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Vegetation patterns in a cut-away peatland in relation to abiotic and biotic factors: a case study from the Šumava Mts., Czech Republic

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We studied the natural regeneration of a cut-over peat bog in the Šumava Mountains, Czech Republic. The spontaneous revegetation by vascular plants has been limited by extreme abiotic conditions left after peat mining. Only 1–2% of the total area was recolonized by *Sphagnum* mosses. This was mainly because drainage channels are still drying out the bog. Only plants tolerant to water stress such as *Juncus effusus, Molinia caerulea*, *Eriophorum angustifolium* and *E. vaginatum* were able to establish there. A key species colonizing bare surface is a clonal plant *E. angustifolium*. It forms circular polycormons of densely aggregated ramets. As in other radially spreading phalanx plants, the oldest (central) part of the system gradually dies, previously connected ramets become separated, and ring polycormon becomes open to recolonization by other plant species. We analyzed the relationships between species richness of the ring and their size, percentage litter cover, distance to seed sources, and soil fertility. The number of plant species was higher in the middle of the polycormons. The soil was more fertile in the central area than in the surroundings. We conclude that the restoration of highly disturbed habitats can be facilitated by clonal behavior of pioneer populations.

Keywords: *Eriophorum angustifolium*, cut-away peat bog, plant colonization, clonal plant

Introduction

Peatlands are rare ecosystems that are being rapidly destroyed by human activities. Removal of the original vegetation, extensive drainage, and the extraction of horticultural or fuel peat are the main factors that threaten in Europe and North America these unique habitats for which few restoration measures were considered until recently (Lappalainen 1996). Attempts to restore these ecologically and economically important landscapes by natural means are often unsuccessful for the extreme abiotic conditions left after peat mining. The natural processes of recolonization and succession may take decades or more especially in those areas in which peat moss extraction was carried out by modern mechanical vacuum methods (Joosten 1995, Pfadenhauer & Klötzli 1996, Desrochers et al. 1998, Lavoie et al. 2003). The impacts of vacuum mining are more severe than those of manual block-cut mining in that it leaves a more uniform peat surface topography. Homogeneous bare peat surfaces are prone to cracking and crust formation, frost heaving and erosion by wind and water, restricting the establishment of plant propagules (Girard et al.

2002). These conditions severely inhibit the re-establishment of *Sphagnum* mosses, the primary peat forming vegetation. Hence, re-establishment of the former vegetation cover in post-mined peatlands represents an important challenge for ecologists and conservation managers.

Recent restoration measures in post-mined peatlands aim to re-establish the original vegetation cover by introducing plant diaspores and reducing moisture deficiencies in the open fields created by the vacuum mining. Blocking draining ditches is a first necessary prerequisite for improving moisture conditions and stimulating regeneration of mosses and bog plants (Price 1997, Stoneman & Brooks 1997). Other possibilities to ameliorate the surface conditions, reduce the water stress and loss of diaspores in the open fields are to create open water reservoirs that decrease lateral seepage, to alter the surface microtopography, and use shading devices and straw mulches (Price et al. 1998, Schouwenaars 1995, Robert et al. 1999, Horn & Bastl 2000). Price et al. (1998) proposed the use of mulches to assist the development of a vegetation cover and stabilize the peat surface. The mulching has been shown to ameliorate soil moisture and temperature conditions through its effect on the energy balance. Price (1997) showed that the use of mulch keeps soil water suction lower during dry summer, which increases the survival of bog plants (Campeau & Rochefort 1996). Using this and other similar restoration techniques, successful establishment of mosses and mire plants has been reported frequently, whereas case studies documenting revegetation solely through natural processes are rather rare.

In Central Europe, many peat bogs have been abandoned and left without management after the end of mining activities, usually due to various economic reasons. Some of these have gradually been overgrown by woody species, notably *Betula pubescens* and *Pinus sylvestris*, but others remained only sparsely vegetated. The plant succession appears to be particularly inhibited in abandoned mountain peatbogs of colder regions with acid and nutrient-poor bedrock (Horn & Bastl 2000). The Šumava Mts., Czech Republic, include several such cut-over and abandoned peatlands. The intent of this paper is to investigate the patterns of plant colonization/succession in post-mined peatland at a locality "Soumarský most" in Šumava Mts. The peat-bog has an extensive open area created by peat mining. Pioneer plant populations that colonize bare surface rarely progress beyond the initial invasion phase of succession. An exception is a clonal plant *Eriophorum angustifolium* which is able to form dense cover and build-up a critical standing crop. This can lead to habitat improvement and establishment of other plant species. This study aims to examine (i) the relationship among the different habitats present in disturbed and undisturbed parts of cut-away peat bog; (ii) their hydrological conditions and (iii) if the *Eriophorum* facilitates ecesis of other plants.

Material and methods

Study area

The data were collected at "Soumarský most" peat bog in the Šumava Mts., South Bohemia, Czech Republic (Fig. 1). The "Soumarský most" peat-bog is a continental raised bog (sensu Neuhäusl 1972) dominated by *Pino rotundatae-Sphagnetum* community, *Oxycocco-Sphagnetea* class. The bog covers an area of 90 ha at an elevation of 650 m in Vltava river floodplain. The bedrock consists of acid, nutrient-poor granit and clay (Kodym 1961). The region is characterized by a humid climate with ca. 1000 mm mean annual precipitation (the Lenora meteorological station, 4 km north-west of "Soumarský most").

The "Soumarský most" peat-bog was disturbed several times during the last 200 years. Between 1958 and 1999, the site was intensively mined for horticultural peat using the milling method, which needs effective drainage because heavy machinery is used and milled peat is dried on the surface of the strips to a moisture content of 40% (Frilander et al. 1996). A grid of drainage ditches was first dug out creating rectangular units. The surface vegetation was than removed and put aside. The mining of moss and peat layers followed, altering the relief and hydrological properties of the site. The bog surface is now flat, with maximum of residual peat reaching the depth of approximately 1 m. One main drainage channel demarcates the peatland into N and S part. The channel was excavated to the present depth

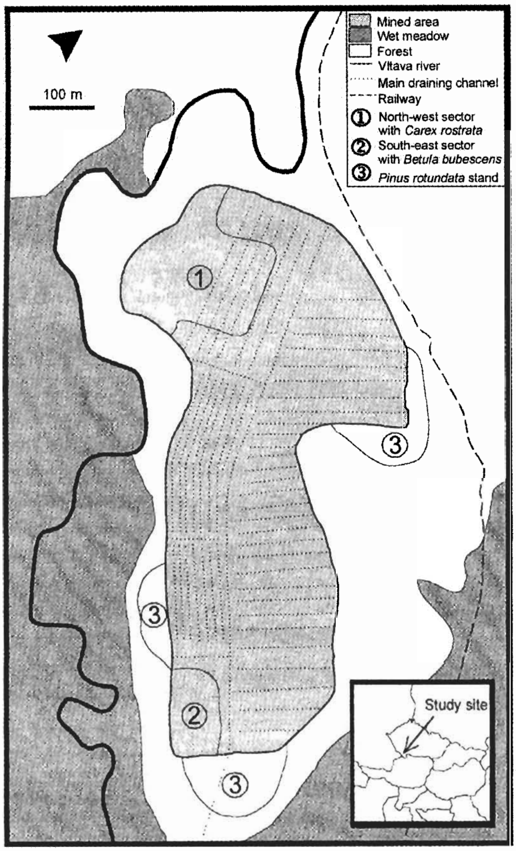


Fig. 1. The study area and its location within Central Europe.

of 2.5–3 m in order to drain away water from secondary ditches, which are running alongside and across the main channel in S and N parts, respectively. In 2000, the secondary ditches in S part were already manually blocked by the breakdown of palisade dams cut through the peat (see Stoneman & Brooks 1997). Water accumulates successfully only in some ditches, with no distinguishable flow.

Data collection

Plant distribution

Plant species distribution was recorded in a total of 50 randomly located quadrates, distributed across seven habitats delineated within the peatland area and the nearest surroundings of: (i) bare post-mined surface; (ii) drainage channels; (iii) old primary *Pinus rotundata* forest; (iv) bog spruce forest; (v) periodically flooded area, i.e., wet meadows; (vi) forest composed of dominant *Pinus sylvestris* trees and (vii) secondary young forest. Cover of all vascular plants were estimated by using the Braun-Blanquet scale. The area of sample quadrates ranged from 25 to 200 m^2, because different scale in forest and open area had to be taken into account (see Moravec et al. 1994). For statistical analysis, species cover values were transformed using 1–9 scale (van der Maarel 1979). Hydrological data were recorded one to three times per month at six sites during vegetation season 2000 for a totaling of 11 measurements in each site. Water table depth was measured relative to the soil surface in perforated 1.5 m long, polyvinyl-chloride pipes (6 cm in diameter) inserted permanently in the peat.

Eriophorum angustifolium

E. angustifolium (Cyperaceae) is a clonal plant which forms distinct rings of densely aggregated ramets on bare surfaces left after peat mining. *E. angustifolium* develops new ramets intravaginally within each shoot. The older shoot increments are re-oriented downwards to form a creeping stem covered with dead leaves. The ramet population expands radial and after some time a wide ring of densely aggregated ramets is formed. As in other radially spreading phalanx plants such as *Carex humilis* (Wikberg & Mucina 2002), the oldest (central) part of the system dies and previously connected parts become separated, i.e. *E. angustifolium* forms rings rather than filled circles. Consequently, the ring habitat can be divided into three concentric zones: Centre — the zone with low ramet density in the middle of ring and high accumulation of litter; Ring — the band with high ramet density around the Center, Surroundings — the bare surfaces among the rings (see Fig. 2).

In August–September 2002, we described fifty randomly selected *Eriophorum* rings localized within the whole harvested area in terms of size, shape, litter area, spatial location and the abundance of bryophytes and other vascular plants. One 80 x 80 cm relevé was recorded in the center of each ring and then four relevés were recorded in the Ring zone of *Eriophorum* (in southern,

Fig. 2. A key species colonizing bare surface is a clonal plant *E. angustifolium* which forms circular polycormons of densely aggregated ramets.

northern, western and eastern part). Due to a small diameter of several polycormons, only one relevé was recorded from the Ring zone. In total, we sampled 184 relevés. We further counted the number of seedlings (< 10 cm in height), saplings (10–130 cm in height) and trees (>1.30 m) of *Betula pubescens* and *Pinus sylvestris* in each ring. In addition, distance (in m) from the nearest drainage channel, i.e. from a diaspores source, was measured. The area of Ring and Centre zone was estimated as an area of ellipse based on two perpendicular measurements approximating major and minor axes. From each ring and the nearest surrounding, 120 ml soil samples were collected from 5–15 cm depth. Each sample was weighted and then dried to constant weight at 105°C to determine water content. We further collected 40 soil samples, always 20 from Centre zone and 20 from Surroundings, to determine extractable phosphorus concentration by a modified ammonium molybdate-ascorbic acid method (Olsen & Sommers 1982). Nomenclature follows Rothmaler (1976) for vascular plants and Kučera & Váňa (1997) for mosses.

Data analysis

The phytocoenological relevés were classified by UPGMA (average clustering) hierarchical procedure with Ward's method using squared euclidean distance coefficient (Sokal & Rohlf 1995). The variability in plant distribution was also analyzed by method of unconstrained ordination, detrended correspondence analysis (DCA), using the program CANOCO (ter Braak & Šmilauer 1998). DCA ordination diagrams showing plant species scores on the first two axes were produced using CANODRAW software (ter Braak & Šmilauer 1998). For each of phytocoenological relevés, obtained in Centre and Ring zones of *Eriophorum* circles, the Shannon-Wiener and Evenness diversity indices (Magurran 1988) were calculated. Both indices describe general relationship between species and their percent covers. Obtained values compared using a GLM (STATISTICA software, Anon. 1996). Differences in underground water level between contrasting peat bog habitats were evaluated by one-way ANOVA. Vegetation of *Eriophorum* rings was analyzed by constrained ordination, redundancy analysis (RDA), with the ring zone type (Center versus Ring) as the only explanatory variable. The species score on the first (i.e. constrained) axis corresponded to the relative position of species' abundances with respect to Centre and Ring zone. A Monte Carlo permutation was used to test for the significance of the RDA model (499 permutations).The number of species, number of tree individuals and ring diameters were $\log(x+1)$ transformed prior to the analysis, in order to improve compliance with equal variance and normality assumption.

Results

Plant communities and water table fluctuations in relation to disturbance

Plant species composition differed between the seven habitate types of the peatland area. A total of 50 relevés were divided into 7 main clusters in that corresponded to 7 different vegetation types (Fig. 3). Similarly, DCA ordination determined 7 different groups connected with similarity in species composition, although the boundaries among them were not pronounced (Fig. 4). According to the dendrogram based on species composition, first vegetation type is a late successional *Pinus rotundata* community. Second type is a species rich wet meadow, occurring on flooded zone along the Vltava river. Third is secondary young forest composed mainly of juvenile stage of *Betula pubescens* and *Pinus sylvestris*. Fourth type is early succession habitat of bare peat surface, with low vegetation cover and dominance of *Juncus effusus*, *Carex canescens* and *Carex rostrata*. Fifth type is spruce forest, which is considered as a natural habitat in the neighboring area of the "Soumarský most" bog. Sixth type is artificial forest dominated by *Pinus sylvestris*. The last type is a young natural stands along draining channels with dominating *Betula pubescens* trees.

Fig. 1 shows a high cover of *Carex rostrata* and *Juncus effussus* (vegetation type of the bare peat surfaces in DCA diagram) in the northwest sector. The northwest sector was characterized by higher water levels that seems crucial for the establishment and survival of mire vegetation. In contrast, the southeast part of the peatland was abandoned earlier and was rapidly recolonized by a dense cover of shrubs and trees. The southeast part is located at a lower plateau. Here, protecting effect of surrounding trees of *Pinus sylvestris* may had evolved. This stand has the higher abundance of *Betula pubescens* saplings, and *Molinia caerulea* and *Juncus effusus* tussocks. *M. caerulea* is considered as a typical grass of peat bogs affected by severe summer droughts. Its presence indicates more favorable conditions for mineralization and mineral release. Along the draining channels *M. caerulea* is replaced by *J. effusus* and *Eriophorum vaginatum*, plants behaving typically as early colonists of bare peat with sufficient water supply.

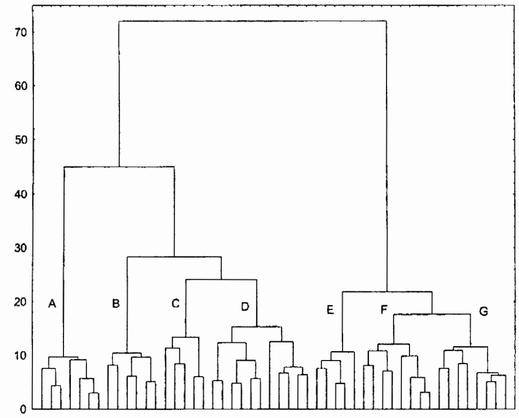
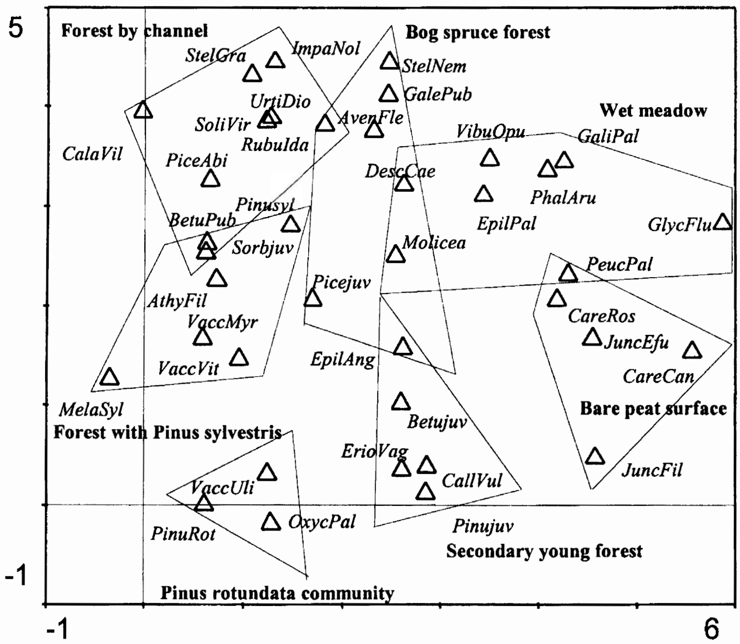


Fig. 3. Dendrogram of clustering of 50 reléves representing seven habitate types in a peatland. The main types of habitat are marked with letters: A — secondary young forest, B — wet meadow, C — bare peat surface, D — bog spruce forest, E — forests by channels, F — forest with planted *Pinus sylvestris*, G — old forest with *Pinus rotundata*.

The depth and seasonal variations in water table differed mainly between undisturbed natural *Pinus rotundata* stand and disturbed peatland (Fig. 5). Water table was the highest in natural forest of *Pinus rotundata* and the lowest in a young stand of *Betula pubescens* (Fig. 5). Water table fluctuation during the vegetation season 2000 was highest at the bare peat surface and lowest in *Pinus rotundata* forest.

Eriophorum angustifolium ring polycormons

Eriophorum had a mean ring diameter of 4.43 ± 0.26 (mean ± standard error) m, with some polycormons 12 m wide. Both the number of species and of tree individuals increased significantly with diameter of *Eriophorum* rings, especially with increasing the Centre zone. Both characteristics tend to decrease with distance from the nearest draining channel (Fig. 6). The average number of species per ring was 3.86 ± 0.29; average number of *Pinus* seedlings, saplings and tree individuals per *Eriophorum* ring were 0.58 ± 0.17, 2.58 ± 1.39, 0.06 ± 0.04 respectively, and the number of *Betula* seedlings, saplings and tree individuals per ring were 5.82 ± 1.55, 13.46 ± 3.27, 0.5 ± 0.20 respectively. Results of GLM



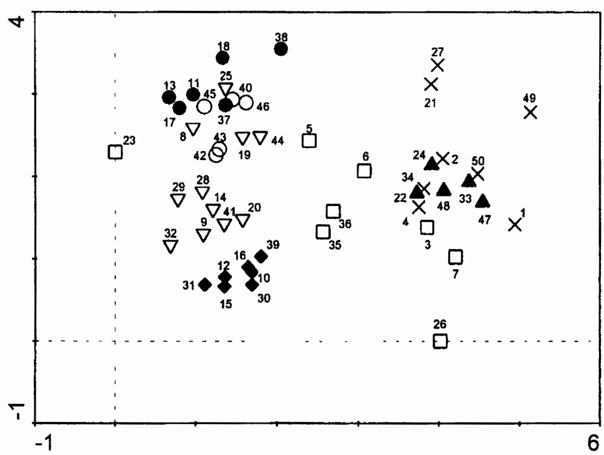


Fig. 4. DCA ordination diagram for vegetation relẽves (lower diagram) and plant species sampled at "Soumarský most" peat-bog. Different groups of samples arise from the UPGMA classification. First two ordination axes explain 17.5% variability of species data. Only species with fit range from 5 to 100% are shown. Abbreviations: *OxycPal* = *Oxycoccus palustris*, *PinuRot* = *Pinus rotundata*, *VaccUli* = *Vaccinium uliginosum*, *Pinujuv* = *Pinus sylvestris* (in juvenile stage), *CallVul* = *Calluna vulgaris*, *ErioVag* = *Eriophorum vaginatum*, *Betujuv* = *Betula pubescens* (in juvenile stage), *EpilAng* = *Epilobium angustifolium*, *Picejuv* = *Picea abies* (in juvenile stage), *AvenFle* = *Avenella flexuosa*, *GalePub* = *Galeopsis pubescens*, *StelNem* = *Stellaria nemorum*, *DescCae* = *Deschampsia caespitosa*, *Molicea* = *Molinia caerulea*, *VibuOpu* = *Viburnum opulus*, *EpilPal* = *Epilobium palustre*, *PhalAru* = *Phalaris arundinacea*, *GaliPal* = *Galium palustre*, *GlycFlu* = *Glyceria fluitans*, *PeucPal* = *Peucedanum palustre*, *CareRos* = *Carex rostrata*, *Carecan* = *Carex canescens*, *JuncEfu* = *Juncus effusus*, *JincFil* = *Juncus filiformis*, *ImpaNol* = *Impatiens noli-tangere*, *Rubulda* = *Rubus idaeus*, *UrtiDio* = *Urtica dioica*, *StelGra* = *Stellaria graminea*, *SoliVir* = *Solidago virgaurea*, *CalaVil* = *Calamagrostis villosa*, *PiceAbi* = *Picea abies*, *BetuPub* = *Betula pubescens*, *PinuSyl* = *Pinus sylvestris*, *Sorbjuv* = *Sorbus aucuparia* (in juvenile stage), *AthyFil* = *Athyrium filix-femina*, *MelaSyl* = *Melampyrum sylvaticum*, *VaccMyr* = *Vaccinium myrtilus*, *VaccVit* = *Vaccinium vitis-idaea*. Symbols in lower diagram: squares — Secondary young forest, open circles — Bog spruce forest, filled circles — Forest by channels, crosses — Wet meadow, down-triangles — Forest with *Pinus sylvestris*, up-triangles — Bare peat surface, diamonds — *Pinus rotundata* community.

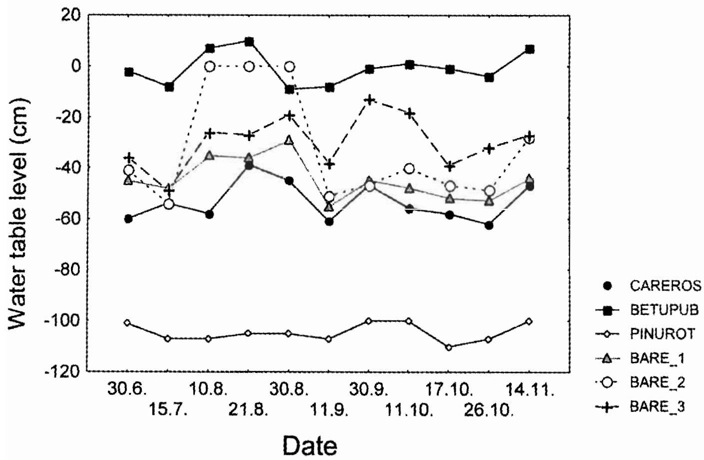


Fig. 5. Water Table fluctuation in six sites. Sites: CAREROS — northwest sector with high *Carex rostrata* cover; BETUPUB — southeast sector with *Betula pubescens*; PINUROT — *Pinus rotundata* stand; BARE_1, BARE_2, BARE_3 — sites on naked peat bog.

analyses are summarized in Table 1. Shannon-Wiener diversity index (SW) differed significantly between Centre and Ring zones within the ring, but evenness indices did not. This indicates that more species is concentrated in the Centre than in the Ring zone, but in terms of evenness there is relatively uniform proportional percent cover between species. Values of SW and evenness indices did not differ among *Eriophorum* rings.

RDA analyses show that species composition significantly differed between the Centre and Ring zones (Table 2). Obviously, *E. angustifolium* is abundant in the Ring zone, while other species with rather low percent cover are concentrated in the Centre zone (Fig. 7). Species composition among *Eriophorum* rings was rather similar, i.e. it showed little changes with the ring size (Table 2). The circle × zone interaction was significant.

Table 1. Differences between Center and Ring zones and differences between *Eriophorum* circles in Shannon-Wiener index and Evenness.

	df	MS	F	p
Shannon-Wiener index				
Circle	1	0.02	1.15	0.28
Zone	1	0.42	20.35	<0.001
Error	202	0.02		
Evenness				
Circle	1	4.50	0.03	0.84
Zone	1	54.99	0.44	0.50
Error	202	122.77		

Thus, it depended where the plant communities were positioned.

Comparison of water content in soil samples taken from *Eriophorum* rings did not reveal any significant difference between the Centre litter-rich zone and the outer Ring zone ($t = -1.62$, $df = 98$, $p = 0.1084$). The mean soil moisture was 59.28 ± 1.79 g 120 ml^{-1} soil (max 92.07) and 63.23 ± 1.66 (max 92.50) ml inside and outside *Eriophorum* rings respectively. However, the soil in Centre zone had a higher phosphorus content (1.62 ± 0.06 ¼g g^{-1} of dry soil; max 2.13) than in Surroundings (1.36 ± 0.08; max 2.12). Analysis of exchangeable phosphorus content showed that Centre zone differed significantly from Surroundings ($t = 2.4$, $df = 38$, $p = 0.0214$).

Discussion

Large scale pattern in vegetation of the cut-away bog

The "Soumarský most" peat-bog was highly disturbed during the last 100 years, mainly from 1960's on. The mining of 70% of the peatland was by far the main disturbance. During this period, the vegetation was removed and an extensive network of drainage ditches created. This led to high water removal from the rest of the peat deposit. After the cessation of mining, the spontaneous revegetation by vascular plants and mosses was successful only along the draining channels, presumably because of higher water supply and a protective shading by established *Betula pubescens*. The high moisture habitats were recolonized almost exclusively by typical fen and peatland species such as *Juncus effusus, Carex rostrata, Carex canescens, Juncus filiformis, Potentilla palustris* and *Eriophorum vaginatum*. Although the spontaneous revegetation by vascular plants was successful in some parts, *Sphagnum* mosses (*S. russowii, S. magellanicum*) colonized only 1–2% of the peat surface. In fact, the drainage ditches are still drawing off a large quantity of water during the vegetation season, resulting in high water table fluctuation across the cut-away peatland (Wind-Mulder et al. 1996, Price 1997). All these factors contribute to drying out the bog and restrict recolonization by *Sphagnum* mosses. Overall, most of the cut-away peatland is scarcely vegetated, especially in those places where mining activities ceased 3 years ago.

It is known that the course of revegetation in cut-away peatlands frequently relies on moisture conditions (Girard et al. 2002), but also the initial species pool after disturbance (Campbell et al. 2003). We recorded a high cover of *Carex rostrata* and *Juncus effusus* in the northwest sector of the peatland (Fig. 1), which is characterized by relatively high and stable water table level. This factor seems crucial for the establishment and survival of mire vegetation (Schouwenaars 1995, Price 1997, Stoneman & Brooks 1997), and could lead to dominancy of several plants as was observed in our case. *C. rostrata* and *J. effusus* are both clonal plants with fast rhizome (*C. rostrata*) and tiller (*J. effusus*) growth, and are thus able to occupy nearly whole part of the northwest sector. Only some subordinate species such as carrot *Selinum carvifolia* and sedge *Carex canescens* survived there.

A different situation occurred at the southeast part, where the peatland was abandoned earlier and was rapidly recolonized by a dense cover of shrubs and trees. The southeast part is located at a lower plateau. Here, protecting effect of surrounding trees of *Pinus sylvestris* may had evolved. Therefore, saplings of the downy birch (*Betula pubescens*) could establish here in high density. Further, *Molinia caerulea* and *Juncus effusus* tussocks also occurred here.

Molinia caerulea is considered as a typical grass species of mined peat bogs that are affected by severe summer droughts. Its presence indicates more favorable conditions for mineralization and mineral release (Schouwenaars 1995). *Molinia* belongs together with *Eriophorum vaginatum* to colonizers which are able quickly spread over the bare peat surface in the first phase of the vegetation succession. We found that this phenomenon is valid for conditions of our study locality. The fact that *Molinia* is regarded as species of relatively drier sites was supported by our observation, when it was replaced by *Juncus effusus* and *Eriophorum vaginatum* on wetter sites along the draining channels.

Compared to disturbed areas, natural undisturbed pine stands had lower water table fluctuation, possibly by retaining water in active peat layer (acrotelm) during extreme weather condi-

Table 2. Results of RDA analyses of cover estimation. % expl. variability = species variability explained by all ordination axes (measure of explanatory power of the explanatory variables). p-value is corresponding probability value obtained by the Monte Carlo permutation test.

Tested hypothesis	Explanatory variable	% expl. variability	F	p
A1: There are differences among Eriophorum rings. NO	Circles	4.0	1.04	0.3
A2: There are differences between Centre and Ring zones. YES	Zone	38.0	142.29	0.002
A3: There are differences between zones in relation to Eriophorum rings. YES	Circles × Zone	38.6	72.46	0.002

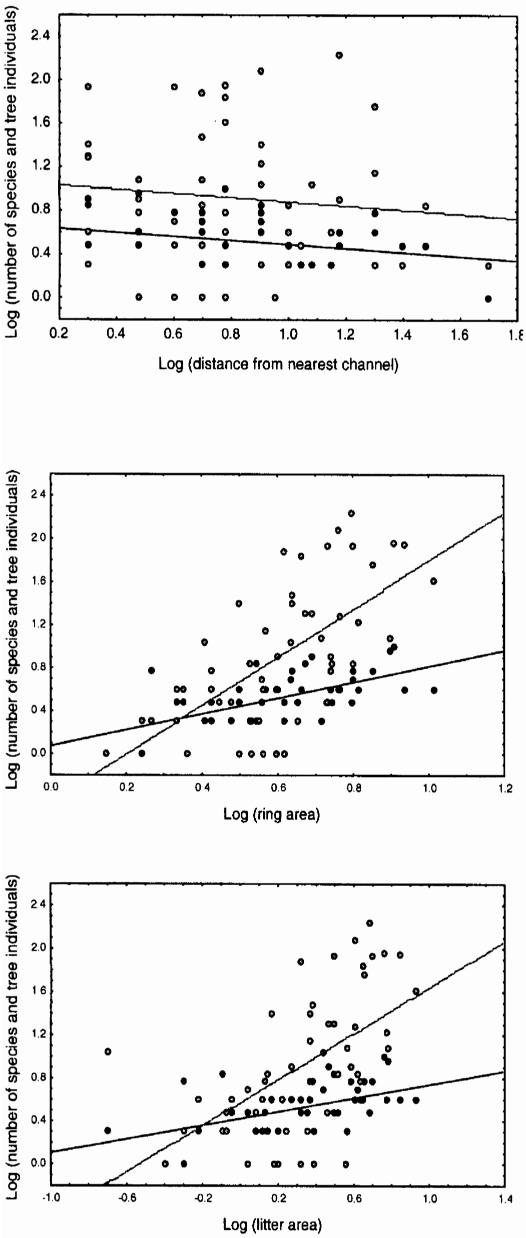


Fig. 6. Relationships between number of species (full line, black circles) and number of tree individuals (dotted line, gray circles) and independent variables, which are distance from the nearest channel, litter amount and ring area. The total number of species depended on the ring area (r^2=0.32, p<0.001) and litter amount (r^2=0.19, p<0.001), but did not correlate with the distance from the nearest channel (r^2=0.04, p=0.08). The number of tree individuals depended on the ring area (r^2=0.41, p<0.001) and litter amount (r^2=0.31, p<0.001), but not on the distance from the nearest channel (r^2=0.00, p=0.50).

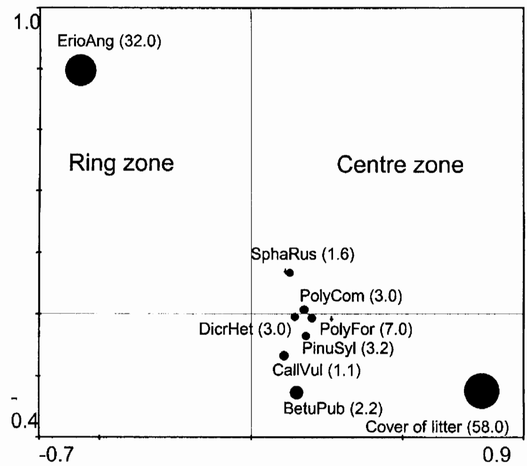


Fig. 7. Result of RDA analysis (attribute plot), where zones are used as nominal explanatory variables (only species with fit range 2–100% are shown). In brackets: cumulative fit per species (=in % explained variability by a species). Abbreviations: ErioAng = *Eriophorum angustifolium*, SphaRus = *Sphagnum russowii*, PolyCom = *Polytrichum commune*, Polyfor = *Polytrichum formosum*, DicrHet = *Dicranella heteromala*, PinuSyl = *Pinus sylvestris*, CallVul = *Calluna vulgaris*, BetuPub = *Betula pubescens*.

tions (Stoneman & Brooks 1997). Kučerová et al. (2000) showed that water table fluctuation is closely connected with a plant species dominating in a particular environment. In our case, the water table level highly fluctuated in *Betula pubescens* stands. *Betula* with deeper roots is more effective in sucking water than *Sphagnum* carpets which are dependent on water diffusion and capillarity. Schowenaars (1995) documented more intense evapotranspiration in the tree stands than those dominated by *Sphagnum* mosses.

Small scale pattern in vegetation of cut-away bog

This study shows that spontaneous revegetation of the bare peat surface is facilitated by clonal nature of *Eriophorum* growth. *E. angustifolium* was able to establish locally and covered the bare peat surface at high densities. This led to habitat improvement and establishment of other plant species. We see the facilitation effect (sensu Callaway 1995) through the high abundance of several plant species and mosses in the Center zone of *Eriophorum* polycormons (Fig. 7). Their establishment was probably caused by accumulating litter that substantially changed microclimatic conditions and soil fertility. Newly created favorable environment inside the rings increased the possibility not only for other plant species to become established but also for faster growth rates, especially in tree saplings. This positive association can be referred to as the "nurse plant effect" (Callaway & Walker 1997, Groeneveld & Rochefort 2002). The number of plant species was positively correlated with the area of Ring and Centre (litter) zone. Significant size effect of *Eriophorum* ring on establishment of a number of plant species supports the hypothesis that intensity of facilitation increases with benefactor size in adverse environment (Callaway et al. 1996, Chambers 2001, Haase 2001). The mechanism of *Eriophorum* facilitation probably involves the direct positive effect on moisture and evapotranspiration. The occurrence of successfully established vascular plants and mosses native to fens and peat bogs in the Centre zone of the *Eriophorum* circle suggest this mechanism. For example, Salonen (1987) compared the species number and composition in the seed rain with those of the actual vegetation, and found a sparse germination of species abundant in the seed rain. He explained this by unfavorable moisture conditions on the post-mined peat surface. It is the same situation which was occurred at the "Soumarský most", however, in our case, the facilitation mechanism improved the bare peat surface to faster recolonization by vascular plants. Similar study was conducted in Finland, where Tuittila et al. (2000) showed that many peatland species benefited from the sheltering effect of *Eriophorum vaginatum* tussocks in cut-away peat fields.

We found non-significant relationship between litter accumulation and soil moisture. However, phosphorus content was significantly higher in Centre zone of litter accumulation. Consequently, the plant species establishment inside the rings can be at least in part explained by increased phosphorus content. Sundberg & Rydin (2002) likewise found that the establishment of *Sphagnum* spores was promoted by *Betula pubescens* litter and the amount of phosphate released. Generally, phosphorus together with nitrogen are limiting ions in fens and peat-bogs (Wheeler & Proctor 2000). A floristic composition in peatlands is often strongly correlated with phosphorus and nitrogen availability. Recently, peatland vegetation is becoming less limited by nitrogen because of increased nitrogen input from air-borne pollutants (Aerts et al. 1992, Økland et al. 2001).

Conclusively, this study shows that natural revegetation process at the "Soumarský most" has been initiated through the facilitation effect of *Eriophorum* vegetation. The mechanism of litter accumulation is important to the better establishment of tree seedlings and saplings. We are aware that such process can lead to the development of dominant birch and pine forest, but not to peat formation. Regardless of this, the facilitation effect seems to be the main process that provides suitable conditions for establishment and growth of mire plant species at the highly disturbed "Soumarský most" peat-bog.

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