

# On the relations between water regime, mass accretion and formation of ombrotrophic conditions in *Sphagnum* mires

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## SUMMARY

(1) I explore the hypothesis that the water regime is one of the major determinants of the difference between bog and fen in *Sphagnum* mires because of its effects on the decay loss and the mass accretion rate. This article deals with the recent mass balance and water regime and the variation in mass accretion rate during the last millennium, studied at two mires in southern Sweden.

(2) At one bog site and one fen site in the Åkhult mire the recent litter input to the acrotelm and mass accretion in the catotelm were 210 and 38 g m<sup>-2</sup> a<sup>-1</sup> at the bog site and 300 and 21 g m<sup>-2</sup> a<sup>-1</sup> at the fen site, respectively. The difference in productivity reflected the availability of plant nutrients and the pH. The smaller loss of mass at the bog site was a result of smaller water table amplitude and a higher median time water level (MTWL) than at the fen site. Through its effects on hummock formation, the water regime is also a major determinant of the surface structure.

(3) Around 1000 cal. BP the precipitation and the supply of mineral soil water to the two sites increased and the bog vegetation of that time was replaced by fen vegetation. Mass accretion first increased to 180 g m<sup>-2</sup> a<sup>-1</sup> but with the upward growth of the mire surface the rate decreased. The recent conditions at the fen site became established ~800 cal. BP, probably as a result of increased water table amplitudes. At the bog site the water regime changed from geogenous to ombrogenous ~600 cal. BP, contemporary with a decrease in precipitation. This change resulted in a rapid increase in mass accretion by 150 % followed by a slow decrease until recent times with low values. The same development was found to have occurred twice at the Store Mosse mire. Such an initial increase in the peat accretion rate must be important for the formation of permanently ombrotrophic conditions in raised bogs.

**KEY WORDS:** bog formation; minerotrophic fen; ombrotrophic bog; past climate changes; vegetation shift

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## SYMBOLS AND ABBREVIATIONS

*DBD*: dry bulk density.

[*X*]: concentration of substance 'X', mass basis.

*M/N*: dry mass / nitrogen, mass basis.

*MTWL*: Median Time Water Level - the water table is above this level during half of the period studied.

*NPL*: Nitrogen Peak Level - the depth of maximum [*N*].

*NPP*: Net Primary Production.

*DDL*: Decay Decrease Level - the depth at which the decay rate reaches a constant, low value.

*LDL*: Litter Deposition Level - the depth at which the input of litter to the acrotelm takes place.

*DOM*: Dissolved Organic Matter.

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## INTRODUCTION

The most characteristic feature of peatlands is their unique capacity to accrete structural organic matter as peat in deep water-saturated anoxic layers (the catotelm) over long periods of time, and this results

in a gradual upward growth of the surface. The formation of peat is due to the incomplete decomposition of plant litter in the predominantly oxic acrotelm (depth ~0.2–0.4 m below the surface) which has a varying water table level and lateral movement of the water. In the catotelm below, the

decay rate is about three orders of magnitude smaller than in the acrotelm and the movement of water is very slow (Ingram 1983). Because of these differences between acrotelm and catotelm the two-layer model proposed by Ingram (1978) has been applied in studies on peat formation and other processes in the surface layers of mires (e.g., Clymo 1984, Clymo & Pearce 1995, Malmer & Wallén 2004, Belyea & Baird 2006, Malmer *et al.* 2011, Morris *et al.* 2011).

The macrofossil content of the peat provides information regarding the peat-forming vegetation and its changes over time. Determination of the variation in dry bulk density (DBD) combined with dating allows studies of the variation in the mass accretion rate over time due to climatic or other external changes and to autogenic processes in the acrotelm (Malmer *et al.* 1997, Belyea & Malmer 2004). The rate of accretion of dry mass ( $M_A$ , structural organic matter) in the catotelm is controlled by the mass balance in the acrotelm (Clymo 1984, Malmer *et al.* 2011), as expressed by the equation:

$$M_A = M_0 - (M_D + M_E) \quad [1]$$

The mass accretion rate is determined by the difference between the litter input to the acrotelm ( $M_0$ ) which results from the NPP (net primary production) and the two main components of mass loss from the acrotelm brought about by litter decomposition ( $M_D$ ), releasing gaseous carbon compounds to the atmosphere, and by export of non-structural organic matter ( $M_E$ ) as DOM (dissolved organic matter) in the runoff taking place mainly in the acrotelm (Ingram 1983, Clymo 2004).

Although the decay rate of the litter in the acrotelm increases with temperature (Clymo *et al.* 1988) the total loss of mass is determined by its residence time and its decay resistance, which is high in most *Sphagnum* litter (Clymo 1965, Belyea 1996). The major determinant of the residence time is the thickness of the acrotelm; which depends upon the equilibrium between water supply, evapotranspiration, resistance to the flow of water exerted by the vegetation and structural organic matter in the acrotelm, and the slope of the mire surface (Belyea & Malmer 2004, Belyea & Baird 2006, Morris *et al.* 2011). Measurements of the drainage water export and eddy correlations of the gas exchange show that both the annual export of DOM and the decay loss follow annual variations in the climatic conditions (Roulet *et al.* 2007, Malmer *et al.* 2011) more closely than do the net primary

production (NPP) and litter input to the acrotelm. Compared with the litter input, the mass accretion in the catotelm is a slow process and the measured rates usually represent averages over decades.

In *Sphagnum* mires (peatlands dominated by *Sphagnum* mosses) the mass accretion often varies between different parts of the mire resulting in differences in the rate of rise of the usually hummocky surface. Because of that two different types of soil wetness develop in many *Sphagnum* mires, namely (1) minerotrophic fen areas of poor fen type with geogenous soil wetness (Sjörs 1948) supplied by water of either topogenous or soligenous origin from the surrounding mineral ground in addition to the precipitation water and (2) ombrotrophic bog areas with ombrogenous soil wetness which are supplied with precipitation water only. Most bogs are more acid and poorer in Ca, Al, and Fe than nearby fen sites. In practice, the delimitation of a bog from a fen is carried out using indicator species for fen vegetation (exclusive fen plants) such as *Menyanthes trifoliata* and several species of *Carex* and *Sphagnum*.

The mire vegetation forms a continuous gradient (the poor–rich gradient) extending from the bog vegetation through the different types of poor and rich fen vegetation (Sjörs 1948, Malmer 1962, 1986; Wheeler & Proctor 2000, Økland *et al.* 2001; but see also Du Rietz 1954). Bog vegetation is usually poorer in species, in particular of vascular plants, than are most fen vegetation types. Despite a low NPP in bogs, the mass accretion and growth in height are greater there than in fens (Malmer 1975). Accordingly, the formation of a bog from a fen requires an increase in the mass accretion rate sufficient to compensate for the decrease in NPP.

In *Sphagnum* mires the lower nutrient availability and pH in bogs offer an established explanation for differences in vegetation and NPP compared to fens (Malmer 1986) but the relevance of these variables for the difference in mass accretion is unclear. The present study aims to provide evidence pertaining to the hypothesis that differences in water regime (through its influence on the decay process in the acrotelm) are a major determinant of the variation in mass accretion rate and the existence of the two systems (fen and bog). In particular, the annual water table amplitude and its variation are considered to be important for the decomposition of the litter in the acrotelm and the formation of hummocks. The main part of the study was carried out in a *Sphagnum* mire where data relating to productivity, decomposition and mass accretion could be combined with the results of

earlier studies concerning hydrology and the water regime at the same sites. The study also includes relevant data regarding the peat stratigraphy of this and another mire to explore the extent to which the results about recent conditions are in line with the development of the mires during the last millennium.

## METHODS

### The Åkhult mire

Most of the study was carried out in the Åkhult mire (57° 10' N / 14° 30' E, altitude 225 m, size ~1 km<sup>2</sup>; see Malmer 1962) in a rural area within the boreo-

memoral region of southern Sweden. During the period 1961–1990 the monthly mean temperature ranged from -3 °C (February) to +16 °C (July), the vegetation growth period (>5 °C) was ~190 days and the mean precipitation ~700 mm a<sup>-1</sup> (Raab & Vedin 1996).

The Åkhult mire is a *Sphagnum* mire with a large raised bog (Malmer 1962). The present study was carried out in the northern part of the mire (the Stattute area) with topogenous fen areas receiving drainage water from ~0.8 km<sup>2</sup> of forested land. The macrotopography is rather flat (Figure 1). The limit between bog and fen is, therefore, topographically indistinct there but hydrological studies have shown that it closely follows the distribution limit of *Narthecium ossifragum*, a fen plant in the region.

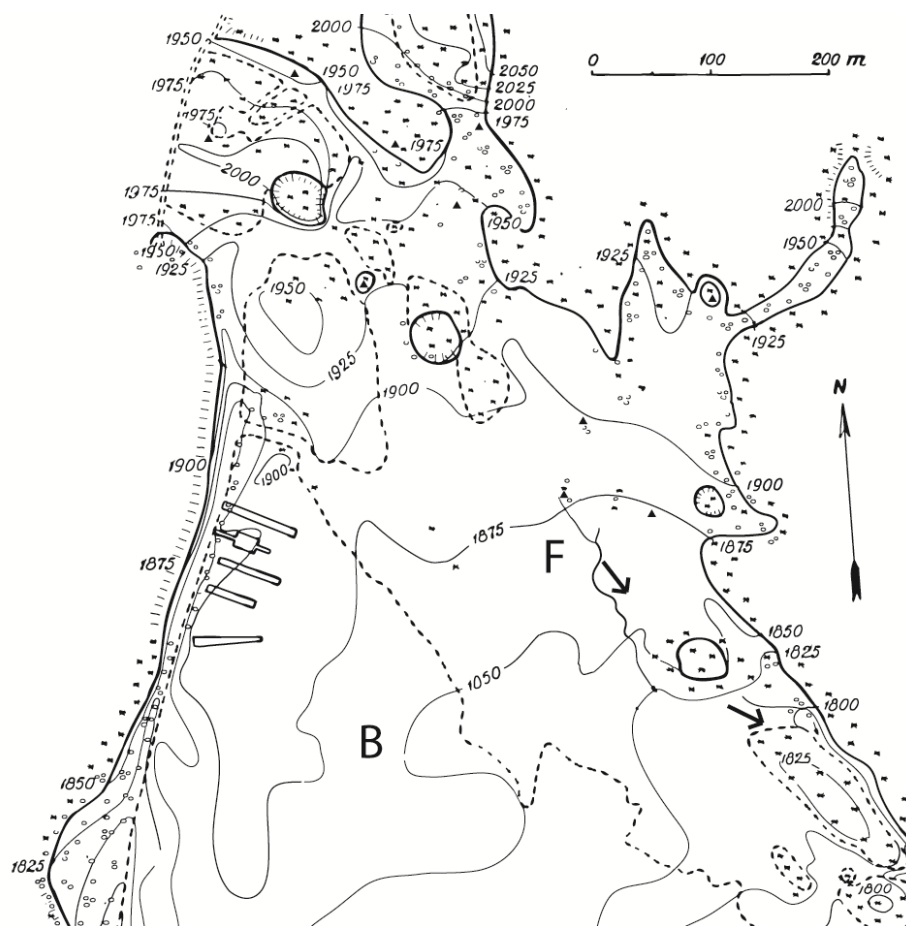


Figure 1. Map of the northern part of the Åkhult mire covering the Stattute area and its surroundings indicating the two sampling sites (B and F for the bog and fen sites, respectively), the macrotopography (contour lines, cm compared to a fixed point, interval 25 cm), the main water track of brook pools (arrows), the fen plant limits in 1940 (dashed lines), wooded areas (small crosses), boulders (filled triangles), and peat cuttings that were abandoned long ago (the pattern of narrow rectangles at the western margin of the bog). Part of the original map in Malmer (1962) as revised in Malmer *et al.* (2011).

In the central part of the bog, deep layers of Late Glacial lake sediments are found (Fries 1965, Svensson 1979). Peat formation there began early in the Atlantic period, beginning with *Cyperaceae* peat rich in woody remains. From the beginning of the Early Sub-Boreal period up to recent times, bog peat formed mainly by *Sphagnum fuscum* dominates (maximum depth 8.5 m). During this period the mire also expanded northwards (Figure 1) and from the Early Sub-Atlantic period the *S. fuscum* bog reached into the Stattute area (see sub-section “Stratigraphy and macrofossils” in Results).

### Sampling and treatment of the samples

#### Sampling sites

All sampling was performed in the non-wooded parts of the Stattute area. One bog site and one fen site (areas ~0.5 ha) were sampled (Figure 1). The bog site was characterised by ombrotrophic bog vegetation (Malmer 1962). The minerotrophic vegetation at the fen site was richer in species and included exclusive fen plants such as *Menyanthes trifoliata*, *Narthecium ossifragum*, *Eriophorum angustifolium*, *Sphagnum majus* and *S. pulchrum*. The lawn vegetation there was dominated by *S. papillosum* instead of *S. magellanicum*; *S. balticum*, *S. cuspidatum* and *S. tenellum*, all common at the bog site, were lacking; and *Eriophorum vaginatum* was less abundant. At the bog site various types of hummock vegetation covered 58 % and lawn vegetation 33 % of the surface, the rest being without macrophyte vegetation (Malmer *et al.* 2011). At the fen site, hummocks covered only 11 % of the surface and lawns the rest of it.

#### Water level

In the autumn of 1953, points for water table measurements were established all over the Stattute area in hollows bare of vegetation (mud-bottoms) where wooden sticks (length  $\geq 1.5$  m) were pushed down  $\geq 1.3$  m into the peat. In 1954 the position of the water table was measured  $\geq 24$  times from snowmelt at the end of March to freeze-up in mid-November (240 days, precipitation 681 mm; Malmer 1962) and are presented here as water table residence curves. Measurements for other purposes after 1954 (e.g. Malmer *et al.* 2011) confirm that the 1954 measurements were typical of later years too.

#### Litter input

The rate of litter input to the acrotelm was measured

using a  $^{14}\text{C}$  labelling technique (Malmer & Wallén 1996, 1999). In *Sphagnum*-dominated hummocks and lawns  $^{14}\text{C}$ -labelled plots (size 0.04 or 0.10 m<sup>2</sup>) were established in 1980 and 1981. Cores were sampled from the plots in the autumns of 1986 (short treatment period) and 1992 (long treatment period) and deep frozen within a day. Prior to analysis, the frozen cores were cut into consecutive 1.25 cm slices. After being dried (80 °C) their dry bulk density was determined. The  $^{14}\text{C}$  activity was analysed separately in bulk samples and in fine root litter through combustion in a Packard Tri Carb Sample Oxidizer, the  $^{14}\text{C}$  activity being measured in a Packard Tri Carb Scintillation Counter. The upper surface of the slice with the highest  $^{14}\text{C}$  activity in the bulk sample (the  $^{14}\text{C}$  horizon) was taken to represent the surface at the time of labelling, the mass above this level being assumed to have been added after labelling. The amount and composition of the biomass is assumed to remain constant throughout the experiment (Malmer *et al.* 2011).

#### Litter decay

The decay of the litter in the acrotelm was studied using surface cores (diameter 10 cm) extending through the acrotelm and the top of the catotelm, sampled 1980–1987 in *Sphagnum*-dominated lawns and in low hummocks, six at the bog site and nine at the fen site; three of these cores at each site were in hummocks. The cores were deep frozen and later cut into 2.5 cm consecutive slices before being dried (80 °C) and then analysed for dry bulk density (DBD), [C] (Leco CR-12 auto analyzer), and [N] (Kjeldahl-N). For details, see Malmer & Wallén (1993, 1999).

In *Sphagnum* communities most of the litter input to the acrotelm takes place just below the euphotic zone a few centimetres below the surface at a level rich in senescing mosses and fine roots (Wallén 1983, 1986, 1992; Malmer & Wallén 1993). This level, the litter deposition level (LDL), separates the carbon sequestering green moss layer from the rest of the acrotelm dominated by decaying litter and roots. Before litter formation begins, N is continuously re-located to the growing parts of the plants (Aldous 2002). In the cores the LDL is therefore set at the upper surface of the slice having the lowest [N] (Malmer & Wallén 1993, 2004). Because N is conserved, the decay in the acrotelm results in [N] increasing with depth to the N peak value or NPL. If the amount of nitrogen originally added to the system ( $N_0$ ) equals that at time  $t$  ( $N_t$ ) the loss of mass through decomposition during this period can be calculated from the equation:



$$\ln(M_t/N_t) = \ln(M_0/N_0) - k t \quad [2]$$

where  $M_0$  is the original mass,  $M_t$  is the amount remaining after time  $t$  and  $k$  is the proportional decay constant, dimension  $T^{-1}$ . The cumulative value of  $N$  ( $N_{cum}$  g  $m^{-2}$ ) is used to establish a timescale. For the bog site it has been re-calculated to calendar years by the use of  $^{210}Pb$  (Malmer *et al.* 2011). More detailed accounts of these calculations are presented by Malmer & Wallén (1993, 1999, 2004).

The bottom limit of the acrotelm is the level where the accretion of mass in the catotelm takes place. Ingram (1978) originally related the limit to the amplitude of the water table. Since the limit between acrotelm and catotelm often appears as a transitional zone rather than a distinct level, the lower part of the acrotelm could be treated as a separate layer, the mesotelm (Clymo & Bryant 2008). Clymo & Pearce (1995) give a detailed treatment of the conditions in the acrotelm and distinguish four process zones and four structural layers. The present study uses a simpler definition, setting the limit between acrotelm and catotelm at the decay decrease level (DDL) where no further increase in  $[N]$  can be detected with the present methods because of a very low decay loss and low value of the decay constant ( $k$  in Equation 2).

#### *The catotelm*

At each of the sites two deep cores (the main cores) were taken in *Sphagnum* lawns in 1983 using a Russian pattern (cross section 5 cm) peat corer. One of the cores was cut into 5.0 cm consecutive slices and treated as the short cores were to estimate the variation in the mass accretion rate in the catotelm. This gives the apparent accretion rate ignoring the small decay loss. The second core was used for the analysis of macrofossils and for  $^{14}C$  dating. For these purposes two supplementary cores were also taken later at each site. All the sample depths refer to the upper surface of a sample. The upper limit for the catotelm was set at 15 and 20 cm below the surface for the bog and for the fen site, respectively. The  $^{14}C$  determinations were carried out at the Radiocarbon Dating Laboratory at Lund University.

In each sample plant macrofossils were analysed following Svensson (1986). After sifting, the abundance of the different types of plant remains was estimated using a 5-degree scale for % cover (<1, 1–10, 10–25, 25–50 and > 50), means being calculated using 1, 5, 15, 30 and 60 %, respectively, as the values for the classes. The nomenclature for *Sphagnum* follows Daniels & Eddy (1985) except that *S. rubellum* is treated as a separate species. To

avoid misunderstandings *Palustria* is used for Section *Sphagnum*. The peat-forming vegetation was reconstructed from five groups of plant macrofossils, namely above-ground and below-ground vascular plants and the sections *Acutifolia*, *Cuspidata* and *Palustria* of *Sphagnum*. In particular, these groups of plant macrofossils in the peat reflect both the former conditions at the site and the decay resistance of the litter.

#### **The Store Mosse mire**

Results from studies on the Store Mosse mire, (57° 15' N / 13° 55' E; altitude 160–170 m) - a large mire complex 45 km to the west of the Åkhult mire - have also been included in this study. The climatic conditions and the recent bog vegetation are the same as at the Åkhult mire. Sampling for the present study was at two sites, A and B, in the central and eastern margin, respectively, of the large raised bog in the southern part of the mire complex. Svensson (1988) gives detailed information about the peat stratigraphy and development of that bog. The same methods as for the Åkhult mire have been used. See also the section “About the shift from fen to bog” in the Discussion.

## **RESULTS**

### **The recent acrotelm of the Åkhult mire**

#### *Litter input*

In the  $^{14}C$  labelled plots, both the annual height increment and the accumulation of mass above the  $^{14}C$  horizon were greater in the hummocks than in the lawns at the bog site (Table 1;  $P = 0.002$  and  $< 0.001$ , respectively;  $t$ -test) but not at the fen site ( $P > 0.2$ ). The height increment was greater at the fen site than at the bog site both in the hummocks ( $P = 0.017$ ) and the lawns ( $P = 0.014$ ). The accumulation of mass was also higher in the lawns at the fen site than at the bog site ( $P = 0.002$ ) but not in the hummocks ( $P = 0.063$ ). Adding five short-period samples for the hummocks of the bog site reduced the overall values by only a tiny amount relative to those presented in Malmer *et al.* (2011).

#### *Litter decomposition*

The depth of the *LDL* was less at the fen than at the bog site (Table 2). For the fen site the analyses in the top parts are difficult to interpret because the sampling technique was insensitive to differences

Table 1. Height increment and litter accumulation above the  $^{14}\text{C}$  horizon in the  $^{14}\text{C}$ -inoculated plots at the end of the experimental periods together with the estimated rate of litter input to the acrotelm for each vegetation type. Mean  $\pm$  SD given for growth and accumulation rates. The calculation of the estimated litter input follows Malmer *et al.* (2011). To compensate for the root biomass added below the  $^{14}\text{C}$  horizon during the first six years after inoculation, the accumulated mass in each sample has been increased by 11 %. In calculating the mass lost through decomposition during the experiment the decay constants ( $k$ ) were assumed to be  $0.039\text{ a}^{-1}$  and  $0.050\text{ a}^{-1}$  at the bog and fen site, respectively (see sub-section “Litter decomposition” in Results).

	Vegetation type and site	Number of samples			Height increment ( $\text{cm a}^{-1}$ )	Accumulated since labelling ( $\text{g m}^{-2}\text{ a}^{-1}$ )	Estimated litter input ( $\text{g m}^{-2}\text{ a}^{-1}$ )
		Short period	Long period	Sum			
<i>Hummocks</i>	Bog site	5	13	18	$0.78 \pm 0.15$	$187 \pm 46$	$267 \pm 64$
	Fen site	4	1	5	$1.03 \pm 0.34$	$234 \pm 36$	$343 \pm 116$
<i>Lawns</i>	Bog site	0	7	7	$0.57 \pm 0.14$	$108 \pm 26$	$153 \pm 37$
	Fen site	8	1	9	$1.07 \pm 0.48$	$202 \pm 21$	$298 \pm 92$

Table 2. The depth of the *LDL* (litter deposition level) and the *NPL* (*[N]* peak level) together with the dry bulk density and *[C]* at these levels and in the top layer with living *Sphagnum* mosses in the surface cores. Mean  $\pm$  SD given with the *P* values (*t*-test) for the differences between sites ( $n = 6$  and  $n = 9$  for the bog and fen sites, respectively).

Level	Depth (cm)			Dry bulk density (g dm <sup>-3</sup> )			[C] (mg g <sup>-1</sup> )			
	Site	Bog	Fen	<i>P</i>	Bog	Fen	<i>P</i>	Bog	Fen	<i>P</i>
Top		0	0	-	27±9	15±6	0.006	490±10	484±13	0.194
<i>LDL</i>		7.3±4.0	3.2±2.1	0.014	29±3	13±2	<0.001	478±19	473±13	0.180
<i>NPL</i>		22.8±6.2	28.4±7.1	0.082	81±26	58±29	0.083	508±18	488±21	0.044

between small depths (Figure 2). The depth interval between the *LDL* and *NPL* was greater at the fen than at the bog site ( $26 \pm 7\text{ cm}$  compared with  $15 \pm 5\text{ cm}$ ;  $P = 0.008$ ; mean  $\pm$  SD, *t*-test). *[C]* increased slightly at the bog site, but hardly at the fen site ( $P = 0.033$  and  $P = 0.062$ , respectively; *t*-test). *DBD* increased with depth and was larger throughout at the bog than at the fen site ( $P \leq 0.05$ ).

In the top layer with living mosses the difference in *[N]* between sites was insignificant (means 8.5

and  $9.8\text{ mg g}^{-1}$  at the bog and fen site, respectively;  $P = 0.131$ ; *t*-test). At the *LDL*, too, this difference was insignificant both if calculated on a mass basis as  $\text{mg g}^{-1}$  ( $P = 0.121$ , ranges  $3.9\text{--}5.8$  and  $4.8\text{--}8.9\text{ mg g}^{-1}$  at the bog and fen site, respectively), or on a volume basis as  $\text{mg dm}^{-3}$  ( $P = 0.262$ ; ranges  $0.12\text{--}0.24$  and  $0.07\text{--}0.25\text{ g dm}^{-3}$  at the bog and fen site, respectively). Below the *LDL*, *[N]* increased with depth. At the bottom of the acrotelm it was much larger at the fen site than at the bog site (Table 3).

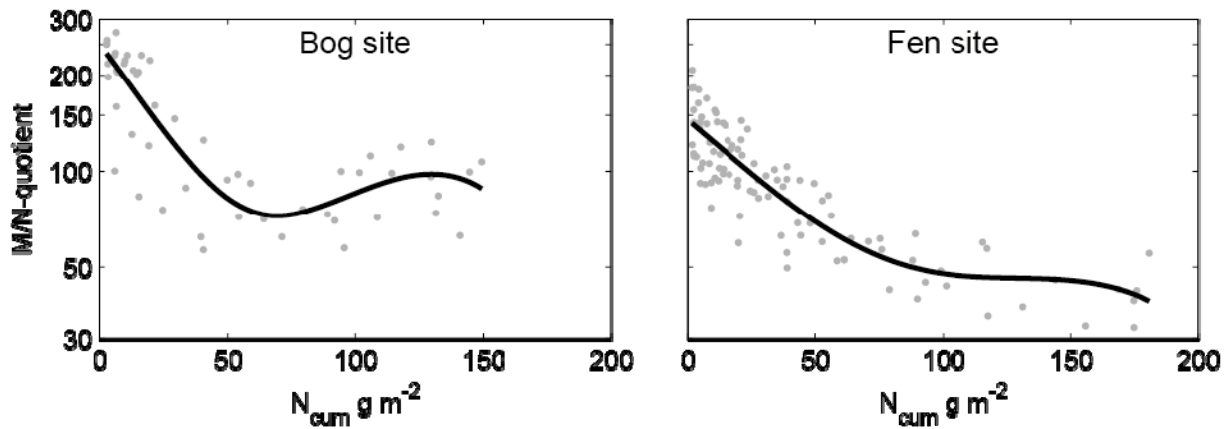


Figure 2. The variation of the  $M/N$  quotient (dry mass/ $N$  mass) with depth as  $N_{cum}$  below the  $LDL$  in the acrotelm and uppermost part of the catotelm. Data from the surface cores. Third degree polynomials fitted to the data with  $R^2 = 0.704$  ( $n = 52$ ) and  $R^2 = 0.784$  ( $n = 101$ ) for the bog site and fen site, respectively.

Table 3. Data for  $LDL$  and  $DDL$  related to the progress of the decay process in the acrotelm. For the  $LDL$  the data refer to the sample with the lowest  $[N]$  for the site (Malmer *et al.* 2011). The depth below surface is obtained from a third degree polynomial of the depth in cm in relation to  $N_{cum}$ . The rest of the data were obtained from the polynomials in Figure 2.

Level	Attribute and (units)	Site	
		Bog	Fen
<i>Litter deposition level (LDL)</i>	$[N]$ ( $\text{mg g}^{-1}$ )	4.0	4.8
	$M/N$ quotient	249	208
<i>Decay decrease level (DDL)</i>	$[N]$ ( $\text{mg g}^{-1}$ )	13.7	25
	$M/N$ quotient	73	41
	$N_{cum}$ ( $\text{g m}^{-2}$ )	71	120
	Depth (cm)	21	27

Concurrently with decomposition of the litter the  $M/N$  quotient decreased with depth below  $LDL$  (Figure 2). At the bog site the slope in the upper part of the fitted polynomial ( $N_{cum} < 10 \text{ g m}^{-2}$ ) gives  $k = 0.039 \text{ a}^{-1}$  (Malmer *et al.* 2011 and Equation 2). At the fen site four cores providing sufficient resolution in the upper samples give  $k = 0.050 \text{ a}^{-1}$ , a somewhat uncertain and probably conservative value. The  $DDL$  was indicated at the bog site by the distinct minimum of the polynomial and at the fen site by the polynomial reaching a constant value at which  $[N]$  and  $N_{cum}$  were both greater than at the bog site (Table 3) indicating a greater total decay

loss and a greater depth to the  $DDL$  than at the bog site. The residence time for the litter in the acrotelm may be longer at the fen site than at the bog site, although not as long as indicated by  $N_{cum}$ .

#### Water level

Whereas high water tables occur in the mire at any time of the year low ones occur only during dry periods in summer (Malmer 1962). During a period with low subsoil water level in the surroundings the water table hardly changed at the fen site despite the fact that at the bog site the precipitation raised it by  $\geq 4 \text{ cm}$  (Figure 3). In contrast, during a period with

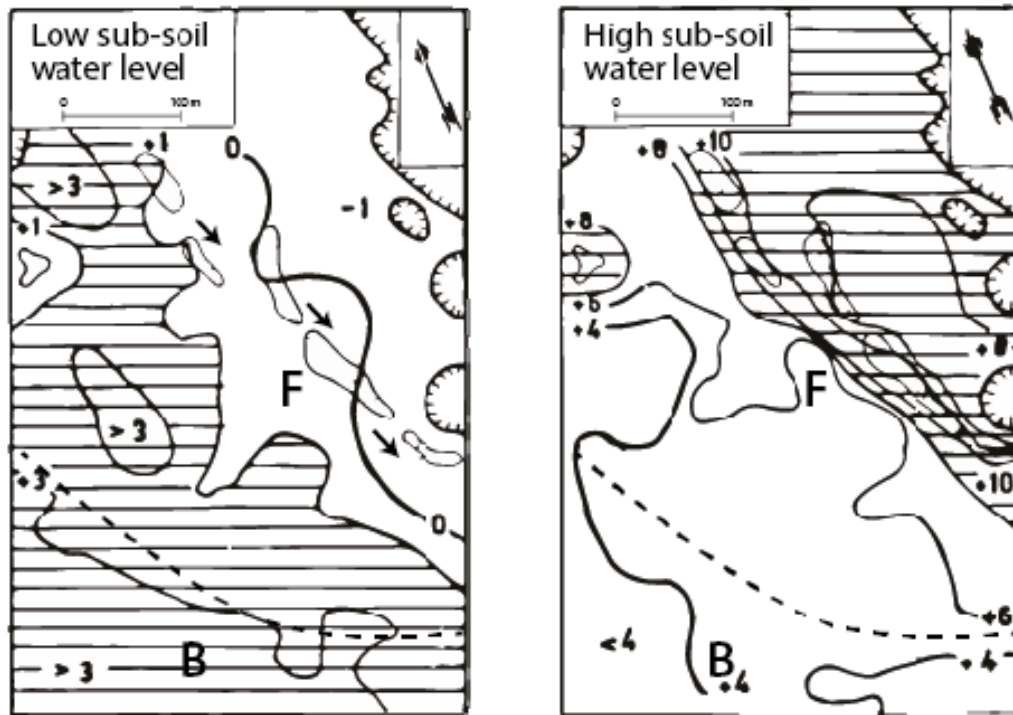


Figure 3. Changes in the water table in the Stattute area during two periods in 1954, one with low (left) and one with high (right) sub-soil water level in the surrounding mineral soils. The maps, based on Malmer (1962) but taken from Malmer & Andersson (1973), cover the central part of the Stattute area (Figure 1). The border to the mineral soil, the hydrologically determined limit between bog and fen (dashed line), the main water track in the fen (arrows), the bog (B) and fen (F) sites, and isolines (continuous lines, equidistance 2 cm) for equal and (only in the left figure) no change in water table are indicated. During the period with low sub-soil water level (June 8 to July 9) the precipitation was 67 mm (5 mm thereof on July 8) and the water table in an abandoned well at a former cottage 0.3 km north of the mire, sunk from 120 to 170 cm below the soil surface. Corresponding values for the period with high sub-soil water level (August 7 to August 16) were 83 mm precipitation and a rise of the water table from 50 to 10 cm below the surface in the well. The shaded parts of the maps indicate the areas with the greatest water table rises,  $\geq 1$  cm and  $\geq 8$  cm at the low and high subsoil water level, respectively. On August 16 the water level was close to its maximum all over the mire. On July 8 it was instead near the *MTWL* (median time water level) on the bog and rather close to its minimum at the fen site.

water-saturated mineral soils precipitation raised the water table in the fen twice as much as it did at the bog site. This shows that, particularly if the mire wetness is topogeneous, a fen (due to the supply of mineral soil water) has a much greater and an annually more variable flow of water than a bog nearby.

The water table residence curves (Figure 4) show that the annual water table amplitude was much less at the bog than at the fen site. This difference coincides with differences in the depth of the *DDL* (Tables 3 and 4). Another characteristic water level

in the residence curves is the median time water level (*MTWL*), defined as the level of the water table at which the cumulative number of days corresponds to half (120 days) of the period with unfrozen peat. Calculated from the fitted curves in Figure 4 it is close to the inflection point (Table 4) and corresponds to the compensation level discussed in Malmer (1962). At both sites the water level varied within  $\pm 2$  cm from the *MTWL* during more than half of the period with unfrozen peat.

On average the surfaces of the lawn communities at the fen and bog sites might be respectively 11 and



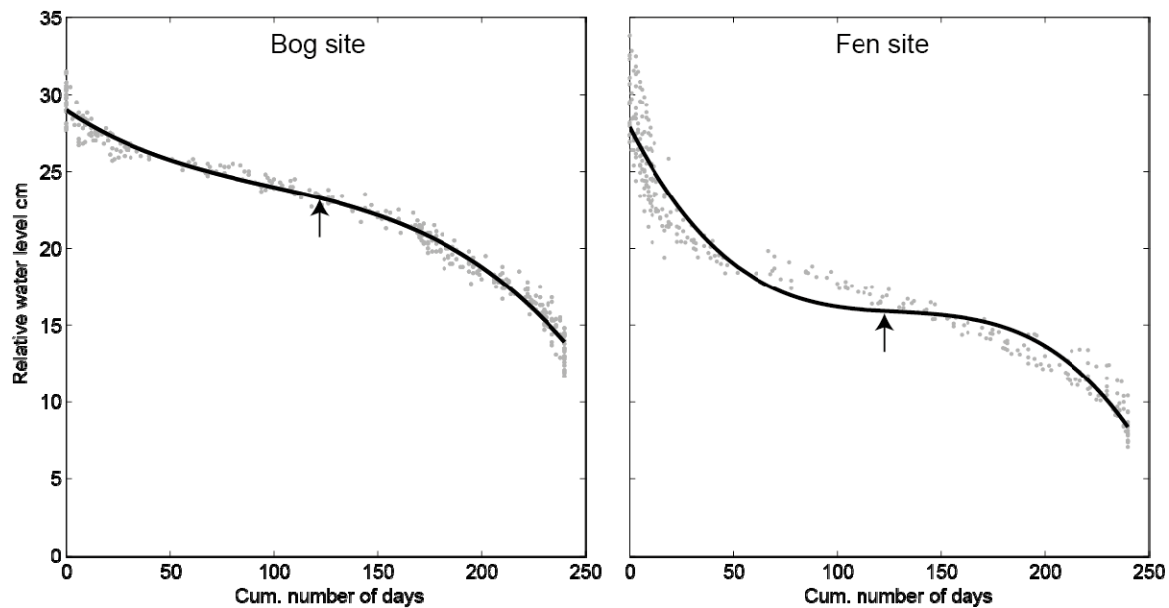


Figure 4. Water table residence curves for the bog (left) and fen (right) sites giving the length of the period with the water level exceeding each cm within the water table amplitude. Data from Malmer (1962). For the bog site the values include 23 measuring points distributed all over the non-wooded bog area. The fen site includes 16 measuring points. To standardise the scale for the measurements of the water table a residence curve was established for each point, a third degree polynomial fitted to this curve, the depth corresponding to the inflection point calculated, and the y-axis scale re-labelled setting the level for the inflection point to 0. Using this common scale the data points for each site (bog site  $n \geq 350$ ; fen site  $n \geq 300$ ) were combined in the figures after rearranging the scales on the y axis setting the mean maximum water level for each measuring point to 30 cm. The third degree polynomials fitted to the data give  $R^2 = 0.978$  and  $R^2 = 0.932$  for the bog and fen site, respectively. The arrows indicate the median day (the 120<sup>th</sup>) and the level of the MTWL obtained from the polynomials.

Table 4. Summary of the annual variation in the water table at the bog site and the fen site in terms of the water table amplitude and the maximum, minimum and median time (MTWL) water levels, as well as the proportional water saturation of the acrotelm within the ranges of water table amplitudes recorded during the period with unfrozen peat. The same data and scale as in Figure 4. Mean  $\pm$  SD given when possible. *T*-tests gave  $P \ll 0.001$  for the difference in water level minimum and amplitude between sites. Water saturation obtained by integration of the polynomials in Figure 4.

Site		Bog	Fen
Number of locations		23	16
<i>Calculated from measurements</i>	Maximum (cm)	$30.0 \pm 1.1$	$30.0 \pm 2.4$
	Minimum (cm)	$13.4 \pm 1.0$	$8.2 \pm 0.9$
	Amplitude (cm)	$16.2 \pm 0.8$	$21.7 \pm 2.7$
<i>Calculated from the fitted polynomials</i>	Inflection point (cm)	24.0	16.2
	MTWL (cm)	23.3	16.3
	Water saturation (%)	57	37

4 cm above the *MTWL* (Malmer 1962). The distance between the maximum water level and the *MTWL* was greater at the fen site than at the bog site (14 and 7 cm, respectively) (Table 4). Thus, the proportion of time during which the lower parts of the acrotelm were water-saturated was greater at the bog site than at the fen site. Also, in wooded bog areas the distance between the maximum water level and the *MTWL* is small despite water table amplitudes being as large as at the fen site (Malmer 1962). Measurements from the bog Ellergower Moss in south-western Scotland (Clymo & Pearce 1995) show not only the same water table amplitude and variation over the year as that at the present bog site but also a *MTWL* close to the maximum water level. For further references to studies with similar results see Malmer (1962, p. 159).

### The catotelm of the Åkhult mire during the last millennium

#### *Stratigraphy and macrofossils*

In the Stattute area peat formation began with *Betula-Cyperaceae* peat followed by *Cyperaceae-Sphagnum* peat which, from the end of the Sub-Boreal period, was replaced successively by the type of *Acutifolia* peat found over most of the mire (Svensson 1979). At both sites the main deep cores (Table 5) extended into this layer (Stage I) that was replaced upwards by *Cuspidata* peat (Stage IIa) followed by *Acutifolia* peat (Stage IIb) and finally by *Palustria* or *Palustria-Radicell* peat (Stage III). The transitions between stages could be recognised without difficulty in the supplementary cores, too. The degree of humification in this uniform

Table 5. Stages in the peat stratigraphy in the main deep cores obtained from lawn communities at the bog site and at the fen site. Depths in cm below the surface. The upper limit for Stage III in these cores is set close to the *NPL* (Table 2). Degree of humification according to the von Post scale.

	Bog site		Fen site	
	Depth (cm)	Peat characteristics	Depth (cm)	Peat characteristics
<i>Acrotelm</i>	0–15	H < 1. Decomposing litter.	0–20	H < 1. Decomposing litter.
<i>Stage III</i>	15–45	H4–5. Uniform <i>Magellanicum</i> peat with a little <i>Cuspidata</i> mixed in.	20–52	H4–7. <i>Palustria-Radicell</i> peat.
	45–73	H3. Uniform <i>Magellanicum</i> peat.		
	73–84	H5–7. <i>Palustria</i> peat with a little <i>Cuspidata</i> .		
<i>Stage IIb</i>	84–120	H3–4. <i>Acutifolia</i> peat mixed with <i>Palustria</i> peat.	60–95	H3. <i>Acutifolia</i> peat.
<i>Stage IIa</i>	120–132	H3. <i>Cuspidata</i> peat.	95–126	H3. <i>Cuspidata</i> peat.
			126–132	H6. <i>Cuspidata</i> peat with numerous radicells.
<i>Stage I</i>	132–180	H2–3. Uniform <i>Acutifolia</i> peat.	132–182	H2–3. Uniform <i>Acutifolia</i> peat.
	180–>200	H2–4. Uniform <i>Acutifolia</i> peat with much <i>Eriophorum vaginatum</i> .	182–>200	H5. Fen stage with <i>Palustria</i> peat.

*Sphagnum* peat did not vary appreciably within the cores.

During Stage I the same type of ombrotrophic bog vegetation rich in hummocks grew at both sites (Table 6). The fen plant limit may then have followed the present row of brook pools (Figure 1). Since macrofossils of exclusive fen plants were found at both sites throughout Stage II, the fen plant limit must have been >300 m from its position during Stage I and farther out on the mire than today. A wet-growing *Sphagnum* vegetation with some graminaceous plants characterised Stage IIa ('wet-growing' is used for species such as *S. cuspidatum*, that normally grow in hollows or pools). During Stage IIb with much *Acutifolia* peat and a lower frequency of exclusive fen plants the vegetation was probably similar to that presently found near the fen plant limit (the *Narthecium* zone, Malmer 1962). For Stage III the macrofossil content indicates the same types of vegetation as those occurring at the sites today and the fen plant limit may have been near its present position (Figure 1). As all cores were taken in lawns, the abundance of *Acutifolia* and *Ericaceous* spp. may have been under-estimated, particularly at the bog site (Svensson 1979). All species recorded as macrofossils also occur in the recent vegetation although *Narthecium ossifragum* was not noted until the end of Stage II.

#### Peat chemistry

At the fen site, the values for *DBD* increased slowly from Stage I to a maximum in the early part of Stage III (Figure 5). At the bog site distinct maxima were found at the ends of Stages II and III and a minimum at the beginning of Stage III. At both sites low *[N]* characterised Stages I and IIa (minimum 2.4 mg g<sup>-1</sup>). At the fen site the low *[N]* increased four-fold through Stage IIb until the transition to Stage III. At the bog site *[N]* instead had a maximum at the end of Stage II but a distinct minimum after the transition to Stage III that was followed by a gradual increase from <5 to 13–14 mg g<sup>-1</sup> at present. The values for *[C]* were usually >500 mg g<sup>-1</sup>, except at the fen site during Stage II.

#### Age determinations

At the fen site the bottom-most layer of the *Acutifolia* peat in Stage I is dated to 1230 cal. BP (Table 7, LuA 5736; AD 720) but at the bog site it may be considerably older. The duration of Stage II is problematic because the 95 % probability range

for the age of the samples approaches the duration of the stage. For the beginning of the stage the range of the dates (bog site Lu 2390, LuA 5730; fen site Lu 2392, Lu 2394, LuA 5666) is 1080–930 cal. BP giving a mean of 1010 cal. BP (AD 940). That value may be the best estimate possible, since the period of changes in the area may have been shorter than a century. The transitions from Stage II to Stage III may not be contemporary at the sites. For the bog site the date 620 cal. BP (LuA 5729; AD 1330) should be preferred for stratigraphical reasons (Malmer *et al.* 2011). For the fen site the mean of sample LuA 5667 and an alternative date for LuA 5734, 830 cal. BP (870–790 cal. BP; 17 %) gives 800 cal. BP (AD 1150) as the date for this transition. The mean of Lu 2393 and LuA 5735 at the fen site gives the date 910 cal. BP for the transition from Stage IIa to IIb. The end of Stage III is arbitrarily given an age for both sites of 100 years prior to sampling or AD 1880 (Malmer *et al.* 2011). For a summary, see Table 8.

#### Peat growth and mass accretion

Calculated separately for each stage, the height increment and mass accretion varied only at the fen site (Table 8). The total mass accretion during Stages II and III was greater at the bog than at the fen site (50 and 34 or as carbon 26 and 18 kg m<sup>-2</sup>, respectively). Neither the height increment (Table 5) nor the N accretion rates differed either between the sites or between Stages II and III (overall rates 0.58 and 0.48 g m<sup>-2</sup> a<sup>-1</sup>, respectively; in a core at another site 0.54 g m<sup>-2</sup> a<sup>-1</sup>). The loss of mass through decomposition in the acrotelm may thus be the main reason for the variation in *[N]* over time during these stages (Malmer *et al.* 2011 and references therein). The lower N accretion rate in Stage I may reflect a lower N supply rate, since a decrease in N around 1000 cal. BP has also been documented at the Store Mosse mire (Malmer *et al.* 1997).

Stage II began at both sites with rapidly increasing rates of mass accretion and height followed by slower decreases (Figure 6). Through Stage III these rates remained low at the fen site while at the bog site they increased rapidly at first and then decreased slowly to present values. For the fen site, in particular, the magnitude of the peak values is somewhat uncertain because of the uncertainty of the age determinations, but similar accretion rates have been estimated for bog peat layers from the same period at the Store Mosse mire (Malmer & Wallén 1999).

Table 6. Macrofossils in the samples from the deep cores. All samples from Stages I to III in the main and supplementary cores are included. The record of *Carex* in Stage I at the fen site refers to roots that had grown down from Stage IIa. At the bog site the record of *C. limosa* in Stage III refers to one sample from the bottom of the stage. The species occurs on bogs in other regions.

Site	Bog site				Fen site			
Stage	I	IIa	IIb	III	I	IIa	IIb	III
Number of samples analysed	23	18	12	9	17	19	21	11
<i>Mean abundance for major groups of plant macrofossils (% cover)</i>								
Vascular plants, above-ground parts	4	2	8	4	4	4	7	12
Vascular plants, below-ground parts	15	20	17	12	13	15	16	47
<i>Sphagnum</i> Section <i>Acutifolia</i>	63	5	36	1	74	8	69	10
<i>Sphagnum</i> Section <i>Palustria</i>	3	32	31	52	2	23	3	17
<i>Sphagnum</i> Section <i>Cuspidata</i>	9	36	7	33	2	46	3	10
<i>Frequencies of selected plant macrofossils (%). For clarity, '0' is shown as '~'.</i>								
<i>Exclusive fen plant species</i>								
<i>Narthecium ossifragum</i>	~	~	17	~	~	16	~	18
<i>Carex</i> , epidermis	~	28	8	~	~	5	19	9
<i>Carex rostrata</i> , below ground	~	44	8	~	6	16	~	55
<i>Carex limosa</i>	~	17	~	11	~	~	~	9
<i>Rhynchospora fusca</i>	~	~	~	~	~	~	5	9
<i>Calliergon stramineum</i>	~	~	~	~	~	11	~	~
<i>Sphagnum majus</i>	~	~	17	~	~	26	~	64
<i>Sphagnum subsecundum</i>	~	~	~	~	~	~	~	18
<i>Uniformly distributed plant species</i>								
<i>Calluna vulgaris</i> , leaves	13	~	~	~	~	~	~	~
<i>Ericaceae</i> , wood & leaves	91	44	75	67	41	58	48	73
<i>Ericaceae</i> , radicells	100	28	83	67	100	79	81	27
<i>Vaccinium oxycoccos</i>	4	11	~	11	~	~	19	9
<i>Eriophorum vaginatum</i> , epidermis	52	83	75	22	12	21	38	64
<i>Eriophorum vaginatum</i> , radicells	91	100	50	67	24	63	76	45
<i>Rhynchospora alba</i>	~	~	~	~	~	~	~	9
<i>Trichophorum caespitosum</i>	~	~	~	56	~	5	14	55
<i>Sphagnum fuscum</i>	83	28	50	~	29	~	100	36
<i>Sphagnum rubellum</i>	87	11	42	~	35	42	86	9
<i>Sphagnum magellanicum</i>	78	72	100	89	24	42	38	36
<i>Sphagnum papillosum</i>	0	6	50	22	12	58	29	36
<i>Sphagnum balticum</i>	9	50	50	~	6	58	19	~
<i>Sphagnum cuspidatum</i>	57	94	50	~	12	58	10	27
<i>Sphagnum tenellum</i>	9	56	33	11	~	37	~	27

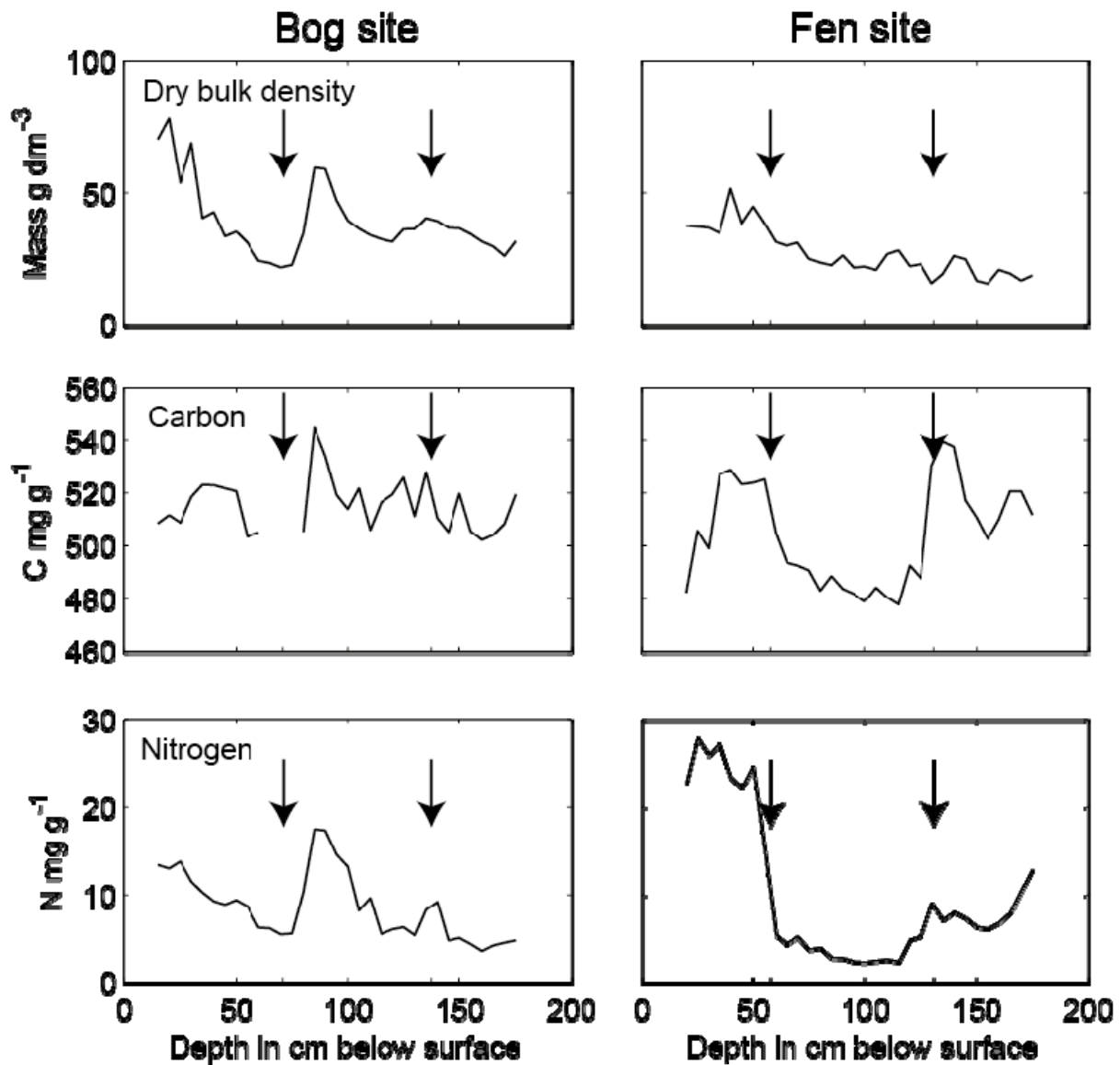


Figure 5. Variation in dry bulk density,  $[C]$  and  $[N]$  with depth in the catotelm at the bog site (left column) and fen site (right column). Data from the main deep cores. The arrows indicate the limits between the stratigraphical stages.



Table 7. All  $^{14}\text{C}$ -age determinations in the deep cores from the two sites. Samples marked Lu refer to the main cores and LuA to the supplementary cores. The SDs of the samples have been revised (Göran Skog, in litt.) prior to the re-calculation to calendar years (Stuiver & Reimer 1993). The estimated age is the median of the age range having the highest probability. Year cal. BP = 0 is AD 1950.

Site	Lab. No.	Depth of sample (cm)	Peat characteristics	$^{14}\text{C}$ -age BP (1 SD)	Estimated age cal. BP (range)	Probability for estimated age (range at 95 %)
<i>Bog site</i>	LuA 5729	80–82	Slightly humified <i>Magellanicum</i> peat above humified peat with <i>Carex</i> .	670 (± 90)	620 (680–550)	68 % (770–510)
	Lu 2389	86–90	Moderately humified <i>Fusum</i> peat below <i>Magellanicum</i> peat.	820 (± 45)	720 (765–675)	68 % (890–660)
	Lu 2390	122–126	Moderately humified <i>Cuspidata</i> peat with <i>Rubellum</i> above <i>Fusum</i> peat.	1110 (± 45)	1010 (1060–960)	68 % (1170–930)
	LuA 5730	98–100	Humified <i>Acutifolia</i> peat below humified peat with <i>Carex</i> .	1155 (± 90)	1080 (1180–970)	68 % (1270–920)
<i>Fen site</i>	LuA 5734	35–38	Humified <i>Fusum</i> peat below <i>Radicell</i> peat.	1025 (± 90)	940 (1010–880)	43 % (1170–730)
	LuA 5667	38–40	Humified <i>Acutifolia</i> peat below <i>Radicell</i> peat.	890 (± 35)	770 (800–730)	32 % (920–720)
	Lu 2393	70–73	Moderately humified <i>Fusum</i> peat above <i>Cuspidata</i> peat.	970 (± 45)	830 (870–790)	39 % (970–760)
	LuA 5735	90–93	Moderately humified <i>Acutifolia</i> peat above <i>Cuspidata</i> peat.	1040 (± 90)	980 (1060–900)	55 % (1180–740)
	Lu 2394	134–137	Moderately humified <i>Rubellum</i> peat below <i>Cuspidata</i> peat.	990 (± 50)	930 (960–900)	37 % (1050–760)
	LuA 5666	137–139	Moderately humified <i>Acutifolia</i> peat below <i>Cuspidata</i> peat.	1060 (± 50)	960 (1000–920)	54 % (1070–790)
	LuA 5736	182–185	Humified <i>Palustria</i> peat above <i>Radicell</i> peat.	1315 (± 80)	1230 (1310–1140)	68 % (1370–1050)
<i>In the fen but outside the fen site</i>	Lu 2392	117–120	Slightly humified <i>Cuspidata</i> peat above limit to <i>Acutifolia</i> peat.	1150 (± 45)	1050 (1140–970)	64 % (1230–930)

Table 8. Ages and means of the height increments and accretion rates for mass, C and N in the three developmental stages at the two sites. Year cal. BP = 0 is AD 1950.

	Stage	Bog site	Fen site
Age of upper level (year cal. BP)	Stage III	70	70
	Stage II	620	800
	Stage I	1010	1010
Duration of stage (years)	Acrotelm	100	100
	Stage III	550	730
	Stage II	390	210
	Stage I	> 300	220
Height increment (cm a <sup>-1</sup> )	Stage III	0.13	0.05
	Stage II	0.13	0.38
	Stage I	-	0.20
Accretion of mass (g m <sup>-2</sup> a <sup>-1</sup> )	Stage III	52.9	19.3
	Stage II	52.9	97.7
	Stage I	47.3	40.8
Accretion of C (g m <sup>-2</sup> a <sup>-1</sup> )	Stage III	26.9	9.91
	Stage II	27.7	48.1
	Stage I	-	21.2
Accretion of N (g m <sup>-2</sup> a <sup>-1</sup> )	Stage III	0.56	0.48
	Stage II	0.61	0.49

## DISCUSSION

### Input and decay in the acrotelm

#### *Mass balance*

On the Åkhult mire the litter input at the bog site was smaller than that at the fen site (Table 9), primarily because the litter input in the lawns at the fen site was twice that at the bog site (Table 1). This difference as well as the difference in plant species occurrences is due to differences in nutrient availability and pH despite the fact that most of the mineral soil water supplied to the Åkhult mire is

topogenous surface water which is poor in plant nutrients (Troedsson 1955, Malmer 1962). The difference in litter input between the sites may be even greater than shown because of the uncertainty in the estimate of the input at the fen site. The input of N to the acrotelm at litter formation ought to be greater at the fen site than at the bog site but the accretion in the catotelm did not differ (Table 8), probably because of greater losses of N as DOM in the runoff.

The recent mass accretion in the catotelm (Table 9, as C ~20 g m<sup>-2</sup> a<sup>-1</sup>) was less than the lowest value (30 g C m<sup>-2</sup> a<sup>-1</sup>) given by Turunen (2003) for

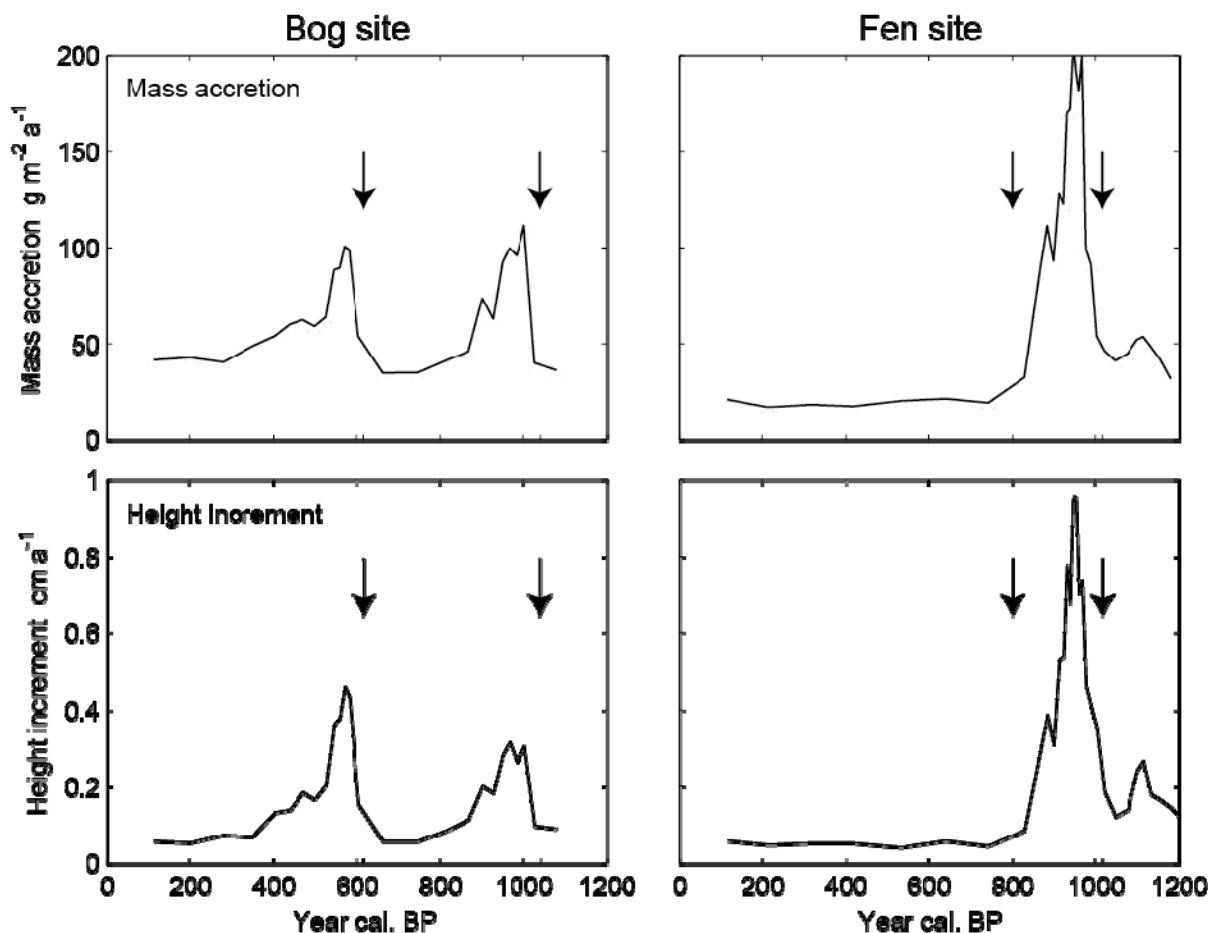


Figure 6. The variation with time in mass accretion (upper row) and height increment (lower row) rates in the catotelm at the bog (left) and fen (right) sites. Data from the main deep cores. The ages (cal. BP) refer to the midpoint of each 5 cm sample and have been calculated separately for each stage using the  $^{14}\text{C}$  dates and N accretion rates in Table 8. The arrows indicate the limits between the stratigraphical stages.

boreal and subarctic mires. It also represented only a small share of the input to the acrotelm (bog site 18 %, fen site 7 %). The total loss of mass in the acrotelm at the bog site was only two thirds of that at the fen site but the mass accretion rate was nearly twice that at the fen site. DOM was nearly 50 % higher at the fen than at the bog site, probably because of a greater water flow (Malmer *et al.* 2011).

#### Processes in the acrotelm

In *Sphagnum* mires the growth in height of hummocks is limited by the water supply to their upper parts (Belyea & Clymo 2001) whereas the maximum water level sets the lower limit for productive hummock vegetation (the “*Calluna*

limit”, Malmer 1962). Thus, water regimes with the *MTWL* (Table 4) close to the maximum water level (as at the bog site) improve the growth of hummocks while a *MTWL* in the lower part of the water table amplitude (as at the fen site) disfavour hummocks at the expense of lawns with smaller *DBD* (Table 2). Thus, the water table regime appears as a major determinant of the surface microtopography. Accordingly, the resistance to water flow in the acrotelm is usually weaker in a fen than in a bog with more hummocks (Ingram 1983, Clymo 2004). The system of hummocks and lawns in *Sphagnum* mires also has a damping effect on the water level variation, in a fen because of the ability to withstand the peak flows and in a bog to maintain an adequate water table close to the *MTWL*.

Table 9. The recent mass balance. For the bog site, all values are taken from Malmer *et al.* (2011). For the fen site the litter input to the acrotelm is taken from Table 1 with account being taken of the proportion of vegetation structures (see sub-section “Sampling sites” in Methods), the decomposition calculated from  $[N]$  at *LDL* and *DDL* (Table 3), the mass accretion in the catotelm from the uppermost sample in the main core (Figure 6) covering a period of ~100 years, and DOM from the difference between total loss and decomposition.

	Specification	Designation in Equation 1	Bog site $\text{g m}^{-2} \text{a}^{-1}$	Fen site $\text{g m}^{-2} \text{a}^{-1}$
<i>Structural organic matter</i>	Litter input to acrotelm	$M_0$	214	302
	Accretion in catotelm	$M_A$	38	21
<i>Loss of organic matter</i>	Decomposition	$M_D$	150	244
	DOM in drainage water	$M_E$	25	37
	Total loss	$M_D + M_E$	176	281

The decay loss in the acrotelm was nearly  $100 \text{ g m}^{-2} \text{a}^{-1}$  greater at the fen site than at the bog site (Table 9). There may be three factors contributing to this greater decay loss: (1) the greater abundance of vascular plants forming a litter which is on average less recalcitrant than *Sphagnum* litter (Johnson & Damman 1993, Belyea 1996) and with roots forming exudates rich in C (e.g., Jauhiainen *et al.* 1998); (2) longer periods with oxic or near oxic conditions in the middle part of the acrotelm because of the lower *MTWL*; and (3) the greater water table amplitude resulting in a deeper acrotelm, cf. Figure 4, Table 4. The first and second of these factors may increase the decay rate in the upper parts of the acrotelm while the third factor creates more time and space for the decay process and perhaps a more diverse microbial community (Clymo & Pearce 1995). Down to the depth with the same *M/N* quotient as at the *DDL* at the bog site (Figure 2, Table 3) the decay loss at the fen site was ~30 % greater than at the bog site despite a shorter period of time for the process. The rest of the greater decay loss at the fen site,  $\sim 50 \text{ g m}^{-2} \text{a}^{-1}$ , took place at a smaller rate below that level. Obviously, the water table regime appears to be a major determinant of the mass accretion rate in *Sphagnum* mires. These results concern the non-wooded mire expanse type of *Sphagnum*-mire vegetation (Sjörs 1948, Malmer 1962, 1986). This type is different from wooded

*Sphagnum*-mire vegetation (e.g., mire margin vegetation) where the water level amplitudes may be considerably greater because of the influences on the water table of the sub-soil water in the mineral soil.

#### Variation of the mass accretion rate in the catotelm

##### *Interpretation of the past development*

From bogs in Denmark and the UK Mauquoy *et al.* (2002) report minima in C accretion rates for periods during the Little Ice Age (*ca.* AD 1350–1850) as a result of lower *NPP* due to low temperatures and short growing seasons. Further, in a survey of the C accretion in peatlands (ombrotrophic and minerotrophic peatlands treated together) during the last millennium all over the high latitudes of the Northern Hemisphere, Charman *et al.* (2013) conclude that the variability in *NPP* may be more important than decomposition in determining the C accretion rate over time. The average decrease in the C accretion was  $0.0026 \text{ g m}^{-2} \text{a}^{-1}$ . On the other hand, in two mires in eastern boreal Canada the greatest C accretion rates were correlated with either wet conditions or high percentages of recalcitrant plant litter suggesting that the residence time in the acrotelm and the

nature of plant material had both influenced the mass accretion rates (Loisel & Garneau 2010). At the bog of the Store Mosse, south Sweden, the mass accretion decreased on average by  $\sim 0.14 \text{ g m}^{-2} \text{ a}^{-1}$  (as C  $\sim 0.07 \text{ g m}^{-2} \text{ a}^{-1}$ ) during the period AD 1150–1850 (Malmer & Wallén 1999). Bog formation there is dated to 5380 cal. BP and since then the variation in mass accretion rate has closely followed the variation in lake water levels with high and low water levels being contemporary with high and low mass accretion rates, respectively (Malmer *et al.* 1997). Obviously, this variation in mass accretion rate depended on the sum of decay loss and DOM export ( $M_D$  and  $M_E$  in Equation 1) which, in addition, increases with the growth in height of the bog surface improving the drainage and results in a thicker acrotelm and longer residence time there for the litter (Belyea & Malmer 2004).

#### *The catotelm during the last millennium*

The recent mass accretion rates in the catotelm of the Åkhult mire (Table 9, as C  $19 \text{ mg g}^{-2} \text{ a}^{-1}$ ) were close to the long-term average accretion rate ( $21 \text{ g C m}^{-2} \text{ a}^{-1}$ ) for northern mires (Clymo *et al.* 1998) but less than the lowest value ( $30 \text{ g C m}^{-2} \text{ a}^{-1}$ ) given for a number of boreal and subarctic mires (Turunen 2003). In the catotelm of the present sites the mass accretion rates most of the time varied in the range  $20\text{--}60 \text{ g m}^{-2} \text{ a}^{-1}$  but with peak values  $> 150 \text{ g m}^{-2} \text{ a}^{-1}$  (Figure 6). Obviously, the variation was the result of both autogenic and externally triggered processes affecting either the *NPP* or the decay process or both in the acrotelm.

At the present sites rough estimates of the variation over time in the total percentage loss of mass in the acrotelm show that the greatest values ( $> 90\%$ ) may be 2 to  $\sim 3$  times greater than the lowest ones. Over time the litter input to the acrotelm cannot be expected to have varied that much, particularly since the variation in *NPP* mainly depends on the supply of N and P (Aerts *et al.* 1992). However, an increase in the litter input rate to the acrotelm may have taken place at the shift from Stage I to Stage II because of the change to minerotrophic conditions (Figure 6). At the bog site a change in the litter input rate at the shift from Stage II to Stage III seems unlikely, particularly because of the small differences between *NPP* in fen lawns and bog hummocks (Table 1). Low decay resistance in the litter may have contributed to the high decay losses in Stage III at the fen site but any clear effects due to differences in that respect between the *Sphagnum* species are hardly detectable. Therefore, changes in the decay

conditions and DOM export must have been the main reason for the observed changes in mass accretion (Figure 6).

At both sites the vegetation in Stage I (Table 6) was similar to that in the recent bog and indicated ombrotrophic conditions. The mass accretion rate may have been about the same as at the present bog site (Figure 6). Since  $[N]$  was lower than at the present *DDL* (Figure 5, Table 3) both the decay loss in the acrotelm and the litter input to the acrotelm at the bog site may have been less than at present, as has also been observed at the Store Mosse bog (Malmer *et al.* 1997).

The bog of Stage I became colonised  $\sim 1000$  cal. BP (AD 950) by wet-growing *Sphagnum* species forming a pioneer type of vegetation with fen plants (Stage IIa, Table 6). That indicates an abrupt change to minerotrophic conditions and higher water tables over the whole Stattute area. Also the mass accretion rate increased more at the fen than at the bog site (Figure 6, peak values 5–10 times the recent ones) and more due to smaller losses than higher productivity. A pollen diagram from the mire shows contemporary increases in *Corylus*, *Fagus*, *Picea* and *Juniperus* indicating vegetation changes in the surrounding landscape as well (Svensson 1979). A contemporary increase in precipitation can be inferred from rising lake water levels (Digerfeldt 1988, Hammarlund *et al.* 2003) and precipitation reconstructions (Büntgen *et al.* 2011). At the Store Mosse bog, similar increases in the mass accretion rate have been dated to 1070–940 cal. BP (Malmer *et al.* 1997). Further, along the margin of that bog *Carex-Cuspidata* peat layers indicate contemporary flooding (Svensson 1988). Several other mire studies suggest similar climatic changes in other parts of Sweden during this period (Rundgren 2008, Andersson 2010, and references therein).

Further development (Stage IIb) resulted at both sites in the establishment of a hummock/lawn fen community (Table 6) and decreasing mass accretion rates due to increasing decay losses because of a progressively deeper acrotelm (Figure 6). In short, the development during Stage II appears to have been initiated at both sites by a “catastrophic” event of climatic origin in which a bog ecosystem was replaced by a dynamic fen ecosystem with a large mass accretion rate. The subsequent autogenic succession ended in two different, still persisting systems (Stage III) which are dealt with separately in the following two paragraphs.

At the fen site the transition to Stage III  $\sim 800$  cal. BP (AD 1150) is seen as a change to a lawn vegetation richer than before in vascular plant



species but with fewer hummock plant species (Table 6). Occurrences of fen plants indicate continued minerotrophic conditions. At the same time the mass accretion and height increment rates suddenly decreased to the same values as today (Figure 6). These changes may have been triggered by changes in the directions of the flow of water to and through the fen owing to rapid peat accumulation during Stage II and resulting in increased water table amplitudes as indicated by the decrease in abundance of *Acutifolia* spp. Since then the water table regime disfavoured the formation of hummocks and thus preserved the conditions once they were established.

At the bog site the supply of mineral soil water ceased at the beginning of Stage III, 620 cal. BP (AD 1330) as indicated by the disappearance of fen plants (Table 6). The new ombrogenous water regime rapidly facilitated an expansion of the hummock vegetation (Svensson 1979), decreased decay loss and increased mass accretion and height increment rates (Figure 6). The start of this development was contemporary with the upper limit of one of the layers with *Carex-Cuspidata* peat at the margin of the Store Mosse bog dated to 680 cal. BP (Svensson 1988;  $^{14}\text{C}$ -age 770 BP). A contemporary decrease in climatic humidity as indicated by Digerfeldt (1988) and Büntgen *et al.* (2011) may have triggered the process.

Since ~500 cal. BP the mass accretion and height increment rates at the bog site have been decreasing (Figure 6) due to the progressively improved drainage resulting in the same autogenic process as that which is going on at the same time in the Store Mosse bog (Belyea & Malmer 2004). In ombrotrophic peat  $[\text{N}]$  seems rarely to exceed 14–15 mg g<sup>-1</sup> (Malmer & Wallén 1993, 1996, 1999; Malmer *et al.* 1997). A possible interpretation could then be that the recent balance between litter input and mass accretion (Table 9) should be rather stable but the recent mass accretion is ~20 % less than during the 19<sup>th</sup> century (Malmer *et al.* 2011). The fen plant limit, although fluctuating slightly (Gunnarsson *et al.* 2002), may have been close to its present position (Figure 1) since the beginning of Stage III. During the last 200 years the height increment rate at both sites has been the same, 0.6 mm a<sup>-1</sup>. Despite the mass accretion rate at the bog site being higher than at the fen site (Figure 6) it is hard to imagine any appreciable ongoing changes in the hydrology along this limit. It probably acts as a kind of water divide since most of the bog in the Stattute area drains in a SSE direction (Figure 1).

### About the shift from fen to bog

Shifts from fen to bog in peat layers usually seem to be contemporary with indications of a decrease in climatic humidity (Almquist-Jacobson & Foster 1995, Malmer *et al.* 1997, Hughes & Barber 2004). Moreover, in recent times the drainage of a fen resulted within a few years in a change to a type of bog vegetation (Tahvanainen 2011). In experiments comparing the growth of the bog species *Sphagnum fuscum* with that of two rich fen *Sphagnum* species at different water levels, Granath *et al.* (2010) found two thresholds supposed to affect the shift in vegetation from rich fen to bog, namely a low water level minimising the risk of flooding and a higher water level at which bog mosses became the most competitive species. The two thresholds differ in the same way as the position of the *MTWL* does between the fen site and bog site (Figure 4, Table 4). At the studied sites on the bog of the Store Mosse mire (Table 10) the development at the shifts from fen to bog was very similar to that at the bog site on the Åkhult mire (Figure 6). At Site A on the Store Mosse mire the macrofossils point to a development that ought to be expected from the results presented by Granath *et al.* (2010), namely a shift involving three successive stages of increase in the mass accretion and height increment rates from rich fen through poor fen to bog vegetation as a result of changes in both the quality of the supplied mineral soil water and the water regime. At Site B the shift from fen to bog 4750 years later is indicated by the expansion of bog hummock vegetation over vegetation dominated by lawns and carpets and with poor fen plants. At both sites the samples with *Sphagnum fuscum* peat represent peak values for the mass accretion rate and were followed by successively decreasing rates in an autogenic process like that at the Åkhult bog site. Both shifts are also contemporary with distinct decreases in lake water levels (Digerfeldt 1988). Changes in the *NPP* and litter input rate at these two shifts cannot be excluded but the distinct decreases in  $[\text{N}]$  at the transitions show that the main reason for the increased mass accretion rates was decrease in decay loss following the change from a geogenous to an ombrogenous water regime just as was found at the bog site of the Åkhult mire. Such an initial increase in mass accretion may strengthen the isolation of a mire area from the supply of mineral soil water and must be an important part of the process resulting in the formation of the permanent ombrotrophic conditions in raised bogs.

Table 10. Mass accretion and height increment rates in peat layers representing shifts from fen to bog in cores from the bog of Store Mosse mire. Means  $\pm$  SD are given. On Site A in the central part of the bog the shift from poor fen to bog peat has been dated to 5380 cal. BP (Malmer *et al.* 1997, Malmer & Wallén 1999). At Site B the data refer to a core sampled in 2002 (Malmer & Svensson, unpublished data) between the cores E24 and E25 in Svensson (1988) and the shift dated to 630 cal. BP (LuA 5662, 650–615 cal. BP, 28 %). The *P* values refer to *t*-tests of the differences between the layer with bog peat and the layer with poor fen peat below that.

Type of peat	Type of vegetation	Type of soil wetness	Length of period (yr)	<i>n</i>	[N] mg g <sup>-1</sup>	Mass accretion g m <sup>-2</sup> a <sup>-1</sup>	Height increment cm a <sup>-1</sup>
<i>Site A (depth 445–490 cm)</i>							
<i>Sphagnum fuscum</i> peat	Bog	Ombrogenous	140	3	4.9 $\pm$ 0.8	75 $\pm$ 11	0.12 $\pm$ 0.03
<i>Carex-Sphagnum</i> peat	Poor fen	Geogenous	430	3	11.4 $\pm$ 1.2	32 $\pm$ 3	0.03 $\pm$ 0.01
Radicell-brown moss peat	Rich fen	Geogenous	1160	3	22.1 $\pm$ 1.1	16 $\pm$ 0.8	0.01 $\pm$ 0.001
<i>t</i> -test				6	<i>P</i> = 0.001	<i>P</i> = 0.001	<i>P</i> < 0.001
<i>Site B (depth 100–140 cm)</i>							
<i>Sphagnum rubellum</i> peat	Bog	Ombrogenous	60	4	5.3 $\pm$ 0.2	113 $\pm$ 4	0.35 $\pm$ 0.02
<i>Sphagnum-Carex</i> peat	Poor Fen	Geogenous	130	4	11.0 $\pm$ 1.2	58 $\pm$ 17	0.16 $\pm$ 0.03
<i>t</i> -test				8	<i>P</i> = 0.006	<i>P</i> < 0.001	<i>P</i> < 0.001

## CONCLUSIONS

Both the productivity and the loss of mass in the acrotelm at the Åkhult mire were smaller at the bog site than at the fen site (Table 9). Due to the differences in the origin of the water supply the annual water table amplitude at the bog site was less and the *MTWL* closer to the maximum water level than at the fen site. That made the decay process less efficient at the bog site than at the fen site because of smaller acrotelm thickness and longer periods of

water-saturation there. The variation in the water table regime is thus a major determinant of the total loss of mass in the acrotelm and should be recognised as an important reason for the differentiation between bog and fen in *Sphagnum* mires and a major determinant of the vegetation structure.

During the last millennium the mass accretion has ranged from 40 to 110 g m<sup>-2</sup> a<sup>-1</sup> at the bog site and from 18 to ~180 g m<sup>-2</sup> a<sup>-1</sup> at the fen site, with the peak values at the beginning of Stage II and the

minima in recent times. The development of the peat layers shows that the water regime depended very much on the climatic humidity although an uneven peat accumulation changing the water track also seems to have brought about a change in the water regime in the fen. Depending on the effects on the water table regime, both increases and decreases in the climatic humidity triggered increases in the mass accretion rate. On the other hand, during periods with constant climatic humidity the mass accretion rate either remained constant or decreased with time because the height increment of the mire surface improves the drainage and in that way increases the thickness of the acrotelm and the decay loss.

For the development of an ombrotrophic raised bog from a topogenous fen the results presented from both mires give support for a process in two steps. The first step is an externally triggered decrease in the supply of mineral soil water. The increased influence of precipitation water on the water regime then results in smaller water table amplitudes and a rise of the *MTWL* from the lower to the upper part of the water table amplitude. This development facilitates an expansion of the hummock vegetation and rapid increases in the rates of mass accretion and height increment which enhance the isolation of the bog area from the supply of mineral soil water and make it permanent.

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## REFERENCES

- Aerts, R., Wallén, B. & Malmer, N. (1992) Growth-limiting nutrients in *Sphagnum*-dominated bogs subject to low and high atmospheric nitrogen supply. *Journal of Ecology*, 80, 131–140.
- Aldous, A.R. (2002) Nitrogen translocation in *Sphagnum* mosses: effects of atmospheric nitrogen deposition. *New Phytologist*, 156, 241–253.
- Almquist-Jacobson, H. & Foster, D.R. (1995) Toward an integrated model for raised-bog development: theory and field evidence. *Ecology*, 76, 2503–2516.
- Andersson, S. (2010) *Late Holocene Humidity Variability in Central Sweden*. Dissertations from the Department of Physical Geography and Quaternary Geology, 20, Stockholm University, 58 pp.
- Belyea, L.R. (1996) Separating the effects of litter quality and microenvironment on decomposition rates in a patterned peatland. *Oikos*, 77, 529–539.
- Belyea, L.R. & Baird, A.J. (2006) Beyond “The limits to peat bog growth”: cross-scale feedback in peatland development. *Ecological Monographs*, 76, 299–322.
- Belyea, L.R. & Clymo, R.S. (2001) Feedback control of the rate of peat formation. *Proceedings of the Royal Society of London*, B, 268, 1315–1321.
- Belyea, L.R. & Malmer, N. (2004) Carbon sequestration in peatlands: patterns and mechanisms of response to climate change. *Global Change Biology*, 10, 1043–1052.
- Büntgen, U., Tegel, W., Nicolussi, K., McCormick, M., Frank, D., Trouet, V., Kaplan, J.O., Herzog, F., Heussner, K.U., Wanner, H., Luterbacher, J. & Esper, J. (2011) 2500 years of European climate variability and human susceptibility. *Science*, 331, 578–582.
- Charman, D.J., Beilman D.W., Blaauw, M., Booth R.K., Brewer, S., Chambers, F.M., Christen, J.A., Gallego-Sala, A., Harrison, S.P., Hughes, P.D.M., Jackson, S.T., Korhola, A., Mauquoy, D., Mitchell, F.J.G., Prentice, I.C., Linden, M. van der, De Vleeschouwer, F., Yu, Z.C., Alm, J., Bauer, I.E., Corish, Y.M.C., Garneau, M., Hoh, V., Huang, Y., Karofeld, E., Le Roux, G., Loise, J., Moschen, R., Nichols, J.E., Nieminen, T.M., MacDonald, G.M., Phadtare, N.R., Rausch, N., Sillasoo, Ü., Swindles, G.T., Tuitila, E.-S., Ukonmaanaho, L., Väliranta, M., Bellen, S.van, Geel, B.van, Vitt, D.H. & Zhao, Y. (2013) Climate-related changes in peatland carbon accumulation during the last millennium. *Biogeosciences*, 10, 929–944.
- Clymo, R.S. (1965) Experiments on breakdown of *Sphagnum* in two bogs. *Journal of Ecology*, 53, 747–758.
- Clymo, R.S. (1984) The limits to peat bog growth. *Philosophical Transactions of the Royal Society of London*, B, 303, 605–654.
- Clymo, R.S. (2004) Hydraulic conductivity of peat at Ellergower Moss, Scotland. *Hydrological*

- Processes*, 18, 261–274.
- Clymo R.S. & Bryant, C.L. (2008) Diffusion and mass flow of dissolved carbon dioxide, methane, and dissolved organic carbon in a 7-m deep raised bog. *Geochimica et Cosmochimica Acta*, 72, 2048–2066.
- Clymo, R.S. & Pearce, D.M.E. (1995) Methane and carbon dioxide production in, transport through, and efflux from a peatland. *Philosophical Transactions of the Royal Society of London*, A, 350, 249–259.
- Clymo, R.S., Turunen, J. & Tolonen, K. (1998) Carbon accumulation in peatland. *Oikos*, 81, 368–388.
- Daniels, R.E. & Eddy, A. (1985) *Handbook of Sphagna*. Institute of Terrestrial Ecology, Huntingdon, 262 pp.
- Digerfeldt, G. (1988) Reconstruction and regional variation of Holocene lake-level fluctuations in Lake Bysjön, South Sweden. *Boreas*, 17, 162–182.
- Du Rietz, G.E. (1954) Die Mineralbodenwasserzeigergrenze als Grundlage einer natürlichen Zweigliederung der nord- und mitteleuropäischen Moore. (The mineral soil water limit as foundation for a natural division of the north and central European mire vegetation into two parts). *Vegetatio*, 5–6, 571–585 (in German).
- Fries, M. (1965) The Late Quaternary vegetation of Sweden. *Acta Phytogeographica Suecica*, 30, 269–280.
- Granath, G., Strengbom, J. & Rydin, H. (2010) Rapid ecosystem shifts in peatlands: linking plant physiology and succession. *Ecology*, 91, 3047–3058.
- Gunnarsson, U., Malmer, N. & Rydin, H. (2002) Dynamics or constancy in *Sphagnum* dominated mire ecosystems: a 40-year study. *Ecography*, 25, 685–704.
- Hammarlund, D., Björck, S., Buchardt, B., Israelson, C. & Thomsen, C.T. (2003) Rapid hydrological changes during the Holocene revealed by stable isotope records of lacustrine carbonates from Lake Igelsjön, southern Sweden. *Quaternary Science Reviews*, 22, 353–370.
- Hughes, P.D.M. & Barber, K.E. (2004) Contrasting pathways to ombrotrophy in three raised bogs from Ireland and Cumbria, England. *The Holocene*, 14, 65–77.
- Ingram, H.A.P. (1978) Soil layers in mires: function and terminology. *Journal of Soil Science*, 29, 224–227.
- Ingram, H.A.P. (1983) Hydrology. In: Gore, A.J.P. (ed.) *Mires: Swamp, Bog, Fen, and Moor, General Studies*. Ecosystems of the World, 4A, Elsevier, Amsterdam, 67–158.
- Jauhainen, J., Wallén, B. & Malmer, N. (1998) Potential  $\text{NH}_4^+$  and  $\text{NO}_3^-$  uptake in seven *Sphagnum* species. *New Phytologist*, 138, 287–293.
- Johnson, L.C. & Damman, A.W.H. (1993) Decay and its regulation in *Sphagnum* peatlands. *Advances in Bryology*, 5, 249–256.
- Loisel, J. & Garneau, M. (2010) Late Holocene palaeoecohydrology and carbon accumulation estimates from two boreal peat bogs in eastern Canada: potential and limits of multi-proxy archives. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 291, 493–533.
- Malmer, N. (1962) Studies on mire vegetation in the archaean area of southwestern Götaland (South Sweden). I. Vegetation and habitat conditions on the Åkhult mire. *Opera Botanica*, 7:1, 322 pp.
- Malmer, N. (1975) Development of bog mires. In: Hasler, A.D. (ed.) *Coupling of Land and Water Systems*, Ecological Studies 10, Springer-Verlag, Berlin-Heidelberg-New York, 85–92.
- Malmer, N. (1986) Vegetational gradients in relation to environmental conditions in northwestern European mires. *Canadian Journal of Botany*, 64, 375–383.
- Malmer, N. & Andersson, F. (1973) Botanisk ekologi (Plant ecology). In: *Svensk Naturvetenskap 1973 (Swedish Natural Science 1973)*. Sveriges Naturvetenskapliga Forskningsråd, Stockholm, 7–40 (in Swedish).
- Malmer, N., Svensson, G. & Wallén, B. (1997) Mass balance and nitrogen accumulation in hummocks on a South Swedish bog during the late Holocene. *Ecography*, 20, 535–549.
- Malmer, N., Svensson, G. & Wallén, B. (2011). Carbon and mass balance in a south Swedish ombrotrophic bog: processes and variation during recent centuries. *Mires and Peat* 8(1), 1–18.
- Malmer, N. & Wallén, B. (1993) Accumulation and release of organic matter in ombrotrophic bog hummocks - processes and regional variation. *Ecography*, 16, 193–211.
- Malmer, N. & Wallén, B. (1996) Peat formation and mass balance in sub-arctic ombrotrophic peatlands around Abisko, northern Scandinavia. *Ecological Bulletins*, 45, 79–92.
- Malmer, N. & Wallén, B. (1999) The dynamics of peat accumulation on bogs: mass balance of hummocks and hollows and its variation throughout a millennium. *Ecography*, 22, 736–750.



- Malmer, N. & Wallén, B. (2004) Input rates, decay losses and accumulation rates of carbon in bogs during the last millennium: internal processes and environmental changes. *The Holocene*, 14, 111–117.
- Mauquoy, D., Engelkes, T., Groot, M.H.M., Markesteijn, F., Oudejans, M.G., van der Plicht, J. & van Geel, B. (2002) High-resolution records of late-Holocene climate change and carbon accumulation in two north-west European ombrotrophic peat bogs. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 186, 275–310.
- Morris, P.J., Belyea, L.B. & Baird, A.J. (2011) Ecohydrological feedbacks in peatland development: a theoretical modelling study. *Journal of Ecology*, 99, 1180–1201.
- Økland, R.H., Økland, T. & Rydgren, K. (2001) A Scandinavian perspective on ecological gradients in north-west European mires: a reply to Wheeler and Proctor. *Journal of Ecology*, 89: 481–486.
- Raab, B. & Vedin, H. (eds.) (1996) *Klimat, Sjöar och Vattendrag (Climate, Lakes and Rivers)*. Sveriges Nationalatlas (National Atlas of Sweden), Swedish Meteorological and Hydrological Institute, Norrköping, 176 pp. (in Swedish).
- Roulet, N.T., Lafleur, P.M., Richard, P.J.H., Moore, T.R., Humphreys, E.R. & Bubier, J. (2007) Contemporary carbon balance and late Holocene accumulation in a northern peatland. *Global Change Biology*, 13, 397–411.
- Rundgren, M. (2008) Stratigraphy of peatlands in central and northern Sweden: evidence of Holocene climatic change and peat accumulation. *Geologiska Föreningen i Stockholm Förhandlingar*, 130, 95–107.
- Sjörs, H. (1948) Myrvegetation I Bergslagen (Mire vegetation in Bergslagen, Sweden). *Acta Physiographica Suecica*, 21, 298 pp. (in Swedish with an extensive summary in English).
- Stuiver, M. & Reimer, P.J. (1993) Extended  $^{14}\text{C}$  database and revised CALIB radiocarbon calibration program, Rev. 3.0.3. *Radiocarbon*, 35, 215–230.
- Svensson, G. (1979) *Utvecklingshistoriska Studier av Åkhultmyren. (Studies on the Development of the Åkhult Mire)*. Licentiate Thesis, Department of Plant Ecology, Lund University, Sweden, 127 pp., 4 Tables, 15 Figures and 29 diagrams (in Swedish).
- Svensson, G. (1986) Recognition of peat-forming plant communities from their peat deposits in two south Swedish bog complexes. *Vegetatio*, 66, 95–108.
- Svensson, G. (1988) Bog development and environmental conditions as shown by the stratigraphy of the Store Mosse mire in southern Sweden. *Boreas*, 17, 89–111.
- Tahvanainen, T. (2011) Abrupt ombrotrophication of a boreal aapa mire triggered by hydrological disturbance in the catchment. *Journal of Ecology*, 99, 404–415.
- Troedsson, T. (1955) *Vattnet i skogsmarken: studier med särskild hänsyn till ytvattnets, sjunkvattnets och grundvattnets uppkomst och sammansättning (Water in the Forest Soil: Studies with Special Reference to the Development and Composition of the Surface Water, Sinking Water and Sub-soil Water)*. Kunglig Skogshögskolans skrifter (Bulletin of the Royal School of Forestry), 20, 215 pp. (in Swedish).
- Turunen, J. (2003) Past and present carbon accumulation in undisturbed boreal and subarctic mires: a review. *Suo*, 54, 21–31.
- Wallén, B. (1983) Translocation of  $^{14}\text{C}$  in adventitiously rooting *Calluna vulgaris*. *Oikos*, 40, 241–248.
- Wallén, B. (1986) Above and below ground dry mass of the three main vascular plants on hummocks on a subarctic peat bog. *Oikos*, 46, 51–56.
- Wallén, B. (1992) Methods for studying below-ground production in mire ecosystems. *Suo*, 43, 155–162.
- Wheeler, B.D. & Proctor, M.C.F. (2000) Ecological gradients, subdivisions, and terminology of north-west European mires. *Journal of Ecology*, 88, 187–203.

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