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The effect of dam construction on the restoration succession of spruce mires in the Giant Mountains (Czech Republic)

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Spruce mires are rare and endangered plant communities of central and western Europe. In the Czech Republic, they were intensively destroyed and drained during the 1970s. To start the regeneration of spruce mires, palisade dams sealed with peat were used to block draining ditches in the Giant Mountains. Four years after construction of the dams, there were significant differences in vegetation above and below the dams. Vegetation above the dams successfully developed towards plant communities characteristic to spruce mire forests. Below the dams, the colonization by forest floor species continued. These differences indicate that palisade dams effectively retain water and help the regeneration of spruce mire forests. Our results support construction of palisade dams in such habitats.

Key words: community structure, dam, drainage ditch, RDA, restoration, spruce mire

Introduction

Spruce mires are rare plant communities of central and western Europe. In recent decades, they were intensively destroyed by human activity and their area decreased dramatically throughout Europe. Drainage of spruce mires has a long tradition in the Giant Mountains (Krkonoše in Czech). The first attempt to drain them comes from the 19th century. Paradoxically, the catastrophic flood of 1897 stopped this effort. Drainage of mire forests and deforestation of mountain belts were considered to be the main reasons for the catastrophe (Lokvenc 1994). In the 1970s and the 1980s, spruce mires were destroyed by severe drainage and air pollution in the Giant Mountains. Drainage was performed despite the conservation status of the Krkonoše National Park. In the Czech Republic, all types of wetlands were drained as a part of existing government policy, which tried to increase agricultural and horticultural land production. Wetland drainage causes mineralization, peat decomposition and leaching of minerals (Kuntze 1988, Wind-Mulder *et al*. 1996, Sundström *et al*. 2000). These processes result in a decrease or disappearance of stress-sensitive species with weak competitive ability and narrow ecological amplitudes, and an invasion or increase of ubiquitous and nitrophilous strong competitors, often with wide ecological amplitudes (Lavoie *et al*. 2003).

Excavation of draining ditches leads to an increase in lateral seepage from the wetlands (Schouwenaars 1995, Horn & Bastl 2000). To reduce water loss caused by ditching, a key activity is usually blocking or preferably filling any ditches. To regenerate wetlands, blocking requires insertion of a series of impermeable (or nearly so) barriers (dams). The damming raises water table levels in the ditch (Mawby 1995, Price 1996) and stimulates establishment and spreading of mosses and mire plants (Pfadenhauer & Klötzli 1996, Robert *et al*. 1999, Price *et al*. 2003). Many successful attempts have been recorded from the insertion of plastic, plywood or palisade dams at regular distances to complete refilling of drains with peat (Rowell 1988, Wheeler & Shaw 1995, Stoneman & Brooks 1997).

To start regeneration of spruce mires, palisade dams sealed up with peat were used to block draining ditches in the Giant Mountains. Palisade dams were used because of low cost and because they do not disturb landscape patterns. The aim of our study was to evaluate the effectiveness of dam construction on vegetation development in draining ditches.

Methods

Site description

The study site (Mrtvý vrch) is located 3 km north of the town of Harrachov in the Czech Republic (50°48´15´´, 15°26´45´´). The altitude of the site is 1058 m a.s.l., with mean annual temperature of 4 °C and mean annual precipitation of 1400 mm (Harrachov and Szrenica meteorological stations). Mrtvý vrch is a topogenic raised peatland (Dohnal 1965). According to the phytosociological nomenclature (Moravec *et al*. 1995) the vegetation of the study site was classified as *Sphagno-Piceetum* (spruce mire) with some refuges of *Oxycocco-Empetrion hermaphroditi* (mire vegetation). *Avenella flexuosa* and *Calamagrostis villosa* were the most dominant species, co-occurring with *Molinia caerulea*, *Vaccinium myrtillus*, *Galium saxatile*, *Agrostis tenuis*, *Carex canescens* and *Eriophorum vaginatum*. In the early 1980s, spruce trees (*Picea abies*) dominants died out because of air pollution and were removed. At the same time, draining ditches were excavated to lower the water level and to increase productivity. The spruce mire is situated in a slightly shallow depression of a granite pluton form. The peatland surface has a moderately south-facing slope. The maximum depth of peat accumulation is 2 m. A mire macrotope of the peatland is composed from two raised mire mesotopes (here called locality 1 and locality 2).

The first mesotope (locality 1) has a central drainage ditch (75 cm deep) that was dug out around the central mire. Two ditches were excavated to collect water from the central ditch. To control water run-off and to stimulate regeneration of the mire, palisade dams were installed in ditches and sealed up with peat from the neighborhood in the summer of 1997. A total of 14 dams were installed, approximately in 10–15 m distances apart from each other.

In the second mesotope (locality 2) only one drainage ditch (75 cm deep) was excavated. Three dams (in 15 m distances) were installed there in the summer of 2000. Damming resulted in effective retaining of the water (above dams), shown as large differences in water level between above and below parts of dams.

Data collection

To monitor the effectiveness of dam construction, 28 relevés were laid out at locality 1 in July 2001. We estimated visually the vegetation cover using pairs of 1 m^2 plots established in draining ditches. Each pair consists of plots on either side of a particular dam, placed 1 m away from the inside of the ditch. This experimental design is based on the presumption of the same vegetation composition in each pair of plots before the dams were established in 1997.

To compare alternative ways of restoration succession we used permanent plots to monitor temporal changes in vegetation at locality 2. Vegetation cover was estimated visually in permanent 1 m^2 plots using a continuous grid of nine 0.33 × 0.33 subplots in three paired plots established in the draining ditch. Each pair consists of plots on either side of a particular dam,

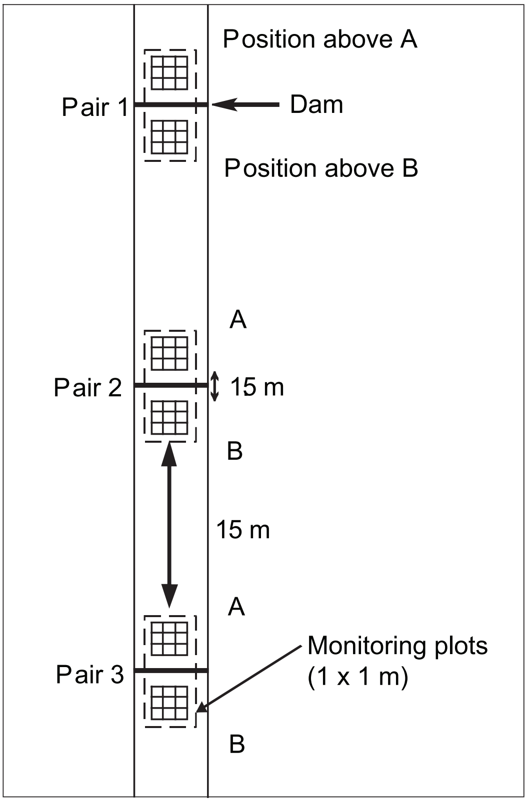

Fig. 1. Spatial arrangement of the experiment at locality 2. Vegetation cover was estimated in permanent 1 × 1 m plots using a continuous grid of nine 0.33 × 0.33 m subplots in three paired plots established in a draining ditch.

placed ca. 0.75 m away (for spatial arrangement of the experiment *see* Fig. 1). An initial vegetation recording was conducted immediately in August 2000, after dam building in order to obtain baseline data for each plot. First vegetation changes after dam building we monitored in three consecutive years (August 2002, July 2003 and July 2004). To evaluate the effect of damming to species diversity of both vascular species and mosses, the number of species per plot was counted.

Immediately after damming of the ditch we measured the actual water level as a height of water column above and below the dam six times during the vegetation season of 2001 at locality 2. In the following years, we did not measure the water table because there were remarkable differences between above and below parts of the dam.

Nomenclature of vascular plant species according to Neuhäuslová and Kolbek (1982), of *Senecio hercynicus* according to Hodálová (1994), and of bryophytes according to Váňa (1997).

Data analysis

We used constrained ordination method redundancy analysis (RDA) to analyze differences in vegetation of locality 1 caused by damming. Redundancy analysis is a direct gradient analysis method based on the assumption of a linear response, and was used because data sets were relatively homogeneous (the length of the first DCA axis was 3.114). The species score on the first (i.e. constrained) axis corresponded to the relative position of species' abundances with respect to position above and below the dams. A Monte Carlo permutation was used to test for the significance of the RDA model (299 permutations). We analyzed both the non-standardized data and the data standardized by sample norm. With non-standardized analyses we investigated if damming affected species cover. With standardized analyses we studied if damming caused changes in species proportion.

We used the RDA to study successional change in vegetation of locality 2. We used RDA models because the data set was relatively homogenous (the length of the first DCA axis was 2.819) and the explanatory variables were categorical. For hypotheses testing with Monte Carlo permutation tests (499 permutations) we used split-plot design appropriate for our experimental design (ter Braak & Šmilauer 2002). Permutations were performed within each pair of plots. For RDA analyses of the species composition of the established plant community, data were taken from 0.33 × 0.33 subplots with permutation test reflecting this hierarchical procedure (i.e. permuting the whole 1 m^2 plots together). As the data form repeated observations that include the baseline (before treatment) measurements, the interaction of time and treatment (plot position above or below dams) is of greatest interest and corresponds to the effect of the experimental manipulation. The significant effect of time and position interaction indicates divergent temporal development of plots located above and below dams. Plot identifiers (coded as dummy variables) were used as covariates, when the influence of plot position (above or below a dam) on time changes in plant composition was tested. Time was considered as a categorical variable (we created four dummy variables for four observation years). The biplot ordination diagram was used to visualize the results of the analyses. Only the species with highest fit to ordination axes are shown in the ordination diagrams.

Species scores on the constrained axis of the non-standardized analysis (that was processed on coverage data sampled above dams), where time was the only linear variable and codes of individual plots treated as covariables, were considered characteristic of the species response to time: cover of species with negative values of the RDA score decreased and cover of species with positive values increased. Then posterior classification of species into simple functional types, using data from the local flora of Šourek (1969) for vascular plants, was tested as a possible predictor of this response. We recognized the following three categories: mosses, forest vascular species and mire vascular species. Then we processed the data with a simple ANOVA analysis. We used the ANOVA for repeated measurements to analyze univariate data of species diversity. To improve normality and homoscedasticity we log-transformed species diversity data.

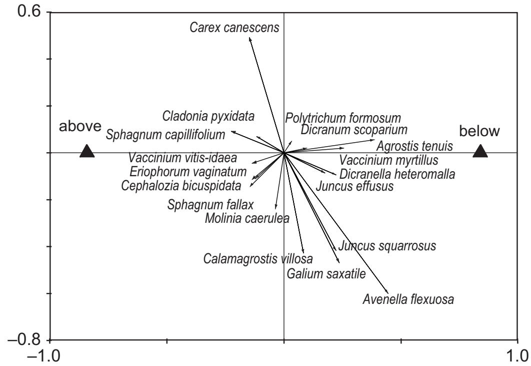

Fig. 2. Ordination diagram showing the results of RDA analysis for locality 1 where the position of reléves above and below dams was used as only one environmental variable (nonstandardized test).

Results

Water table measurements

The building of dams resulted in an increase of the below-ground water level. The values varied from –8 to –18 cm (mean value –15 cm) below and from –4 to 14.5 cm (mean value –7 cm) above dams.

Species composition at locality 1

Four years after the dams were built there was a significant difference in plant species composition between above and below dams. Damming affected species cover (RDA; Non-standardized test: the first canonical axis, RDA I, explained 7.9% variation, $F = 2.604$, $P = 0.038$) as well as the relative proportion of the species (RDA; Standardized test: RDA I = 8.1%, $F = 2.905$, $P = 0.025$). Above dams, *Sphagnum capillifolium* and *S. fallax* were the only bryophytes present, but below dams, *Dicranella heteromalla* and *Dicranum scoparium* had the highest cover among bryophytes. Among vascular plants, *Carex canescens*, *Eriophorum vaginatum* and *Vaccinium vitis-idaea* were more abundant above dams, while *Avenella flexuosa*, *Agrostis tenuis* and *Galium saxatile* were more abundant below dams (Fig. 2).

Species composition at locality 2

Regardless of the type of analysis used (standardized and non-standardized RDA), the species composition of plant and moss community varied significantly between years (both tests $P < 0.01$, *see* Table 1). However, no clear directional trend was observed during the four study years that would be common to all sample plots (Fig. 3).

Significant differences between positions above and below a dam were detected (Table 1, analyses A1 and A1st). The mire mosses as *Dicranella cerviculata*, *Sphagnum* sp. and *Brachythecium rutabulum*, and vascular plants as seedlings of *Salix caprea*, grasses *Avenella flexuosa*,

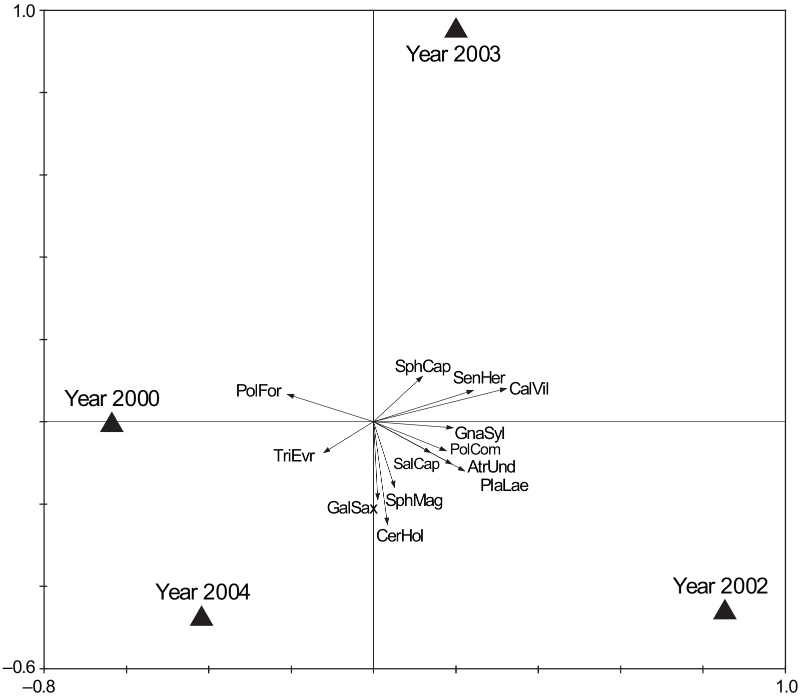

Fig. 3. The distribution of plant species and mosses during different years of the experiment (locality 2). Results of non-standardized RDA test (Table 1, analysis A2, species cover). Time was coded as four dummy variables. AtrUnd = *Atrichum undulatum,* CalVil = *Calamagrostis villosa*, CerHol = *Cerastium holosteoides*, GalSax = *Galium saxatile*, GnaSyl = *Gnaphalium sylvaticum*, PlaLae = *Plagiothecium laetum*, PolFor = *Polytrichum formosum*, PolCom = *Polytrichum commune*, SalCap = *Salix caprea*, SenHer = *Senecio hercynicus*, SphCap = *Sphagnum capillifolim*, SphMag = *Sphagnum magelanicum*, TriEvr = *Trientalis europaea*.

Calamagrostis villosa, and forb of *Cirsium palustre* were the species that most thrived above dams (Fig. 4). Typical forest species such as *Galium saxatile*, *Trientalis europaea* and *Gnaphalium sylvaticum* survived better below the dams. The moss *Polytrichum commune* performed better above the dams, whereas *P. formosum* increased below the dams. *Viola palustris*, the mire species most promoted by damming, nevertheless performed better below the dams (Fig. 4). The total cover values did not differ between plots (cover close to 100%), therefore the results of standardized and non-standardized analyses were very similar to each other (Table 1).

The difference between the results of standardized and non-standardized RDA analyses shows that variation in species composition in relation to position above or below a dam in both studied localities is a consequence of the general response of plants to positions (non-standardized RDA) rather than of changes in species proportions itself (standardized RDA).

Table 1. Results of the RDA analyses of cover estimates in 1 m × 1 m plots at locality 2. Data are centered by species and either standardization (St) by sample norm (Y = yes) was applied or data were not standardized (N = no). Env. var. = Environmental variables, Covar. = Covariables, % axis 1 = Percentage of species variability explained by axis 1; measure of the explanatory power of the environmental variables, *r* axis 1 = species environment correlation on axis 1, *F* = *F*-statistics for the test on the trace (all axes), *P* = corresponding probability value obtained by the Monte Carlo permutation test (499 permutations, i.e. Type I error probability in testing the hypothesis that the effect of one explanatory variables is zero). Position = location of the plots above or below a dam; Yr = time coded as four dummy variables; PlotID = plot identifiers of each plot coded as many dummy variables. * = interaction between terms.

	Env. var.	Covar.	St	% axis 1	*r* axis 1	*F*	*P*
A1	Yr × Position	Yr, PlotID	N	6.8	0.667	8.890	0.002
A1st	Yr × Position	Yr, PlotID	Y	1.6	0.548	2.394	0.002
A2	Yr	Yr × Position	N	6.9	0.668	8.077	0.002
A2st	Yr	Yr × Position	Y	4.0	0.585	5.415	0.002

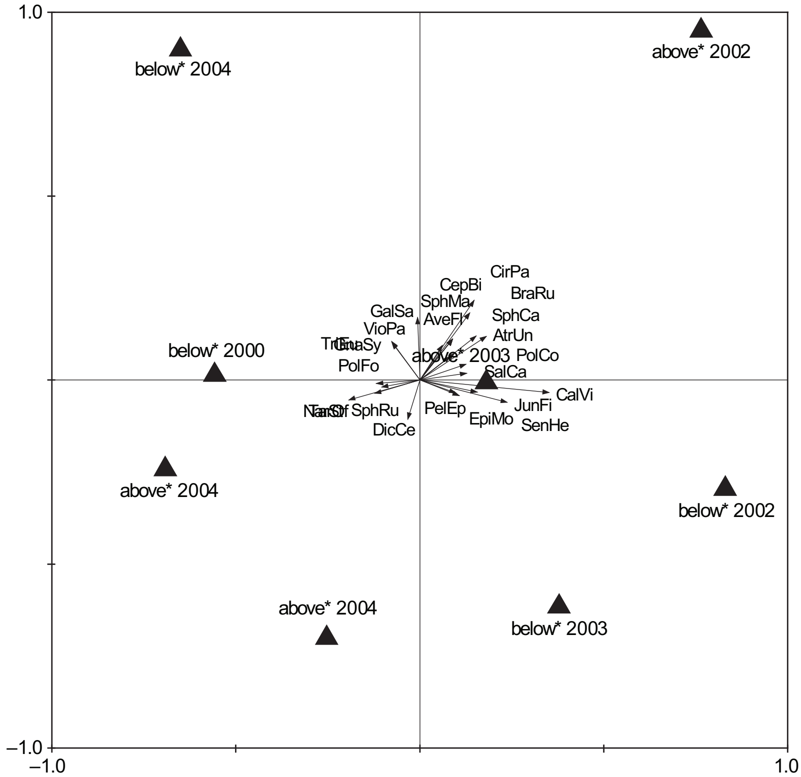

Fig. 4. Redundancy analysis biplot (Table 1, analysis A1, species cover) of the year to year difference in the individual species response to the positions above and below dams (locality 2). Abbreviations: AtrUn = *Atrichum undulatum*, AveFl = *Avenella flexuosa*, BraRu = *Brachythecium rutabulum*, CalVi = *Calamagrostis vilosa*, CepBi = *Cephalozia bicuspidata*, CirPa = *Cirsium palustre*, DicCe = *Dicranum cervicullata*, EpiMo = *Epilobium montanum*, GalSa = *Galium saxatile*, GnaSy = *Gnaphalium sylvaticum*, JunFi = *Juncus filiformis*, NarSt = *Nardus stricta*, PelEp = *Pellia epiphylla*, PlaLa = *Plagiothecium laetum*, PolCo = *Polytrichum commune*, PolFo = *Polytrichum formosum*, SalCa = *Salix caprea*, SenHe = *Senecion hercynicus*, SphCa = *Sphagnum capillifolium*, SphMa = *Sphagnum magelanicum*, SphRu = *Sphagnum rusowii*, TarOf = *Taraxacum* sect. *Ruderalia*, TriEu = Tientalis europaea, VioPa = *Viola palustris*. * = interaction of environmental variables. Each centroid (triangles) represents position of plot in a year. Only species with highest fit are shown.

There was a significant difference in the response to the time between three functional types of grouped species in the data set sampled above dams (Fig. 5; ANOVA: df = 2, $F = 6.71$, $P = 0.003$). Tukey's post-hoc comparison test showed that the response of forest vascular species significantly differed from the response of mosses ($P < 0.05$). Responses of the mosses and mire plants to time were rather similar (Tukey test: $P > 0.05$). The scores of the canonical axis indicated that cover of species with positive values increased and with negative values decreased with time in relation to time as an environmental factor. Therefore species with increased cover were mostly mosses such as *Sphagnum capillifolium* and *Polytrichum commune* (Fig. 5). The cover of forest species declined except for three species (*Calamagrostis villosa*, *Avenella flexuosa* and *Galium saxatile*); those had positive values of canonical scores.

Species diversity

The time–position interaction term in univariate repeated measures ANOVA was not significant (df = 3, $F = 0.30$, $P = 0.82$) during the study period. Thus, the total species diversity was not influenced by damming of the draining ditch and the succession was similar above and below

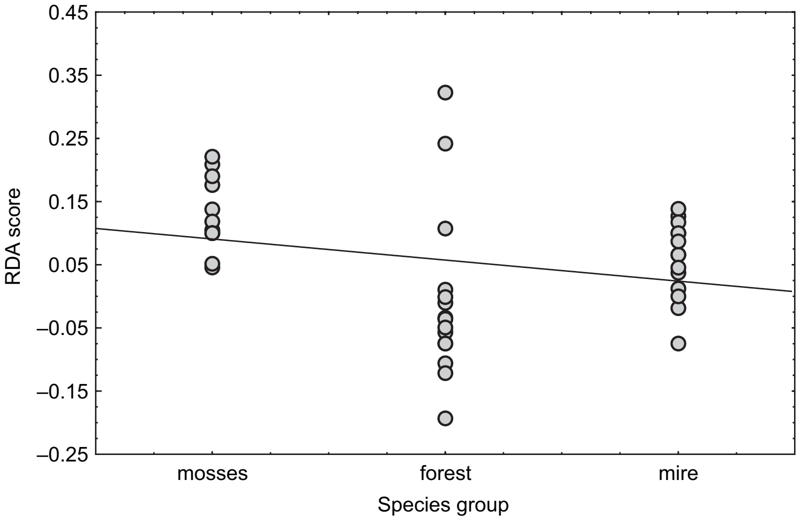

Fig. 5. Relationships between functional types and species responses to the time as an environmental factor.

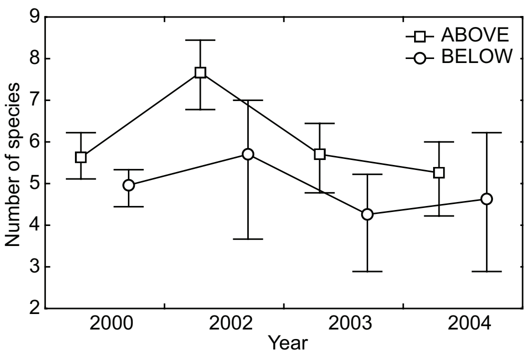

Fig. 6. Mean numbers of plant species per 1 m^2 over four years of investigation at locality 2. Min and max values are indicated by the vertical lines.

dams in terms of species diversity. However, the numbers of species were higher in locations above the dams (*see* Fig. 6).

Discussion

Vegetation monitoring in the draining ditches revealed changes in vegetation above and below the dams during the study period 2000–2004. Construction of the woody dams led to clear differentiation of the vegetation at both studied localities within the spruce mire of "Mrtvý vrch".

The sites above the dams were occupied mainly by mosses which were infrequent below the dams. However, at locality 1, we recorded several mosses below the dams; e.g. *Polytrichum formosum*, *Dicranum scoparium* and *Dicranella heteromalla*. These mosses are considered as forest floor mosses (Pilous & Duda 1960) and in our study were overgrown by the mire mosses above the dams. At locality 2, such early moss colonists were *Polytrichum formosum*, *Dicranella cerviculata* and *Funaria hygrometrica*. Similarly to our results, Robert *et al*. (1999) observed rapid replacement of early successional mosses by *Sphagnum* species after blocking a draining ditch.

More favorable hydrological conditions above the dams led to a colonization of all *Sphagnum* mosses recorded in plots. Lower suitability of drained sites than blocked sites for *Sphagnum* canopy regeneration was observed because of the lowest water tension there (Price 1997). *Sphagnum* colonization also depends on a source of diaspores (Salonen 1987) and suitable environmental conditions for their establishment (Campbell *et al*. 2002, Price *et al*. 2003). *Sphagnum* is often regarded as a characteristic component of mire vegetation, but it also helps to re-establish acrotelm and to stabilize the hydrochemical conditions, and also to moderate microclimatic fluctuations (Rochefort 2000).

Above the dams, the coverage of dominant grasses gradually decreased, although the coverage of some clonal plants such as *Agrostis tenuis*, *Avenella flexuosa* and *Calamagrostis villosa* was higher at locality 2. It could be explained by a lower moisture content above the dams for some parts of the year. Furthermore, wet profiles were partially retarded because of an increase in temperature during spring, which reduces the release of nutrients, oxygen supply, length of growing season, and therefore the speed of peat mineralization (Wheeler & Proctor 2000). Our study demonstrates that the presence of clonal grasses may play an important role in the vegetation dynamics of developing communities in drained mires as found earlier by Laine *et al*. (1995).

Eriophorum vaginatum and *Carex canescens* were two vascular plants most abundant above the dams (Fig. 2). Both indicate differentiation in water conditions in relation to position. Similarly, Komulainen *et al*. (1999) found *E. vaginatum* and *C. canescens* to benefit from rewetting. According to Tuittila *et al*. (1999) *Eriophorum vaginatum* behaves as an early colonist of bare peat surfaces after disturbance.

The rather xerophilous lichen *Cladonia pyxidata* occupied bare peat among the dwarf shrubs of both *Vaccinium* species below the dams, which corresponds with findings that this lichen grows only on hummocks (Laine & Vasander 1996).

Excavation of draining ditches led to the colonization by forest species that continued, in particular below the dams, after damming of drainage ditches. Prostrate herb *Galium saxatile* is moderately shade-tolerant and can coexist with more robust species of higher competitive ability, also in mires and aquatic habitats. *Vaccinium vitis-idaea* and *V. myrtillus* are long-lived and slower-growing shrubs of acid soils. Leaves of *Vaccinium* species have larger area as compared with that of other mire species — this characteristic enables them to maximize production per unit of limiting minerals in nutrient poor conditions (Kučerová *et al*. 2000). Both species that are generally more abundant in mires in the Czech Republic (Dohnal 1965, Neuhäusl 1972) benefited from wetter conditions.

The succession studies over longer periods of time usually confirm year-to-year variation (Tuittila *et al*. 2000). The reason for these variations is most likely weather conditions (Price *et al*. 2003). Therefore, a slow decrease in species diversity during the four years of the study after construction of the dams can be caused by several summer droughts in 2002 and 2003. In our case, as seen in Fig. 5, this effect of the droughts was more pronounced, with delay, in 2003 and 2004. In our plots, where the diversity was similar in all years, grouping the plant species into three ecological types showed that species grouping is a good predictor of species response to the time. In other words, each group responded to the time as a unit. It could be caused by subjective classification into three distinct groups that may, however, have completely different physiological and environmental requirements.

Our results showed that location of dams in 15 m distance from each other supported restoration succession of forest mires in the Giant Mountains. These are considered very specific and endangered habitats in the Czech Republic. They are characterized by specific site conditions and are suitable for the survival of a very specialized flora and fauna. Drainage and removal of the original vegetation destroyed the functional relationships founded within an intact mire. The restoration by damming can help the area to revert to its original habitat type, although the longer the area has been drained, the more difficult it is to fully recreate its original state (Laine *et al*. 1995). The construction of dams for hydrological management of disturbed mires is the simplest mean for creating a large water-storage capacity. It aims to lead to a new state, often different from the original, but nevertheless recognizable as some other peatland habitat type. The blocking of drainage ditches seems to be a fairly good method for achieving spruce mire regeneration in the Giant Mountains. As a start to forest mire regeneration, palisade dams sealed with peat seem to be a sufficient and inexpensive means for water retention and are a necessary step for the restoration of spruce mires. The study showed that raising the water level to, or above, soil surface promotes conditions wet enough for a rapid succession towards closed mire vegetation.

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