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Factors affecting the re-vegetation of abandoned extracted peatlands in Estonia: a synthesis from field and greenhouse studies

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Abstract. Re-vegetation of extracted peatlands is a slow and sporadic process. The aim of our study was to clarify whether this process is affected by the distance from vegetated areas and propagules arrival or by the conditions for propagules germination and plant growth. Our analysis is based on three extracted peatlands in Estonia, abandoned 26–31 years ago. In all study areas vegetation was analysed on the gradient from a neighbouring vegetated area towards the central part of the peatland. In addition, peat blocks were collected from the marginal and central parts of the peatlands, held in favourable moisture conditions for seed germination in a greenhouse, and half of them were fertilized with a complex fertilizer.

Our study showed the species pool to be present everywhere on abandoned extracted peatlands, but the germination was influenced by different factors such as water table, peat chemistry, etc. The species richness on extracted peatlands was higher close to the neighbouring vegetated areas and decreased towards the central part of the peatland, but for the peat blocks held in the greenhouse, the number of species was higher for the blocks collected from the central parts of the peatlands. The proximity of the vegetated area did not increase the number of species developed in the greenhouse whereas higher moisture and temperature conditions initiated the growth of many additional species not found on the extracted peatlands. Our study demonstrated that fertilization with a complex fertilizer did not have an overall influence on the number of species, indicating that the re-vegetation of extracted peatlands is more controlled by moisture conditions than by the availability of nutrients or propagules arrival.

Key words: fertilization, germination, plant assemblages, species arrival, species pool, succession.

INTRODUCTION

Peatlands have been used for peat extraction for centuries. This practice has left behind spoiled landscapes without vegetation. According to the Estonian legislation, all mining areas, including extracted peatlands, should be recultivated after the end of mining (Raudsep, 2011). Although 20–30 years ago areas where peat harvesting had ceased were sometimes used for agricultural purposes and forestry, most of them were just abandoned during and after the end of the Soviet period up to the early 1990s by the state-owned companies. Only very few extracted peatland areas have currently been recultivated. For successful restoration a better understanding of factors affecting this process and its regional peculiarities is necessary (Campbell et al., 2003; Lavoie et al., 2003; Triisberg et al., 2011).

Abandoned extracted peatlands with deep drainage have a negative impact on the hydrology and microclimate of their surroundings; they cause changes in the local outflow of water rich in dissolved organic carbon and the fragmentation of natural areas. These areas have a high fire risk and they reduce habitat diversity. Currently peat is extracted from 20 000 ha in Estonia and the total area of abandoned extracted peatlands is 9371 ha, but in the coming decades their area will be doubled because of the depletion of peat deposits on mining areas (Ramst & Orru, 2009). Extracted and drained peatlands have a dense drainage system and they are an increasing source for man-induced CO_2 emission caused by accelerated peat decomposition in such areas (Paavilainen & Päivänen, 1995; Salm et al., 2009). In Estonia drained and extracted peatlands emit annually about 10 million tonnes of CO_2, being the second most important CO_2 source in this country after industry and exceeding the emissions from traffic (Ilomets, 2001).

The exposed residual peat layer after peat harvesting is often several thousands of years old where seeds/spores are decomposed or not capable of germination (Salonen, 1987, 1994). Therefore, all the propagules for re-vegetation have to be carried here from elsewhere, mostly by the wind. Due to the unfavourable and highly variable growth conditions on the surface of the extracted peatlands, discussed thoroughly by several authors (e.g. Price et al., 1998; Campbell et al., 2002; Campbell & Rochefort, 2003), the propagules have to go through several ecological filters such as human-imposed barriers, intensive agriculture etc. before arriving the extracted peatlands (Belyea, 2004). Moreover, only a few propagules can germinate and form plant assemblages able to survive there for a longer period (Egawa et al., 2009). Hence, the spontaneous re-vegetation of abandoned extracted peatlands is very slow and uneven. Still, this process offers a useful opportunity to study and understand the propagules arrival, their germination, plant survival, and the formation of early plant assemblages, i.e. the peculiarities of the respective succession. There are several studies about the role of some early arriving species, such as *Eriophorum vaginatum* and *E. angustifolium*, which create more suitable conditions for other mire plant species (Tuittila et al., 2000; Groeneveld & Rochefort, 2002; Koyama & Tsuyuzaki, 2010), but these results are to some extent discordant. As we pointed out earlier (Triisberg et al., 2011), considering that the dispersal distance of propagules is limited, there can be differences in plant species number and species content between the marginal parts of larger extracted peatlands close to vegetated neighbouring areas and in the central parts located further from the potential propagules source. Salonen & Setälä (1992) showed that besides the seed rain from the adjacent plant communities, the quality of substrate and its microbial activity affect the composition of vegetation in extracted peatlands. However, it is not fully clear how far into the extracted peatlands the propagules could be carried, how much the re-vegetation is influenced by the type of the adjacent vegetated areas, and how much the germination of the arriving propagules and the survival of plants depend on the growth conditions or on autecological differences between plant species.

The main aims of the current study were to clarify on the basis of field studies and a greenhouse experiment (i) whether the slow natural re-vegetation of abandoned extracted peatlands is affected mainly by the propagules arrival or by their germination and juvenile plant survival in unfavourable conditions, (ii) whether the areas of extracted peatlands located close to the forest have a higher potential for re-vegetation than the central parts of the peatlands, and (iii) whether the lack of nutrients influences the germination of the arriving propagules and the number of species and plants.

MATERIALS AND METHODS

Study sites

Field studies were carried out on three abandoned extracted peatlands: Viru, Tähtvere, and Visusti bogs, located in northern, southern, and central Estonia, respectively. On all these peatlands, abandoned 26–31 years ago, peat had been harvested using a milling technique.

In the northern part of Viru bog (Tables 1 and 2) peat was extracted from 1966 to 1986 on 37 ha (centre co-ordinates 59°28′31″N, 25°39′26″E). The surface of the extracted peatland is flat, with some seasonally flooded depressions and large, almost bare peat areas. In May 2010 the water table depth close to the forest edge was 25–30 cm and in central parts 45–47 cm below the surface. Close to the forest edge some ditches are almost overgrown by vegetation (coverage 90–100%), whereas on flat central parts and ditch margins (0–3 m from the ditches) the vegetation coverage is 3–5% and 5–10%, respectively (Triisberg et al., 2011).

In Tähtvere bog (Tables 1 and 2) peat was extracted on 61.5 ha (58°23′57″N, 26°38′25″E) in 1968–1982. In May 2010 the water table depth close to the forest edge was 65–67 cm and in the central parts 57–60 cm below the surface. The total vegetation coverage on flat areas and ditches located in the central part is ~3%. Close to the forest edge it is up to 40%, in ditches and on ditch margins up to 45–90% and 25–90%, respectively.

In Visusti bog (Tables 1 and 2) peat was harvested on 36.5 ha (58°38′30″N, 26°30′23″E) in 1983–1987. The extracted area is mainly plantless: in the central part of the peatland the vegetation cover is <5% and the peat surface is very muddy, but close to the forest edge in the northern part *Vaccinium angustifolium* has been sowed. In May 2010 the water table depth close to the forest edge was 40–43 cm and in the central part of the peatland >1.3 m below the surface. Close to the forest edge the vegetation in ditches and ditch margins has a coverage of 80–100% and in the central part 5–40%.

The botanical nomenclature for vascular plants follows Leht (2010) and for mosses Ingerpuu et al. (1998).

Table 1. General characteristics (mean ± SD) of the study sites (according to Orru, 1992; Ramst et al., 2005, 2006; and data from the Loksa, Tartu (Tõravere), and Jõgeva stations of the Estonian Meteorological and Hydrological Institute)

Characteristic	Peatland		
	Viru	Tähtvere	Visusti
Average thickness of residual peat, m	2.5	2.8	2.2
Average peat type and decomposition of residual peat (whole area)	Upper peat layer (0–1 m) is slightly decomposed *Sphagnum* peat, lower part is well decomposed *Eriophorum–Sphagnum* peat	Upper peat layer (0–0.6 m) is slightly decomposed *Sphagnum* peat, middle part is well decomposed with slightly decomposed interlayers of *Eriophorum–Sphagnum* peat, lowest part contains *Phragmites–Sphagnum* peat	Upper peat layer (0–1.9 m) is slightly decomposed *Lignum–Eriophorum–Sphagnum* peat, lower part *Phragmites–Carex* peat
Precipitation, mm:			
Annual (last 10 yrs)	596 ± 117	721 ± 121	688 ± 128
June–Aug (last 10 yrs)	73 ± 44	86 ± 46	85 ± 46
Temperatures, °C:			
Annual (last 10 yrs)	+6.0 ± 0.6	+6.1 ± 0.6	+5.6 ± 0.6
Extreme mean monthly (last 10 yrs)	–8.5 in Feb +21.9 in Jul	–10.3 in Feb +22.6 in Jul	–10.3 in Feb +22.6 in Jul

Table 2. Characteristics of peat solution and residual peat in May 2010 (mean ± SD). Notations: pH1 and pH2 – pH values of the soil solution at depths of 0–10 cm and 10–20 cm, respectively; EC1 and EC2 – electrical conductivity values (μS cm^{-1}) of the soil solution at depths of 0–10 cm and 10–20 cm, respectively; DD1 and DD2 – decomposition rates H (von Post scale) of residual peat at depths of 0–10 cm and 10–20 cm, respectively; M-part and C-part – field samples collected from the marginal (M) and central (C) parts (~150 m from the marginal part) of the peatland, respectively

Characteristic	Viru bog		Tähtvere bog		Visusti bog	
	M-part	C-part	M-part	C-part	M-part	C-part
pH1	3.9 ± 0.1	4.1 ± 0.2	4.2 ± 0.1	4.1 ± 0.1	4.5 ± 0.4	4.4 ± 0.3
pH2	4.0 ± 0.1	4.1 ± 0.1	4.2 ± 0.2	4.3 ± 0.3	4.4 ± 0.3	4.4 ± 0.2
EC1	217 ± 34	241 ± 61	273 ± 76	224 ± 45	303 ± 247	306 ± 349
EC2	196 ± 20	222 ± 34	298 ± 67	221 ± 44	327 ± 30	315 ± 241
DD1	H3	H3	H4	H5	H4	H4
DD2	H3	H3	H4	H4	H4	H4

Vegetation and residual peat analyses in field

The vegetation analyses of abandoned peatlands were carried out in July 2010. Considering the main wind direction (from W, SW) in Estonia (Jõgi & Tarand, 1995), in every peatland five localities were established representing a gradient from the marginal part of the abandoned peatland towards its centre. The first locality was situated at a distance of 2–5 m from the marginal ditch of the peatland's western edge, the distance to each next locality was 15–25 m. In addition five localities characterizing the central part of the abandoned peatland situated randomly at a distance of 10–15 m as a cluster were sampled. In every locality the coverage (%) of every plant species and litter was assessed on three randomly placed 1 m × 1 m sample plots. In that way the total number of sample squares was 90. In the bordering forests a plant species list was compiled.

After the vegetation analyses two peat cores were collected from each sample square using a plastic tube with a diameter of 6 cm: one from the depth of 0–10 cm and the other from the depth of 10–20 cm. The degree of peat decomposition was assessed in the field according to the von Post scale (Hulme & Birnie, 1997). For determining the electrical conductivity of peat solution, the peat cores were treated according to the European Standard 'Determination of electrical conductivity in soil, sewage sludge and biowaste' (2005). The peat solution pH was measured using a PE-06HD pH-212 model pH Electrode, and the electrical conductivity ($\mu S\ cm^{-1}$) was determined with a Microcomputer 900.

Greenhouse experiment

To reveal the potential effect of germination conditions on the re-vegetation of abandoned milled peatlands, a greenhouse experiment was carried out parallel with the field study. In every peatland sampling was performed in two sites: one in its western marginal part (~10 m from peatland edge) bordering with natural forest and the other in its central part, 125–175 m from the peatland margin. In both sites uppermost 10 cm thick peat blocks were taken as samples from 10 randomly selected points using a saw. The samples were mounted into plastic boxes (28 cm × 42.5 cm = 0.12 m^2). As seeds often require cold stratification for dormancy break (Baskin & Baskin, 1998), the peat samples were collected after the end of winter, at the beginning of May 2010.

For viable seed bank estimation, the peat blocks were held in the greenhouse till mid-September 2010 (126 days). To keep the moisture conditions stable, to prevent the access of flies, and to avoid the dispersal of propagules from the nearby boxes, all sample boxes were covered with a fibric shade cloth. Samples were kept in the greenhouse at natural day light and moderately wet by watering after every few days. Daytime temperatures in the greenhouse varied in May in the range of 20–24 °C; in June, July, and August 22–32 °C; and in September 19–24 °C.

Sottocornola et al. (2007) suggested that the optimal dose of phosphate rock to encourage plant re-establishment in peat bog restoration is in the range of 15–25 g m^{-2}. We used the maximal suggested dose and fertilized half of the peat samples from every site with a complex fertilizer (granules) equivalent to 25 g m^{-2} N : P : K 11–11–21 fertilizer (Yara Mila Cropcare; components: NO_3 4.4%, NH_4 6.6%, P_2O_5 11%, K_2O 21%, MgO 2.6%, SO_3 25%, B 0.05%, Cu 0.01%, Fe 0.1%, Mn 0.25%, Mo 0.002%, Zn 0.04%). To inhibit the growth of algae, all samples were once treated with a $KMnO_4$ solution at the beginning of June. The plants were allowed to grow to a size that enabled their species identification. The number of plant individuals was counted for each peat block and thereafter these plants were removed. In addition the coverage of the mosses was assessed. Mosses remained very small and their identification was mostly performed at the end of the experiment using a microscope.

Data processing

The values of the distance of the study areas from the closest forest were log-transformed. The compositional pattern of vegetation was analysed with Canonical Correspondence Analysis (CCA; Ter Braak & Šmilauer, 2002). The significance of environmental variables to be included in the CCA model was validated by the conditional effects and Monte Carlo permutation tests. The characteristic species for different peatlands and their study areas were ascertained according to the Indicator Species Analysis (Dufrêne & Legendre, 1997) implemented in PC-ORD ver. 5.2 (McCune & Mefford, 1999). The distinctness of species assemblages among peatlands and among their study areas was tested with the Multi-Response Permutation Procedures (MRPP; McCune & Mefford, 1999).

RESULTS

Species richness

All in all 27 moss and vascular plant species were identified on the studied abandoned peatlands and 25 in the greenhouse. These numbers differed notably between certain peatlands and greenhouse samples, being the lowest in Viru bog and the highest in Visusti bog (Table 3). The large variation was characteristic also of the mean number of species on 1 m × 1 m sample squares and of the greenhouse peat blocks. The total number of species for fertilized and non-fertilized peat blocks in the greenhouse was similar: 19 and 18 species, respectively. In all peatlands the total number of plant species was higher in their marginal parts than in their central parts. This difference was especially great in Tähtvere bog. The increase of the distance from the forest edge had a significant negative impact ($p_{ANOVA} < 0.001$) on plant species number (Fig. 1). However, neither the mean nor the total number of species showed this regularity for the peat blocks kept in the greenhouse (Table 3). Fertilization had an inconsistent effect on plant species number for samples kept in the greenhouse (Table 3).

Table 3. Species richness in the field and the greenhouse experiment. Notations: Non-fert and Fert – plant samples from non-fertilized and fertilized peat blocks in the greenhouse; p.b. M-part and p.b. C-part – peat blocks from marginal and central parts, respectively

Peatland											
Viru				Tähtvere				Visusti			
Number of plant species from the field study											
12				21				25			
M-part		C-part		M-part		C-part		M-part		C-part	
11		9		20		9		14		13	
Number of plant species in 1 m × 1 m sample squares (mean ± SD; n = 90)											
2.6 ± 1.6		3.5 ± 1.4		4.6 ± 2.6		1.9 ± 1.4		2.7 ± 2.0		2.5 ± 1.6	
Number of plant species from the greenhouse											
10				15				21			
p.b. M-part		p.b. C-part		p.b. M-part		p.b. C-part		p.b. M-part		p.b. C-part	
6		9		11		14		17		15	
Non-fert	Fert	Non-fert	Fert	Non-fert	Fert	Non-fert	Fert	Non-fert	Fert	Non-fert	Fert
6	4	5	9	6	8	10	7	14	11	10	12
Number of plant species per peat block of 0.12 m^2 (mean ± SD, n = 30)											
1.2 ± 0.9		2.3 ± 1.5		2.0 ± 1.5		3.7 ± 2.1		5.3 ± 1.8		4.5 ± 1.3	
Non-fert	Fert	Non-fert	Fert	Non-fert	Fert	Non-fert	Fert	Non-fert	Fert	Non-fert	Fert
1.6 ± 0.9	0.8 ± 0.8	1.2 ± 0.8	3.4 ± 1.1	2.2 ± 1.8	1.8 ± 1.3	4.2 ± 2.6	3.2 ± 1.5	6.4 ± 1.3	4.2 ± 1.6	4.2 ± 1.6	4.8 ± 0.8

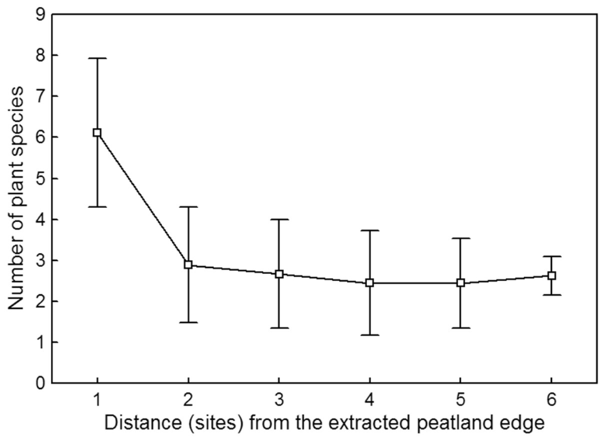

Fig. 1. Summarized relationship between the number of assessed plant species and the distances from the abandoned Viru, Tähtvere, and Visusti extracted peatland edges. Notations: 1 – sites close to the forest (2–5 m from the marginal ditch), 2 – sites 15–25 m from the forest, 3 – sites 15–25 m from the previous locality, 4 – sites 15–25 m from the previous locality, 5 – sites 15–25 m from the previous locality, 6 – sites from the central parts of the extracted peatlands. Data of central sample quadrats are averaged. Vertical bars denote the 0.95 confidence interval.

Species composition

The most common species in all studied peatlands were *Pinus sylvestris* (in 61% of the sample squares), *Eriophorum vaginatum* (56%), and *Polytrichum strictum* (42%) (Appendix 1). The same species together with *Betula* spp. were also the most frequent in greenhouse peat blocks, but these often included several ruderal or forest species absent in the peatlands or even in their neighbouring forests, e.g. *Chenopodium* spp., *Cirsium* spp., *Epilobium* spp., *Galinsoga cilicata*, *Senecio vulgaris*, etc. The bryophytes *Bryum* spp. and *Marchantia polymorpha* were represented in all greenhouse peat blocks but were not recorded in the extracted peatlands (Appendix 1).

Close to the forest edge several plant species were recorded in the peatlands that were missing in the bordering forest zone: *Drosera rotundifolia*, *Carex panicea*, *C. viridula*, *Oxycoccus palustris*, *Salix* spp., *Quercus robur*, *Rhynchospora alba*, *Dicranella cerviculata*, and *Pohlia nutans*. At the same time, many species, including common mire species, were represented in the neighbouring ca 100 m wide forest belt, but were missing in the extracted peatlands, e.g. *Melampyrum pratense*, *Rubus chamaemorus*, *Vaccinium myrtillus*, *Aulacomnium palustre*, *Cladina* spp., *Pleurozium schreberi*, and some *Sphagnum* species (Appendix 1).

The species composition of the greenhouse peat blocks collected from the marginal and central parts of the peatlands was quite different (Table 4 and Appendix 1), e.g. *Pinus sylvestris* and *Empetrum nigrum* occurred only in peat blocks from the marginal parts of the peatlands, while *Populus tremula*, *Pteridium aquilinum*, and *Vaccinium uliginosum* were present only in blocks from the

Table 4. Significance of differences (*p*-values of Multi-Response Permutation Procedures test) in the composition of plant species collected from abandoned Viru, Tähtvere, and Visusti extracted peatlands and from the peat blocks in the greenhouse. Notations: ns – non-significant; Non-fert and Fert – samples from non-fertilized and fertilized peat blocks in the greenhouse experiment, respectively; p.b. M-part and p.b. C-part – peat blocks from marginal and central parts of peatlands, respectively

Difference between plant species composition	*p*
Field vs greenhouse samples	<0.001
Field C-part vs field M-part	ns
p.b. C-part vs p.b. M-part	0.041
Fert vs Non-fert	ns
Fert C-parts vs Fert M-part	0.02
Non-fert C-part vs Non-fert M-part	ns
Non-fert C-parts vs Fert C-part	0.036
Non-fert M-part vs Fert M-part	ns

central parts. The species recorded from non-fertilized peat blocks and not found in the field were *Galinsoga ciliata*, *Mycelis muralis*, *Senecio vulgaris*, and *Chenopodium* spp., whereas *Cirsium oleraceum*, *Cirsium palustre*, *Epilobium hirsutum*, and *Populus tremula* occurred only on fertilized peat blocks in the greenhouse. *Bryum* spp., *Epilobium adenocaulon*, *E. montanum*, *Leptobryum pyriforme*, *Marchantia polymorpha*, and *Taraxacum* spp. were recorded in both fertilized and non-fertilized peat block samples, but not on the extracted peat fields (Appendix 1). *Andromeda polifolia*, *Calluna vulgaris*, *Ledum palustre*, *Oxycoccus palustris*, *Polytrichum strictum*, *Rhynchospora alba*, *Vaccinium vitis-idaea*, *Dicranella cerviculata*, and *Cladonia* spp. found in the field did not appear on any greenhouse peat blocks (Appendix 1).

Abundance of plant individuals

The most frequent species that emerged on greenhouse peat blocks, regardless of their collection sites in peatlands, were *Betula* spp., *Salix* spp., and *Epilobium montanum*. In central parts *Eriophorum vaginatum*, *Marchantia polymorpha*, and *Pohlia nutans* and in marginal parts *Bryum* spp. and *Pinus sylvestris* were abundant.

According to the MRPP test, the species composition on fertilized and non-fertilized peat blocks in the greenhouse did not differ significantly (Table 4); *Betula* spp. were dominating on both types of treatment. On non-fertilized peat blocks also *Salix* spp. and among fertilized samples *Eriophorum vaginatum* were abundant.

Results from the greenhouse experiment did not support the hypothesis that the low abundance (number) of plant individuals on spontaneously vegetated extracted peatlands could be limited by the lack of nutrients: in the greenhouse samples the number of vascular plant individuals was higher on non-fertilized peat blocks: 113 plant individuals on non-fertilized peat blocks and 69 on fertilized blocks. The total coverage of mosses and their coverage per peat block were very low (0.1–0.3%) and almost similar for non-fertilized and fertilized peat blocks. Comparison of the number of vascular plant individuals on peat blocks collected from the marginal and central parts of the peatlands shows that it was higher for the blocks from the central part, i.e. 79 plant individuals vs 103 plant individuals. The coverage of the mosses, on the contrary, was slightly higher for the blocks collected from the marginal parts of the peatlands.

Analysis of the indicator species (Appendix 2) using various groupings of data gave ambiguous results. For the Tähtvere extracted peatland *Eriophorum vaginatum*, *Pinus sylvestris*, *Dicranella cerviculata*, and *Pohlia nutans* were more significant indicator species in comparison with other peatlands. However, this result was expected already on the ground of the highest species number found in the field. For the Viru extracted peatland only *Oxycoccus palustris* and for the Visusti peatland *Betula pubescens* and *Eriophorum vaginatum* were identified as indicator species. At the same time, comparison of plant species composition in the marginal and central parts of peatlands showed a rather stochastic pattern of indicator species for all three studied peatlands as well as for the corresponding greenhouse peat blocks. The indicator species for the marginal or central parts on different peatlands did not overlap at all or the significant indicator species were just missing. *Marchantia polymorpha* turned out to be a significant indicator species for the greenhouse (mainly fertilized) peat blocks, whereas the indicator species for the non-fertilized peat blocks were *Betula* spp. and *Salix* spp.

Environmental conditions

Peat samples from Viru bog, especially from its marginal parts, were somewhat less decomposed and the peat solution was more acidic than the residual peat from other abandoned peatlands. The peat solution had relatively higher pH values for the Visusti residual peat. The values of electrical conductivity were higher (~200–300 µS m^{-1}) in all extracted peatland samples in comparison with those from natural bogs (average ~60 µS m^{-1}; Karofeld & Pajula, 2003). The highest electrical conductivity values were measured for the Visusti residual peat samples (Table 1).

The CCA biplot of binarized species data and values of environmental variables reveal a strong positive inter-set correlation on the first ordination axis with the litter coverage ($r = 0.69$), the total coverage of vegetation ($r = 0.57$), and the peat solution pH from the depth of 10–20 cm below surface ($r = 0.26$). Correlations on the second axis correspond to the variation of vegetation induced mainly by the studied properties of the upper 0–10 cm peat layer, i.e. with the pH ($r = 0.63$), electrical conductivity ($r = 0.25$), and the degree of decomposition ($r = -0.35$). Moreover, significant factors that determined the vegetation development on abandoned extracted peatlands were also the distance from the marginal forest stand ($r = -0.17$ for the second axis) and the degree of decomposition of the peat at a depth of 10–20 cm ($r = -0.29$ for the first axis) (Fig. 2).

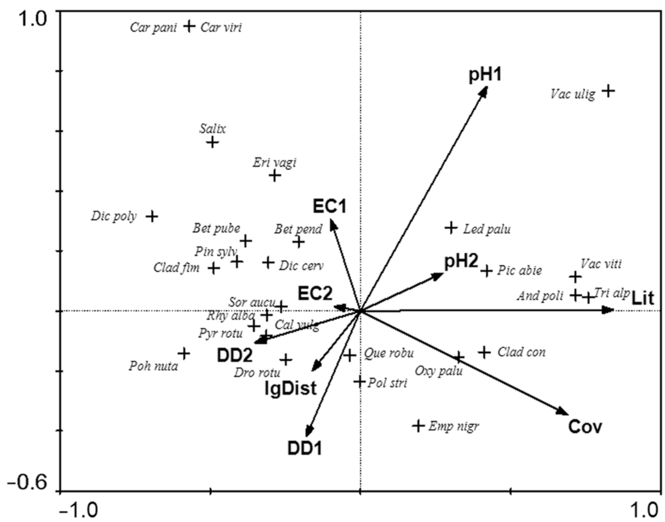

Fig. 2. CCA biplot of the environmental factors and field collected vegetation data for abandoned Viru, Tähtvere, and Visusti extracted peatlands. Correspondence of the data was 45.8% for the first and 41.0% for the second axis. Notations: Cov – total species coverage on sample squares (%); Lit – total litter coverage on sample squares (%); pH1 and pH2 – pH values of the soil solution at depths of 0–10 cm and 10–20 cm, respectively; EC1 and EC2 – electrical conductivity values ($\mu S\ cm^{-1}$) of the soil solution at depths of 0–10 cm and 10–20 cm, respectively; DD1 and DD2 – decomposition rates H (von Post scale) of residual peat at depths of 0–10 cm and 10–20 cm, respectively; lgDist – distance from the forest (logarithmed). Full names of plant species: *Bet pend – Betula pendula*, *Bet pube – Betula pubescens*, *Pic abie – Picea abies*, *Pin sylv – Pinus sylvestris*, *Que robu – Quercus robur*, *Sor aucu – Sorbus aucuparia*, *Salix – Salix* spp., *And poli – Andromeda polifolia*, *Cal vulg – Calluna vulgaris*, *Emp nigr – Empetrum nigrum*, *Led palu – Ledum palustre*, *Vac ulig – Vaccinium uliginosum*, *Vac viti – Vaccinium vitis-ideae*, *Rhy alba – Rhynchospora alba*, *Car pani – Carex panacea*, *Car viri – Carex viridula*, *Dro rotu – Drosera rotundifolia*, *Eri vagi – Eriophorum vaginatum*, *Oxy palu – Oxycoccus palustris*, *Pyr rotu – Pyrola rotundifolia*, *Tri alp – Trichophorum alpinum*, *Clad con – Cladonia coniocreae*, *Clad fimb – Cladonia fimbriata*, *Dic cerv – Dicranella cerviculata*, *Dic poly – Dicranum polysetum*, *Poh nuta – Pohlia nutans*, and *Pol stri – Polytrichum strictum*.

DISCUSSION

The difference between the species composition from abandoned extracted peatlands and peat blocks kept in the greenhouse was noteworthy. The species observed in the field were mostly typical bog species, while in the greenhouse mainly forest or ruderal species appeared. The occurrence of such species in the peat samples kept in the greenhouse could be explained by spatial competition or by the shortage of nutrients. It is also possible that typical bog species need more time to germinate and stabilize their growth but in our study their germination was limited by the short duration of the experiment. This difference of species in extracted peatlands and greenhouse samples confirms that the propagules of forest or ruderal plant species are able to arrive on the extracted peatlands, but the unfavourable environmental conditions there do not enable their germination and growth (Belyea, 2004). Poor germination ability is also illustrated by the low total and mean number of plant species both in abandoned extracted peatlands and in the greenhouse peat blocks. The most abundant species in our study had some trait similarities: they disperse mainly by wind, to a lesser extent vegetatively, and have similar demands to some environmental conditions, such as openness to light, (moderately) acidic soil, but are rather indifferent to the moisture content or prefer moderate to wet habitats (Ellenberg et al., 1992; Ingerpuu et al., 1998; Leht, 2010). It remains open whether the highest total number of plant species in the Visusti extracted peatland could, in addition to other factors, have been caused by a relatively short exploitation period (4 years) during which only a thin layer of peat was extracted and so the residual peat may contain some viable propagules.

It was interesting that the species composition in the central and marginal parts of the abandoned extracted peatlands, but also the composition of species germinated in the greenhouse peat blocks, were often rather different or coincided only marginally. It is most likely that propagules are distributed on peatland surface unevenly and, therefore, the species number recorded in the sites of extracted peatlands on a larger total area is much higher than that represented in greenhouse samples having a limited surface. Nevertheless, many species recorded in the greenhouse samples were registered neither on the extracted peatlands nor the bordering forest areas. Consequently, propagules of these species arrived into the extracted peatlands randomly but were able to germinate only in suitable moisture and temperature conditions, mimicked in greenhouse conditions.

Growth of the plant species on the extracted peatlands is inhibited by the level and dynamics of the water table (Price et al., 2003), peat chemistry (Salonen, 1994), wind erosion (Campbell et al., 2002), and frost heaving (Groeneveld & Rochefort, 2002) as well as by changed peat pore structure with soil becoming more dense and humified (Price, 1997). Our study confirmed the strong influence of peat properties on the re-vegetation of the extracted peatlands where peat properties (pH, peat deposit thickness, etc.) influence the vegetation composition (Girard et al., 2002; Triisberg et al., 2013). In addition, in the first stages of re-vegetation the species pool in the neighbouring communities is surely very important, but in the course of succession, when some vegetation has already formed, the autogenic modification of growth conditions becomes more important. This result is in good accordance with the conclusions drawn in Groeneveld & Rochefort (2002, 2005) and Tuittila et al. (2000), who ascertained that the pioneer species *Polytrichum strictum*, *Eriophorum vaginatum*, and *Eriophorum angustifolium* reduce frost heaving, prevent residual peat erosion by wind, and facilitate the growth of other species (such as *Sphagnum* spp.) in abandoned extracted peatlands. The impact of litter cover is also substantial for keeping favourable moisture conditions necessary for propagules germination and plant growth. Moreover, the decomposed organic matter from litter enriches the upper layer of residual peat with nitrogen (Anggria et al., 2012) enhancing also the plant growth in nutrient-poor conditions.

Local species richness is positively related to species evenness in the seed pool (Myels & Harms, 2009). Still, Huopalainen et al. (1998) showed that in extracted peatlands only half of the seeds from the depth of 10 cm of the residual peat are able to germinate. According to our study, the most frequent species from the greenhouse experiment were the vascular plants *Betula* spp., *Salix* spp., *Eriophorum vaginatum*, *Epilobium montanum*, *Taraxacum* spp. and the mosses *Marchantia polymorpha*, *Pohlia nutans*, and *Bryum* spp. However, these results overlap with the studies carried out in Finland only by two species. According to a somewhat similar experiment carried out by Huopalainen et al. (1998), the seeds of *Betula* spp. and *Calluna vulgaris*, as well as spores of the mosses *Pohlia nutans*, *Dicranella cerviculata*, and *Polytrichum longisetum* are viable. In Canada *Betula* spp., *Vaccinium oxycoccus*, *Eriophorum vaginatum*, and *Rubus chamaemorus* show a quick growth on residual peat samples (Campbell & Rochefort, 2003). Those results indicate that even in neighbouring countries the re-vegetation of extracted peatlands can proceed to some extent differently due to the local environmental conditions and that even the presence of viable seeds will not always result in plant growth.

Campell et al. (2003) pointed out that bog species propagation to extracted peatlands depends on the species dispersal abilities. Our study revealed that the number of plant species was higher in the marginal parts of the abandoned extracted peatlands, i.e. in areas close to the vegetated areas (forest etc.), and it decreased towards the central part of the peatlands mainly within the first ca 20 m.

In the greenhouse samples, on the contrary, the number of emerged species was higher in samples collected from central parts of the extracted peatlands. This confirms that the distance from the neighbouring species pool is not decisive for propagules arrival on the extracted peatland, i.e. the propagules are present everywhere; nevertheless, we can speculate that the success of their germination and growth depends on different environmental conditions in the marginal areas and the central parts of peatlands.

Although we found a lowering gradient of species number from the edge toward the central part of peatland, according to the MRPP test the species composition in marginal and central parts was quite similar but different for the respective greenhouse peat blocks collected from the same sites. Some apophytic *Chenopodium* spp., *Cirsium* spp., and *Epilobium* spp. emerged in the peat blocks in the greenhouse but were not recorded in the nearby forest field samples. This indicates that although species are able to spread from long distances, their growth will occur only in localities where moisture conditions and nutrient availability enable germination of propagules. This also explains the difference in the species composition that did not appear in the field conditions but only in the greenhouse with more suitable growing conditions.

Surprisingly, the number of plant individuals in the greenhouse samples was higher for the non-fertilized peat blocks and fertilization did not affect considerably the total number of species either. Although fertilization did not lead to the germination of more plant species it favoured certain species, which resulted also in the larger number of plant individuals. There were not so many indicative species for the greenhouse samples with fertilization treatment. Only one indicative species was found that could explain the vegetation difference in different areas and treatments. It was *Marchantia polymorpha* – representative for the fertilized peat blocks growing naturally on wet environments with moderate acidity and demanding high light conditions (Ellenberg et al., 1992; Ingerpuu et al., 1998). The low number of indicator species for the peat block samples could derive from the random propagules content in the field conditions and from the chance for species with different autecological features to germinate due to the favourable conditions in the greenhouse.

Although comparison of the results of fertilization experiments carried out with fertilizers containing active substances in different proportions is to somewhat irrelevant, certain rough comparisons are still possible. For instance, Ferland & Rochefort (1997) mentioned that phosphorus, included also in the complex fertilizer used in our experiment, favours the recolonization of extracted peatlands by mosses and vascular plants. Development of plant cover can be accelerated also by some other fertilizers. The main species that doubled their coverage due to the added fertilizer were *Polytrichum strictum*, *Pohlia nutans*, and *Aulacomnium palustre*. Sottocornola et al. (2007) noted that the fertilization with granular phosphate rock increases also the coverage of *Eriophorum vaginatum* and *Betula* spp. In Finland the vascular plant coverage on extracted peatland was up to 37% three years after a P–K fertilizer was applied, whereas on unfertilized areas the coverage was less than 7%. Moreover, the P–K fertilizer increased the species richness in five years after fertilization (Huotari et al., 2007). According to our study, it was surprising that the complex fertilizer did not have any notable effect on the number of species; the number of species was in several cases even higher in non-fertilized samples. Although Salonen & Laaksonen (1994) showed that light watering does not have a major effect on plant colonization on extracted peatlands, on the basis of our results we can aver that re-vegetation of extracted peatlands is inhibited mainly by unsuitable moisture conditions and not so much by the nutrient availability: in the optimal moisture conditions kept in the greenhouse several species that were not present in natural areas germinated successfully.

CONCLUSIONS

Based on the results of the field and greenhouse study we found that the plant species pool existed everywhere on abandoned extracted peatlands, but the germination of species was a random process inhibited mainly by unsuitable moisture conditions. The proximity of forest influenced the species richness in extracted peatlands, but the improvement of the moisture conditions (like in the greenhouse conditions) enabled germination of many other species (e.g. some ruderal species) that had randomly arrived by wind. Those species did not form a viable seedbank for the extracted peatlands but in certain environmental conditions they were able to germinate. The N : P : K fertilization increased the total and mean number of plant species only for some peat blocks, therefore we found that the main factor inhibiting the germination was the lack of suitable moisture conditions rather than the lack of nutrients.

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APPENDIX 1

The presence of plant species in the abandoned Viru, Tähtvere, and Visusti extracted peatlands and greenhouse samples. Notations: M-part and C-part – field samples collected from the marginal (M) and central (C) parts of the extracted peatland, respectively; GH – M-part/C-part peat blocks in the greenhouse collected from the peatland marginal (M) or central (C) part, respectively; Forest – forest site; non-fert – non-fertilized peat block; fert – fertilized peat block. The most abundant species are marked with larger crosses in bold

Species	Abandoned Viru extracted peatland							Abandoned Tähtvere extracted peatland							Abandoned Visusti extracted peatland						
	M-part	Forest	GH, M-part, non-fert	GH, M-part, fert	C-part	GH, C-part, non-fert	GH, C-part, fert	M-part	Forest	GH, M-part, non-fert	GH, M-part, fert	C-part	GH, C-part, non-fert	GH, C-part, fert	M-part	Forest	GH, M-part, non-fert	GH, M-part, fert	C-part	GH, C-part, non-fert	GH, C-part, fert
Betula spp.		**+**	**+**	+		+	+			+	**+**		**+**	**+**			**+**	+		**+**	+
Betula pendula					+			+	**+**							**+**					
Betula pubescens								+	**+**			+			**+**	**+**			**+**		
Picea abies								+	+							+			+		
Pinus sylvestris	**+**	**+**	+	+	**+**			**+**	**+**		+	**+**			**+**	**+**	+		**+**		
Populus tremula							+														
Quercus robur								+													
Sorbus aucuparia									+			+				+					
Salix sp.							+	+		+		+	**+**		+		**+**		+	**+**	+
Andromeda polifolia								+								+					
Arctostaphylos uva-ursi																+					
Calluna vulgaris	**+**				**+**			+	**+**						+	**+**			+		
Empetrum nigrum	+							+	**+**		+	**+**				**+**			+		
Ledum palustre		**+**						+	+						+	+					
Vaccinium myrtillus		+														**+**					
Vaccinium uliginosum	+	+			+			+	**+**			+			+	+			+	+	
Vaccinium vitis-ideae		**+**						+								**+**			+		
Rhynchospora alba								+													
Carex panacea															+						
Carex viridula															+						
Chenopodium spp.													+				+			+	
Cirsium oleraceum																		+			
Cirsium palustre																		+			
Deschampsia caespitosa		+																			
Drosera rotundifolia								+							+				+		
Epilobium adenocaulon													+					+		+	
Epilobium angustifolium		+															+	+			+
Epilobium hirsutum														+							

APPENDIX 1. *Continued*

Species	Abandoned Viru extracted peatland							Abandoned Tähtvere extracted peatland							Abandoned Visusti extracted peatland						
	M-part	Forest	GH, M-part, non-fert	GH, M-part, fert	C-part	GH, C-part, non-fert	GH, C-part, fert	M-part	Forest	GH, M-part, non-fert	GH, M-part, fert	C-part	GH, C-part, non-fert	GH, C-part, fert	M-part	Forest	GH, M-part, non-fert	GH, M-part, fert	C-part	GH, C-part, non-fert	GH, C-part, fert
Epilobium montanum										+	+		+	+			**+**	+			+
Eriophorum vaginatum	**+**	+	+	+	**+**	+	**+**	**+**			+	+			**+**	+	+	+	**+**		**+**
Galinsoga ciliata													+				+				
Lycopodium annotinum									+							+					
Melampyrum pratense		+																			
Mycelis muralis																	+				
Orthilia secunda																+					
Oxycoccus palustris	+							+				+									
Poa trivialis							+														
Pteridium aquilinum		+																		+	+
Pyrola rotundifolia																			+		
Rubus chamaemorus																+					
Senecio vulgaris																	+				
Taraxacum spp.							+				+			+			+	+		+	+
Trichophorum alpinum								+	+			+				+					
Tussilago farfara																					
Aulacomnium palustre																+					
Bryum spp.			+			+	**+**			**+**			**+**				**+**	**+**		**+**	**+**
Cladonia spp.									**+**							**+**					
Cladonia coniocraea	+				+			**+**							+						
Cladonia fimbriata	+																				
Cladina spp.		**+**														+					
Dicranella cerviculata	+				**+**			+							+						
Dicranum polysetum															+	+			+		
Hylocomium splendens		+																			
Hypogymnia physodes		+														+					
Leptobryum pyriforme													+							**+**	+
Marchantia polymorpha			+			+	**+**			+	+		+	+			**+**	**+**		+	**+**
Pleurozium schreberi																**+**					
Pohlia nutans	+		+	**+**	+	+	+			+			**+**				**+**	**+**		+	+
Polytrichum strictum	+				**+**			**+**	+			**+**			**+**	**+**			**+**		
Rhytidiadelphus triquetrus		+																			
Sphagnum capillifolium																+					
Sphagnum fuscum																+					
Sphagnum magellanicum																+					

APPENDIX 2

Correlated CCA plant sample variables and their significant *p*-values. Notations in combination with each other: M-part - All and C-part - All – field samples collected from the marginal (M) and the central (C) part of all peatlands, respectively; Viru, Tähtvere, Visusti - All – both the marginal and central part species together for the same peatland; M-part and C-part – field samples collected from the marginal (M) and the central (C) part of the peatland, respectively; Non-fert - All and Fert - All – plant samples from all non-fertilized and fertilized peat blocks in the greenhouse, respectively; Viru, etc. p.b. – plant samples from the peatland peat blocks in the greenhouse; * – species are equally frequent in both variable groups

Plant sample variables						
The first correlated variable	The second correlated plant sample variable					
Field samples						
Indicator species	C-part - All			M-part - All		
Eriophorum vaginatum				<0.001		
Cladonia coniocraea				0.004		
	Viru - All		Tähtvere - All		Visusti - All	
Betula pubescens					0.001	
Eriophorum vaginatum			0.002		0.002	
Oxycoccus palustris	0.001					
Pinus sylvestris			<0.001			
Dicranella cerviculata			0.004			
Pohlia nutans			0.002			
Cladonia coniocraea	0.002					
	Viru		Tähtvere		Visusti	
	M-part	C-part	M-part	C-part	M-part	C-part
Betula pendula		0.33				
Empetrum nigrum				0.041		
Eriophorum vaginatum					<0.001	
Oxycoccus palustris			0.042			
Pinus sylvestris	<0.001					
Vaccinium vitis-ideae			0.024			
Dicranella cerviculata		0.006				
Pohlia nutans		0.002				
Polytrichum strictum			0.002			
Cladonia coniocraea			0.001			
Greenhouse samples						
	Non-fert - All			Fert - All		
Betula spp.	<0.010					
Salix spp.	<0.001					
	C-part - All			M-part - All		
Marchantia polymorpha	0.016					
Pohlia nutans	0.036					
	Non-fert - C-part - All			Fert - C-part - All		
Marchantia polymorpha				0.014		
	Non-fert - M-part - All			Fert - M-part - All		
Salix spp.	0.018					
	Viru p.b.		Tähtvere p.b.		Visusti p.b.	

APPENDIX 2. *Continued*

Plant sample variables						
The first correlated variable	The second correlated plant sample variable					
Salix spp.					0.004	
Bryum spp.					<0.001	
Pohlia nutans			0.024			
	M-part	C-part	M-part	C-part	M-part	C-part
Epilobium montanum					0.041	
Pohlia nutans				0.009		
Pteridium aquilinum						0.022
Salix spp.						0.040
Bryum spp.					<0.001	

	Viru p.b.			
	Non-fert, M-part	Fert, M-part	Non-fert, C-part	Fert, C-part
Marchantia polymorpha				0.016

	Tähtvere p.b.			
	Non-fert, M-part	Fert, M-part	Non-fert, C-part	Fert, C-part
Betula spp.			0.013	
Marchantia polymorpha			0.015*	0.015*

	Visusti p.b.			
	Non-fert, M-part	Fert, M-part	Non-fert, C-part	Fert, C-part
Salix spp.			0.048	

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