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MUD-BOTTOMS IN MÄNNIKJÄRVE BOG, CENTRAL ESTONIA

Edgar KAROFELD^a and Mare TOOM^b

^a Institute of Ecology, Tallinn University of Educational Sciences, Kevade 2, 10137 Tallinn, Estonia; edgar@eco.edu.ee

^b Institute of Botany and Plant Ecology, University of Tartu, Lai 40, 51005 Tartu, Estonia; mareto@ut.ee

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Abstract. The distribution, plant cover, and development of mud-bottoms were studied on three transects in Männikjärve raised bog. Mud-bottoms were common in level bog areas (slopes 0.001-0.003) and almost absent on slopes steeper than 0.004. They were most frequent in grass-hollow bog type and rare in wooded pool-ridge complexes. The mean number of vascular plant species in mud-bottoms was only three and the mean total coverage 10.6%. The surface layer of mud-bottoms was a 2–3 mm thick layer of algae, dominated by *Zygogonium ericetorum*. Of the mud-bottoms studied (n = 41) 19 had formed in hollows, 10 on hummocks, and 12 on lawn communities. The area of 27 mud-bottoms was increasing, whereas 7 were decreasing and 7 had a stable area. In an experiment, after prolonged floods of more than 20 days *Sphagnum cuspidatum* mosses became infested with hyphae and algae. A typology of mud-bottoms is also proposed.

Key words: algae, bog surface pattern, degradation of *Sphagnum*, Estonia, microtopography of mire, raised bog.

INTRODUCTION

Bog hollows with aquatic *Sphagnum* mosses and *Rhynchospora alba* and *Scheuchzeria palustris* at the edges are typical features of the raised bog micro-topography in the Boreal zone. In addition, the so-called mud-bottom hollows with a blackish bare peat surface and sparse vegetation are common. The bare peat bottom is composed of a compact leathery layer of algae and remnants of *Sphagnum* shoots. Only a few individuals of weak *R. alba, Vaccinium oxycoccus*,

and *Drosera anglica* may be found. During wet periods the mud surface is flooded, whereas in summer it dries out. Different terms such as *mud-bottom* hollow, *mud-bottom*, bare or naked peat area, flark, regressive complex, etc. have been used. The term *mud-bottom* hollow is employed most widely (after Sjörs, 1948); however, in its strict sense, this term is misleading. Hence, in this paper the term *mud-bottom* will be used (Sjörs, 1983; Damman & French, 1987).

Mud-bottoms are common in bogs of Estonia (Thomson, 1924; Masing, 1958, 1982), Scandinavia (Sjörs, 1948, 1990; Du Rietz, 1949; Malmer, 1962, 1965), and Finland (Eurola, 1962). Paasio (1934) pointed out their higher frequency and larger area in northern regions. They have been described in NW Russia (Bogdanowskaya-Guiheneuf, 1928, 1969), in West Europe (Boatman & Armstrong, 1968; Goode, 1970; Hulme, 1976; Lindsay et al., 1985), and in North America (Sjörs, 1963; Damman & French, 1987). It may be concluded that mud-bottoms occur in most of the area of the raised bogs and that their general appearance is quite similar in different regions.

The degradation of Sphagnum mosses followed by the formation of mudbottoms may be caused by different factors. The hypothesis about the degradation of Sphagnum mosses in flooded depressions by abundant algae has found the strongest support (Bogdanowskaya-Guiheneuf, 1928; Zinserling, 1938; Du Rietz, 1949; Zauer, 1950; Masing, 1958; Malmer, 1962; Sjörs, 1963; Boatman & Armstrong, 1968; Hulme, 1976; Seppäla & Koutaniemi, 1985), but its exact mechanisms are not known. Auer (1920) pointed out the possible importance of poor oxygen content in standing water and later spring melt in depressions. Katz (1923) added the possible impact of gases from peat decomposition. The effect of bog gases was later discussed by Thomson (1924), Bogdanowskaya-Guiheneuf (1969), and Ivanov & Kuzmin (1982). Droughts and drying out may favour weakening of the Sphagnum mosses especially on the top of ridges and lead to their replacement by lichens or liverworts (Bogdanowskaya-Guiheneuf, 1928; Paasio, 1934; Masing, 1958). Masing (1958) and Bogdanowskaya-Guiheneuf (1969) described the lethal effect of calcareous bird droppings on sphagna.

Mud-bottoms can play an important role in the differentiation of the bog surface pattern, further development of a bog, and emission of bog gases. Because of retarded peat accumulation (Bogdanowskaya-Guiheneuf, 1928; Hulme, 1976) and intensive decomposition processes in mud-bottoms they become lower than the surroundings with continuous peat accumulation (Sjörs, 1961, 1963; Hulme, 1986). Once formed, depressions will be flooded during wet periods and may become hollows. It is well documented that the halted carbon fixation, caused by the degradation of *Sphagnum* mosses from mud-bottoms, is combined with an increased methane emission compared with other bog areas (Crill et al., 1992; Frenzel & Karofeld, 1998). The aims of the present study were to (1) find out the regularities in the location of mud-bottoms in Männikjärve bog, (2) describe the vegetation on the mud-bottoms and the peat beneath them, (3) develop a typology of mud-bottoms, and (4) clarify their formation and development.

MATERIAL AND METHODS

The study area, Männikjärve bog (320 ha, maximum peat depth 7.5 m), situated in Central Estonia (58°52' N, 26°14' E), is a bog of East-Estonian type (Masing, 1984). The bean-shaped convex raised bog has a well developed hollow-ridge-pool complex in the centre and wooded bog margins (Veber, 1974; Masing, 1982). It is one of the best studied bogs in Estonia (Kimmel, 1998) with abundant background information available.

Three transects were set up from the genetical bog centre crosswise to the longitudinal axis of microtopographic forms toward the bog margin in summer 1998 (Fig. 1). To calculate the slope of bog surface (height difference against the distance) the levelling stations situated at every 50 m at the water level of hollows and pools were used. On *c*. 10 m wide transects the location of all mud-bottoms was marked; the bog type and the shape, contours, and surface type (flat and naked or with decaying *Sphagnum* shoots and some plants, etc.) of mud-bottoms were described. The coverage, the abundance (1 = rare, 5 = abundant) and vitality (1 = weak, 3 = luxuriant) of plant species on the mud-bottoms' surface were estimated. The nomenclature of vascular plants and mosses follows Eurola et al. (1992). Altogether 41 mud-bottoms were studied on the transects. In addition measurements, descriptions, and visual observations were made of mud-bottoms from other bog areas ($n \sim 30$).

Special attention was paid to the transition zone between the mud-bottom with bare peat and the vegetated surroundings (clear and sharp or smooth replacement). The state of *Sphagnum* mosses was described after Masing & Trass (1955) on a 5-grade scale:

1. Sphagnum has settled only lately covering small plots; no Sphagnum patches are present.

2. A *Sphagnum* carpet occurs as young viable moss pads; their round contours are indicators of possible expansion.

3. The *Sphagnum* carpet is viable, without signs of expansion or degeneration, liverworts are absent or rare.

4. The *Sphagnum* carpet bears signs of degeneration. *Sphagnum* mosses are obviously weak, liverworts are abundant, small plots of brown dying sphagna can be seen.

5. The *Sphagnum* carpet is dead, covered with an algae layer or replaced by liverworts; *Sphagnum* mosses become slimy in hollows during the high water table.



Fig. 1. Männikjärve bog with the location of the established transects. Map redrawn from Remm & Sons (1996).

For a more detailed survey of the peat beneath the mud-bottoms, the samples were taken from the uppermost 20–25 cm thick peat layer. The type, colour, and degree of decomposition (in % scale) of peat were described (Tyuremnov, 1976). The thickness of the algal film was measured and its colour and nature were described, and samples were taken to determine the algal species composition (nomenclature follows Teiling, 1954; Kosinskaya, 1960; Tikkanen, 1986). In July 1997, the temperature on the surface and at various depths in the hollows and mud-bottoms was measured (n = 6 at each depth) with a microprocessor thermometer type J-K. The pH value of bog water near the surface was measured with HANNA Instruments HI 9025 and the dissolved oxygen content with the thermo-oxymeter Marvet. To study the nocturnal oxygen regime, an O₂ detector

was inserted into a small flooded depression (diameter 60 cm) with decaying *Sphagnum cuspidatum* and algae. To halt photosynthesis, the depression was covered with black plastic. The O_2 content and saturation were measured next morning and measurements were repeated after removing the cover at daylight.

To study the possible role of floods in the degradation of *Sphagnum* mosses the *S. cuspidatum* samples from a wet hollow (water table -1 cm) were placed into perforated plastic tubes (height 11 cm, diameter 3.5 cm) for four series, six replicates in each in May 1998. Before installing, the length of the green part of *Sphagnum* shoots in all the replicates was measured. Samples of series 1 were fixed at a floating platform in the pool with *Sphagnum* capitulae 1 cm above the water level. Samples of series 2, 3, and 4 were fixed in water at a depth of 10 cm for 10, 20, and 30 days, respectively. Thereafter the samples were lifted near the water similarly to series 1 for 10 days. Then the samples were taken to the laboratory for measuring their length increment and for algological research.

To determine the possible contribution of mud-bottoms to the hollow formation, peat samples from hollows were taken from the transition zone between brown hummock or lawn peat and yellow hollow peat using a Russian type peat sampler. In the laboratory the samples were studied for algae to compare them with the species in mud-bottoms.

RESULTS

Location of mud-bottoms in the bog

The transects, bog types, and location of mud-bottoms are shown in Fig. 2. Mud-bottoms on transects A and B were grouped in certain bog areas, whereas on transect C they were distributed more evenly in the level central part and absent on the marginal slope. The biggest number of mud-bottoms (14) was found in wooded hollow-ridge and wooded dwarf-shrub bog types. In the wooded dwarf-shrub hollow-ridge and wooded pool-ridge complexes only one mud-bottom was found in each bog type. However, if the number of the mud-bottoms per 1 m of the transect is considered the results will be somewhat different: the highest occurrence was found in grass-hollow and wooded-grass bog type (0.031 m^{-1} and 0.026 m^{-1} , respectively) and the lowest in grass bog type and wooded pool-ridge complexes (0.0075 m^{-1} , 0.0027 m^{-1}). Mud-bottoms occurred on bog slopes of various steepness (0.0001-0.007), being most frequent on 0.001-0.003 and rare on slopes steeper than 0.004 (Fig. 3). Even within different or absent.

The diameter of mud-bottoms varied from c. 10–20 cm between the *R*. *alba* clumps to up to 8 m for well-developed mud-bottoms. From 41 mud-bottoms on the transects only 9 had clear contours; the rest had undulating borders and included small plant clumps, which made their shape and size quite irregular.



Fig. 2. The distribution of mud-bottoms on the transects. \leftarrow , levelling stations; location and number of the mud-bottoms with increasing (\bullet), decreasing (\circ), or stable area (*).





Ecological conditions in mud-bottoms

The water level in mud-bottoms and hollows depends on the season and precipitation. In spring they were both flooded for several weeks (water depth 10–20 cm), but in summer the water table was just under the surface, at a depth of c. 1 cm. The pH values (3.4-3.9) of bog water were practically the same in the mud-bottoms and hollows with a *Sphagnum* carpet. The bog water in the hollows was oxygen-rich $(6.8 \pm 1.2 \text{ mg L}^{-1}$, saturation $76 \pm 13\%$) whereas the water in mud-bottoms had a low oxygen content $(0.9 \pm 0.3 \text{ mg L}^{-1}, 9 \pm 3.1\%)$. During spring the water in flooded areas with *Sphagnum* mosses and algae was often oversaturated (110–120%) with oxygen, and gas bubbles were observed on plants. Measurements of the nocturnal oxygen regime in a flooded depression covered with black plastic showed intensive oxygen consumption during the night when the O₂ content dropped to 1.6 mg L⁻¹ (saturation 16%). Within 40 min after the removal of the cover in daylight the oxygen content rose to 3.6 mg L⁻¹ (saturation 38%) and in 2.5 h up to 6.8 mg L⁻¹ (saturation 76%).

The temperature at the bog surface varied due to changes in radiation, shadows, wind speed, etc. more widely than in the underlying peat. In general, the mean surface temperature of mud-bottoms was higher and varied more $(25.2 \pm 5.1 \,^{\circ}\text{C})$ than in *S. cuspidatum* hollows $(22.3 \pm 4.9 \,^{\circ}\text{C})$. The mean temperature decreased with depth and so did the difference between the temperature in mud-bottoms and hollows. At a depth of 5 cm the mean temperature was $18.7 \pm 2.3 \,^{\circ}\text{C}$ and $18.1 \pm 1.7 \,^{\circ}\text{C}$, respectively.

Vegetation in mud-bottoms

The surface of mud-bottoms had sparse vegetation. Often remnants of *Rhynchospora alba* and *Sphagnum* shoots could be found on the bare peat. Usually *R. alba, Andromeda polifolia, Drosera anglica,* and *Vaccinium oxycoccus* were represented only by a few weak individuals (Table 1). Only eight vascular plant species were found in mud-bottoms and the mean number of species within one plot was much smaller (from 3 ± 1.8 in mud-bottoms of type III to 3.8 ± 1.9 in type IV). The coverage of plant species varied largely, from almost 0 to 45% (mean 10.6%), being $7.6 \pm 8.4\%$ in mud-bottoms of type II, $13.3 \pm 21.5\%$ for type III, and $13.7 \pm 14.7\%$ for type IV. Coverage was higher in small mud areas between *R. alba* clumps. The abundance and vitality of plant species in mudbottoms were fairly low. In a 3-grade scale, the highest mean vitality (2) was recorded for *Eriophorum angustifolium* and *Scheuchzeria palustris*. From common species *D. anglica* (1.5) and *D. rotundifolia* (1.3) had the highest mean vitality. Specimens of *R. alba* in mud-bottoms were mostly weak (vitality 1.1), yellowish green, lower (*c.* 10–15 cm high) and less fertile than the individuals in the hollow edges. The mean vitality of *V. oxycoccus*, represented on the mud surface by nonfertile runners rooted outside the mud-bottom, was even lower (1). The mean abundance, estimated on a 5-grade scale, was also very low (1–1.8) for all plant species. *R. alba* had the highest abundance (1.8); however, estimation of plant abundance in clumps is complicated and it is likely to be underestimated because vegetative reproduction.

Transition zone between mud-bottoms and plant-covered area

Observations of more than 60 mud-bottoms with different contours revealed the most distinct contour between the mud surface and an expanding *S. magellanicum* carpet. The height of the *Sphagnum* carpet above the mud surface was *c*. 5 cm, the outermost shoots were inclined toward the mud surface, creeping 5–10 cm on it. The expanding *Sphagnum* carpet was not fixed on the mud surface and could be easily lifted up with hands. Mud-bottoms had steep banks with *R. alba* when they occupied the whole area of a well-developed hollow (common in bogs of West-Estonian type; Karofeld, 1989). The contact was much smoother if the mud surface was bordered by a 10–20 cm wide flooded zone of decaying *Sphagnum* with transition to a green *S. cuspidatum* or *S. magellanicum* carpet. The contact was least distinct in small mud plots formed between the *R. alba* clumps where the mud surface was bordered by decaying *Sphagnum* under *R. alba*. The described sharp contour between the mud surface and *S. magellanicum* carpet indicates an expansion of *Sphagnum* and a decreasing mud-bottom area, while the two other situations refer to an expansion of the mud-bottom area.

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	68				1010	pill		No.	of the	-pnu	botton	1 a					o mi	one	0.04
	1	2	3	4	5	9	7	8	6	10	11	12	13	14	15	16	17	18	19
						T	ansec	tA			ribit	ines ria 1		NOP 1	18 2		Nac'	atio	8
ndromeda polifolia			+		+		+			+	+								+
)rosera anglica	1		+	+	1	1	5	+	1	+		+					+		
). rotundifolia	+				+	+													
Ahynchospora alba	10	5	7	5	5	5	5	5	3	3		+	+	5	+	10	5	5	2
cheuchzeria palustris							1	1			+				+				
'accinium oxycoccus	+	+	+	+	+	+		+	+	+						+			
phagnum cuspidatum	1	+				+	5		3	+									
. magellanicum			1	+				+											
otal coverage (5.2 ± 4.3%)	12	5	8	5	9	9	16	9	7	3	+	+	+	2	+	10	5	5	5
Number of species (3.1 ± 1.7)	5	3	5	4	5	5	5	5	4	5	2	2	1	1	2	2	7	1	1
tate of Sphagnum	2/3	3	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4
ype of mud-bottom	IVa	IIb	Ш	IIa	IVa	qII	IIIb	dII	dII	dII	dII	IVb	IIb	dII	Ш	IIb	IVb	IVb	dII
ype of mud-bottom surface	5	1/5	1/5	4	5	1/5	5	5	1/5	1	4/2	4	4/2	4	4	5	5/1	5	4/5

Table 1. List of plant species, coverage (%), and some characteristics of mud-bottoms studied on the transects

224

Table 1 continued

	1				No.	of th	e mu	d-bot	tom ^a				
curred side by side, while	1	2	3	4	5	6	7	8	9	10	11	12	13
			Tra	nsect	B								
Andromeda polifolia	+	5	5		+			+	+				
Carer limosa		-	5	+									
Drosera anglica	5	+	+	+	+	+	+	+	+				
Rhynchospora alba	40	otto	d-h	+	5	+	8	5	T				
Scheuchzeria palustris	10				2	+		5	+				
Vaccinium oxycoccus	+	+	+		+			+					
Sphagnum magellanicum			+	+	+								
Total coverage $(7.8 \pm 14.1\%)$	45+	5+	5+	+	5+	+	+	5+	5+				
Number of species (3.5 ± 0.88)	4	3	4	4	5	3	2	4	3				
State of Sphagnum	3	2	2	2	3/4	4	4	4	4				
Type of mud-bottom	Ш	IIb	IIb	IIb	IIb	IIb	IIb	IIb	IIb				
Type of mud-bottom surface	5	4/6	6	6/4	5	5	5	5	4/5				
			Tra	nsect	С								
Andromeda polifolia			+	15		10	5	+		+		30	+
Carex limosa								+					
Drosera anglica			+	+		2	5	+	+	+		5	
D. rotundifolia						2	+	+		+		+	+
Eriophorum angustifolium				+				+					
Rhynchospora alba	+	20	30	10	20	+	5	+	25	45	+	5	+
Vaccinium oxycoccus		+	+			1		+	+	+		+	
Sphagnum magellanicum												+	10
Total coverage (8.8 ± 14.4%)	+	20	30	25	20	15	15	+	25	45	+	40	10
Number of species (3.6 ± 1.9)	1	2	4	4	1	5	4	7	3	5	1	6	4
State of Sphagnum	4	4	4	3/4	4	4/5	4/5	4	4	3/4	2/3	4	4
Type of mud-bottom	IVb	IIb	IIb	IIb	IIb	IVa	IVa	IVa	IVa	IVa	III	IVa	IVb
Type of mud-bottom surface	5	5	5	5	5/0	5	5	5/0	5	5/0	1/3	5	1

^a See Fig. 2 for location of mud-bottoms.

The majority of mud-bottoms (n = 27) studied on the transects distinguished by the character of the transition zone and plant cover showed signs of expansion, seven mud-bottoms were decreasing and seven seemed to be in a stable state (Fig. 2). Near the bog centre on transect B and, especially, A mudbottoms with increasing, decreasing, or stable areas occurred side by side, while in the marginal areas of the bog all mud-bottoms were expanding (Fig. 2). This regularity was not noted on transect C with a level bog slope, where the majority of mud-bottoms were increasing in area.

Surface of mud-bottoms

The surface of mud-bottoms was mostly rather flat and covered with a black, greenish, or reddish 2–3 mm thick layer of algae. Remnants of *Sphagnum* shoots or *R. alba* tussocks could be found. During dry summers the surface layer became completely dry and cracked into polygons (diameter 20–30 cm) with winded up edges. The lower sides of this leathery surface layer remained always green. Sometimes small (diameter 10–15 cm) bubble- or crater-like humps, caused by intensive emission of bog gases, were observed. The total number of algal species in mud-bottoms was 22 (Table 2), but on individual plots it varied from 4 to 13. *Zygogonium ericetorum* and *Tetmemorus brebissonii* were always dominant. *Z. ericetorum* can form an almost continuous mat. Species diversity was higher in wet mud-bottoms with a greenish black slimy surface but lower in dried-out black surfaces. Sometimes the surface of mud-bottoms was covered with a blackish carpet of liverworts (*Cladopodiella fluitans, Cephalozia lunulifolia*).

Peat type beneath the mud-bottoms

From 41 mud-bottoms studied, 19 had formed on hollow peat dominated by *S. cuspidatum*, 12 on *S. magellanicum* lawn peat, and 10 on hummock peat dominated by *S. fuscum* and *S. rubellum*. Under the surface algal film a 3–5 cm thick watery greenish slimy peat layer rich in algae (Table 2) with a degree of decomposition of 10–20% occurred in mud-bottoms formed in hollows. Deeper it was replaced by less decomposed (5%) yellow *S. cuspidatum–R. alba* or *S. magellanicum* hollow peat. In a few cases friable, crumbly yellow *S. cuspidatum* peat occurred directly under the algal layer. Beneath the mud-bottoms formed on lawns, well-decomposed (15–20%) watery, slimy *S. magellanicum–R. alba* peat was most typical, which deeper was replaced by less decomposed (5%) light brown lawn peat. Watery and slimy, up to 5 cm thick greenish well-decomposed (15–20%) brown hummock peat under the layer of algae was typical in mud-bottoms formed on hummocks. When sampling the peat under mud-bottoms often sulphur compounds could be smelt.

Table 2. List of algal species from different habitats in Männikjärve bog

Species	ar	bs	000	1005	6 50	H	labita	nt ^a		i.wi	noiti	"Test"	120m
	1	2	3	4	5	6	7	8	9	10	11	12	13
Actinotaenium sp.	*									*	*	*	
A. cucurbita		*					*	*			*		*
A. minutissimum						*							
A. trachypolum									*				
Anabaena sp.		*											
Aphanothece clathrata		*											
Bacillariophyta	*		*										
Coccomyxa dispar		*											
Cosmarium obliquum var.		*		*			*	*	*	*		*	
Cylindrocystis crassa		*		*	*		*	*	*				
Dinobryon divergens									*				
Gloeocapsa minor f. smithii		*											
Gloeocapsa turgida	+		*								*		
G. turgida f. maxime										*		*	
Gloeocystis vesiculosa								*	*	*		*	
Mesotaenium sp.								*		*		*	
Mougeotia sp.		*						*	*				
Navicula sp.		*		+	*	*			*				
Netrium digitus		*								*		*	
Penium sp.	*		*										
P. cylindrus				*				*	*				
P. polymorphum				*	*			*	*				
P. phymatosporum				*									
P. silvae-nigrae var. parallel.		*		*			*	*	*				
P. spirostriolatum							*	*					
Pleurotaenium minutum	*	*	*				*						*
Pseudanabaena sp.		*											
Scenedesmus quadricauda								*					
Staurastrum sp.	*		*						*				
Zvgogonium ericetorum	+	+	+	+	+	+	+	*	*	*	*	*	*
Tetmemorus brebissonii	*		*	*	+	*	*	*		*	*	*	*
T. intermedius		*					*						
Tetrarcus sp.												*	
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^{1,} on *S. cuspidatum* in a flooded hollow; 2, on brownish capitulae of *S. cuspidatum* in a flooded hollow; 3, on *S. magellanicum* in a flooded lawn; 4, 5, greenish black surface layer in a mudbottom (m-b); 6, dry dense surface layer in m-b; 7, brownish green watery surface layer in m-b; 8, brownish black slimy surface layer in m-b; 9, flooded green surface layer in m-b; 10, brownish black dense surface layer in m-b; 11, uppermost 1 cm thick slimy *Sphagnum* hummock peat under the 10th sample; 12, uppermost 5 cm thick slimy greenish peat layer under m-b; 13, peat sample from the transition zone from hummock to hollow peat.

* present, + abundant.

Peat samples (n = 6) from the hollows at depths from 30 to 120 cm, from clear transition from hummock to hollow peat, contained quite a low number of algae, most of them with empty cells and decomposed. The number of different algal species was smaller than in the surface layer, but all species were typical of mud-bottoms as well (Table 2).

Types of mud-bottoms and their surfaces

Four types of mud-bottoms were differentiated according to their location, underlying peat type, shape, and contour:

I. mud-bottoms covering the entire area of a former well-defined hollow;

II. mud-bottoms with sharp contours (a) or with indistinct contours (b) covering some part of a well-developed hollow;

III. mud-bottoms with distinct contours on hummock or lawn peat;

IV. mud-bottoms with indistinct contours on hummock or lawn peat (a) or on hollow peat (b).

The typology of mud-bottom surfaces takes into account the nature of the surface, occurrence of plants, shoots of dead sphagna, etc.:

0. mud surface with decaying Sphagnum mosses;

1. mud surface with remnants of decayed Sphagnum shoots;

2. mud surface with remnants of plant (R. alba) tussocks;

3. mud surface interrupted by intensive emission of bog gases;

4. flat, bare peat/mud surface;

5. mud surface with few plant tussocks or clumps;

6. mud surface with expanding S. magellanicum or R. alba lawn.

Most of the mud-bottoms studied were of type II (n = 24); type IV was represented by 13 and type III by 4 mud-bottoms only (Table 2). No mudbottoms of type I occurred on the transects studied, these are more common in bogs of West-Estonian type. Mud-bottoms of type II were dominating on transects A and B with a steeper bog slope, whereas on transect C with a slopeless plateau type IV was more common. Mud-bottoms of type II had the highest mean number of plant species (3.1) but the lowest mean coverage (10.7%) whereas type III was characterized by the highest total coverage (24.5%) of plants and type IV by the smallest number of plant species (2.4). The majority of the surfaces of mud-bottoms (29) were of type 5. Type 4 was represented on ten and type 1 on eight mud-bottoms. The mud surface was interrupted by intensive emission of bog gases (type 3) on only one mud-bottom.

Flooding experiment

The biggest length difference of the green parts of *Sphagnum* shoots was observed during the experiment of series 2, flooded for 10 days. Series 3 and 4, flooded for 20 and 30 days, respectively, showed smaller length difference

(Table 3). However, the statistical analyses (MANOVA, regression analysis) indicated that the effect of the duration of the flooding on the changed length of the green parts of sphagna was not significant (r = 0.3715, p < 0.88366). There were visible differences in sphagna after the experiment of series 3 and 4, which were slimier and had a specific smell. On mosses from series 1 and 2 only a few algae (Xanthidium antilopeum + Oocystis spp. and Mougeotia spp. + Navicula spp., respectively) with some hyphae were found. The number of algal species increased on mosses from series 3 (Cosmarium spp., Epithenia spp., Euastrum binale, Hapalosiphon faktinalis, Mougeotia spp., Navicula spp., Oedogonium spp., Oocystis spp., Penium silvae-nigrae, Z. ericetorum) but none of them were as abundant as the dominating hyphae. Series 4 was generally similar to series 3 (Actinotaenium cucurbita, Binuclearia tatrana, Cosmarium depressum, E. binale, Mougeotia spp., Oedogonium spp., Oocystis lacustris, P. silvae-nigrae, Z. ericetorum, T. brebissonii), only O. lacustris was more abundant with hyphae dominating again. The sphagna from flooded depressions looked often slimy and weak, infested with algae. The species composition of algae in the top layer of flooded (water depth 10-15 cm) Sphagnum carpets is given in Table 2. The diversity of species was the highest in samples of decaying Sphagnum with brownish and slimy capitulae. Dominant species were Z. ericetorum and Pleurotaenium minutum.

ing talestates provident and	in the second second	Length (mean ±	SD; n = 6), cm	San Parks
the state house side	Series 1	Series 2	Series 3	Series 4
Before the experiment	7.08 ± 0.49	6.70 ± 0.57	6.25 ± 0.76	6.75 ± 0.52
After the experiment	8.83 ± 1.12	8.58 ± 0.92	7.50 ± 0.70	8.33 ± 0.58
Length difference	1.75 ± 1.30	1.88 ± 1.70	1.25 ± 0.70	1.58 ± 0.80

Table 3. The length of the green uppermost part of *Sphagnum cuspidatum* shoots before and after the flooding experiment, and difference after the experiment

DISCUSSION

Mud-bottoms were evenly distributed in level bog areas, whereas in bog areas with a steeper bog slope they occurred in groups (Fig. 2). Because no correlation was found between the number of mud-bottoms and bog slope, it was suggested that differences in bog hydrology, microtopography, etc. in different bog types are more important. Conditions for mud-bottom formation are the most unsuitable in well-drained wooded pool-ridge complexes, and the most favourable in wooded-grass and grass-hollow bogs (ground layer dominated by *Eriophorum vaginatum* and *R. alba*) where the water table is higher and depressions become flooded more regularly. Mud-bottoms with an increasing, decreasing, or stable

area, located side by side, may indicate a high spatial heterogeneity of factors affecting the degradation of *Sphagnum* mosses and the formation of mudbottoms. Expansion in the area of all mud-bottoms in certain bog areas indicates the continuing process of their formation. No regularities were found between the location and the type of mud-bottoms, but transect A showed a much diverser pattern than transects B and C. As shown earlier (Karofeld, 1985) the location of mud-bottoms does not correlate with the thickness of the underlying hollow peat as supposed by Ivanov & Kuzmin (1982).

The types of mud-bottoms, except the ones distinguished by the type of the underlying peat, should be treated as stages of the development rather than fixed types. The same is valid for the described states of the mud surface: type 1 indicates the beginning of *Sphagnum* degeneration, types 3 and 4 show temporal stability, whereas types 5 and 6 show reduction of the mud-bottom area by overgrowing.

Mud-bottoms were most common in depressions flooded in spring. Therefore, first of all one has to search for the factors that may kill *Sphagnum* in these habitats. Since no relevant pH value differences between hollows and mud-bottoms were found, other factors must cause the die-back of sphagna. A high oxygen content in hollow water is caused by the intensive photosynthesis and good aeration, while a low O_2 content in a mud-bottom is not a likely reason for its formation but a result of died sphagna and intensive oxygen consumption in decomposition processes.

Prior to the formation of mud-bottoms during prolonged floods, *Sphagnum* became infested with algae, which later formed a dense layer on the mud-bottom surface. Thus, one can assume an important role of algae in the die-back of sphagna. During the daytime in spring water temperature and oxygen content are quite high in shallow flooded depressions and conditions become favourable for algae and they cover *Sphagnum* mosses as a slimy layer. Sphagna become weak and unhealthy (Zinserling, 1938; Sjörs, 1963; Boatman & Armstrong; 1968; Goode, 1970; Hulme, 1976), reducing the radiation intensity for photosynthesis and aggravating the metabolism by clogging the leaf pores. Baker & Boatman (1985) reported about the difficulties to grow *S. cuspidatum* in laboratory because mosses became heavily infested with algae. However, the exact impact of floods on the growth of *Sphagnum* mosses is unclear and should be studied in more detail.

The toxic effect of bog gases could also have an essential role in the degeneration of *Sphagnum* mosses. The effect of H_2S on bog plants is not sufficiently studied, but it is known to reduce the permeability of membranes, which may result in cell death. Hulme (1986) showed that in the places with algae-infested *Sphagnum* the upper limit of H_2S is higher than in the areas with algae-free healthy *Sphagnum*. However, in his experiment the possible role of H_2S was probably shadowed by differences in water tables at the sites. As to CH₄, it itself is not harmful in natural concentrations, but as a strong oxidant it

has an effect on plant cells. Methane oxidation in the aerobic zone will result in an increased O_2 consumption and CO_2 release. It is difficult to find out whether the increased emission of bog gases may cause the degradation of *Sphagnum* mosses and the formation of a mud-bottom or vice versa: mud-bottom formed by some other reasons will cause increased gas emission because of higher temperature and a thin aerobic oxidation layer (Frenzel & Karofeld, 1998). Bog gases may have the greatest effect on plants when captured under the ice in flooded depressions in early spring and late autumn. This, in combination with the destruction of water filled capitula cells during repeated freezing in spring nights, may explain the higher frequency and larger area of mud-bottoms in northern regions.

The degradation of *Sphagnum* mosses in hollows and depressions may be caused by the flood induced factors, but on the top of hummocks *Sphagnum* can be weakened by droughts and thereafter replaced by lichens or liverworts. Silvola (1990) reported a very sharp decrease in the photosynthesis of *S. fuscum* when it becomes dry. Bird droppings may also play some role but only in limited plots below the bird nest and in the sea gulls' colonies.

R. alba, the most typical plant species around and on the surface of mudbottoms, can spread vegetatively and by seeds. Masing (1955) showed that seeds of *R. alba* are relatively heavy and mainly transported by water and that in some cases the bare peat areas may be even more suitable for seeds than the *Sphagnum* carpet. During the second half of the summer, a large number of *R. alba* shoots may appear on the mud surface. In West Estonian bogs we described the invasion of the *R. alba* carpet on the mud surface by 20–30 cm without rooting on it (Karofeld, 1989). The zone of decaying sphagna around the mud-bottoms does not always indicate their increasing area because at the same time the centre of the mud-bottom may overgrow with *R. alba* (Table 1).

Ecological conditions (temperature, aeration, floods, dryness, substrate for seeds, etc.) in mud-bottoms were very variable and differed essentially from other bog areas. This makes the invasion of plants on the mud surface harder. In dry summers, the dried out surface of a mud-bottom is not favourable for plant seeds and a number of them will be eaten by birds. The similarity of water tables, beside proximity, is a possible reason why the majority of plant species able to grow on the mud surface are typical in hollows.

The liverwort species occurring on the surface of mud-bottoms in Männikjärve bog are Holarctic species (Laasimer, 1953). *Cladiopodella fluitans* typically grows in bog hollows, on mud, and between *Sphagnum* shoots, whereas *C. lunulifolia* grows on peaty soil and decaying wood (Ingerpuu et al., 1994). *Gymnocolea inflata, Mylia anomala, Odontoschisma denudatum, Microlepidozia setacea*, and *Calypogeia neesiana* were also found in Männikjärve bog on decaying sphagna (Masing, 1958). *C. inflata (Jungermannia inflata)* alone and in combination with *R. alba* is common on different mires (Bogdanowskaya-Guiheneuf, 1928; Sjörs, 1983; Damman & French, 1987).

Algae on the surface of mud-bottoms dry out in summer and form a leathery blackish or purple layer. According to Voronikhin (1954), the purple colour is caused by the pigment from *Z. ericetorum*'s cell membrane and fluid. A dense film of algae on the surface halts the evaporation from peat below, and humid, warm conditions, suitable for algae, develop under the surface layer. The lower side of the film is always green and the uppermost 3–5 cm peat layer greenish and slimy. As shown by Zauer (1950), the number of algal species is the highest at a depth of about 5 cm, not in the surface layer with changing and temporarily unfavourable conditions. Among algal species represented on flooded *Sphagnum* mosses and on the surface of mud-bottoms, *Z. ericetorum* has the dominating role (Bogdanowskaya-Guiheneuf, 1928; Voronikhin, 1954; Masing, 1958; Pork, 1958; Malmer, 1962; Sjörs, 1963, 1983; Hulme, 1986), able to form algal mats.

A transition zone of decaying, often flooded *Sphagnum* mosses around a mudbottom indicates its expansion. Sometimes the contact zone was characterized by *R. alba* clumps with decaying, slimy *Sphagnum*. In general there were four pathways for revegetation and reduction of the mud-bottom area: (a) by a creeping *Sphagnum* (*magellanicum*) carpet with a clear border on the mudbottom; (b) by a *R. alba* carpet with a relatively high and clear border on the mud-bottom surface or by single tussocks; (c) by a combination of *R. alba* and *Sphagnum* as a carpet or as single tussocks; and (d) by a combination of all three types mentioned.

The total plant coverage alone does not give full information on the direction of further development of mud-bottoms. The mud-bottom can be overgrown from the edges by *S. magellanicum* or *R. alba*, with the centre remaining almost plantless. On the other hand, the coverage with *R. alba* may be quite high, but plants are weak, with underlying decaying *Sphagnum* indicating that the area of the mud-bottom is increasing. To forecast the further development of mud-bottoms, the character of the transition zone between the mud-bottom and plant cover, the state of plants on the mud surface, etc. have to be considered.

Data from long-term monitoring of mud-bottoms are lacking. As shown above, mud-bottoms could be overgrown and disappear or stay for a longer time. In summers the surface of the mud-bottoms becomes dry and due to high temperature and good aeration mineralization processes are accelerated (Sjörs, 1961, 1963; Foster & Fritz, 1987). Ceased peat accumulation in mud-bottoms combined with continuous peat accumulation on their banks makes mud-bottom depressions deeper. Because of rising water table these depressions become flooded and are occupied by algae and aquatic hollow species. This hypothesis is supported by the greenish slimy interlayer sometimes found between the ridge and hollow peat. Unfortunately, most algal species do not survive in peat for a longer time and their actual species composition in the areas which become later hollows cannot be reconstructed. Under certain conditions mud-bottoms may become bog pools with an open water table (Thomson, 1924; Ivanov, 1981; Foster & Fritz, 1987). Surprisingly, mud-bottoms in shell craters in KõnnuSuursoo bog in a former Soviet army military training area in North Estonia are somewhat similar to bare peat areas (Karofeld, 1998).

It may be concluded that mud-bottoms occurred most often in grass-hollow bog type where initial depressions become flooded most frequently due to a high water table. This will result in the infestation of *Sphagnum* mosses with algae and their degradation, which leads to the formation of mud-bottoms. Mudbottoms can become overgrown (mainly by *S. magellanicum* and *R. alba*) or, if existing for a longer time, turn into a hollow and pool.

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MUDAÄLVESTE LEVIK MÄNNIKJÄRVE RABAS JA NENDE ISELOOMUSTUS

Edgar KAROFELD ja Mare TOOM

Männikjärve rabas tehtud uuringud näitasid, et valdavalt mustja vetikakilega (*Zygogonium ericetorum*) kaetud mudaälved on sagedasemad väikese languga (0,1–0,3%) rabaosades, olles kõige tüüpilisemad rohu-älverabas ning harvad laukarabas. Mudaälved võivad tekkida nii älvestes, mätastel kui ka siirdekoosluste foonil. Nende tekkele eelnev turbasammalde hävimine võib olla tingitud kevadistest üleujutustest ja turbasammalde kattumisest seeneniidistiku ja vetikakilega ning eeldatavasti ka külmumisprotsessidest ning soogaaside eraldumisest. On analüüsitud mudaälveste taimkatet ja edasist arengut ning esitatud nende tüpoloogia.