Substrate quality and spontaneous revegetation of extracted peatland: case study of an abandoned Polish mountain bog

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SUMMARY

If peatland is left without any restoration treatments after mechanical peat extraction ceases, the process of secondary transformation of peat continues. The resulting changes in peat properties severely impede the recovery of vegetation on cutover peatland. The aim of this study was to assess how secondary transformation of peat affects spontaneous revegetation, and the relative importance of different factors in controlling the re-establishment of raised bog species on previously cutover peat surfaces. The study was conducted on two sectors of a raised bog in southern Poland where peat extraction ended either 20 or 30 years ago. Where the residual peat layer was thin (~ 40 cm or less) and the water table often dropped into the mineral substratum, the development of vascular plants (including trees) was favoured, and this further promoted the secondary transformation of peat. In such locations the vegetation tended towards a pine and birch community. Revegetation by *Sphagnum* and other raised bog species (*Eriophorum vaginatum, Vaccinium uliginosum, Ledum palustre, Oxycoccus palustris*) was associated with thicker residual peat and higher water table level which, in turn, were strongly correlated with hydrophysical properties of the soil. A species - environmental factor redundancy analysis (RDA) showed that any single factor (of those considered) was not important in determining the revegetation pattern, because of their intercorrelations. However, water table level appeared to be the most important abiotic factor in determining the degree of soil aeration and, consequently, the stage of secondary transformation attained by the peat.

KEY WORDS: peat extraction, cutover peatland, secondary transformation, peat quality

INTRODUCTION

Peatlands are globally important ecosystems with multiple roles in the natural environment. They serve as water and carbon reservoirs and are known for their specific biodiversity (Minayeva *et al.* 2017). They are also natural archives of data on palaeoenvironmental, climatic and hydrological changes as well as human impact (*e.g.* Joosten & Clarke 2002, Chambers & Charman 2004). Since the beginning of the 19th century, the global area of mires and peatlands has declined significantly due to climate change and human activities, especially drainage for agriculture and forestry. The largest losses have occurred on the European continent, where the remaining mire area is about 52 % of the former extent of mires (Joosten & Clarke 2002). In Poland (central Europe), mires cover about 0.6 % of the country and their loss in relation to former extent is estimated at 84 % including about 4 % of peatland degraded by peat extraction (Bragg & Lindsay 2003). It is especially important to restore extracted areas on former raised bogs because only 4.4 % of all the mires in Poland belong to this type (Ostrowski *et al.* 1995).

The first requirement for mechanical extraction of peat is drainage, which is usually provided by open ditches at about 20 m spacing that are gradually deepened as peat extraction proceeds. The next step involves removal of the acrotelm, which is a singular hydrologically self-regulating component of a natural peat bog (Ingram 1978). Thus, peat extraction drastically affects both the peat and the vegetation, and some of the changes are irreversible.

After removal of the acrotelm the denser (more decomposed) peat of the catotelm is exposed, and this in turn undergoes changes. The transformation of peat under the aerobic conditions imposed by lowering of the water table is known as secondary transformation (primary transformation takes place during the initial peat formation process) (*e.g.* Kalisz *et al.* 2015). The effects of drainage on the physical properties of peat are shrinkage, compaction, oxidation and consequent peat subsidence (Eggelsmann 1986, Lipka *et al.* 2017). Following drainage, bulk density increases and pore spaces

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decrease in size (Price 1997); soil moisture content, specific yield and hydraulic conductivity decline; and the amplitude of water level fluctuations increases (Price *et al*. 2003, Van Seters & Price 2001). The water retention capacity of peat is enhanced by compaction, but the availability of water to non-vascular plants may become limited (Price & Whitehead 2001). Intensified oxidation of the organic matter may result in nutrient regime changes in the peat and groundwater (Wind-Mulder *et al.* 1996, Andersen *et al.* 2010) and may significantly enhance acidity (Juckers & Watmough 2014). It also results in a rise in CO_2 emissions from cutover peatland (Wilson *et al.* 2013).

When peatlands are left without any restoration treatments (*i.e*. 'abandoned') after peat extraction operations are terminated, spontaneous revegetation may be observed. The revegetation process is influenced by multiple factors, the most important being the degree of damage to the peat bog, the thickness of residual peat and its nutrient content, the water level and water sources, the surface topography, and the time that has elapsed since peat extraction ceased (Wheeler & Shaw 1995). Conditions may vary widely between and within sites, and this affects the rate and pattern of revegetation. The most desirable outcome is reinstatement of the original plant community including, in the case of a raised bog, an acrotelm composed mainly of *Sphagnum* mosses. However, extracted areas are hostile and highly challenging habitats for recolonising mire plants, mainly because of poor water availability, exposure to desiccation and erosion, lack of diaspores (Quinty & Rochefort 2003), and high acidity accompanied by low nutrient content in the cutover surface peat (Salonen 1994). Moreover, *Sphagnum* species are particularly sensitive to difficulties of acquiring water by transfer from the finer-textured cutover peat (McCarter & Price 2015).

Early recognition of the potential for regeneration of a specific site may be helpful when planning ecological restoration activities aimed at encouraging the development of target plant communities by modifying environmental conditions (Campbell *et al.* 2000). In order to determine the local potential for spontaneous revegetation, it is essential to know which factors are important for species typical of raised bogs. We hypothesise that the secondary transformation of peat after drainage results in changes in quality of the uppermost soil layer which might in turn affect the establishment of bog species. The water-holding capacity index W_1 proposed by Gawlik (*e.g*. 1992) is a quantitative characteristic of water retention by the soil that reflects changes in the physical, hydrophysical and chemical properties of peat when subjected to drying (Gawlik 2000, Sokołowska *et al.* 2005), and can be used to quantitatively assess the secondary transformation stage of peat.

The aim of this study was to investigate: 1) how secondary transformation of peat on an area of extracted peatland affects revegetation; 2) the relative importance of a range of factors in controlling the establishment of raised bog species; and 3) whether the W_1 index, as a single measure of secondary transformation, may be a useful predictor of revegetation trajectories for extracted areas.

METHODS

Study site

The research was carried out on the Bór za Lasem bog, which is located in Czarny Dunajec commune in southern Poland (Figure 1). It is one of a group of 27 peatlands belonging to the European Ecological Network Natura 2000. These bogs were formed within the Orava - Nowy Targ Basin, which is a depression flanked to the north and south by mountain ridges. The climate of the basin is moderately warm with some local peculiarities (Kondracki 2011). For the part with bogs, Olszewski (1988) gives a mean annual air temperature of + 5.5 °C (highest and lowest monthly means: + 16 °C for July, - 6 °C for February) and total annual precipitation 750–825 mm, which is considerably less than in the surrounding higher-altitude areas but much greater than in the Polish lowlands. Basic weather characteristics were recorded in 2016 with a Davis Vantage Pro 2 weather station located near the study site (49° 25' 31.33" N, 19° 48' 42.24" E; Figure 1). At this location, mean daily air temperature between June and August (2016) was 15.4 °C, with daily maximum 37.0 °C and daily minimum -2.9 °C. The total precipitation recorded during the same period was 375 mm.

The Bór za Lasem bog was initiated by paludification of a sparingly permeable clay substratum under the influence of shallow groundwater, and subsequently developed into a raised bog. This is reflected in the peat stratigraphy by the presence of strongly decomposed and transitional (poor-fen) *Sphagno-Cariceti* peat near the base, overlain by *Eriophoro-Sphagneti* and *Eusphagneti* peats formed under conditions of ombrogenous water supply. Average degree of peat decomposition within the deposit, determined by a microscopic method (*e.g*. Tobolski 2000), is 30 % and average ash content is 2.2 %. Average thickness

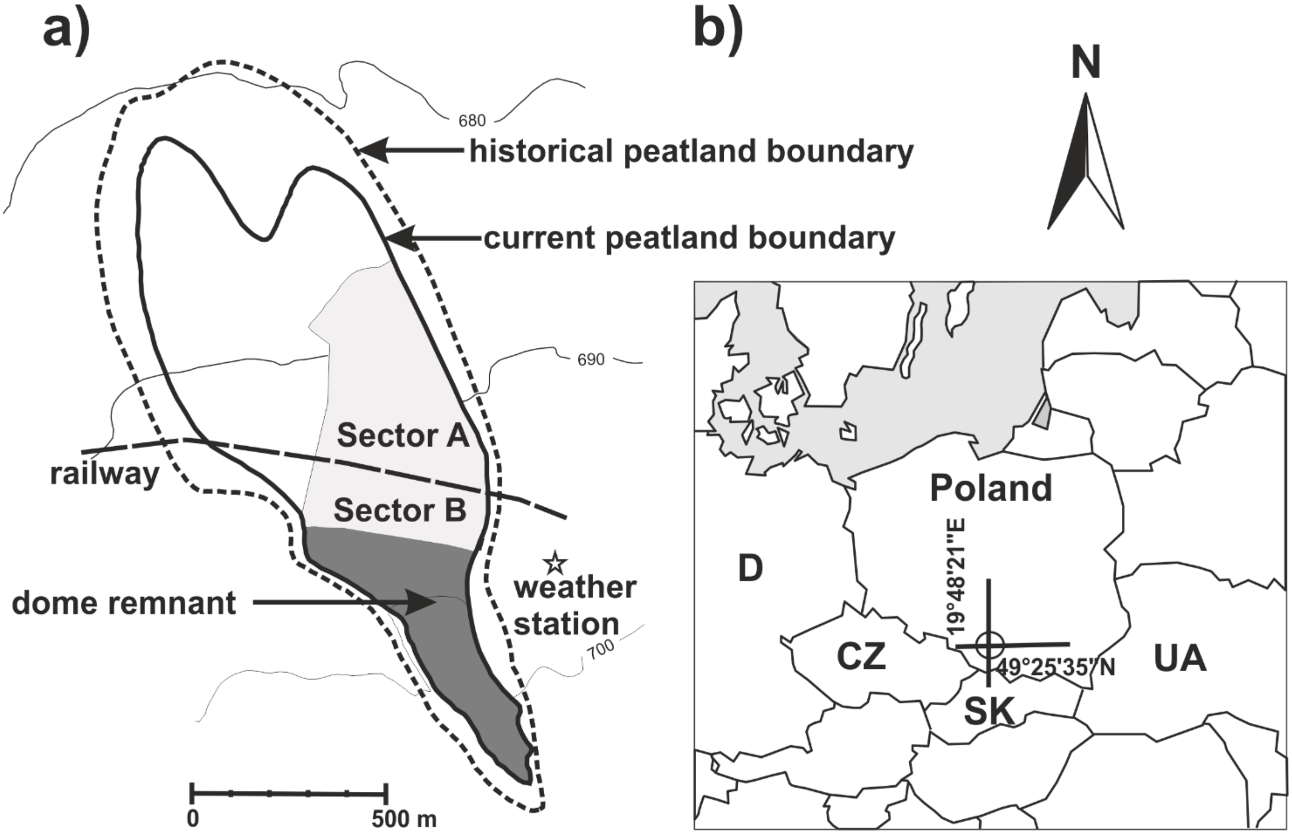

Figure 1. Map of the Bór za Lasem peat bog showing the two investigated sectors of the extracted area (adapted from Łajczak 2006) (a), and location map (b).

of the deposit is about 1.8 m, and its maximum thickness is 3.65 m (Lipka & Zając 2014).

The current area of the bog is 55 ha. Almost the entire perimeter of the bog dome has been intensively exploited by local people for centuries. After World War II, industrial extraction of peat by the block-cutting method commenced, using heavy machinery. The extracted area is bisected by a railway embankment. The northern sector (Sector A, ~16 ha) is bordered by the railway to the south and by forest and grassland to the north, while the southern sector (Sector B, ~ 8 ha) is delimited by the railway to the north and a surviving part of the bog dome to the south (Figure 1). Peat was cut on Sector A from the beginning of the 1960s until the beginning of the 1980s, then operations moved onto Sector B where extraction continued until the early 1990s (Mr Bogusław Sroka, Peat Production Plant "Bór za Lasem" in Czarny Dunajec, personal communication 2016). Thus, peat extraction ceased approximately ten years earlier in Sector A than in Sector B. The site was subsequently left untouched. Across both sectors there is a network of secondary ditches spaced at about 20 m that discharge water into main ditches. Most of the secondary ditches are currently overgrown with vegetation and some of them are blocked. The main ditches discharge water mainly during floods associated with major rainfall events and spring thaws.

Study plots

Studies in the extracted sectors of the Bór za Lasem bog were conducted during the years 2015 and 2016. Within each sector, twenty 5 m × 5 m study plots were set out in a W-shaped transect (40 study plots in total). The plots were arranged in a regular pattern but they were placed to avoid ditches, standing water and dense groups of trees.

Analysis of peat

At each study plot the mean thickness of residual peat was measured with a soil probe and surface peat samples were taken for laboratory analysis. The peat samples were collected from 0–10 cm depth. Samples of undisturbed structure were collected in small metal rings (250 cm^3, two *per* plot, 80 in total) and placed in plastic bags for transport. A further (disturbed) sample was collected into a plastic bag from each of the 40 plots and subsequently divided into two parts for analysis (*i.e.* all analyses were duplicated). To determine the type of peat that was left at the surface when extraction ended, additional samples were collected from just below the surface layer that had subsequently degraded, at eight randomly selected locations in each sector.

Degree of peat decomposition was estimated by von Post's method (von Post 1924). Peat type was determined by a microscopic method based on plant macrofossil analysis (Kac *et al.* 1977, Tobolski 2000). To determine bulk density (ρ_b) plus volumetric (θ_v) and saturated (θ_s) moisture content, the samples with undisturbed structure were dried to constant weight at 105 °C. For θ_s, the samples were soaked with water for three weeks before drying, and gravimetric moisture content was converted to volumetric basis using bulk density. Volumetric shrinkage (S_v) was estimated as the difference in volume of the sample between saturated and oven-dry (105 °C) state divided by its volume in saturated state. Volumes were calculated from measurements of sample height plus top and bottom diameter (mean of four measurements with a micrometer for each dimension; Oleszczuk *et al*. 2003). Ash content (A) was determined by a loss on ignition method (6 hours at 550 °C). Specific density (ρ) was calculated from ash content (A) using the equation $\rho = 0.011 \cdot A + 1.451$ (Okruszko 1971) and total porosity (n) was calculated from specific density and bulk density. pH and electrical conductivity (EC) were measured in a 1:10 (weight of soil : volume of liquid) mixture using a potentiometric method; EC was measured in distilled water only, while pH was measured in both distilled water and 1 M KCl. The resulting EC values were corrected for H^+ ions (Sjörs 1950). Total carbon (C) and total nitrogen (N) were determined using a CNS analyser (LECO CNS-200), and the mineral nitrogen forms nitrate (NO_3^-) and ammonium (NH_4^+) using a flow injection analysis (FIAstar 5000, FOSS) method. Available phosphorus (P) was determined by the Egner-Riehm method based on soil extraction with calcium lactate solution acidified with hydrochloric acid (Lityński *et al.* 1976).

The stage of secondary transformation of peat was assessed on the basis of water-holding capacity index (W_1) according to the procedure proposed by Gawlik (1996). This index is the quotient of the (minimum) water-holding capacity of the soil when absolutely dry and its (maximum) water-holding capacity in fresh condition. It was determined as the water capacity of a soil sample dried at 105 °C divided by that of a sample in fresh (field) condition. The soil samples were divided into two batches. Samples that were to remain in fresh state were soaked with distilled water for seven days, while their counterparts were dried to constant weight at 105 °C before soaking (also for seven days). Then each sample was centrifuged at 1000 × g for one hour, at an ambient temperature of 10 °C. The water content of each soil sample was determined gravimetrically, then the W_1 index was calculated. The values of W_1 were classified as follows (Gawlik 2000):

$W_1 = 0.36–0.45$: I - initial secondary transformation;
$W_1 = 0.46–0.60$: II - weak secondary transformation;
$W_1 = 0.61–0.75$: III - medium secondary transformation;
$W_1 = 0.76–0.90$: IV - strong secondary transformation;
$W_1 > 0.90$: V - completely degraded.

Water table coefficient

A dipwell made from PVC pipe (ø 50 mm) was installed at each study plot. The wall of the dipwell was perforated for one-third of its length and coated with a geotextile screen to prevent silting. Water table depth (cm below peat surface) was measured manually every two weeks between April and November 2016. The degree of drying of the cutover peat layer was expressed as a coefficient calculated as (mean water table depth ÷ thickness of residual peat in cm). Thus, a coefficient of zero indicated that the water table was level with the peat surface and a coefficient of unity meant that there was no water table within the peat layer.

Vegetation survey

The vegetation inventory was carried out by estimating the cover of plant species on the plots using a decimal scale (Londo 1976), separately for the tree, shrub, and herb layers. The cover of bryophytes and bare peat was recorded in 0.5 × 0.5 m subplots located in the four corners of each plot. Bryophytes were identified at genus level. Species that are characteristic of the classes *Scheuchzerio-Caricetea nigrae* and *Oxycocco-Sphagnetea* according to Ellenberg *et al.* (1992) were considered to be raised bog species.

Statistical analysis

The data for soil properties were tested for normality using the Shapiro-Wilk test ($p > 0.05$). Variables that did not follow normal distributions were subjected to log transformation. For some variables, this did not provide the expected result so Spearman's non-parametric correlation coefficient was used to evaluate correlations. Although not replicated, we assessed differences in peat properties between Sectors A and B using a parametric t test for normally distributed variables and a non-parametric U-Mann Whitney test for variables with non-normal distributions. Results were deemed significant at $\alpha = 0.05$ but were interpreted with caution in view of the pseudoreplication. The statistical analysis was performed in Statistica 12 (2016 version, Dell Inc.).

The comparison of plant species composition between the two sectors was based on the frequency of occurrence and mean plant cover on the plots. The Shanonn–Wiener index (Lepš 2005) was used as the metric of species diversity. Analyses of vegetation and abiotic factors affecting the occurrence of plants were carried out using multivariate methods, Detrended Correspondence Analysis (DCA) and Redundancy Analysis (RDA), in Canoco software (ter Brak & Smilauer 2002). The linear method (RDA) was used with a gradient length of 3.0 SD (standard deviation) in the DCA analysis. The significance of partial and marginal effects in RDA analysis was calculated on the basis of a Monte Carlo permutation test. In marginal analyses, only one factor at a time was included as an environmental variable. This provided information about the importance of specific factors without reference to their correlations with other variables (Lepš & Šmilauer 2003). In partial analyses, each factor was tested as an environmental variable using the other factors as covariables.

RESULTS

Peat characteristics

When peat extraction ended, the cutover surfaces in the two sectors consisted of different types of peat. In Sector B the surface peat was composed of cottongrass-*Sphagnum* (*Eriophoro*-*Sphagneti*) peat with degree of decomposition H4–H6 on the von Post scale. In the older Sector A, a layer of pine-*Sphagnum* (*Pino*-*Sphagnum*) peat and sapric peat with pine wood residues (H4–H8) had been exposed. One-third of the study plots in the latter sector featured a compressed moss layer at depth 5–6 cm, as well as traces of fire.

The average thickness of the residual peat layer differed significantly between Sectors A and B (Table 1), as did water level ($p < 0.1$; Mann-Whitney U-test). A significant ($p < 0.05$) negative correlation ($r = -0.771$) was observed between residual peat thickness and water table depth. Water table depth also significantly ($p < 0.05$) correlated with θ_v ($r = -0.701$), W_1 ($r = 0.650$), S_v ($r = -0.492$), NH_4^+ ($r = -0.518$) and corrected EC ($r = 0.667$).

In general, between April and November 2016 the water table was lower in Sector A than in Sector B (Table 1). From June to August it dropped to 13–22 cm below the base of the peat layer in study plots with peat thickness ~40 cm or less. This was recorded for 17 % of the plots in Sector B and 58 % of the plots in Sector A. In the rest of the plots (where the water table always remained within the peat profile), water table depth was 3–37 cm (mean 25 cm) in Sector A and 1–42 cm (mean 16 cm) in Sector B. The water table coefficient indicated that the peat in Sector A was markedly drier than that in Sector B (Figure 2). It is likely that this caused differences between the sectors in some physical and hydrophysical properties of the uppermost 10 cm of peat (Table 1). Values of n, S_v, θ_v and θ_s were all higher in Sector B while values of W_1 were higher in Sector A. On the basis of W_1 index, the secondary transformation class of top-layer peat in Sector A was ‘weak’ to ‘strong’, whereas Sector B featured less-transformed peat, between ‘initial’ and ‘medium’. As far as chemical properties are concerned, the sectors differed in NH_4^+ content, pH and corrected EC. NO_3^- outweighed NH_4^+, although the difference was markedly lower in Sector A. Both sectors were characterised by low content of available P and extremely low pH, with higher values of both attributes in the older Sector A (Table 1).

Vegetation characteristics

For all study plots the mean cover of raised bog species was 46 %, while the mean cover of species not usually associated with raised bogs was 85 %. There was no difference between the two sectors in the number of species *per* plot and species diversity (Shannon-Wiener index). The cover of herbaceous plants was significantly higher in Sector B, while moss cover (with prevalence of true mosses) was higher in Sector A. No differences were found for shrub layer cover or bare peat, while tree layer cover was higher in Sector A (Table 2). The raised bog plants *Sphagnum* spp., *Ledum palustre* and *Oxycoccus palustris* were more common in Sector B; indeed, the last of these species was not found in Sector A. *Sphagnum* (cover 12 %) occurred mainly in the form of isolated cushions and did not form a continuous acrotelm. *Eriophorum vaginatum* and Ericaceae such as *Calluna vulgaris*, *Vaccinium uliginosum*, *V. vitis-idaea* and *V. myrtillus* were common in both sectors but *Eriophorum vaginatum* cover in Sector B was double that in Sector A. Tree species *(Pinus sylvestris*, *Betula pendula)* occurred in all vegetation layers. However, *Pinus sylvestris* in the shrub layer was associated with Sector B (Table 3).

Effect of peat quality on revegetation

The first and second axes of the DCA ordination diagram shown in Figure 3 explain 16.9 % and 8.9 %, respectively, of the variability in plant species composition. The first axis reflects the main differences in species composition. Thus, the left-hand part of the diagram contains raised bog plants such as *Sphagnum* spp., *Eriophorum vaginatum, Oxycoccus palustris* and *Ledum palustre* while the

Table 1. Comparison of soil properties for the uppermost 10 cm of peat, between Sector A and Sector B. Significance was tested with a parametric t-test or a non-parametric Mann-Whitney U-test; *comparison of medians with non-parametric Mann-Whitney U-test. Key: SD = standard deviation; n.s. = non-significant at $p < 0.05$; b.g.l. = below ground level.

Soil properties	Units	Sector A				Sector B				Sector A *vs.* B
		min.	max.	mean	SD	min.	max.	mean	SD	
Peat depth	cm	19	98	39.3	21.8	32	113	64.6	23.9	$p < 0.001^*$
Total porosity (n)	%	78	89	84	3	77	91	86	3	$p < 0.05$
Bulk density (ρ_b)	Mg m^{-3}	0.16	0.33	0.25	0.05	0.14	0.35	0.22	0.06	n.s.
Specific density (ρ)	Mg m^{-3}	1.50	1.73	1.59	0.06	1.47	1.78	1.57	0.10	n.s.*
Ash content (A)	%	4.24	25.35	12.69	5.81	1.99	30.34	10.94	9.41	n.s.*
Volumetric shrinkage (S_v)	%	15.75	53.12	31.68	9.07	19.14	59.93	45.07	10.40	$p < 0.001$
Volumetric moisture content (θ_v)	vol.%	12.48	67.66	34.65	17.87	58.95	88.59	76.05	8.75	$p < 0.001^*$
Saturated moisture content (θ_s)	vol.%	61.14	90.85	73.00	7.15	75.87	88.69	81.86	3.06	$p < 0.001^*$
Water-holding capacity index (W_1)	-	0.53	0.76	0.61	0.07	0.39	0.68	0.55	0.08	$p < 0.05$
Total C	%	47.45	58.14	53.79	2.81	33.84	63.07	55.57	6.71	n.s.*
Total N	%	1.38	2.02	1.70	0.17	1.19	2.02	1.65	0.21	n.s.*
C/N	-	25	39	32	3	27	48	34	5	n.s.
NO_3^-	mg kg^{-1}	0.83	37.08	3.30	8.22	0.44	6.24	1.51	1.26	n.s.*
NH_4^+	mg kg^{-1}	7.68	44.58	16.19	9.03	35.84	172.46	77.54	33.79	$p < 0.001^*$
Available P	mg kg^{-1}	10.09	48.77	23.30	9.98	2.62	41.94	17.92	9.70	n.s.
pH_{H2O}	-	3.56	3.96	3.72	0.12	2.96	3.60	3.29	0.21	$p < 0.001^*$
pH_{KCl}	-	2.35	3.24	2.82	0.23	2.52	2.90	2.68	0.13	$p < 0.05^*$
Corrected electrical conducticity (EC)	µS cm^{-1}	119.00	252.08	177.79	38.34	60.62	264.00	134.58	50.35	$p < 0.01$
Water table depth	cm b.g.l.	50	0	30.4	7.0	51	0	17.9	5.9	$p < 0.1^*$

right-hand part lacks raised bog species and is rich in trees and true mosses (mainly *Pleurozium* sp.). The plots located in the older Sector A are clustered in the right-hand part of the diagram, whereas those in the younger sector B appear in the left-hand part. However, the central part of the diagram contains plots from both sectors that harbour raised bog species (*Vaccinium uliginosum*) and plants that are typical for oligotrophic habitats but not peat-forming (*e.g*. *Calluna vulgaris*).

The main gradient of change in species composition correlated with water table depth and soil factors (Figure 4) that reflect the secondary transformation stage of the uppermost layer of cutover peat. Plots with raised bog species were characterised by higher water level, lower W_1 and ρ_b, higher n, θ_v, θ_s, S_v, NH_4^+ content, total C and C/N, as well as greater residual peat depth. The second axis correlated (weakly) only with available P, total N and pH. The RDA analysis of the significance of individual variables for plant species composition showed that twelve of them (Table 4) were significant when each was analysed as an individual variable (marginal effect). The most important attribute seemed to be water table depth, which accounted for 35 % of the variation. However, the strong intercorrelation of significant variables meant that the effects of individual variables without the influence of all other variables (partial effect) were non-significant in all cases (Table 4).

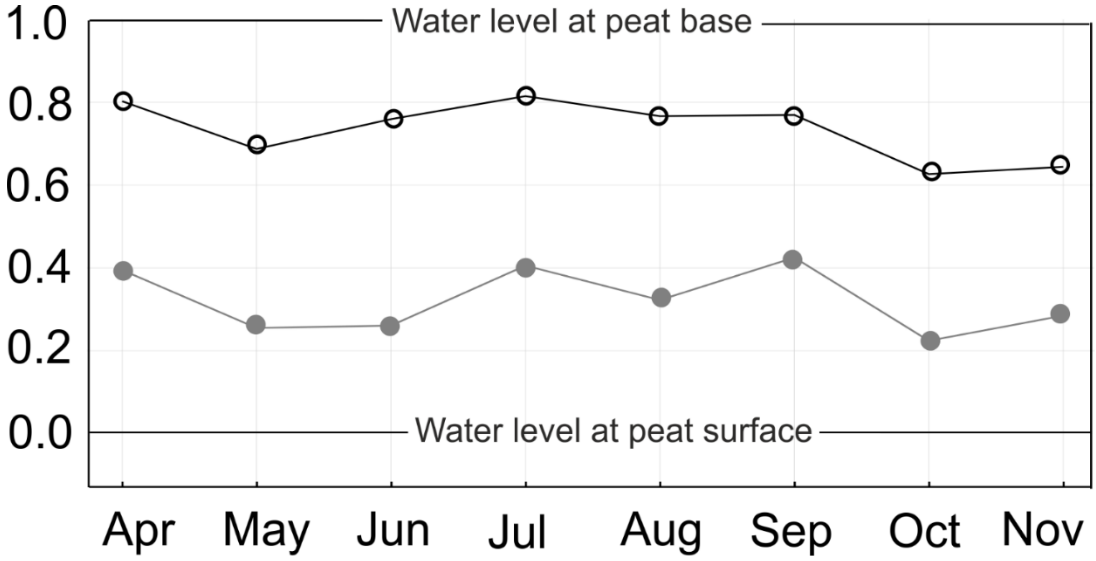

Figure 2. Variation of the water table coefficient (mean water table depth ÷ thickness of residual peat) during the period April to November 2016, for Sector A (unfilled circles) and Sector B (filled circles).

Table 2. Diversity measures and mean cover (%) of plant species typical of raised bogs; other plant species (not characteristic for raised bogs); the tree, shrub and herb layers; and bare peat, in the two extracted sectors of the Bór za Lasem bog.

Attribute	Sector A	Sector B	p	Mean for both sectors
Mean number of species *per* plot	11.5	10.6	0.23	11.1
Shanonn-Wiener index	1.8	1.6	0.13	1.7
Raised bog species cover	28	65	0.00	46
Non raised bog species cover	93	76	0.00	85
Tree layer cover	11	1	0.00	6
Shrub layer cover	10	10	0.95	10
Herb layer cover	44	80	0.00	83
Moss layer cover	23	11	0.00	17
Bare peat cover	18	22	0.37	20

Table 3. Frequency of occurrence (%) of plant species and mean plant cover (%) calculated only for plots where the species was present. Only species with frequency > 50 % and raised bog species (**bold**) are presented.

Species	Sector A		Sector B	
	Frequency	Mean cover	Frequency	Mean cover
Oxycoccus palustris	0	0	35	4
Sphagnum **spp.**	32	4	55	12
Pinus sylvestris (shrub layer)	16	7	45	10
Ledum palustre	42	3	90	8
Eriophorum vaginatum	95	23	95	49
Pleurozium schreberi	89	19	75	9
Calluna vulgaris	84	17	80	24
Vaccinium uliginosum	84	18	80	13
Brachythecium spp.	68	2	60	4
Pinus sylvestris (herb layer)	68	1	50	2
Betula pendula (shrub layer)	58	11	45	8
Polytrichum spp.	84	10	80	6
Aulacomnium palustre	74	2	20	1
Betula pendula (herb layer)	53	2	35	1
Vaccinium myrtillus	53	7	35	3

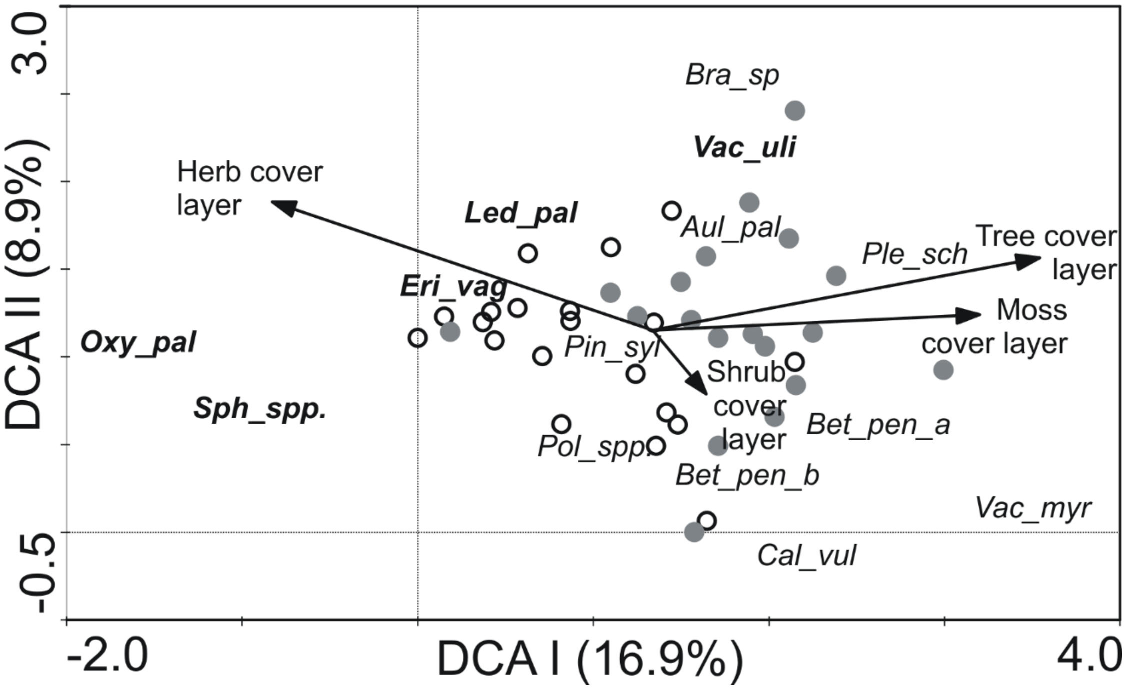

Figure 3. Unconstrained ordination diagram (DCA) of plots (filled circles - Sector A, unfilled circles - Sector B) and vegetation data. Only raised bog species (in **bold**) and species with the highest weight are presented. Abbreviations of species names: *Aul_pal* = *Aulacomnium palustre, Bet_pen_a* = *Betula pendula* in tree layer, *Bet_pen_b* = *Betula pendula* in shrub layer, *Bra_spp.* = *Brachythecium species, Cal_vul* = *Calluna vulgaris, Eri_vag* = *Eriophorum vaginatum, Led_pal* = *Ledum palustre, Oxy_pal* = *Oxycoccus palustris, Pin_syl* = *Pinus sylvestris, Ple_sch* = *Pleurozium schreberi, Pol_spp.* = *Polytrichum* species, *Sph_spp.* = *Sphagnum* species, *Vac_myr* = *Vaccinium myrtillus, Vac_uli* = *Vaccinium uliginosum, Vac_vit* = *Vaccinium vitis-idaea.*

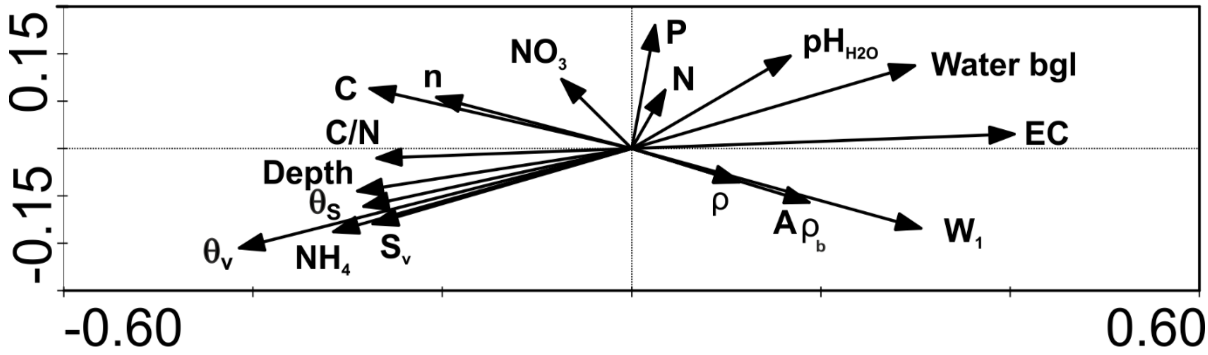

Figure 4. Unconstrained ordination diagram (DCA) of all environmental variables (arrows) shown as the passive ones. Abbreviations of variables: Water bgl = water table depth (below ground level), Depth = depth of residual peat, n = total porosity, ρ_b = bulk density, ρ = specific density, A = ash content, S_v = volumetric shrinkage, θ_v = volumetric moisture content, θ_s = saturated moisture content, W_1 = water-holding capacity index, C = total carbon, N = total nitrogen, NO_3 = nitrate nitrogen, NH_4 = ammonium nitrogen, P = available phosphorus, EC = corrected electrical conductivity.

Table 4. Results of the constrained ordination (RDA). Marginal effects of the environmental variables and their partial effects on the vegetation based on forward selection (Monte Carlo permutation test). Only variables with significant marginal effect are presented.

Variable	Marginal effect			Partial effect		
	Explained variability (%)	p	F	Explained variability (%)	p	F
Water table depth	35	0.002	11.92	2	0.616	0.58
Volumetric moisture content	26	0.002	7.78	3	0.408	1.10
Corrected electrical conductivity	24	0.002	6.96	2	0.592	0.73
Sector	16	0.012	4.10	1	0.710	0.36
Total C	15	0.010	3.95	2	0.492	0.92
Water-holding capacity index W_1	15	0.010	3.87	2	0.638	0.54
Peat depth	13	0.020	3.42	3	0.584	0.70
NH_4^+	13	0.022	3.18	2	0.486	0.93
Volumetric shrinkage	12	0.026	3.05	3	0.584	0.71
C/N	11	0.042	2.74	2	0.526	0.86
Total porosity	10	0.044	2.58	1	0.690	0.50
Bulk density	10	0.048	2.43	2	0.608	0.65

DISCUSSION

Because of their intercorrelations, the factors investigated were not individually important in determining the revegetation pattern on the extracted parts of the Bór za Lasem bog. However, water table depth seemed important as the abiotic factor that determined the degree of soil aeration and, consequently, the secondary transformation stage of the peat. Therefore, it may be concluded that the interactions of water table depth with peat soil properties further promote the importance of water conditions on extracted areas.

Soil properties which explained plant species composition (W_1, θ_v, n, ρ_b, S_v, corrected EC, NH_4^+, C, C/N) were associated with water table position, as confirmed by partial DCA. Except for NH_4^+ content, edaphic factors (*e.g*. pH, NO_3^- content, available P) did not affect vegetation development at Bór za Lasem, even though a role has been demonstrated in other studies (Salonen 1994, Graf *et al.* 2008, Konvalinková & Prach 2010). This was probably due to the very small variation in these factors within the two cutover areas investigated here. The values of the soil properties tested indicated that secondary transformation of peat was more advanced in Sector A, which was abandoned about ten years earlier than Sector B.

The revegetation patterns on the two extracted sectors of Bór za Lasem bog were similar to those observed on extracted areas of other peatlands in Europe, *e.g*. by Poschlod *et al*. 2007 (Germany), Konvalinková & Prach 2014 (Czech Republic), Triisberg *et al.* 2014 (Estonia) and Orru *et al.* 2016 (also Estonia). In our study areas, the water table often dropped into the poorly permeable mineral (clay) substratum, especially where the peat layer was thin (< 0.4 m). This favoured the development of vascular plants including trees, whose roots can access nutrients by growing into the rich mineral substratum. Trees promote drying of the peat layer through transpiration and interception of water arriving as precipitation (Van Seters & Price 2001, Limpens *et al.* 2014), and this further enhances the processes that cause secondary transformation of peat. Such conditions prevailed in Sector A, where revegetation was tending towards a pine and birch community. Common inhabitants of this sector were species typical of coniferous forest such as *Vaccinium myrtillus*, *V. vitis-idaea* and *V. uliginosum*, along with mosses belonging to the genera *Polytrichum* and *Brachythecium*, *Pleurozium schreberi* and *Aulacomnium palustre*. These mosses are usually associated with forest communities where trees are providing considerable shade (Hedwall *et al.* 2017).

The revegetation by *Sphagnum* and other raised bog species (*Eriophorum vaginatum*, *Vaccinium uliginosum*, *Ledum palustre*, *Oxycoccus palustris*) was associated with areas of deeper residual peat and high water table, which in turn were strongly correlated with hydrophysical soil properties such as volumetric moisture content θ_v and water-holding capacity index W_1. High water level is a prerequisite for *Sphagnum* re-establishment because it mitigates the effect of radically differing hydrophysical properties between the regenerating moss cover and the cutover peat (McCarter & Price 2015). *Sphagnum* lacks roots and vascular channels, so water uptake and transport processes differ from those in vascular plants (Schouwenaars & Gosen 2007). Price & Whitehead (2001) formulated limit values to define hydrological conditions suitable for the development of *Sphagnum*, which included a mean water table depth of 24.9 ± 14.3 cm below the ground surface, $\theta_v > 50$ % and soil-water pressure above -100 mb. Soil-water pressure was not evaluated in our study, but θ_v and mean water table depth indicated potentially favourable conditions for *Sphagnum* development in the younger Sector B and unfavourable conditions in Sector A. The difference in θ_v between the two sectors was important. There were serious consequences for regeneration of typical raised bog plant species including, most notably, *Sphagnum* spp. Reduced moisture content (and, thus, high soil water tension) in the uppermost peat layer inhibits *Sphagnum* development because these mosses are unable to take up water from the substrate when the pore-water pressure is below -100 mb (Hayward & Clymo 1982 *op. cit*. Price 1997). On the other hand, the root systems of vascular plants can collect water from deeper soil layers and nutrients from mineralised organic matter (Malmer *et al.* 2003) and/or from the mineral substratum underlying a thin layer of peat. Therefore, they are capable of colonising extracted peatland areas at a faster rate.

In our study, DCA revealed correlations between the establishment of *Sphagnum* and other raised bog species and the water-holding capacity index W_1. Bog species were present on the study plots showing lower W_1 index values, *i.e*. where the peat was transformed to a lower degree. This relationship is most important for *Sphagnum*, which does not have roots and is thus more highly dependent than vascular plants on water conditions in the uppermost layer of cutover peat. Thus, the W_1 index may be useful not only for evaluating the secondary transformation stage of peat, but also as an indicator of the potential for spontaneous regeneration of vegetation composed of *Sphagnum* species on degraded bogs. However, in view of the relatively low representation of

Sphagnum on the peatland that we investigated here, this suggestion must be explored in further research before it can be verified.

There is a possibility that interventions to help raise the water table in Sector B may promote further expansion of *Sphagnum.* Local conditions such as the proximity of the bog dome remnant and thus of a diaspore bank (Konvalinková & Prach 2014), as well as the small area (Triisberg *et al.* 2011, Kollman & Rasmussen 2012), may favour the establishment of bog species. Recovery towards raised bog might be positively affected by the great abundance of *Eriophorum vaginatum*, which is nearly two times more common (with larger individual plants) in Sector B. This species prefers areas of thick peat with low ash content, predominance of NH_4^+ over NO_3^- (Salonen 1994), water table depth no greater than 30–40 cm and $\theta_v > 70$ % (Lavoie *et al.* 2005), which is consistent with our results. Various studies have suggested that plants such as *Eriophorum* (Soro *et al.* 1999), ericaceaous shrubs or young trees (Pouliot *et al.* 2011a) and *Polytrichum strictum* (Groeneveld *et al.* 2007) may facilitate *Sphagnum* colonisation by improving the microclimate and shaping microtopography.

We found a strong negative correlation between water table depth and residual peat thickness. Differences between these two environmental factors were expressed in terms of a coefficient that clearly illustrated the contrast in conditions between the two sectors. In 2016, 80 % and 40 % of the residual peat layer in Sectors A and B, respectively, was above the average water table level (and, thus, usually unsaturated) during the growing season. Where residual peat thickness was less than 40 cm, the water table was below the organic soil horizon for the entire observation period. This suggested that a certain depth of residual peat was required to stabilise the water level, *i.e.* it helped to limit water table fluctuations. However, further observations (in progress) are needed to confirm this hypothesis. Assuming that satisfactory peat thickness and degree of peat decomposition are preconditions for successful recovery of mire vegetation, it may be concluded that the residual peat layer on the investigated sectors was in general too thin and decomposed. There is no strict threshold for the minimum residual peat depth required for restoration but the value that is most often recommended is at least 0.5 m for well-decomposed peat ($H \geq 7$) and 1.0 m for less-decomposed peat (H5–H7) (Wheeler & Shaw 1995, Quinty & Rochefort 2003). Successful restoration has been performed on Canadian sites with less than 1.0 m depth of less-decomposed peat (González & Rochefort 2014). On the other hand, Poschlod *et al.* (2007) consider that the peat thickness values stated above are insufficient in the conditions of southern Germany, and Triisberg *et al.* (2014) state that raised bogs with less-decomposed peat in the boreo-nemoral region should be restored when residual peat thickness is greater than 2.3 m.

Spontaneous regeneration of cutover bogs is possible only under favourable conditions. It is also a long-term process that may take more than a century to complete (Pouliot *et al.* 2011b). Restoration of a properly functioning hydrological system is a crucial element of rehabilitation for any type of peatland (Chimner *et al* 2017). There are many techniques for improving hydrological conditions on extracted peatlands (see, for example, Wheeler & Shaw 1995, Price *et al.* 2003, Graf *et al.* 2012), but the effects of a residual peat layer that is too shallow may be sufficiently serious to prevent the restoration of a raised bog. Thus, leaving behind only a shallow peat layer at the end of peat extraction operations may be justified only if the recovery of peat-forming bog vegetation is not an objective for the peatland.

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