Sphagnum decay patterns and bog microtopography in south-eastern Finland

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SUMMARY

This study addresses differences in *Sphagnum* decay in the context of variations in physico-chemical peat properties linked to bog microtopography. The decay rates of six *Sphagnum* species were studied using litter bag techniques at Haukkasuo, a concentric raised bog in south-eastern Finland. The *Sphagnum* species were buried in their native microhabitats in oxic, intermittently anoxic and anoxic peat layers for one or two years. The hummock species generally decayed at slower rates than species growing in hollows and transitional zones of hollows (lawns). The average mean loss in mass of all *Sphagnum* species was 17.7 % after the first year and 18.6 % after two years. The mass loss correlated most positively with oxygen, carbon/nitrogen quotient and sodium, and most negatively with nitrogen, carbon, iron and depth in the native microhabitat. Knowledge about the litter quality of *Sphagnum* species is important for improving our understanding of ecosystem functions in northern peatlands, and particularly in relation to the development of microtopography.

KEY WORDS: chemical and physical peat properties, Haukkasuo, hollow, hummock, lawn, litter bag

INTRODUCTION

A recent estimate of the global peatland carbon stock is 436 Gt (Loisel *et al.* 2014), which is more than 50 % of the carbon present as CO_2 in the atmosphere (IPCC 2013). Much of this carbon is in the form of partially-decomposed remains of *Sphagnum* mosses accumulated due to an imbalance between growth and decomposition (Turetsky *et al.* 2008, Laing *et al.* 2014, Bengtsson *et al*. 2018).

Several studies have investigated the decomposition of *Sphagnum* species using the litter bag method (*e.g*. Clymo 1965, Rosswall *et al*. 1975, Rochefort *et al*. 1990). Inter-species differences are important because they may be critical for the development of microtopographical patterns (*e.g*. alternating hummocks and hollows) (Johnson & Damman 1991). Hummock *Sphagnum* species may be more chemically resistant to decay than hollow species, as demonstrated by studies investigating the preservation of cellular details in *Sphagnum fuscum* (Karunen & Ekman 1982) and *Sphagnum magellanicum* (Dickinson & Maggs 1974). *Sphagnum* species form their own substrate of dead plant parts in which aerobic decomposition of plant material takes place, especially while it remains above the water table (*e.g*. Johnson *et al*. 1990, Johnson & Damman 1991). The thickness of the acrotelm, defined approximately as the thickness of organic material above the summer water table (Clymo 1978), is generally much greater in hummocks than in hollows (Malmer 1988). Depending on the amplitude of water table fluctuations, dead *Sphagnum* may be exposed to aerobic conditions for over 100 years in hummocks with a 30–40 cm thick acrotelm, and lose up to 80 % of its original carbon content before it is added to the slowly decaying peat deposit (catotelm) (Malmer & Holm 1984). In hollows, total carbon losses occurring due to aerobic decay processes should be less because of the much thinner (~10 cm) acrotelm and the consequently shorter residence time of organic material before it is added to the catotelm (Hogg 1993). Products of the slow decay of peat in waterlogged and anoxic conditions are mainly removed from the catotelm as carbon dioxide, methane and dissolved organic carbon (DOC) (Clymo 1984, Alm *et al.* 1997, Chanton *et al.* 2008).

To explore *Sphagnum* decay patterns and links to bog microtopography, in this study we aimed: (1) to measure differences in decay rates of six *Sphagnum* species in a hummock, transitional zones of a hollow and a hollow after one and two years using litter bags; and (2) to study some chemical and physical properties and environmental factors of *Sphagnum* species in relation to decay.

METHODS

Haukkasuo

Haukkasuo (60° 9' N, 26° 57' E) was selected for this study as a good example of a well-preserved large raised bog. It is located in the zone of concentric raised bogs in south-eastern Finland (Ruuhijärvi 1983). The bog is pristine except at the margins, and it is protected within Finland's national mire protection programme.

Haukkasuo (Figure 1) covers 280 ha and lies 54–59 m above sea level. It was intensively investigated during the national peat resource inventory by the Geological Survey of Finland (Mäkilä & Grundström 1984), the evolutionary history of the Haukkasuo bog complex was studied by Hyyppä (1966) and Tolonen & Ruuhijärvi (1976), and the development of the bog was described by Mäkilä (1997) and Puranen *et al.* (1999).

The longitudinal (north–south) profile of Haukkasuo indicates a typical domed bog (Figure 2A), whereas in cross-section it appears to have a fairly flat centre. The age of the basal peat is a little more than 10,000 years and the thickness of the peat layer in the study area for this project is 5.3 m.

Litter bag experiments

Sphagnum decomposition was studied using the litter bag method (*e.g*. Johnson & Damman 1991). Plants of *S. fuscum, S. magellanicum, Sphagnum angustifolium, Sphagnum rubellum, Sphagnum balticum* and *Sphagnum majus* were collected in August 1994. The capitulum - the cluster of actively growing branches at the apex of each moss shoot - was discarded and the next 20 mm of the shoot was retained for use in the litter bags. This part of the shoot was chosen to ensure that all of the material used was of the same age (Johnson & Damman 1991).

We made 28 litter bags for each species (total 168). The shoots were laid out individually and air-dried (22 ºC) for at least a week before making them up into samples and weighing. Immediately after weighing, the shoots were dampened with distilled water to prevent crumbling. The samples were then inserted into nylon mesh bags (5 × 5 cm, 0.2 mm mesh) and the bags closed by heat sealing. The fine mesh size prevented *Sphagnum* leaves from falling out of the bags. Subsamples of the air-dried mosses were oven dried (110 ºC for 24 h) so that the sample weights could be expressed as oven-dry weights.

Figure 1. Oblique aerial photograph of the southern and central part of Haukkasuo showing the concentric pattern of hummocks and hollows. The arrow indicates the location of the study area on the main transect (see also Figure 2a). Photo: Rami Immonen (The Finnish Defence Forces) 1997.

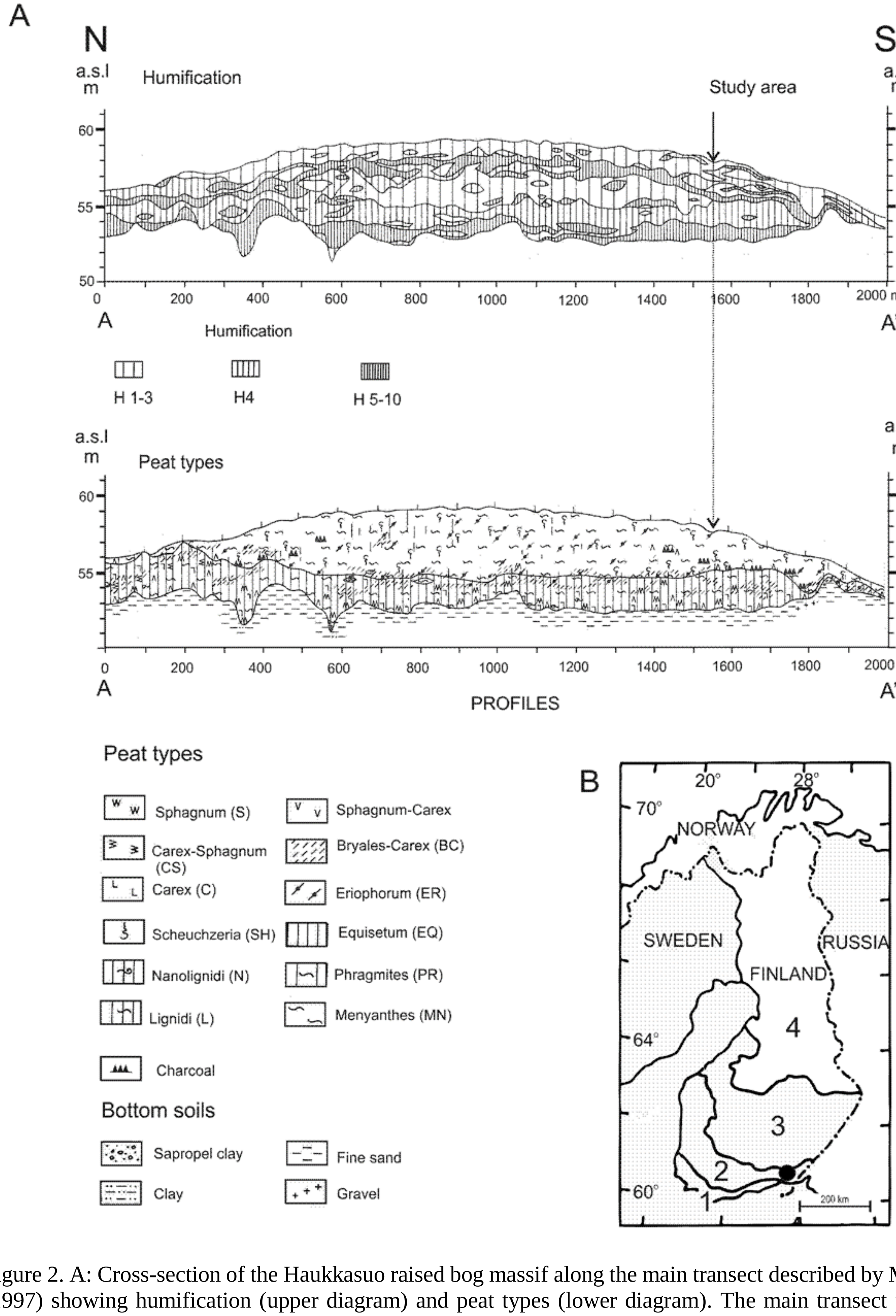

Figure 2. A: Cross-section of the Haukkasuo raised bog massif along the main transect described by Mäkilä (1997) showing humification (upper diagram) and peat types (lower diagram). The main transect passes through the centre of the bog in a north-south direction. The study area for the work described here, containing Study Sites A 1550 and A 1585, was located near this main transect at the point indicated (see also Figure 1). B: Map showing the location of Haukkasuo (large black dot) in south-eastern Finland, relative to the zones of mire complex types: 1 - plateau bogs, 2 - concentric bogs, 3 - eccentric and *Sphagnum fuscum* bogs, 4 - aapa mires (after Ruuhijärvi 1983).

The two study sites (A1550, A1585) were on open patterned bog, close to a transect line established during previous projects (Figures 1 and 2). The litter bags, each containing shoots of one of the six *Sphagnum* species under investigation, were buried in the oxic, intermittently anoxic and anoxic layers of peat beneath their native microhabitats at the beginning of November 1994. Litter bags containing *S. fuscum* and *S. magellanicum* were buried in a hummock at depths of 10 cm, 30 cm and 50 cm below the hummock surface, while bags containing *S. angustifolium*, *S. balticum* and *S. rubellum* were placed at 10 cm and 30 cm depth in the transitional ('lawn') zone between hummock and hollow, and those containing *S. majus* were inserted at the same two depths in a hollow (Figure 3). In each case, two or three bags containing the same *Sphagnum* species were bound onto a nylon line. The line with bags attached was inserted at the desired depth, arranging so that the distance between the bags was 20 cm.

The average water table depth in the study area was 16 cm below ground surface (range 6–33 cm) (eleven-year record at Site A 1585). As the distance between the two study sites A 1550 and A 1585 was only 35 metres, the same water table data were applicable to both.

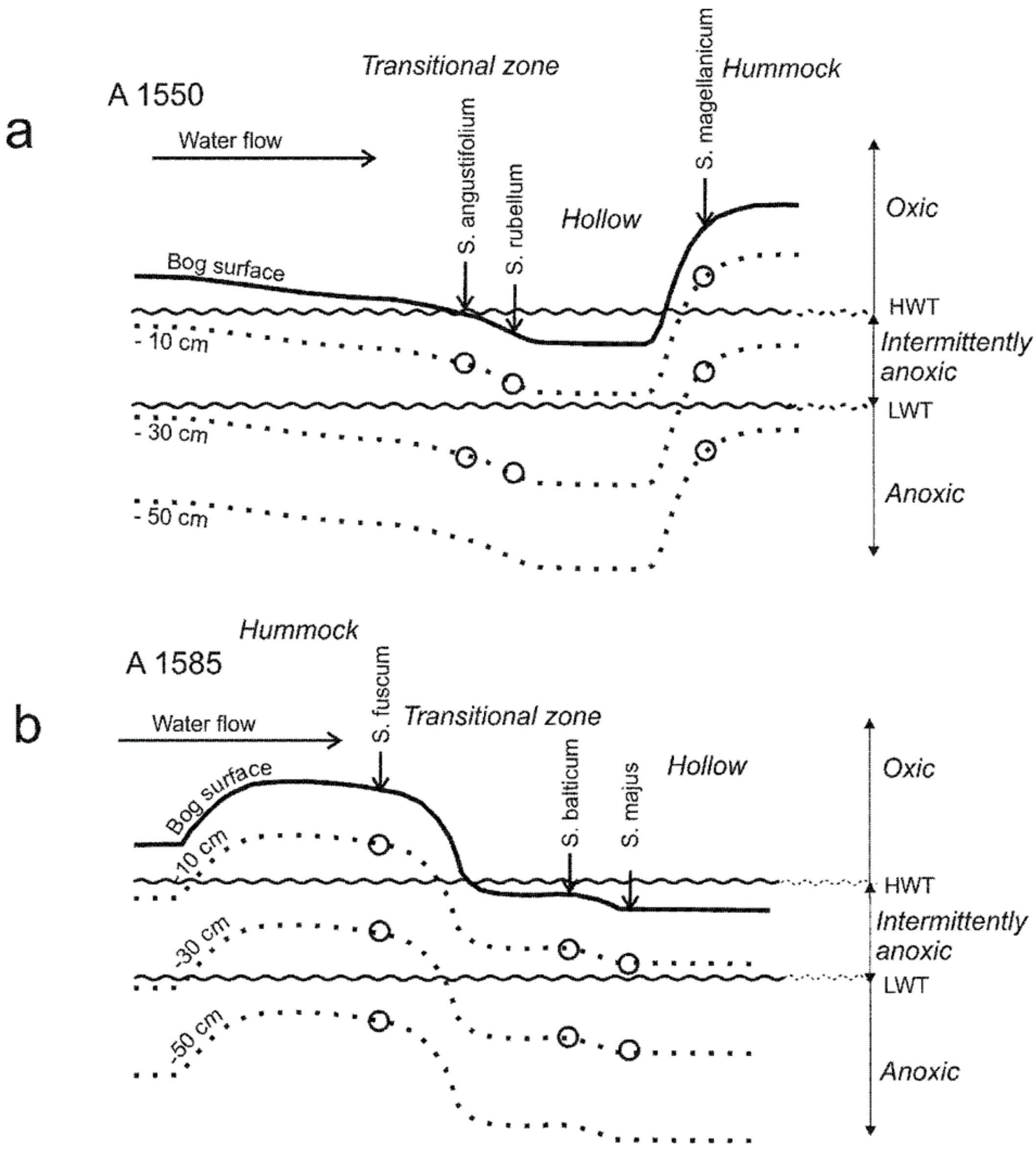

Figure 3. Locations of the litter bags in hummock (*S. fuscum, S. magellanicum*), hollow (*S. majus*) and lawn (*S. balticum, S. angustifolium, S. rubellum*) habitats in relation to depth, degree of oxygenation and water table fluctuation (HWT = highest water table, LWT = lowest water table). In a) (Site A 1550) the litter bags were buried on the 'upstream' side of a hummock, *i.e.* on the side facing into the surface water flow; in b) (Site A 1585) they were placed on the 'downstream' side of a hummock.

Half of the litter bags (84, *i.e*. 14 *per* species) were collected after one year and the remainder after two years. Immediately after collection they were put into lidded plastic boxes that contained distilled water to prevent them from drying out during transit.

In the laboratory, the outside of each litter bag was washed carefully with a gentle stream of distilled water, after which the bag was lightly pressed under running distilled water to remove the colloidal humus. Then the bags were oven-dried at a temperature of 110 °C for 24 hours before weighing. Using a dissecting microscope, new fine roots and extraneous plant material were removed from the outside of each bag, the material removed was weighed and this weight was subtracted from the weight of the sample.

Environmental data

Intact peat cores were extracted from the study sites to a depth of 50 cm using a side-filling Russian pattern peat corer (5 cm diameter) with a chamber volume of 500 cm^3. The main peat type and the fractions of minor constituents were determined according to the specifications provided by Lappalainen *et al*. (1984) by visual inspection of the peat cores, and humification was estimated according to the 10-degree scale of von Post (1922). The pH values of wet samples were measured with a portable meter Sentron 1001.

Further analyses were carried out in the laboratory of the Geological Survey of Finland. Dry samples of the different *Sphagnum* species were ground using a pestle and mortar. One part of each dried sample was used to determine carbon, nitrogen, hydrogen and sulphur content and a different part was used to determine ash content. The calorific value (heating value HV) was determined for total dry matter using a Leco AC 300 calorimeter. The ash content was determined by igniting samples at a temperature of 815 ± 25 °C and expressed as a percentage of dry weight. A Leco SC 132 sulphur analyser was used to determine sulphur content and a Leco CHN 600 to determine carbon, nitrogen and hydrogen contents. The oxygen content (%) was approximated by subtracting the carbon, hydrogen, nitrogen, sulphur and ash contents from 100. Dry bulk density and water content were determined from volumetric samples, dried to constant weight at 105 ºC. The contents of seven selected elements (Ca, K, Mg, Na, P, Fe, Ti) were determined using inductively coupled plasma atomic emission spectrometry (lCP-AES). The results were expressed as parts per million (ppm) in total dry matter.

The correlations between mass loss and other measured variables were studied with variance analysis and Spearman's correlation, using the IBM SPSS 25.0 Statistics software package.

RESULTS

Mass loss after one and two years

The mean dry mass loss of all the studied *Sphagnum* species was 17.7 % after the first year (Table 1). Mass loss was generally lowest for *S. fuscum* and *S. magellanicum* in the intermittently anoxic (30 cm depth) and anoxic parts (50 cm depth) of the hummock. The highest dry mass losses occurred from *S. angustifolium* and *S. balticum* in the intermittently anoxic (10 cm) and anoxic (30 cm) layers of peat beneath the lawns (Table 1). After one year, standard deviation ranged from 1.1 in *S. magellanicum* to 7.5 in *S. majus*. Avarage standard deviation for all species was 3.6 (Table 1).

The mean dry mass loss across all species and microhabitats after two years was 18.6 % (0.9 % higher than the mass loss after one year) (Table 1). The greatest mass losses during the second year occurred in the anoxic zone (30 cm) for *S. majus* (hollows), in the oxic zone (10 cm) for *S. fuscum* and in the intermittently anoxic zone (30 cm) for *S. magellanicum* (Table 1). After two years, standard deviation varied from 0.8 in *S. magellanicum* to 11.8 in *S. fuscum*. Average standard deviation for all species was 3.7 (Table 1).

Half of the litter bags, especially those containing *S. rubellum* and *S. majus* in the intermittently anoxic zone, gained mass during the second year (Table 1). This could be due to algal growth in the bags or because hollows tend to accumulate colloidal matter which is washed in by rain from the surroundings (Johnson & Damman 1991). It is most likely that some decay of *Sphagnum* continued in all bags during the second year, but the resulting loss in mass was exceeded by gains for these bags.

Two-way analysis of variance indicated that variation in the rate of decay depended mainly on *Sphagnum* species but also on depth (as a proxy for degree of oxygenation). The coefficient of determination after one year was 40 % and after two years it was 38 %. Depth and *Sphagnum* species together explained 45 % of the variance after one year and 41 % after two years (Table 2).

Overall, there was additional mass loss during the second year in all microhabitats. The greatest average mass loss was for *S. majus* in hollows (Figure 4).

Table 1. Mean, median (Med.), standard deviation (SD), minimum (Min.) and maximum (Max.) (n = 3–8) mass remaining as a percentage of the original mass after one and two years for: *S. fuscum* and *S. magellanicum* at depths of 10, 30 and 50 cm below the mire surface in hummocks; *S. angustifolium, S. rubellum* and *S. balticum* at depths of 10 and 30 cm below the surface in lawns; and *S. majus* at depths of 10 and 30 cm below the surface in hollows.

Zone	Year	*Sphagnum* species	Mean	Med.	SD	Min.	Max.	n
Oxic 10 cm	1	*fuscum*	14.7	13.7	2.1	12.9	17.3	5
		magellanicum	18.9	18.4	5.7	14.7	24.3	5
	2	*fuscum*	18.3	19.6	8.1	6.4	28.7	5
		magellanicum	18.8	18.7	2.8	16.3	21.6	4
Intermittently anoxic 30 cm	1	*fuscum*	13.4	12.2	7.1	6.3	24.4	5
		magellanicum	12.8	13.0	1.1	11.1	14.4	6
		angustifolium	26.2	25.7	6.1	23.5	29.9	4
		rubellum	22.7	21.9	2.8	20.4	26.5	4
		balticum	23.6	24.0	2.0	20.1	25.8	6
		majus	15.5	15.6	7.5	8.7	19.3	7
	2	*fuscum*	13.6	13.7	11.8	10.5	16.3	4
		magellanicum	15.1	13.7	2.5	13.6	18.0	3
		angustifolium	26.3	28.3	4.1	24.4	29.3	5
		rubellum	20.4	21.2	2.9	15.1	23.7	4
		balticum	23.5	22.3	2.7	20.8	27.5	8
		majus	15.2	15.1	3.7	10.8	19.8	4
Anoxic 50 cm	1	*fuscum*	13.9	15.1	2.9	10.8	16.9	5
		magellanicum	12.2	12.8	2.4	8.9	15.4	6
		angustifolium	20.3	20.7	3.9	17.7	21.9	4
		rubellum	20.4	21.2	1.8	17.1	22.1	4
		balticum	18.4	19.1	2.2	14.7	20.6	6
		majus	14.4	14.4	2.5	11.2	18.6	7
	2	*fuscum*	13.3	13.1	1.0	12.3	14.7	4
		magellanicum	11.3	11.4	0.8	10.4	12.0	3
		angustifolium	22.9	22.2	4.4	20.4	27.0	4
		rubellum	19.8	19.5	1.4	18.1	22.3	4
		balticum	20.8	20.3	2.7	17.2	25.0	8
		majus	20.6	20.6	3.5	15.3	26.1	4
All	1	All	17.7	17.7	3.6	14.2	21.2	74
	2	All	18.6	18.6	3.7	15.1	22.3	64

Table 2. Two-way analysis of variance for percentage mass losses after one and two years from *Sphagnum* litter bags placed at intermittently anoxic and anoxic levels within hummock, lawn and hollow microhabitats.

Source of Variation	Years	Sum of Squares	DF	Mean Square	F	Sig.
Main Effects	1	925	6	154.1	9.2	0.00
	2	762	6	127.1	7.6	0.00
Depth	1	99	1	99.4	5.9	0.02
	2	59	1	59.5	3.6	0.07
Species	1	826	5	165.0	9.8	0.00
	2	703	5	140.6	8.4	0.00
Depth*Species	1	70	5	13.9	0.8	0.50
	2	198	5	39.7	2.4	0.05
Corrected Model	1	1008	11	91.6	5.4	0.00
	2	968	11	88.0	5.3	0.00
Error	1	1045	62	16.8		
	2	886	53	16.7		
Corrected total	1	2052	73	28.1		
	2	1854	64	29.0		

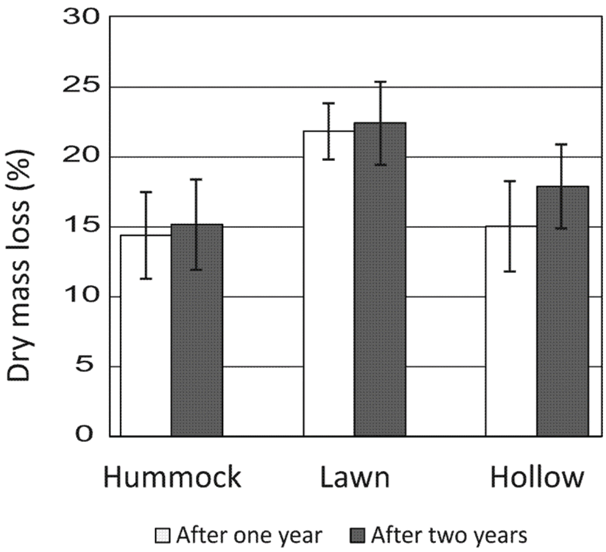

Figure 4. Average dry mass loss (%) and standard deviation in different microhabitats after one and two years, including all burial depths.

Peat properties

The chemical properties of the buried *Sphagnum* moss material indicated that the highest oxygen content and C/N quotient, as well as the lowest ash and nitrogen contents, were found in lawns (Table 3). Nitrogen and carbon contents decreased from the hummock species *S. fuscum* and *S. magellanicum* to the hollow species *S. balticum*. The highest nitrogen content was in the hollow species *S. majus* (Table 3).

The surface material of the hummock (*S. fuscum* and *S. magellanicum*) had the lowest C/N-quotient, oxygen content and pH value and the highest carbon content of the *Sphagnum* species studied. The species in lawns (*S. angustifolium, S. rubellum and S. balticum*) had the highest C/N-quotients and oxygen contents as well as the lowest nitrogen and carbon contents. The hollow species *S. majus* had the highest nitrogen, sulphur and ash contents and the highest pH value. Ash content was highest in the intermittently anoxic layers of all microhabitats studied (Table 3).

Dry bulk density was highest in the hummocks (*S. fuscum*) and lowest in the hollows (*S. majus*). In the uppermost 30 cm in wet hollows, the dry material of *S. majus* was about half of the dry material in the corresponding layers of hummocks (*S. fuscum*) (Table 3). According to our field measurements, the hummocks were most acidic (pH 3.0–3.3) and the hollows were least acidic (pH 3.3–3.6) (Table 3).

Essential elements such as nitrogen (N), phosphorus (P) and especially potassium (K) were recycled to the upper parts of the *Sphagnum* peat layer. The concentrations of magnesium (Mg) and sodium (Na) decreased with depth. Nitrogen (N), calcium (Ca), iron (Fe) and titanium (Ti) increased with degree of humification of the peat (Table 3).

Mass loss correlated most positively with oxygen, C/N quotient and sodium, and most negatively with nitrogen, carbon, iron, depth, dry bulk density and titanium (Table 4).

Table 3. Chemical and physical properties of different *Sphagnum* species in their native microhabitats. Samples were taken from the surface moss (S), from (depth) 5–15 cm oxic (O), 25–35 cm intermittently anoxic (IA) and 45–55 cm anoxic (A) layers. Units and abbreviations: Depth: cm; C, H, O, N, S, ash: % of dry mass; WC (water content): % of wet mass; DD (dry density *in situ*): kg m^{-3}; HV (heating/calorific value): MJ kg^{-1}; Ca, K, Mg, Na, P, Fe and Ti: mg kg^{-1}; ML yr1 (mass loss after one year): %; ML yr2 (mass loss after two years): %, VP: H (1–10) on the von Post scale. Missing data were not collected.

Sphagnum species	Oxyg.	Depth (cm)	pH	C	H	O	N	S	Ash	C/N	WC	DD	HV	Ca	K	Mg	Na	P	Fe	Ti	ML yr1	ML yr2	VP
S. fuscum	S	0	3.0	52.0	6.3	38.8	0.9	0.1	1.9	57.8	-	-	-	-	-	-	-	-	-	-	-	-	1.0
	O	10	3.3	52.1	6.3	38.8	0.8	0.1	1.9	65.1	89.9	23.9	19.2	1720	2120	456	87	237	420	17	14.7	18.3	1.5
	IA	30	3.2	51.2	6.2	39.2	1.0	0.2	2.2	50.2	91.9	56.5	19.0	1810	869	441	87	200	980	26	13.4	13.6	4.0
	A	50	3.2	51.4	6.3	40.3	0.9	0.1	1.0	56.5	91.3	88.5	19.3	1460	425	383	165	300	540	26	13.9	13.3	3.0
S. magellanicum	S	0	3.3	53.4	6.3	37.8	0.9	0.1	1.5	59.3	-	-	-	-	-	-	-	-	-	-	-	-	1.0
	O	10	3.2	50.1	6.1	41.2	0.9	0.1	1.6	55.7	84.6	21.8	20.4	1630	1630	470	129	320	70	27	18.9	18.8	1.5
	IA	30	3.2	52.9	6.4	36.7	1.4	0.3	2.3	37.8	89.9	32.9	19.9	1960	899	511	109	288	1490	41	12.8	15.1	4.5
	A	50	3.3	52.8	6.6	38.4	1.2	0.1	0.9	44.0	91.0	75.7	20.2	1710	511	423	64	403	630	29	12.2	11.3	3.5
S. angustifolium	S	0	3.2	51.6	6.3	39.8	0.8	0.2	1.3	64.5	-	-	-	-	-	-	-	-	-	-	-	-	1.0
	IA	10	3.3	48.5	6.8	42.7	0.6	0.2	1.2	79.4	93.8	33.4	19.0	1410	1540	575	195	314	590	18	26.2	27.0	2.0
	A	30	3.2	50.7	6.3	41.5	0.9	0.1	0.6	55.7	-	-	-	-	-	-	-	-	-	-	20.3	22.9	2.5
S. rubellum	S	0	3.2	51.6	6.2	39.9	0.7	0.1	1.5	73.7	-	-	-	-	-	-	-	-	-	-	-	-	1.0
	IA	10	3.3	51.1	6.3	40.5	0.6	0.1	1.4	85.2	-	-	-	-	-	-	-	-	-	-	22.7	20.3	1.5
	A	30	3.4	50.0	6.4	41.5	0.6	0.3	1.2	83.3	-	-	-	-	-	-	-	-	-	-	20.4	19.8	3.0
S. balticum	S	0	3.2	48.5	6.4	43.0	0.5	0.1	1.5	97.0	-	-	-	-	-	-	-	-	-	-	-	-	1.0
	IA	10	3.3	48.1	6.4	43.2	0.5	0.1	1.7	96.1	98.7	13.1	18.6	1060	3260	536	789	224	224	8	23.6	23.5	1.0
	A	30	3.4	49.4	6.4	42.3	0.5	0.2	1.2	98.7	97.6	23.4	18.4	1050	259	292	<100	156	363	21	18.4	20.8	1.5
S. majus	S	0	3.4	48.7	6.4	39.7	1.3	0.2	3.7	37.5	-	-	-	-	-	-	-	-	-	-	-	-	1.0
	IA	10	3.6	49.2	6.4	39.5	0.9	0.3	3.7	52.9	98.8	11.3	18.7	1060	3593	552	696	270	352	10	15.5	15.2	1.0
	A	30	3.3	51.3	6.6	37.9	1.7	0.2	2.3	30.1	97.2	28.6	18.6	1045	223	298	100	208	377	35	14.4	20.6	1.5
			pH	C	H	O	N	S	Ash	C/N	WC	DD	HV	Ca	K	Mg	Na	P	Fe	Ti	ML yr1	ML yr2	VP
		min	**3.0**	**48.1**	**6.1**	**36.7**	**0.5**	**0.1**	**0.6**	**30.1**	**84.6**	**11.3**	**18.4**	**1045**	**223**	**292**	**64**	**156**	**70**	**8**	**12.2**	**11.3**	**1.0**
		average	*3.3*	*50.7*	*6.4*	*40.1*	*0.9*	*0.2*	*1.7*	*64.0*	*93.2*	*37.2*	*19.2*	*1447*	*1394*	*449*	*242*	*265*	*549*	*23*	*17.7*	*18.6*	*2.0*
		max	**3.6**	**53.4**	**6.8**	**43.2**	**1.7**	**0.3**	**3.7**	**98.7**	**98.8**	**88.5**	**20.4**	**1960**	**3593**	**575**	**789**	**403**	**1490**	**41**	**26.2**	**27.0**	**4.5**

Table 4. Spearman's rank correlation coefficients *(ρ_s)* relating mass loss of *Sphagnum* shoots in litter bags to the measured microhabitat variables (left column). The statistically most significant relationships at the 0.05 level are indicated by **bold red** type.

Variables	ρ_s
O	**0.87**
C/N	**0.77**
Na	**0.77**
K	0.43
W %	0.43
Mg	0.41
pH	0.22
H	0.18
S	-0.10
Ash	-0.12
P	-0.14
Heating value	-0.46
Ca	-0.59
Ti	**-0.64**
Bulk density	**-0.66**
Depth	**-0.70**
Fe	**-0.75**
C	**-0.76**
N	**-0.81**

DISCUSSION

Our results suggest that the variation in decay rate of *Sphagnum* depends primarily on the intrinsic decay properties of each *Sphagnum* species but is also influenced by depth. Several studies have stressed the importance of variation in the C/N quotient in relation to the decomposition of plant litter, carbon being the energy source for micro-organisms and nitrogen being neccessary for the production of proteins (*e.g*. Malmer & Holm 1984). This ratio reflects litter quality, and degree of decomposition is greater when the C/N quotient is low, as seen in this study. Variation in the C/N quotient mainly follows variation in the nitrogen content of the peat (Malmer 1986). The C/N quotient decreases with depth due to losses of C during decay processes.

Litter quality and anoxic soil conditions are the main factors affecting decomposition rates in peatlands (Bragazza *et al.* 2008). Some *Sphagnum* species are affected more than others by the environmental conditions at the locations where they grow. Any environmental change favouring vascular plants at the expense of *Sphagnum* can potentially reduce peat accumulation by increasing rates of litter decomposition (Bragazza *et al.* 2008). In particular, habitat wetness strongly reduces the rate of decomposition realised in species inhabiting hollows (Bengtsson *et al.* 2016). Although plant litter decomposition rates increase following water table drawdown, the accumulation of new organic matter also increases due to proportionally increased litter inputs (Strakova *et al.* 2012).

Johnson & Damman (1991) found that *S. fuscum* and *S. cuspidatum* lost mass at different rates, independently of whether the *Sphagnum* decayed in hummocks or in hollows. Hollow species (*Sphagnum* section *Cuspidata*) tend to have higher production rates than hummock-forming species (*Sphagnum* section *Acutifolia*) (Rochefort *et al*. 1990, Malmer & Wallén 1999), but also generally decay more rapidly (Johnson & Damman 1991, Belyea 1996). Johnson *et al*. (1990) suggest that the poor preservation of *S. cuspidatum* in hollow peat may be due to fast decay. At a depth of 7–10 cm, nearly all hollow species had completely fragmented into stems and leaves. However, the hummock-forming species, especially *S. fuscum*, remained completely intact to a depth of at least 25 cm (Johnson *et al*. 1990). Our results also show that *Sphagnum* macrostructure is better preserved in hummocks than in hollows down to a depth of 25 cm, and that the chemical decay properties of *Sphagnum* hummock species are more decay-resistant than those of hollow species.

Decomposition rates show a negative correlation between species and their positions in the microtopography, as species that grow on hummocks decompose slowly but hummock microhabitats promote rapid decomposition (Turetsky *et al.* 2008). By forming litter that degrades slowly, hummock mosses appear to maintain pore structures (air-filled porosity, pore shape and size distribution) in the surface peat of hummocks that aid water retention (Johnson *et al.* 1990). According to Rochefort *et al.* (1990), decomposition of *S. fuscum* is lower due to a combination of low pH, higher uronic acid content, drier peat and sturdier, denser construction. The hummocks exhibit the lowest pH in the peatland (*e.g.* Clymo 1963, Vitt *et al*. 1975), and it is likely that this acidity contributes greatly to the lower decay rate. The acidity of peat decreases from hummock to hollow, as seen in this study.

Mires and Peat, Volume 21 (2018), Article 13, 1–12, http://www.mires-and-peat.net/, ISSN 1819-754X

Peat decomposition is enhanced when the level of the water table fluctuates greatly during the growing season (Malmer 1986). The decomposition of *S. angustifolium* is probably high because of the enhanced cycle of moisture and drought at its location close to the water table, enhanced nutrients from contact with more active water flow, higher pH and a faster fragmentation rate (Rochefort *et al.* 1990). Our study has also shown that there is remarkable dry mass loss from *S. angustifolium* and *S. balticum*, especially in the anoxic peat zones.

The fluctuations of the water table in hollows cause water to flow and become more oxygenated than in hummocks, which can influence peat decay. Aeration conditions in the uppermost 10 cm of intermediate hollow peat become favourable for decomposition only intermittently, while in deeper layers the aeration conditions remain unfavourable (Zobel 1986). The wet conditions of the hollow can be expected to induce anoxia and thus slow down decomposition. However, hollows may be less oxygen deficient than was previously thought because of water table fluctuations and oxygen production by algae (Johnson *et al*. 1990) as well as a luxuriant *Sphagnum* carpet.

High nitrogen content in hollows can be due to bacteria and cyanobacteria that bind free nitrogen from the atmosphere. This occurs especially in wet flarks (Dickinson 1983). The increase in the atmospheric supplies of nitrogen and sulphur during recent decades can mean increased peat accumulation (Turunen *et al.* 2004). In our study, the average N concentration values are of the same magnitude as values found in the literature (*e.g.* Turunen *et al.* 2004). Thus, the results obtained here can be considered in this wider context. It is possible that the higher N concentrations found in hollows in this study (Table 3) reflect the currently high N deposition values (1–3 g m^{-2} yr^{-1}), which may reduce growth and accelerate the decomposition of *Sphagnum* mosses (*e.g*. Jauhiainen *et al*. 1994, Bragazza *et.al*. 2006, Gerdol *et al*. 2007).

ACKNOWLEDGEMENTS

We extend our thanks to all colleagues who contributed to this work, especially Professors Matti Saarnisto and Harri Vasander, senior researcher Jukka Turunen and Carrie Turunen for translating and checking the English of the manuscript.

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Submitted 26 Jun 2017, final revision 11 Jun 2018
Editor: Richard Payne

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