restoration projects?

Material and methods

Study sites

This study was done at mined peatlands in the Czech Republic (Fig. 1). Seventeen sites were selected for study. The criteria for the selection were: (i) Mining had occurred at bogs with bog pine (*Pinus rotundata*) or its hybrid *P.* ×*pseudopumilio*. (ii) All localities with industrial peat milling were included. (iii) Block-cut sites with a clear history were included. The number of block-cut sites was limited because the primary interest was in milled peatlands and because most block-cut sites are now protected as nature reserves to which access is restricted. The localities were located in four geographical areas: 1 – the Krušné hory Mts (including the Slavkovský les hills), 2 – the Šumava Mts, 3 – the Třeboň Basin and 4 – the Českomoravská vrchovina highlands. The basic climatic and other characteristics are listed for all the localities investigated in Table 1.

Data collection

Field sampling was conducted using phytosociological reléves, 5 × 5 m in size, located in representative parts of the harvested bogs, i.e. in parts at the same successional age, homogenous in vegetation cover and apparently not previously subjected to additional disturbances. Each distinguished successional stage was sampled by 1–3 relevés, depending on its size and heterogeneity. The relevés were located in flat areas, avoiding ditches or standing water. Together, 190 relevés were obtained (39 in block-cut and 151 in milled peatlands). Percentage cover of all vascular plants and bryophytes was visually estimated. In some analyses phytosociological reléves recorded in natural, undisturbed vegetation, representing the respective target stages, were included. They were taken from the Czech National Phytosociological Database (Chytrý & Rafajová 2003) if located within 2 km of a studied mined peatlands. In total, 20 relevés from natural vegetation were used. Nomenclature of vascular plants follows Kubát et al. (2002). For each relevé, the following information was

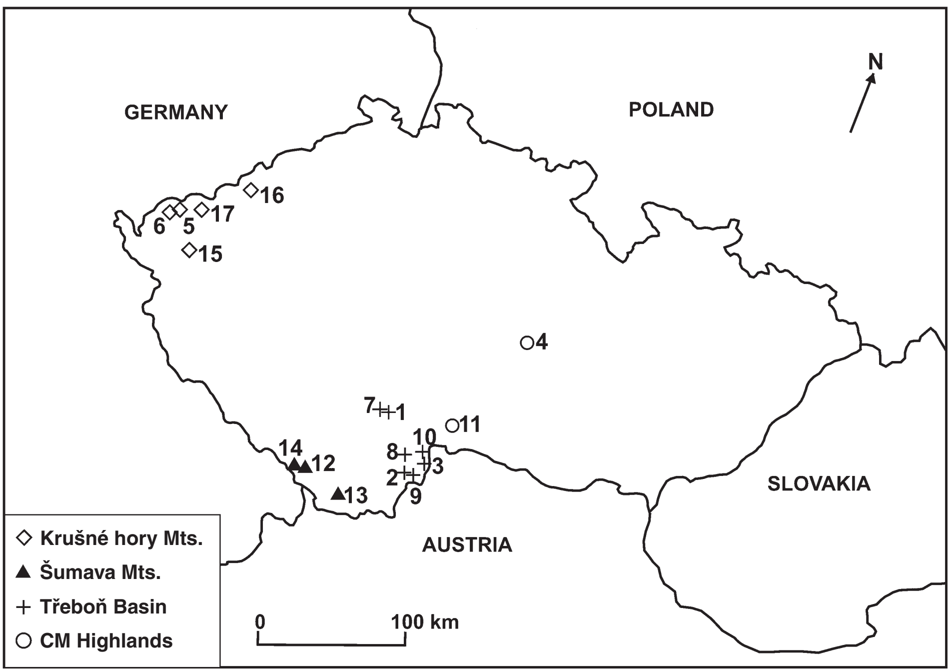

Fig. 1. – Location of the study sites in the Czech Republic. Sites 1–6 were block-cut, sites 7–17 industrially mined. Different symbols indicate location in different geographical areas (regions). For other information see Table 1.

Table 1. – A list of the peatlands studied and their main characteristics. Abbreviations of the geographical areas (regions) where the peatlands are located: TR – Třeboň Basin, CM – Českomoravská vrchovina Highlands, KH – Krušné Hory Mts., SU – Šumava Mts (see Fig. 1).

	Locality	Region	Latitude	Longitude	Altitude (m a.s.l.)	Average annual precipitation (mm)	Average annual temperature (°C)	Time since abandoned	Number of sites sampled
Block-cut peatlands									
1	Kozohlůdky	TR	49°13' N	14°39' E	420	616	7.7	60	10
2	Červené blato	TR	48°52' N	14°48' E	480	673	7.8	60, 100	13
3	Široké blato	TR	48°54' N	14°59' E	490	682	8.0	60	4
4	Radostín	CM	49°39' N	15°53' E	620	771	6.9	60	4
5	Přebuz	KH	50°23' N	12°36' E	880	1120	5.8	50	4
6	Velký Močál	KH	50°24' N	12°39' E	890	1120	5.8	60	3
Milled peatlands									
7	Borkovice	TR	49°14' N	14°37' E	420	616	7.7	27	17
8	Branná	TR	48°57' N	14°48' E	445	617	8.0	12, 16, 25	5
9	Hrdlořezy	TR	48°51' N	14°51' E	460	673	7.8	1, 6, 16	14
10	Příbraz	TR	49°02' N	14°57' E	470	690	7.6	1, 3, 6, 10, 13, 15, 30	28
11	Člunek	CM	49°07' N	15°08' E	540	789	7.6	1, 6, 15	13
12	Soumarský Most	SU	48°54' N	13°50' E	750	851	5.6	7, 20	5
13	Světlík	SU	48°43' N	14°12' E	770	737	6.1	7, 10, 15	13
14	Vlčí Jámy	SU	48°55' N	13°47' E	780	851	5.6	5,15	5
15	Krásno	KH	50°06' N	12°46' E	780	619	6.5	8, 15, 18	12
16	Hora sv. Šebestiána	KH	50°31' N	13°14' E	850	798	5.7	12,19	13
17	Abertamy	KH	50°22' N	12°48' E	880	1018	5.7	10	3

gathered: Age was based on information from the mining companies in the case of milled peatlands, from the local nature conservation authorities in the case of block-cut peatlands, literature and historical aerial photographs. Altitude was obtained from detailed maps and climatic data (average annual temperature and precipitation) from the nearest meteorological station (data from the Czech Hydrometeorological Institute, www.chmi.cz).

At sites where the successional vegetation was sampled, boreholes were dug and the position of the water table manually measured in July, September, October 2006 and May 2007. Water pH and conductivity of water samples taken from the boreholes were directly measured in the field, using a portable pH and conductivity meter.

Because of our primary interest in milled peatlands other characteristics of the peat were measured at these sites: Thickness of the remaining peat deposit was assessed down to a depth of 1 m by coring. Three peat samples were randomly taken from the top 10 cm around each relevé, mixed, dried and sieved (2 mm sieve). Peat samples were analyzed for pH, conductivity, SO_4, NO_3, PO_4, NH_4, K and organic C content using standard methods. All these factors were measured in a 5:1 mixture of distilled water and peat. Conductivity was corrected for H^+ ions (Sjørs 1952).

Data analysis

Multivariate analyses (DCA and CCA) were conducted using the CANOCO program (ter Braak & Šmilauer 2002). Species cover data were log-transformed. Unimodal methods were used because of the length of the gradient (Lepš & Šmilauer 2003), which was 7.0 SD units in the DCA analysis of the whole data set. In the DCA of the whole data set, the age of natural, undisturbed sites was arbitrarily set as 200 years. Milled and block-cut sites were analyzed separately by CCA. In CCA, the inter-sample distance and Hill's scaling were used. Forward selection with a Monte Carlo permutation test (999 permutations) was performed to reveal variables with significance of at least 5%. Partial and marginal effects were also calculated. In the partial analyses, each factor was tested as an environmental variable with other factors as covariables. In the marginal analyses, only the tested factor was set as an environmental variable. This provides information on the importance of the factor disregarding its correlations with other variables (Lepš & Šmilauer 2003). In the case of the characteristics that were available only for the whole locality, i.e. altitude, average annual precipitation and temperature, separate analyses were done with species data pooled for each locality. Geographical area was coded as the dummy variable (Lepš & Šmilauer 2003).

Results

Results of the unconstrained ordination (DCA) of all relevés are presented in Fig. 2. The sites were arranged (Fig. 2A) according to the 1st axis, which reflected successional age ($R = 0.676$, $P < 0.001$). The samples from undisturbed bogs formed a clear and rather homogenous group. The positions of the samples from the block-cut sites were close to those of the undisturbed sites. The samples from milled sites formed a very large cluster. Some samples, especially those from the oldest sites (see isolines in Fig. 2A) were also close in their species composition to those of the undisturbed sites, but not most of the young sites. Moreover, the former were from sites with a high water table, low pH, thick peat deposits and where there were remnants of the bog close by (the last based only on field observations, not quantified in this study). Among the milled sites, a certain geographical pattern is seen, with the samples from the Třeboň Basin and the Krušné hory Mts forming groups with nearly no overlap. Samples from the Šumava Mts and the Českomoravská vrchovina Highlands (named as CM Highlands in the figures) are more heterogeneous. The 2nd axis seems to reflect altitude ($R = 0.591$, $P < 0.001$). Species (Fig. 2B) were clearly arranged along the 1st axis reflecting their successional status, with species typical of undisturbed bogs located on the right hand side of the diagram. Species typical of early successional stages at various disturbed sites are located on the left of the diagram, being represented by *Calamagrostis epigejos, Rumex acetosella* and *Juncus effusus.* Only altitude and age are shown as passive variables, because these were the only variables available for all samples (water measurements were not available for relevés extracted from the Czech National Phytosociological Database). Species typical for late successional stages of three distinguished subseres (see Discussion) are marked.

Results of the forward selection, partial and marginal CCA analyses are shown in Table 2. Marginal effects of all measured variables appeared to be significant, while partial effects of some variables, notably the depth of remaining peat and some water chemical proper-

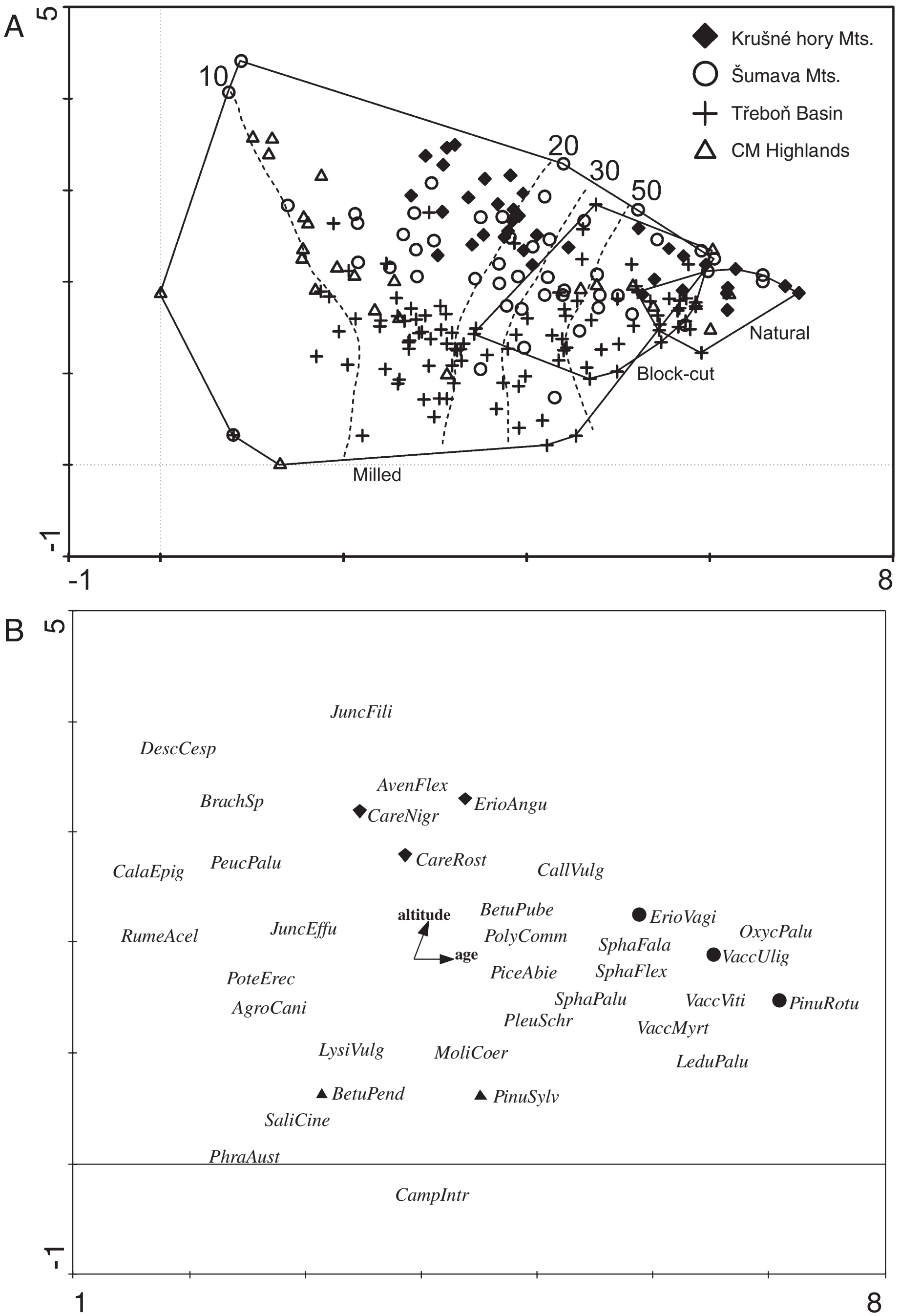

Fig. 2. – (A) Unconstrained ordination (DCA) of samples. Different symbols indicate location of samples in different geographical areas (see Fig. 1). Three types of samples are delimited by envelops: industrially mined (milled), block-cut and natural peatlands. The contour lines indicate successional age. (B) Unconstrained ordination (DCA) of species, which best fitted the model. The dominant species in the late successional stages of three subseres are indicated by different symbols: ◆ fen vegetation, ● bog vegetation, ▲ birch-pine woodland. Abbreviations of species names are composed of the four first letters of the generic and specific names (see Electronic Appendix 1).

Table 2 – Results of the constrained ordination (CCA) of samples based on forward selection of environmental variables, and their marginal and partial effects on the vegetation pattern. In italics, there are variables that were available only for the whole locality but not for particular samples.

	Forward selection (F)	Forward selection (P)	Partial F	Partial P	Explained variability (%)	Marginal F	Marginal P	Explained variability (%)
Milled peatlands								
Age	1.774	0.001	1.655	0.001	1.7	2.050	0.001	1.9
Water level	1.997	0.001	1.728	0.001	1.8	2.080	0.001	1.9
Water pH	1.441	0.014	1.413	0.032	1.5	1.980	0.001	1.8
Peat deposit	1.147	0.185	0.962	0.554	1.0	2.011	0.001	1.8
Soil pH	2.514	0.001	1.762	0.001	1.9	2.514	0.001	2.3
Soil conductivity	1.354	0.020	1.170	0.144	1.2	1.689	0.001	1.6
Organic C	1.483	0.004	0.951	0.590	1.0	2.183	0.001	2.0
NH_4	1.006	0.393	0.850	0.636	0.9	1.849	0.024	1.7
NO_3	1.778	0.001	1.415	0.026	1.5	1.973	0.001	1.8
PO_4	2.501	0.001	1.417	0.031	1.5	2.423	0.001	2.2
K	1.556	0.024	1.495	0.030	1.6	1.512	0.048	1.4
SO_4	0.888	0.740	0.895	0.721	1.0	1.642	0.003	1.5
All abiotic site factors	—	—	1.518	0.001	15.2	1.633	0.001	15.6
Geographical area	—	—	2.501	0.001	7.5	3.071	0.001	8.1
Altitude	2.034	0.001	1.249	0.221	15.1	2.034	0.001	18.4
Precipitation	1.096	0.372	1.096	0.383	13.5	1.517	0.016	14.4
Temperature	1.159	0.271	1.212	0.241	14.8.	1.942	0.001	17.7
Block-cut peatlands								
Age	1.692	0.013	1.387	0.062	4.2	1.997	0.001	5.3
Water level	2.303	0.003	2.671	0.001	7.7	2.316	0.002	6.0
Water pH	2.821	0.001	2.330	0.001	6.8	2.821	0.001	7.4
Geographical area	—	—	2.285	0.001	12.5	2.445	0.001	12.3
Altitude	1.197	0.384	1.354	0.316	40.4	1.939	0.007	32.7
Precipitation	1.974	0.008	1.346	0.385	40.2	1.974	0.008	33.0
Temperature	1.270	0.348	1.270	0.332	38.8	1.802	0.036	31.1

ties, were not significant in the case of milled peatlands. Age, depth of water table and water pH, are significantly associated with the vegetation in both types of mining (block-cutting and milling), however, the range of these variables differed. Depth of water table ranged between 3 and 67 cm below the surface, with an average of 17±14 cm at block-cut sites, and between 0 and more than 100 cm, with an average of 45±22 cm at milled sites, respectively. Water pH ranged from 3.0 to 5.4, with an average of 4.0±0.7 at block-cut sites, and from 3.8 to 7.3, with an average of 5.4±0.6 at milled sites. The largest marginal and partial effect of the abiotic site characteristics at milled sites was substratum pH, which ranged from 3.5 to 5.6, with an average of 4.5±0.4, with geographical area the more influential among the individual factors. Abiotic site factors collectively accounted for the greatest proportion of vegetation variability, followed by geographical area and then by successional age. In the case of the altitude and climatic characteristics of whole localities, all marginal effects were significant while partial effects were not due to mutual correlations. Altitude was significant in the forward selection in the case of milled peatlands and precipitation in the case of block-cut sites. Geographical area accounted for more of the variability than any other variable tested in the analyses based on all the relevés of both milled and block-cut peatlands, being even more important than successional age (Table 2).

Discussion

All traditionally harvested, i.e. block-cut sites, recovered spontaneously. All are older than 50 years and seem to be similar in their species composition to undisturbed sites (Fig. 2A, Electronic Appendix 1). This is already reported from one of the geographical areas included in our study, the Třeboň Basin, by Bastl et al. (2009), based on a different data set. The convergence towards typical bog vegetation composed of species of the class *Oxycocco-Sphagnetea* (Chytrý & Tichý 2003) is seen in Figs 2A and B. Regeneration of typical peatland vegetation after block-cutting is reported, for example, by Poulin et al. (2005), Girard et al. (2002), Lavoie & Rochefort (1996), Robert et al. (1999) and Soro et al. (1999). However, even after 50 years the vegetation at the block-cut sites was different from that at undisturbed sites (see also Soro et al. 1999), with various impoverished forms of raised bog vegetation. If the peat layer is nearly completely removed, the expectation is a higher participation of species typical of class *Scheuchzerio-Caricetea fuscae* or *Phragmiti-Magnocaricetea,* which may represent valuable alternative targets (Dierssen & Dierssen 2001, Grootjans et al. 2006). The above mentioned trends are only possible if the water table remains high, which was the case at all block-cut sites but only at some milled sites. Spontaneous recovery of natural vegetation at the milled sites is less evident and more variable.

Based on field experience and the phytosociological relevés three successional developments can be distinguished (see the dominant species of late successional stages marked in Fig. 2B): (i) The gradual establishment of woodland composed of *Pinus sylvestris* and *Betula* spec. div., which later on are often accompanied by *Picea abies*. This vegetation develops at sites where the water table is usually deeper than 0.5 m (see Bastl et al. 2009). (ii) Recovery of bog vegetation with at least some participation of bog pine, *Pinus rotundata* or its hybrids, and other typical bog species, especially *Eriophorum vaginatum* and *Vaccinium uliginosum*. This can be expected at sites with a high water table, a layer of peat at least 0.5 m thick and remnants of bog at the edges of the mined peatland, which act as a source of diaspores (Salonen 1987, Poulin et al. 1999). This type of recovery is recorded at most block-cut sites (see Electronic Appendix 1). However, only the initial stages of this development occur at the milled sites, especially those where the height of the water table was artificially increased after peat extraction as a part of the restoration management. (iii) Development towards fen vegetation (class *Scheuchzerio-Caricetea fuscae* and *Phragmiti-Magnocaricetea*), mainly seen at sites where the peat was mostly or completely removed and the height of the water table remained high, as mentioned above. A fourth successional development, not evident in our data set, but recorded, is an aquatic sere in water basins that remain after peat mining. Gradual terrestrialization is typical of such sites where the development approaches that recorded under (ii) or (iii) above.

The importance of a high water table is reported in all studies dealing with regeneration of disturbed peatlands. However, the CCA analyzes of the results for milled sites indicate it is not as important as one expects. This is probably because of the large geographical (altitude and climatic) differences among the sites, with precipitation modifying site moisture conditions and thus masking the role of the water table. An artificially high water table may be created by blocking ditches or it may be naturally high at sites where the peat was extracted down to the mineral-rich groundwater level (Sliva & Pfadenhauer 1999, Price et al. 2003, Schrautzer 2007).

Water level and thickness of the remaining peat deposit are generally thought to be preconditions for the spontaneous recovery of bog vegetation (Salonen 1990, Rochefort & Campeau 1997). However, the remaining peat has only a marginally significant effect and was not significant in the partial analysis and in the forward selection in the CCA ordination of relevés from the milled peatlands. This may be due to the negative correlation ($r = -0.458$) with substratum pH (see also Girard et al. 2002). Substratum pH appeared to have the most significant effect on the vegetation pattern in the partial analyses. Similar results are presented by Farrell & Doyle (2003) and Herbichowa et al. (2009). The pH is generally thought to determine vegetation in peatland (Dierssen & Dierssen 2001, Hájek et al. 2002) and generally to be an important factor driving succession (Prach et al. 2007). Substratum pH was positively correlated with water level: the deeper the extraction the greater the probability of reaching fen peat formed during the early development of the bog, which is of a different quality, and the closer the new surface is to mineral rich groundwater (Farell & Doyle 2003, Graf et al. 2008, Nishimura et al. 2009). The importance of other edaphic factors, especially NO_3 and PO_4, which were found to significantly influence the vegetation pattern in this study, is repeatedly reported (Salonen & Setälä 1992, Salonen & Laaksonen 1994, Lanta et al. 2004, Poulin et al. 2005, Graf et al. 2008).

Beside the edaphic factors, successional age had a significant influence but did not play a dominant role. Geographical differences and edaphic factors, perhaps together with some undisclosed biotic or random factors probably partly suppressed the role of age, which is usually the main explanatory variable in most successional studies (Walker & del Moral 2003). An assynchronic development at some localities could have contributed: there was almost no vegetation even after 10 years at some sites at Krásno and Borkovice (Table 1), i.e the sites with a thick peat deposit and low water table. A dry peat surface may be a hostile environment for vegetation and thus block succession as is reported for mined peatlands elsewhere (Tuitilla et al. 2000, Poulin et al. 2005, Herbichowa et al. 2009, Orru & Ramst 2009).

Although biotic factors were not directly considered in this study, especially the local species pool and the distance to remnants of bogs, it is likely these factors have an important influence as recorded for other sites disturbed by mining in the Czech Republic (Řehounková & Prach 2006) and for peatland by Salonen & Setälä (1992) and Girard et al. (2002). Local species pools are largely determined by macroclimate, surrounding vegetation and land-use histories (Settele et al. 1996). Average annual temperature and precipitation, reflected in the altitudes of the sites, appear to have significant effects on the vegetation pattern in the marginal CCA analyses. Close mutual correlations between altitude, temperature and precipitation are responsible for the insignificant partial effect of these variables and for why only one of these characteristics was selected in the forward selection (Lepš & Šmilauer 2003). Moreover, all these abiotic factors together with the local species pool are combined and represented by the geographical area, importance of which was clearly demonstrated in this study. The important influence of macroclimate on the course of the various successions, including that on mined peatlands, was quantified by Prach et al. (2007) for the same geographical region. Consequently, it is not surprising there were differences in the vegetation pattern among the geographical areas considered here (Fig. 2A, Table 2). The distance between the most distant sites was 250 km and the altitudes of the sites differed by 470 m. Samples from the area in the Krušné hory Mts were very different from those from the lowland area in the Třeboň Basin, while samples from the other two regions are from intermediate altitudes (Fig. 2a) and well reflect the range of altitudes of localities in the respective regions (Table 1). This accords with the findings of Bastl et al. (2008) who analyzed undisturbed peatlands in the same geographical area.

The main limitation to arriving at firm conclusions when comparing industrially and traditionally mined sites is the fact that, as far as we know, no industrially mined and spontaneously revegetated site is older then 30 yrs and no traditionally mined site is younger than 50 yrs. Thus, the sets of plots available were exclusive in terms of their successional age, which limits parallel comparison of the successional seres in the two types of mined peatlands. Using the space-for-time substitution approach rather than permanent plots may have another limitation (Johnson & Miyanishi 2008). However, because of the high number of sites studied, the latter limitation may not be so important in this case.

Finally, the answers to the questions posed in the introduction are: (i) Despite the rather high variability in the vegetation, especially among industrially mined sites, there is a general and obvious tendency for the spontaneous recovery of peatland vegetation. A geographical pattern was found that reflects mainly the different altitudes and macroclimates at the sites. (ii) Traditionally mined sites, which are all older than 50 years, appeared to be already close in their species composition to undisturbed peat bog vegetation. The younger industrially mined sites exhibit only a certain tendency towards this condition and probably only some of them have the potential to recover without assistance. (iii) All the environmental variables investigated exhibited at least some significant effects on the vegetation pattern, among them the geographical location, soil pH, water table, nitrates, altitude and successional age are the most important. Abiotic factors together explained a much higher proportion of the variability in the vegetation than the successional age. Only the level of the water table can be easily manipulated in order to enable or speed up the recovery of peatland vegetation.

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

Acknowledgements

The study was supported by the following grants: MSM 6007665801, AVOZ 60050516, DBU 91-0041-AZ26858-33/2 and GA AV CR IAA600050702. We thank Tony Dixon for language revision, Rudy van Diggelen and an anonymous reviewer for their comments, and J. Matouš, M. Hátle, L. Rektoris, V. Melichar and E. Vicherová for their help in carrying out this research.

Souhrn

Spontánní sukcese vegetace byla studována na 17 těžbou narušených blatkových rašeliništích ve čtyřech geografických oblastech České republiky. Byla rozlišena jednotlivá sukcesní stadia, na nich zaznamenány fytocenologické snímky (celkem 190), měřena hladina a pH vody a stanoveno chemické složení substrátu. Fytocenologické snímky z 20 nenarušených rašelinišť byly použity jako referenční. Pro jednotlivé lokality byly dále zjištěny nadmořská výška, průměrné roční srážky a teplota. Data byla zpracována mnohorozměrnými metodami (DCA a CCA). Z výsledků vyplynulo především následující: Vegetace na tradičním způsobem (borkováním) těžených lokalitách (všechny byly starší 50 let) se již značně blíží původní vegetaci rašelinišť. Mladší, průmyslově těžené lokality se obnovují obtížněji a jen některé vykazují náznaky obnovy rašeliništní vegetace. Byla zjištěna výrazná geografická variabilita v průběhu sukcese závislá především na nadmořské výšce (a tím i na makroklimatu a místním "species pool", který však nebyl přímo studován). Všechny studované faktory prostředí vykázaly alespoň v některých analýzách statisticky průkazný vliv na průběh sukcese. Mezi nimi největší vliv měly geografická lokalizace, pH substrátu, hladina vody, obsah nitrátů a sukcesní stáří. Určitý vliv měla rovněž hloubka zbylé rašeliny po těžbě. Abiotické stanovištní faktory dohromady vysvětlily mnohem větší část vegetační variability než sukcesní stáří.

References

Bastl M., Burian M., Kučera J., Prach K., Rektoris L. & Štech M. (2008): Central European pine bogs change along altitudinal gradient. – Preslia 80: 349–363.

Bastl M., Štechová T. & Prach K. (2009): Effect of disturbance on the vegetation of peat bogs with *Pinus rotundata* in the Třeboň Basin, Czech Republic. – Preslia 81: 105–117.

Bragg O. & Lindsay R. (eds) (2003): Strategy and action plan for mire and peatland conservation in Central Europe. – Wetlands International, Wageningen.

Businský R. (1998): Agregát *Pinus mugo* v bývalém Československu: taxonomie, rozšíření, hybridní populace a ohrožení [*Pinus mugo agg.* in former Czechoslovakia: taxonomy, distribution, hybrid populations and its endangerment]. – Zpr. Čes. Bot. Společ. 33: 29–52.

Chytrý M. & Rafajová M. (2003): Czech National Phytosociological Database: basic statistics of the available vegetation-plot data. – Preslia 75: 1–15.

Chytrý M. & Tichý L. (2003): Diagnostic, constant and dominant species of vegetation clases and alliances of the Czech Republic: a statistical revision. – Folia Fac. Sci. Nat. Univ. Masaryk. Brun., Biol., 108: 1–231.

Dierssen K. & Dierssen B. (2001): Moore (Ekosysteme Mitteleuropas aus geobotanischer Sicht). – Ulmer, Stuttgart.

Farrell C. A. & Doyle G. J. (2003): Rehabilitation of industrial cutaway Atlantic blanket bog in County Mayo, North-West Ireland. – Wetl. Ecol. Manage. 11: 21–35.

Girard M., Lavoie C. & Thériault M. (2002): The regeneration of a highly disturbed ecosystem: a mined peatland in Southern Québec. – Ecosystems 5: 274–288.

Graf M. D., Rochefort L. & Poulin M. (2008): Spontaneous revegetation of cutaway peatlands of North America. – Wetlands 28: 28–39.

Grootjans A. P., van Diggelen R. & Bakker J. P. (2006): Restoration of mires and wet grasslands. – In: van Andel J. & Aronson J. (eds), Restoration ecology: the new frontier, p. 111–123, Blackwell, Oxford.

Hájek M., Hekera P. &Hájková P. (2002): Spring fen vegetation and water chemistry in the Western Carpathian flysh zone. – Folia Geobot. 37: 205–224.

Herbichowa M., Budys A. & Cwiklinska P. (2009): Experimental re-introduction of mire plant species in milled, raised bogs in Northern Poland. – In: Farrell C. & Feehan J. (eds.): Proceedings of the 13th International Peat Congress 1: 401–404, International Peat Society, Jyväskylä.

Horn P. & Bastl M. (2000): Successional changes of vegetation at the "Multerberské rašeliniště" peat bog in the Šumava Mts during the last 50 years. – Příroda 17: 109–118.

Jankovská V. (1980): Paläogeobotanische Rekonstruktion der Vegetationsentwicklung im Becken Třeboňská pánev während des Spätglazials und Holozäns. – Academia, Praha.

Johnson E. A. & Miyanishi K. (2008): Testing the assumptions of chronosequences in succession. – Ecol. Lett. 11: 419–431.

Kubát P., Hrouda L., Chrtek J. jun., Kaplan Z., Kirschner J. & Štěpánek J. (eds) (2002): Klíč ke květeně České republiky [Key to the Flora of Czech Republic]. – Academia, Praha.

Kučerová A., Rektoris L., Štechová T. & Bastl M. (2008): Disturbances on a wooded raised bog: how windthrow, bark beetle and fire affect vegetation and soil water quality? – Folia Geobot. 43: 49–67.

Lanta V., Doležal J. & Šamata J. (2004): Vegetation patterns in a cut-away peatland in relation to abiotic and biotic factors: a case study from the Šumava Mts., Czech Republic. – Suo 55: 33–43.
Lappalainen E. (ed.) (1996): Global peat resources. – International Peat Society, Jyskä.
Lavoie C., Grosvernier P., Girard M. & Marcoux K. (2003): Spontaneous revegetation of mined peatlands: an useful restoration tool? – Wetl. Ecol. Manage. 11: 97–107.
Lavoie C. & Rochefort L. (1996): The natural revegetation of a harvested peatland in southern Quebec: a spatial and dendroecological analysis. – Ecoscience 11: 97–107.
Lepš J. & Šmilauer P. (2003): Multivariate analysis of ecological data using Canoco. – Cambridge Univ. Press, Cambridge.
Montanarella L., Jones R. J. A. & Hiederer R. (2006): The distribution of peatlands in Europe. Mires and peat, article 1. – URL: [http://www.mires-and-peat.net].
Neuhäusl R. (1972): Subkontinentale Hochmoore und ihre Vegetation. – Studie ČSAV 13: 1–121.
Nishimura A., Tsuyuzaki S. & Haraguchi A. (2009): A chronosequence approach for detecting revegetation patterns after *Sphagnum*-peat mining, northern Japan. – Ecol. Rest. 24: 237–246.
Orru M. & Ramst R. (2009): Revegetation processes in abandoned peat production fields in Estonia. – In: Farrell C. & Feehan J. (eds.): Proceedings of the 13th International Peat Congress 1: 421–423, International Peat Society, Jyväskylä.
Poulin M., Rochefort L. & Desrochers A. (1999): Conservation of bog plant species assemblages: assessing the role of natural remnants in mined sites. – Appl. Veg. Sci. 2: 169–180.
Poulin M., Rochefort L., Quinty F. & Lavoie C. (2005): Spontaneous revegetation of mined peatlands in eastern Canada. – Can. J. Bot. 83: 539–557.
Prach K., Pyšek P. & Jarošík V. (2007): Climate and pH as determinants of vegetation succession in Central-European human-made habitats. – J. Veg. Sci. 18: 701–710.
Price J. S., Heathwaite A. L. & Baird A. J. (2003): Hydrological processes in abandoned and restored peatlands: an overview of management approaches. – Wetl. Ecol. Manage. 11: 65–83.
Řehounková K. & Prach K. (2006): Spontaneous vegetation succession in disused gravel-sand pits: role of local site and landscape factors. – J. Veg. Sci. 17: 583–590.
Robert E. C., Rochefort L. & Poulin M. (1999): Natural revegetation of two block-cut mined peatlands in eastern Canada. – Can. J. Bot. 77: 447–459.
Rochefort L. & Campaeu S. (1997): Rehabilitation work on post-harvested bogs in south-eastern Canada. – In: Parkyn L., Stoneman R. E. & Ingram H. A. P. (eds), Conserving peatlands, p. 287–294, CAB International, Wallingford.
Salonen V. (1987): Relationship between the seed rain and the establishment of vegetation in two areas abandoned after peat harvesting. – Holarct. Ecol. 10: 171–174.
Salonen V. (1990): Early plant succession in two abandoned cut-over peatland areas. – Holarct. Ecol. 13: 217–223.
Salonen V. (1994): Revegetation of harvested peat surfaces in relation to substrate quality. – J. Veg. Sci. 5: 403–408.
Salonen V. & Laaksonen M. (1994): Effects of fertilization, liming, watering and tillage on plant colonization of bare peat surfaces. – Ann. Bot. Fennici 31: 29–36.
Salonen V. & Setälä H. (1992): Plant colonization of bare peat surface: relative importance of seed availability and soil. – Ecography 15: 199–204.
Schrautzer J., Rinker A., Jensen K., Müller F., Schwartze P. & Dierssen K. (2007): Succession and restoration of drained fens: perspectives from Northwestern Europe. – In: Walker L. R., Walker J. & Hobbs R. J. (eds), Linking restoration and ecological succession, p. 90–120, Springer, New York.
Settele J., Margules C., Poschlod P. & Henle K. (eds) (1996): Species survival in fragmented landscapes. – Kluwer, Dordrecht.
Sjørs H. (1952): On the relation between vegetation and electrolytes in north Swedish mire waters. – Oikos 2: 241–258.
Sliva J. & Pfadenhauer J. (1999): Restoration of cut-over raised bogs in southern Germany: a comparison of methods. – Appl. Veg. Sci. 2: 137–148.
Soro A., Sundberg S. & Rydin H. (1999): Species diversity, niche metrics and species associations in harvested and undisturbed bogs. – J. Veg. Sci. 10: 549–560.
Spitzer K. (1994): Biogeographical and ecological determinants of the central European peat bog *Lepidoptera*: the habitat island approach to conservation. – Nota Lepid. Suppl. 5: 45–49.
ter Braak C. J. F. & Šmilauer P. (2002): Canoco reference manual and CanoDraw for Windows user's guide: software for canonical community ordination (version 4.5). – Microcomputer Power, Ithaca.

Tuittila E-S., Vasander H. & Laine J. (2000): Impact of rewetting on the vegetation of a cut-away peatland. – Appl. Veg. Sci. 3: 205–212.
Vasander H., Tuittila E.-S., Lode E., Lundin L., Ilomets M., Sallantaus T., Heikkilä R., Pitkänen M.-L. & Laine J. (2003): Status and restoration of peatlands in northern Europe. – Wetl. Ecol. Manage. 11: 51–63.
Walker L. R. & del Moral R. (2003). Primary succession and ecosystem rehabilitation. – Cambridge University Press, Cambridge.

Received 20 January 2010
Revision received 1 July 2010
Accepted 4 July 2010