Carbon and mass balance in a south Swedish ombrotrophic bog: processes and variation during recent centuries

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SUMMARY

This study, performed in 1982–2007, deals with the processes in the acrotelm and the subsequent addition (accretion) of material to the catotelm of an ombrotrophic bog in southern Sweden. It is based on analyses of C and N in biomass, necromass and mire water combined with age determinations by ^{210}Pb. The C input to the acrotelm was 102 g m^{-2} a^{-1} of which 69% was released through decay and the rest either retained as peat or exported as dissolved organic matter (DOM). The mean C accretion to the catotelm was 20–25% lower in 1900–1980 than in 1800–1900 due to the rising bog surface, continuously increasing acrotelm thickness and total decay loss. Annual runoff, determined indirectly from [Na$^+$] in precipitation and drainage water, varied more (range 200–770 mm) than the concentration of dissolved organic C (DOC; range 25–55 mg L^{-1}) and mainly determined DOC export. During 1993–2007, with high precipitation (mean 880 mm a^{-1}) and mild winters, the mean DOC export and C accretion to the catotelm were equal at 16 g m^{-2} a^{-1}. During 1953–1960, with lower precipitation (~700 mm a^{-1}) and “normal” winters, the DOC export and C accretion were probably about 9 and 23 g m^{-2}, respectively. The release of C to the atmosphere downstream from the bog was correspondingly lower. As a C sink, the bog at present may be half as efficient as it was 50–200 years ago. The DOC exported was accompanied by 25–50% of the N input in litter.

KEY WORDS: climate change, decay loss, DOC export, primary production, nitrogen.

INTRODUCTION

The most characteristic feature of peatlands is their unique capacity to accumulate structural organic matter as peat due to incomplete decay of the plant litter in the predominantly oxic acrotelm (depth ~0.2–0.4 m below the surface). Apart from the peat accreting to the anoxic catotelm, the main end products of the decay process are gaseous C compounds given off to the atmosphere and the non-structural dissolved organic matter (DOM) analysed as DOC (dissolved organic C) and exported in the drainage water. The result of peat formation is that the surface of the peatland rises continuously. This is most evident in ombrotrophic bogs, which are entirely dependent upon precipitation for water. The general significance of the peat formation process is illustrated by the fact that the amount of C permanently accumulated as peat in northern peatlands during the last 10,000 years (460 Gt) is of the same magnitude as the atmospheric C load (Clymo *et al.* 1998).

A framework for a model to study the conditions for peat growth and C accretion in an ombrotrophic bog should include the three main components of the mass and C balances of the acrotelm, namely the litter input to the acrotelm (M_0) resulting from C sequestration and net primary production (NPP) in the plant cover, the total loss of mass (M_D) and C during decomposition of the litter in the acrotelm, and the export rate (M_E) of DOM and DOC in the drainage water which travels mainly through the acrotelm (Ingram 1983). The rate of peat formation and the mass (M_A) and C accretion to the catotelm will then be

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

To derive the net C balance for the whole bog ecosystem it is necessary to include also the release of C from the catotelm, which occurs at a rate two or three orders of magnitude lower than for litter in the acrotelm (Clymo 1984).

The total decay loss from the litter in the acrotelm (M_D) increases with increasing temperature but is above all determined by the residence time of the litter in the acrotelm and its decay rate (k). Decay rate depends primarily on the decay resistance, which is particularly high in *Sphagnum* litter (Johnson & Damman 1993, Belyea 1996). The main determinant of litter residence time is the thickness of the acrotelm, which depends on the equilibrium between the rates of water supply, evapotranspiration and runoff, the latter being governed by the resistance exerted by structural organic matter and the slope of the surface (Belyea & Malmer 2004, Belyea & Baird 2006).

The limit between acrotelm and catotelm is to be regarded as a transitional zone rather than a distinct level (Clymo 1992). Dated deep peat cores have revealed variation in the rates of peat growth and C accretion to the catotelm due to both climatic changes and the height increment of the peat that in an autogenic process changes the hydrology and increases the runoff and, as a consequence, the decay loss in the acrotelm (Malmer *et al.* 1997, Belyea & Malmer 2004).

Globally, there are few bog sites for which the main components of the mass and C balances have been estimated (cf. Roulet *et al.* 2007). During recent decades development of the eddy covariance technique has made it possible to measure the exchange of C over areas of peatlands large enough to encompass the variation amongst microtopes (Waddington & Roulet 2000, Lafleur *et al.* 2003, Lund *et al.* 2007, Roulet *et al.* 2007). These studies have revealed astonishingly large variations in both seasonal and annual C balances and demonstrated a close dependence of the C balance on climatic conditions. However, the C balance obtained (net ecosystem exchange, NEE) is not fully comparable with the accretion of C to the catotelm as the NEE also includes both the slow release of C from the catotelm and the effect (although usually small) of changes in the C content of bio- and necromass in the acrotelm (cf. Lovett *et al.* 2006). Also, it does not take account of DOC export (M_E in Equation 1).

Malmer & Wallén (2004) showed that the net input of C to the catotelm of a large bog in southern Sweden had decreased from ~50 to ~8 g m^{-2} a^{-1} during the last millennium. For a smaller bog exposed to high atmospheric N pollution the recent rate of C accretion to the catotelm was almost zero (Gunnarsson *et al.* 2008), meaning that the overall net C balance was probably negative. Franzén (2006) studied 14 raised bogs and concluded that they had switched from being net C sinks to net sources because of increased decay losses. On the other hand, the NEE for a small plateau bog showed a C input to the bog of 21 g m^{-2} a^{-1} (Lund *et al.* 2007). Again, DOC export is not dealt with in any of these studies.

Contradictory results like these call for further studies on the C and mass balances of bogs with account given to all processes contributing to the model presented in Equation 1. The study which follows is based on conventional measurements of biomass and necromass, and focuses on quantifying the processes in the acrotelm and their relative importance for the accretion of mass and C to the catotelm of an ombrotrophic bog in southern Sweden. We expect a decreasing accretion rate during the last few centuries because of increasing decay losses (cf. Belyea & Malmer 2004). In a shorter time perspective we tentatively expect a further decrease in accretion due to increased DOM/DOC export resulting from the increased precipitation and milder winters of recent decades (Lindström & Alexandersson 2004, Alexandersson & Edquist 2006).

METHODS

Study site

This study was conducted on the Åkhult Mire (57°10' N, 14°30' E; altitude 225 m; area ~1 km^2; cf. Malmer 1962), which is situated in a rural area within the boreo-nemoral region of southern Sweden. During the period 1961–1990 the monthly mean temperature of the region ranged from -3°C (February) to +16°C (July), the length of the vegetation growth period (>5°C) was ~190 days and the mean annual precipitation ~700 mm (Raab & Vedin 1996). The runoff in the rivers is ~300 mm (Anonymous 2002). This mire offers unique possibilities for studying the export of DOC because the drainage water from the bog can be sampled without any mixing with minerogeneous water from fen or the surrounding forested areas.

The Åkhult Mire is a *Sphagnum* mire with a large ombrotrophic bog and extensive minerotrophic fen areas (Malmer 1962). Most of the bog (Figure 1) slopes to the south while the northern part, the Stattute area, is flatter. The bog drains to the Fiolen rivulet, partly *via* three brooklets cutting through the steep slope above the rivulet and partly as a diffuse trickling flow of surface water. In contrast to the non-wooded Stattute area the slope has a sparse cover of pine trees. The fen along the north-eastern margin and the adjacent forest drain mostly eastwards, but to a lesser extent also through a fen soak to the Fiolen rivulet.

Sampling and treatment of the samples

Litter input

The input of litter to the acrotelm was measured in the Stattute area of the bog following a ^{14}C labelling method described by Malmer & Wallén (1996, 1999). ^{14}C-labelled plots (0.04 or 0.10 m^2) were established on *Sphagnum*-dominated hummocks and lawns in 1980 and 1981. Cores (depth 30–40 cm) were sampled from the plots in the autumns of 1986

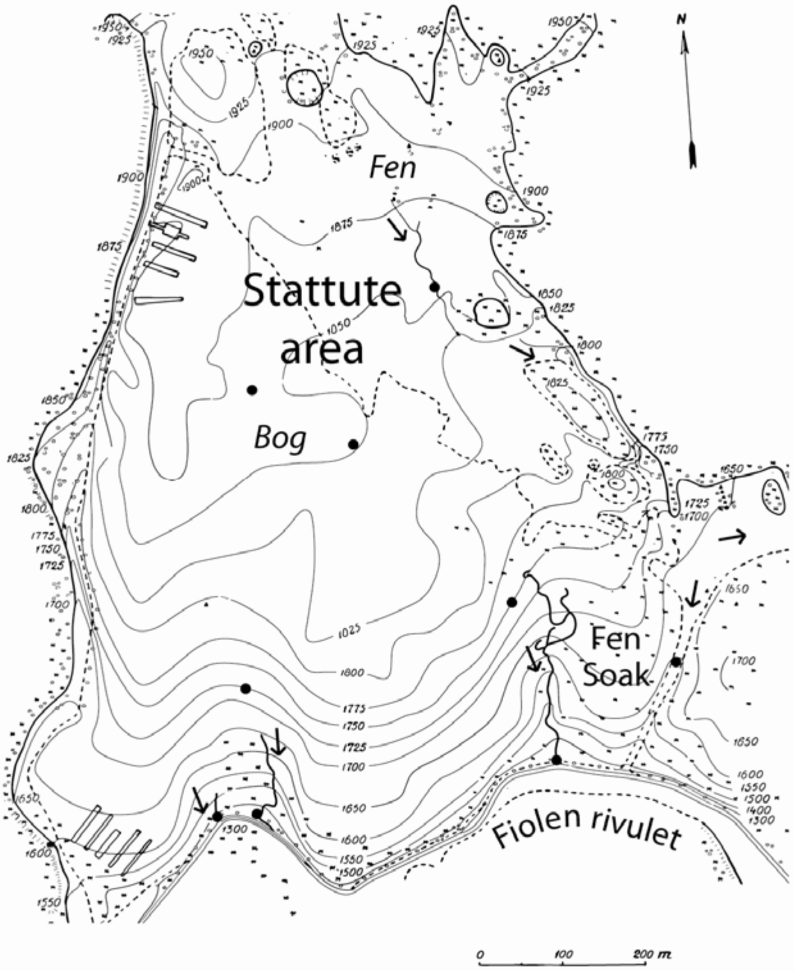

Figure 1. Map of the Åkhult mire indicating, in particular, surface topography and the ombrotrophic bog areas. The border of the mire (continuous lines), the delimitation of ombrotrophic bog areas (dashed lines), contours of altitude (interval 0.25 m) relative to an arbitrary datum, areas with sparse tree cover and old peat cuttings are shown. The three bog brooklets and similar water tracks in the fen are indicated by small arrows. The names mentioned in the text are inserted. Nine black dots indicate all sampling locations except those for trickling water along the Fiolen rivulet between the bog brooklet confluences. Simplified from the original map in Malmer (1962).

(short treatment period) and 1992 (long treatment period) and deep frozen within a day. Before analysis, the frozen cores were cut into contiguous 1.25 cm slices. The dry bulk density of each slice was determined after drying at 80°C. The ^{14}C activity of bulk samples and fine root litter from the dried slices was then determined by combustion in a Packard Tri Carb Sample Oxidizer followed by counting of ^{14}C activity in a Packard Tri Carb Scintillation Counter. The upper surface of the slice with the highest bulk-sample ^{14}C activity was taken to represent the mire surface level at the time of labelling. Living and dead organic matter above this level was assumed to have been added to the acrotelm since labelling, except for above-ground vascular plant biomass whose quantity was assumed to remain constant during the experiment.

Surface cores

Litter decay and peat accretion were studied in surface cores (~0.4 m long) reaching through the acrotelm into the top of the catotelm, which were collected from *Sphagnum*-dominated hummocks and lawns in the Stattute area of the Åkhult mire during the period 1980–1987. The cores were deep frozen and later cut into contiguous 2.5 cm slices before drying at 80°C and analysing dry bulk density, C (Leco CR-12 autoanalyser) and N (Kjeldahl-N). For details, see Malmer & Wallén (1993, 1999).

In *Sphagnum* communities, most of the litter input to the acrotelm takes place a few centimetres below the surface at a level with dying mosses and fine vascular plant roots (Wallén 1986) known as the litter deposition level (LDL; cf. Malmer & Wallén 1993, 2004). The LDL separates the C-sequestering moss layer from the decaying litter of the rest of the acrotelm. It is set at the upper surface of the slice with the lowest [N]. Before litter formation, nutrients like N are relocated to the growing parts of the plants so that the litter is depleted in N (Jonasson & Chapin 1985, Rydin & Clymo 1989, Aldous 2002). In pristine bogs, hardly any N is lost during the subsequent decay of the litter (Rosswall & Granhall 1980, Damman 1988, Malmer & Wallén 1993 and references therein). Thus, decomposition in the acrotelm results in an increase of [N] with depth which can be used to follow the decay of litter until the catotelm is reached and decomposition almost completely ceases. This limit, the decay decrease level or DDL (cf. Malmer & Wallén 1993, 2004) is set at the level where no further increase in [N] can be detected.

The decay loss in the acrotelm was estimated from the increase of [N] with depth in the cores, assuming that the amount of N originally added to the system (N_0) equals that at time t, N_t. The loss of mass through decomposition over a period of time (t) can then be calculated from the equation:

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

where M_0 is the original mass, M_t is the mass remaining after time t, and k is the decay constant. An analogous equation holds for the C/N quotient. For a full account of these calculations, see Malmer & Wallén (1993, 1999, 2004).

N_{cum} (cumulative N, g m^{-2}) was used to establish a timescale for all of the surface cores. To recalculate N_{cum} to calendar years, two surface cores from *Sphagnum* communities, one from a lichen hummock and one from a mud-bottom were dated using ^{210}Pb following Malmer & Holm (1984). The analytical accuracy is about 10%. However, because of the downward transport of Pb in moss carpets (Malmer 1988) we disagree with, e.g., Turetsky *et al.* (2004) in that we do not regard ^{210}Pb dates for the upper parts of peat cores as particularly reliable (Malmer & Holm 1984).

Mire water and runoff

Open water was sampled six times during 2005–2007 at fixed locations in hollows on bog in the Stattute area, above the two main outflows, in the bog brooklets, and from the trickling water on the bog slope along the Fiolen rivulet (Figure 1). A few samples were also taken in the fen areas. In all samples DOC and tot-N were oxidised and analysed with a Shimadzu TOC analyser model TOC-V equipped with a nitrogen module TNM-1. Na$^+$ was analysed with a Perkin-Elmer ICP-AES instrument, model OPTIMA 3000 DV. The analyses were carried out the day after sampling. The median differences between duplicate samples (n = 17) taken in separate water bodies at the sampling locations and then processed separately were: 1.10 mg L^{-1} for [DOC], 0.08 mg L^{-1} for [N] and 0.05 mg L^{-1} for [Na$^+$]. The [DOM] was obtained from [DOC] assuming [C] = 0.511 mg g^{-1} in DOM (cf. section "Dissolved organic matter").

Direct measurements of water flow in the brooklets would not provide an accurate estimate of runoff from the bog, first because it is drained also by trickling water and secondly because catchment areas for the brooklets cannot be defined. Runoff was instead estimated by comparing [Na$^+$] in the draining water with that in the precipitation. Since Na is neither taken up by plants nor retained in peat (e.g. Malmer 1988, 1993), the amount of drainage water W_D (L m^{-2} or mm) over a period of time was estimated according to the following equation:

$$W_D = P \cdot [Na_P^+] / [Na_D^+] \pm \Delta W_S \cdot [Na_D^+] \qquad [3]$$

where P is the amount (L m^{-2} or mm) of precipitation, [Na_P^+] and [Na_D^+] the weighted mean [Na$^+$] in precipitation and drainage water, respectively, for a defined time period, and ΔW_S the change (L m^{-2}) in water storage calculated from the change in water level during the period. Over a year the change in $\Delta W_S \cdot [Na_D^+]$ is at most 0.01 g m^{-2} or <2% of the atmospheric supply.

Monthly precipitation data, along with analyses of Na in precipitation for 1953–1960 (annually; Malmer & Wallén 1980) and 1983–2007 (monthly; Swedish Environmental Research Institute; http://www.ivl.se) are available for the station at Aneboda, 3 km from the mire. Of the ~300 monthly analyses since 1983, six (unfortunately including two from 2007) are missing and have been reconstructed by interpolation from data collected at other stations in southern Sweden.

The water level was measured on each sampling date relative to the top of a wooden stick anchored deep in the peat. To compare the measurements, the highest observed water level at each sampling location was set at 30 cm and the other measurements calculated relative to that. The 30 cm datum corresponded well with the *Calluna* limit (Malmer 1962), defined as the lower limit of dense *Calluna vulgaris* cover and the boundary between hummock and lawn plant communities.

RESULTS

Turnover of the structural organic matter

Litter input in Sphagnum-*dominated sites*

In the cores from the ^{14}C labelled plots, a distinct horizon was found with ^{14}C activity >1000 times that above and below. The maximum in the fine root litter fraction was located 1.5±1.2 cm (mean ±SD, $n = 25$) below that in the bulk samples, the difference being more in hummocks than in lawns. During the experiment, the annual height increment was greater in hummocks than in lawns (Table 1), and the bog surface rose by less than the height increment due to the compaction of litter farther down (Malmer & Wallén 1993).

Almost twice as much organic matter accumulated in hummocks as in lawns during the long treatment period (Table 1; $p < 0.001$, $n = 20$), not least due to the higher below-ground production of vascular plants in hummocks (cf. Flower-Ellis 1980, Wallén 1983, 1986). The annual litter input during the short treatment period was lower, due to the addition of root litter below the ^{14}C horizon during the first few years after labelling; corresponding amounts were added to the results for the long treatment period to give a full estimate of root litter input (Table 1). It is also necessary to account for the decay loss from the litter before sampling as explained in the next section. Note that these additional calculations were not carried out on the smaller set of samples discussed by Malmer & Wallén (1996, 1999).

Decay and peat accretion

In the surface cores the bulk density increased from 20–30 g dm^{-3} at the LDL (depth 3–10 cm below surface) to 70–80 g dm^{-3} at the DDL (depth ~16 and ~25 cm below surface in lawns and hummocks respectively) as a result of decay and compaction (Malmer & Wallén 1993). The total necromass in the acrotelm was higher in hummocks (~7000 g m^{-2}) than in lawns (4500–5000 g m^{-2}).

In the litter, [C] increased by 7% before it was accreted to the catotelm (Table 2). The M/N and C/N quotients were highest at $N_{cum} = 0$ (Table 2) and decreased with depth as indicated by the polynomial in Figure 2. For newly formed litter the summary values M/N = 250 and C/N = 120 (N = 4.0 mg g^{-1}) can be used in relevant calculations (cf. Malmer & Wallén 1999, 2004). The decay constant (k), which does not differ between hummocks and lawns (cf. Malmer & Wallén 1999), decreased with depth as evidenced by the decreasing slope of the tangent to the polynomial (Figure 2). For the top samples ($N_{cum} < 10$), k was 0.035–0.043 a^{-1}, resembling the few values published so far (cf. Johnson & Damman 1993, Belyea 1996, Malmer & Wallén 1999). Therefore, the litter accumulated in the ^{14}C-labelled plots may have lost ~30% of its original mass before sampling. To estimate the initial litter input to the acrotelm this decay loss must be compensated for as indicated in Table 1.

According to the polynomial (Figure 2) the DDL ($k = 0$ cf. Equation 2) was reached at $N_{cum} = 71$ g m^{-2} corresponding to M/N = 75.8. The constant or weakly increasing M/N quotients below the DDL

Table 1. Litter accumulation and the rate of litter input to the acrotelm in the ^{14}C-labelled plots. Values are means ±SD. The litter input rate has been estimated by adding the decay loss during the experiment to the amount accumulated since labelling (see text section “Decay and peat accretion”). The decay loss has been calculated according to Equation 2 with the value for k, 0.039 a^{-1}, obtained from the tangent of the polynomial fitted to the surface core data (Figure 2) at $N_{cum} = 5.5$ g m^{-2} (corresponding to 6 years).

Vegetation type	Number of samples (n)	Time since labelling (years)	Depth to labelled surface (cm)	Height Increment rate (cm a^{-1})	Accumulated since labelling		Estimated litter input rate (g m^{-2} a^{-1})
					Above ^{14}C horizon (g m^{-2} a^{-1})	Below ^{14}C horizon (g m^{-2} a^{-1})	
Lawn	7	12	6.8 ± 1.6	0.6 ± 0.1	108 ± 26	12	153
Hummock	13	11 or 12	9.5 ± 1.9	0.8 ± 0.2	199 ± 42	21	282
Hummock	5	6	4.5 ± 1.0	0.8 ± 0.2	155 ± 41	44	-

Table 2. Characteristics of litter near the LDL and of peat in the uppermost part of the catotelm. The values for $N_{cum} = 0$ are obtained from the intersection of the polynomial in Figure 2 with the y-axis. The other values are means ±SD for relevant samples from the surface cores (Figure 2). Year for the litter input gives the time of input to the acrotelm for the litter within the depth interval, obtained from the ^{210}Pb-datings of the N accumulation rates. The p-values indicate the significance of the differences in concentrations and quotients between the younger and older parts of the catotelm.

Layer	Acrotelm		Catotelm		
Depth below LDL (N_{cum} g m^{-2})	$N_{cum} = 0$	$0 < N_{cum} < 5$	$60 < N_{cum} < 100$	$100 < N_{cum} < 150$	p-value (t-test)
Year for the litter input	1980	1985–1980	1910–1840	1840–1750	
Number of samples	-	6	7	10	17
Concentrations					
[C] (mg g^{-1})	-	477 ± 6	511 ± 15	513 ± 8	0.416
[N] (mg g^{-1})	3.6	4.3 ± 0.45	13.9 ± 2.1	11.0 ± 2.6	0.016
Quotients					
M/N quotient	274	224 ± 23	72.6 ± 12.5	94.0 ± 20.7	0.015
C/N quotient	-	112 ± 12	37.8 ± 7.7	48.7 ± 10.8	0.019

demonstrate that no measurable decay occurred farther down. The limit between acrotelm and catotelm may have varied from time to time, probably in the interval $60 < N_{cum} < 90$. The age of the litter at the DDL was ~70 years in the two ^{210}Pb-dated surface cores from *Sphagnum* communities. This corresponds to litter input to the acrotelm in 1900–1920 and gives an average N accumulation rate of 1.04 g m^{-2} a^{-1} for the whole acrotelm.

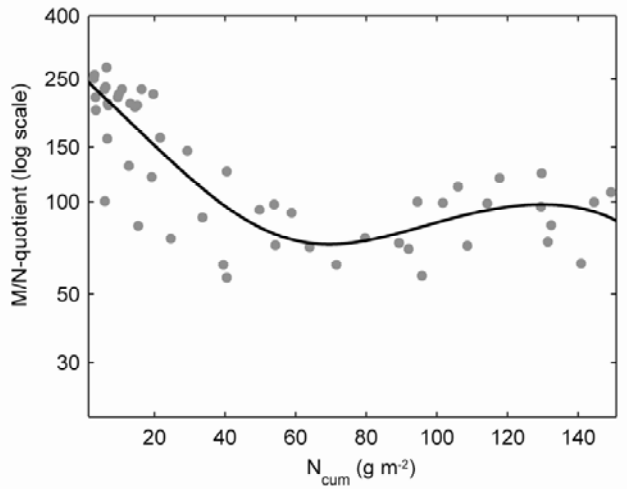

Figure 2. Variation of the M/N quotient with depth (as N_{cum}) from the LDL through the acrotelm and the upper part of the catotelm in the six cores from *Sphagnum*-dominated hummocks and lawns. A third degree polynomial has been fitted to the data ($R^2 = 0.705$; the slope of the tangent is 0 at $N_{cum} = 71$ g m^{-2}). Further explanation in the text.

The present ombrotrophic vegetation became established around AD 1300 (^{14}C-dating: Lu 2389, LuA 5729; Malmer *et al.*, in prep.). Calculated from that point in time, the mean rate of N accretion to the catotelm was 0.48 g m^{-2} a^{-1}. During the first 100 years low [N] also indicated peat accretion rates of up to 80–90 g m^{-2} a^{-1} (cf. Malmer & Wallén 1999, Belyea & Malmer 2004). The peat in the upper part of the catotelm above $N_{cum} = 150$ g m^{-2} (Figure 2) is the result of litter input to the acrotelm from AD ~1750 to AD ~1910 and its subsequent decay (Table 2). For the period AD 1800–1980 (depth interval $60 < N_{cum} < 150$ g m^{-2}) the ^{210}Pb datings show that the rate of N accretion to the catotelm was 0.49±0.06 g m^{-2} a^{-1} (mean ±SD, n = 4) and that the mean mass and C accretion rates were, respectively, 45±3 and 23±2 g m^{-2} a^{-1}. However, the accretion rates for mass and C (Figure 2, Table 3) were 29% higher during the 19th century than during the period 1900–1980. This is consistent with the observations of Franzén (2006) and has also been noted from several other bogs in north-west Europe, eastern Canada and British Columbia (Malmer & Wallén 1993).

Table 3. Rates of peat and C accretion to the catotelm since the beginning of the 19th century. Values are means ±SD for relevant samples in the surface cores (Figure 2). The rates and the time periods for accretion to the catotelm are based on the N accumulation rate for the period AD 1800–1980 (0.49 mg m^{-2} a^{-1}), obtained from dating by ^{210}Pb. The p-values refer to the significance of the difference in accretion rate between the younger and older parts of the catotelm.

Accretion period (year AD)	1900–1980	1800–1900	p-value (t-test)
Depth below LDL (N_{cum} g m^{-2})	$60 < N_{cum} < 100$	$100 < N_{cum} < 150$	
Number of samples	7	10	17
Accretion rates			
Peat accretion (g m^{-2} a^{-1})	37.9 ± 7.0	48.8 ± 10.6	0.016
C accretion (g m^{-2} a^{-1})	19.4 ± 4.0	25.0 ± 5.6	0.019
Peat growth			
Height increment (mm a^{-1})	0.51 ± 0.18	0.86 ± 0.34	0.012

Turnover of the non-structural organic matter

The mire water: level, supply and runoff

Observations since 1953 have shown annual water level amplitudes of 15–20 cm in the non-wooded parts of the bog (Figure 3) and 35–40 cm on slopes and in other wooded parts (Malmer 1962). The water level may fall to 4–10 cm below its maximum close to the *Calluna* limit for more than half of the period when the bog is not frozen. The periods with the highest water levels are short and can occur at any time of year with sufficiently intense precipitation. The lengths of periods with low water levels are variable and dependent on the durations of dry summer periods. The runoff from the bog decreases with decreasing water level and may become low when the water level falls to approximately 12–14 cm below the *Calluna* limit.

The water samples collected during 2005–2007 cover the range of variation in water level on the bog (Figure 3). The lowest water level was measured in July 2006, and the highest water level (April 2006) was ≥ 20 cm above this (29 cm in the bog brooklets). At the highest water levels the flow of water in the brooklets was strong and much trickling water was discharged down the bog slope. At the lowest water level, water samples could be obtained from only two of the brooklets and water levels could not be measured in non-wooded bog.

The mean annual precipitation increased by 25–30% from 1950 to 2000 and its annual mean [Na$^+$] did not change (Table 4; [Na+] in 2007 was exceptional for the whole period). This implies that the annual supply of Na varied mainly with the amount of precipitation and the concentration in the mire water hardly varied. The annual mean [NH_4^+-N + NO_3^--N] in the precipitation has been higher since around 1965 than previously ($p < 0.05$, t-test; Malmer & Wallén 1980).

The analyses of bog water indicate uniform surface water in the ombrotrophic part of the mire (Table 5) with concentrations varying with water level (Figure 4). The somewhat lower and higher mean concentrations in, respectively, trickling water and the brooklets result from differences in the availability of water for sampling at high and low water levels. The mean [Na$^+$] was higher ($p < 0.001$; t-test) at the fen sites than on bog, most probably because of a great inflow of water from surrounding forested areas with high evapotranspiration.

Calculated from Equation 3 using the mean [Na$^+$] in bog drainage water for [Na_D^+], the runoff during 2005–2007 varied from 29% to 81% of the precipitation (Table 5). The runoff in 2007 may have been slightly over-estimated due to an exceptionally high Na supply and lost precipitation samples. The annual runoff and precipitation values for 1993–2007 were correlated with those for 2005 and 2007 as the extremes (Figure 5). This corresponds to an annual evapotranspiration of 430±80 mm (mean ±SD).

Brandesten (1987) measured the water flow from eight segments of the large Komosse mire complex (60 km north-west of the Åkhult mire, altitude 330–340 m, mean precipitation 796 mm a^{-1}) in 1971–1977. In the segment (size 4.10 km^2) with the highest proportion of ombrotrophic bog (92%) the relationship between the precipitation (range 682–1011 mm) and runoff was very similar to that presented in Figure 5 ($R^2 = 0.952$, $n = 7$; slope 1.12, intercept -443 compared to 1.07 and -482; mean runoff 413 mm). For a Canadian bog Roulet *et al.* (2007) give a range of 316–472 mm a^{-1} for the runoff during six years.

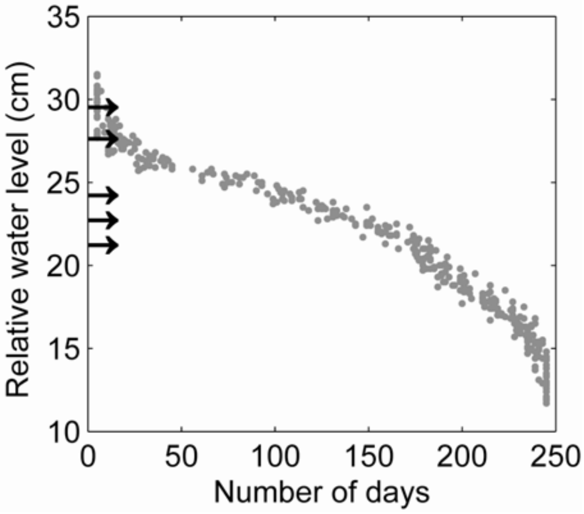

Figure 3. A water table residence curve from the non-wooded ombrotrophic part of the Stattute area. The curve gives the length of the period with the water level exceeding each cm within the amplitude of variation. A third degree polynomial fitted to the data gives $R^2 = 0.978$. The data (from Malmer 1962; field measurements at 23 locations in the Stattute area with ≥ 24 measurements at each location) cover the period from snowmelt at the end of March to the freeze-up in mid-November 1954 (precipitation 834 mm). To standardise the scale of water table measurements for all measurement locations, a water table residence curve with 16–20 data points was established for each location and a third degree polynomial fitted. The point with the lowest (tangent) slope was calculated for each polynomial and the y-axis scale re-labelled setting the level for that point equal to 0. Using this common scale all data points (n ≥350) have been included in the Figure presented and the y-axis scale re-arranged setting the mean maximum water level for the 23 sites to 30 cm (thus making the water level datum comparable to the datum set for this study, see Methods). The arrows indicate the positions of the water level on the 2005–2007 sampling dates except for one occasion when the water level in the non-wooded part of the bog was too low to be measured.

Dissolved organic matter

In the bog water, [DOC] and [tot-N] were inversely proportional to the water level (Figure 4). The outliers for [Na^+], [DOC] and [tot-N] refer to the brooklets on the wooded slope, where the water level is the same as in non-wooded bog in the upper part of the amplitude but drops much more during dry periods (cf. Malmer 1962). [DOC] and [Na^+] were positively correlated (Figure 4), as was [tot-N] with [Na^+] and [DOC] ($R^2 = 0.585$ and $R^2 = 0.665$ respectively; n = 41; $p < 0.001$; data not shown). The C/N-quotient (Table 5; range 31–59) was not significantly correlated with either water level (R^2=0.021) or any of [Na+], [DOC] and [tot-N] (data not shown). It was only four percentage units less in the drainage water (Table 5) than in peat recently added to the catotelm (Table 2). Therefore, layers near the DDL may be the main source of DOM and its [C] is the same as in newly accreted peat (Table 2).

Both the means and ranges for [DOC] (Table 5, Figure 4) agree with results from other bog sites (Urban *et al.* 1989, Fraser *et al.* 2001, Worrall *et al.* 2003, Roulet *et al.* 2007 and references therein) in spite of the fact that the samples represent three years with very different precipitation. However, comparisons with reported concentrations are sometimes difficult to evaluate because the literature values refer either to catchments that are more diverse than an ombrotrophic bog or to samples taken downstream of a bog and thus perhaps after mixing with water from other sources. The deviating concentrations in the fen samples (Table 5) demonstrate that water from minerotrophic sites differs from that at ombrotrophic sites.

The seasonal variation in [DOC] was lower in the water samples than in the runoff. At the summer sampling dates, precipitation was in the range 13–110 mm $month^{-1}$ with [Na^+] = 0.2–0.4 mg L^{-1}. Neglecting changes in the water level (see Equation 3) these values (calculated as monthly drainage water) correspond to 12–20% of the precipitation with [Na^+] = 1.2–2.6 mg L^{-1} and [DOC] = 36–49 mg L^{-1}. In contrast, during the period October–April the precipitation was 40–117 mm $month^{-1}$ with [Na^+] = 0.4–0.7 mg L^{-1}. These values correspond to 32–102% of the precipitation with [Na+] = 1.2–1.8 mg L^{-1} and [DOC] = 25–42 mg L^{-1}.

Since the annual runoff varied much more than [DOC] (Table 5, Figures 4 and 5) the annual DOC export may depend more on variation in the runoff than on the concentration. The uncertainties arising from the estimate of mean [DOC] are not notably large relative to the estimate of DOC export. E.g., for all bog water samples collected at water levels >20 cm (n = 40: cf. Table 5) [DOC] is 33.6±7.8 mg L^{-1} (mean ±SD; n = 40). Using this value instead of 36.2 mg L^{-1} (Table 5) would reduce the DOC export calculated for 1993–2007 by 7% or ~1 g m^{-2} a^{-1}. Moreover, for the samples of drainage water taken at water levels >28 cm [DOC] is 31.9±6.8 mg L^{-1} (mean ±SD; n = 12) but for obvious reasons this value is not suitable for use in the calculations.

Therefore, runoff is tentatively suggested as a sufficient predictor to obtain values for the DOC export integrated over several years. The annual

Table 4. Precipitation and its [Na^+] and [NH_4^+-N+NO_3^--N], runoff, and export of DOC, DOM, and tot-N 1950–2007. Data relating to precipitation from the meteorological station at Aneboda (annual mean 716 mm for 1919–1960; cf. Malmer 1962). The runoff has been calculated annually from Equation 3 or the regression in Figure 5. The values for DOM have been calculated from DOC assuming the same C concentration in DOM as in the peat recently accreted to the catotelm (Table 2). The annual export of DOC, DOM and tot-N for periods before 2005 has been calculated using the mean concentrations in drainage water 2005–2007 (Table 5).

Year/Period	Precipitation				Drainage water			
	Flux density	Na^+	NH_4^+-N+NO_3^--N		Runoff (±SD)	DOC export	DOM export	tot-N export
	mm a^{-1}	mg L^{-1}	mg L^{-1}	g m^{-2} a^{-1}	L m^{-2} a^{-1}	g m^{-2} a^{-1}	g m^{-2} a^{-1}	g m^{-2} a^{-1}
Period with sampling for DOC								
2005	670	0.44	0.81	0.54	197	7.0	13.7	0.17
2006	857	0.65	0.81	0.69	373	13.3	26.0	0.32
2007	950	1.20	0.76	0.72	766	28.7	56.1	0.65
Mean 2005–2007	826	0.76	0.79	0.65	446	16.3	32.0	0.38
Extrapolated data for runoff and DOC								
Mean 1993–2007	875	0.73	0.97	0.73	447 ± 191	16.2	32.6	0.38
Mean 1983–1992	779	0.56	0.84	0.74	348 ± 122	12.6	24.7	0.30
Mean 1953–1960	682	0.78	-		244 ± 101	8.8	17.3	0.21
Mean 1962–1976	670	0.66	1.07	0.72	-	-	-	
Mean 1947–1962	710	0.55	0.67	0.48	-	-	-	

Table 5. Water level position, [Na^+], [DOC], [tot-N], and the C/N-quotients in the mire water. For each group of samples, the values for water level represent the mean water level at all sampling dates and those for concentrations and C/N-quotients the mean ±SD for all samples.

Sampling sites	n	Relative water level (cm)	Na^+ (Mg L^{-1})	DOC (Mg L^{-1})	Tot-N (Mg L^{-1})	C/N
Bog sites						
Stattute area	11	25.4	1.48 ± 0.23	32.3 ± 6.7	0.73 ± 0.17	45.5 ± 8.9
Upstream bog brooklets	8	25.4	1.50 ± 0.30	31.8 ± 5.5	0.71 ± 0.18	46.1 ± 8.6
Mean non-wooded bog	19	25.4	1.49 ± 0.26	32.1 ± 6.1	0.72 ± 0.17	45.8 ± 8.5
Bog brooklets	17	22.5	1.63 ± 0.54	37.6 ± 10.3	0.88 ± 0.23	43.7 ± 9.6
Trickling water	6	29.6	1.08 ± 0.27	32.5 ± 7.6	0.79 ± 0.15	41.1 ± 3.9
Mean bog drainage water	23	24.5	1.48 ± 0.54	36.2 ± 9.7	0.85 ± 0.21	43.0 ± 8.4
Fen sites						
Stattute area	2	-	2.24 ± 1.36	26.5 ±11.2	0.58 ± 0.16	44.8 ± 7.4
Fen soak	4	-	3.08 ± 0.54	28.0 ± 9.7	0.83 ± 0.40	35.9 ± 5.8
Mean fen samples	6	-	2.80 ± 0.86	27.5 ± 9.0	0.75 ± 0.34	38.9 ± 7.3

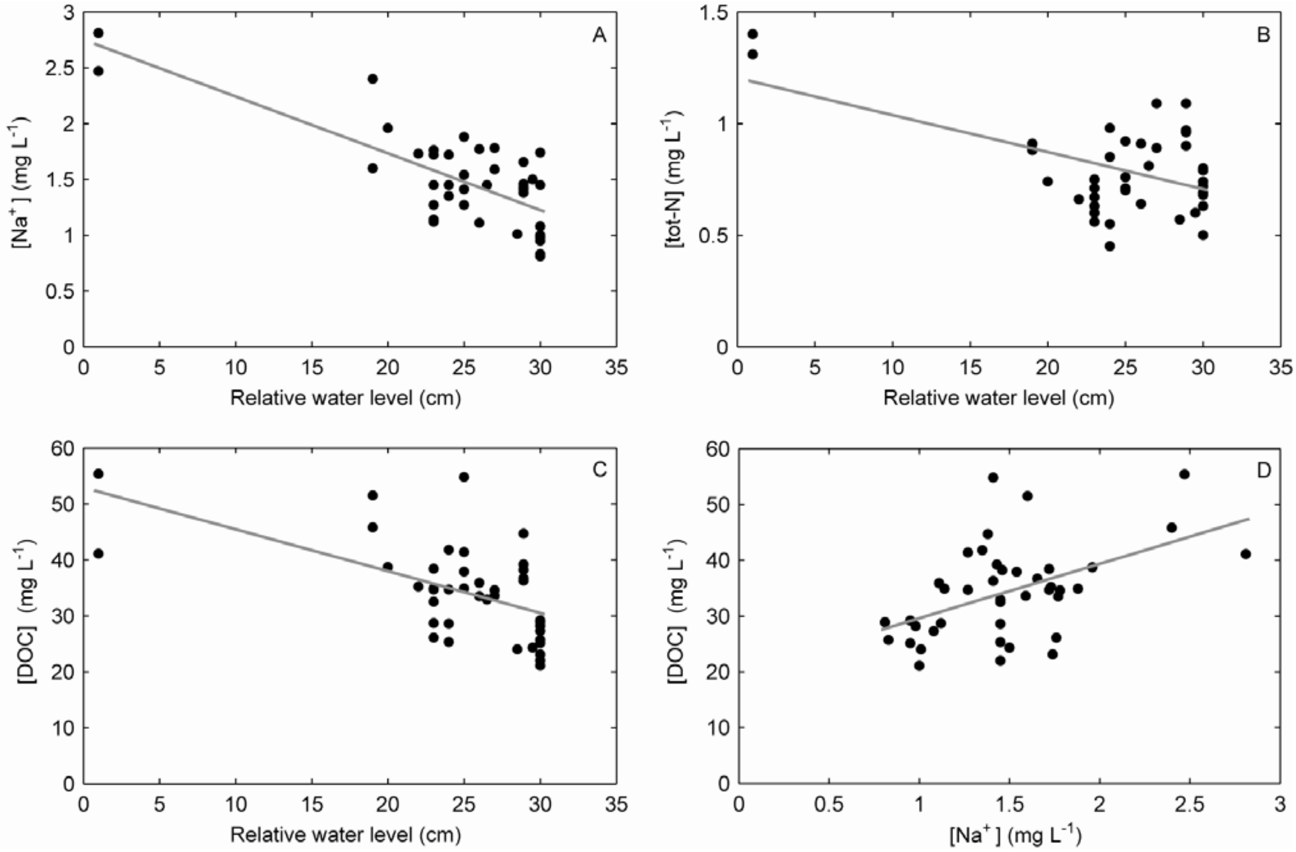

Figure 4. The [Na^+] (A) and [tot-N] (B) in the water in relation to the position of the water level at sampling as well as [DOC] in relation to the position of the water level (C) and [Na^+] (D). All water samples from the ombrotrophic part of the mire are included. Regression lines fitted to the data (R^2 for A: 0.575; for B: 0.277; for C: 0.322; and for D: 0.247; n = 41, $p \leq 0.001$). Excluding the two outliers in A and C gives $R^2 = 0.322$ and $R^2 = 0.271$, respectively ($p \leq 0.001$), and in B $R^2 = 0.004$ ($p>0.01$.)

DOC export for the period 1993–2007 is also the same as for the period 2005–2007 (Table 4) despite the extreme precipitation conditions during the latter period. The mean DOC export for the period 1993–2007 (16 g m^{-2}), its large variation between years (Table 4) and its seasonal variation also correspond with results from a Canadian bog (Roulet *et al.* 2007). The N export varied in the same way as the DOC export, with mean [tot-N] = 0.85 mg L^{-1} in the drainage water (Table 5).

In three bog water samples collected from the Stattute area in August 1949 after a dry summer (Malmer 1950) [DOC] was 47±5 mg L^{-1} (mean ±SD; determined as $KMnO_4$ consumption and, following Erlandsson *et al.* (2008), divided by 3.95). Calculated in the same way, [DOC] was 33 and 73 mg L^{-1} at moderately high and very low water levels, respectively, in samples from one of the brooklets in November 1957 and August 1958 (Malmer 1960). As water levels in the lower part of the full amplitude are over-represented, these data do not contradict a tentative use of the 2005–2007 mean to calculate the DOM/DOC export during this period.

The regression in Figure 5 applied to the annual precipitation during 1953–1960 and 1983–1992 (the latter period coincides with the measurements of litter input and accretion to the catotelm) gives ~200 and ~100 mm lower runoff, respectively, than for the period 1993–2007 (Table 4). In 1957–1959 [Na^+] (mean ±SD) in three water samples from the large brooklet was 2.2±0.8 mg L^{-1} (Malmer 1962) which, from Equation 3 and [Na^+] in precipitation (Table 4), gives 240 mm a^{-1} as the runoff. Therefore, assuming mean [DOC] and [tot-N] to be the same as in 2005–2007, the annual DOC and N export during the 1950s may have been only half of that during 1993–2007 and three-quarters of that in 1983–1992 (Table 4). From July 1985 through June 1986, data in Westling (1990) indicate 400 mm as the measured runoff (precipitation 825 mm) and a DOC export of ~10 g m^{-2}. However, the 2005–2007 variation in the annual DOC export was even larger than the estimated increase in means from 1953 to 2007 (Table 4).

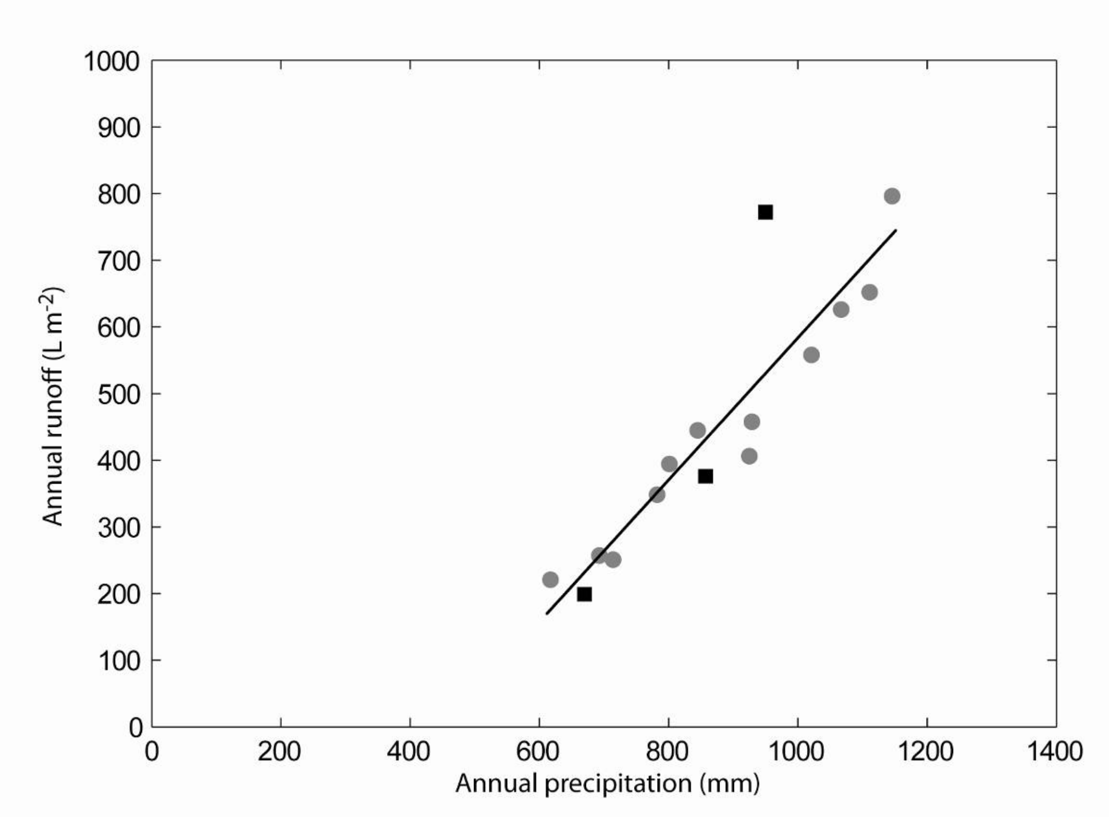

Figure 5. The annual amount of drainage water from the ombrotrophic part of the Åkhult mire in relation to the annual precipitation during the period 1993–2007. The samples from the years 2005–2007 are indicated by filled black squares and the remainder by grey circles. A linear regression line has been fitted to the data ($R^2 = 0.832$: $p < 0.001$; $n = 15$).The annual runoff has been calculated according to Equation 3, inserting the annual mean [Na^+] in precipitation at Aneboda and the mean [Na^+] in the drainage water from Table 5. Note that 1 mm of precipitation is equivalent to 1 L m^{-2}.

DISCUSSION

Litter input to the acrotelm

Although hummocks and lawns with *Sphagnum* mosses form the most recalcitrant litter and thereby contribute most particularly to peat formation, all types of microforms in the patchy bog vegetation have to be considered to arrive at an estimate of the overall NPP and litter input to the acrotelm. In the bog area studied, 34% of the surface is covered by *Sphagnum* hummocks and 33% by *Sphagnum*-dominated lawn and carpet vegetation (Malmer & Wallén 1999). The labelling experiments (Table 1) show an average litter input of 218 g m^{-2} a^{-1} in these microtopes. Heath-like vegetation dominated by dwarf shrubs and *Eriophorum vaginatum* and with mosses other than *Sphagnum* spp., liverworts, lichens or bare peat covered another 24% of the surface. The vascular plants are vital and have a high below-ground productivity (Flower-Ellis 1980, Wallén 1986, 1992) and, therefore, the same litter input rate as in the *Sphagnum* hummocks (Table 1) can be assumed for these sites (cf. Moore *et al.* 2002, Gunnarsson *et al.* 2008). The remaining 9% of the bog surface had no plant cover apart from algae. Neglecting any litter input there, the overall litter input to the bog can be estimated at 214 g m^{-2} a^{-1} or, as C, 102 g m^{-2} a^{-1}. Both experiments and the N/P-quotients in the plants indicate that P is the growth-limiting nutrient (Aerts *et al.* 1992, Malmer & Wallén 2005). Therefore, the increased atmospheric N deposition during recent decades may not have increased the NPP.

Turnover of mass and carbon in the acrotelm

Decay, accretion and net accumulation

The residence time in the acrotelm for the organic matter most recently accreted as peat to the catotelm may on an average have been ~70 years. From the decreases in the C/N- and M/N-quotients (Table 2,

Figure 2) the total decay loss in the acrotelm according to Equation 2 has been about 71% for mass and 69% for C. With an input to the acrotelm of 214 g m^{-2} a^{-1} the remaining mass and C should then be 62 and 32 g m^{-2} a^{-1}, respectively. The mass input to the catotelm was significantly less, viz. the ^{210}Pb-dated long-term rate 45 g m^{-2} a^{-1} and since the beginning of the 20th century 38 g m^{-2} a^{-1} (Table 3). For the period 1983–1992 the sum of the structural organic matter accreted to the catotelm (Table 3) and non-structural organic matter exported in the runoff (Table 4) was 63 g m^{-2} a^{-1} containing 32 g m^{-2} of C and thus not different from the organic matter expected to remain after the estimated decay loss in the acrotelm. Since the share of the non-structural organic matter was as high as 39%, the variation in the DOM/DOC export is doubtless an important determinant of the rate of accretion to the catotelm (Table 4, Roulet *et al.* 2007).

With an estimated mean peat depth of 4.0 m (Svensson 1979) and k = 0.04× 10^{-3} a^{-1} (Malmer *et al.* 1997) the deep peat layers may release 4–5 g m^{-2} a^{-1} of C. With an annual accretion rate of 19 g m^{-2} to the catotelm (Table 3) the bog on the Åkhult mire is still acting as a permanent sink for C but less efficiently than during the 19th century and at only about half the global long term rate of apparent net C accumulation, 21 g m^{-2} a^{-1} (Clymo *et al.* 1998). For the bog Mer Bleue in Quebec, Canada (Roulet *et al.* 2007), the net gain of C (measured as NEE minus DOC export) during 1999–2004 was ~30% higher than for the Åkhult bog, although the input exceeded the losses in only three of the six years of the study period.

Variation over time in accretion

The lower accretion rate in 1900–1980 compared to that during the 19th century (Table 3) may be seen as a continuation of the autogenic bog development with a rising bog surface since the 14th century (Belyea & Malmer 2004). The decreases in the M/N and C/N quotients during this period (Table 2) also show an increase from 59% to 68% in total decay loss from the acrotelm litter. Due to decreasing cover of *Sphagnum* mosses since the beginning of the 20th century (Malmer & Wallén 1999, 2004; Gunnarsson *et al.* 2002) the litter may, on average, have become less recalcitrant than previously. However, the time lag between the input of litter to the acrotelm and the accretion of the decomposed material to the catotelm means that, until around 1980, the main effect of such a change may have been to reduce the necromass stored in the acrotelm.

As a result of the variation in runoff, DOC export varied both annually and as averages over extended periods (Table 4). In particular, it seems that DOC export almost doubled from 1950 to the end of the century and became about equal to the C accretion to the catotelm (Table 6). Thus, the C accretion at the beginning of the 21st century was only two-thirds that during the 19th century (Table 3), a reduction nearly as large as from the 14th to the 19th century. For short periods such changes can scarcely be observed directly as accretion because of the slow height increment (Table 3) and the indistinct transition between acrotelm and catotelm. Indirectly, an increased DOC export also means an increased total release of C to the atmosphere because of an increased release of C from lakes and rivers downstream of the bog (Tranvik 1988, Tranvik & Jansson 2002, Forsberg 1992).

This putative increase in the DOC/DOM export since 1950 (Table 4) is most plausibly attributed to changed climatic conditions increasing the runoff. Particularly since the mid-1980s most winters have been milder with higher precipitation than previously (Alexandersson & Edquist 2006). Since the DOC export is highest during the winter months (cf. Roulet *et al.* 2007), increased winter precipitation and shorter periods with snow cover and frozen acrotelm may increase the DOC export more than heavy rainfall events during the summer. It is notable, though, that the vegetation changes on the Åkhult mire from 1954 to 1997 tend to indicate drying of the surface rather than wetter conditions (Gunnarsson *et al.* 2002) whereas at other bogs in the region vegetation changes since 2002 indicate increased moisture (Gunnarsson & Flodin 2007).

Remarks on the nitrogen balance

With [N] = 4.0 mg g^{-1} in the newly formed litter (Table 2), the 214 g m^{-2} a^{-1} of litter input to the acrotelm would result in an input of 0.86 g m^{-2} a^{-1} of N to the acrotelm. This input based on all cores is somewhat less than that obtained by ^{210}Pb (1.0 g m^{-2} a^{-1}) but slightly higher than in the present atmospheric wet deposition (Table 4). It corresponds fairly well to the sum of N accreted to the catotelm (0.53 g m^{-2} a^{-1}; cf. Tables 2 and 3) and that exported as DOM during 1983–1992 (0.30 g m^{-2} a^{-1}, see Table 4). Since the N contained in the organic matter is much greater than that dissolved in the water, the amount of N exported will vary over time with the DOM export (Table 6). Since 1950, the calculated decrease in the rate of N accretion to the catotelm is about equal to the increase in the N supply rate (Tables 4 and 6). This incomplete calculation of the N balance for the bog also shows that the DOM export contributes to maintaining the low nutrient content of the bog.

Table 6. Effects of the inferred changes in DOC/DOM export on the accretion of mass, C and N to the catotelm since 1950. The calculations assume that the rates of litter input to the acrotelm and release of mass and C in the decay process are constant. Values for litter input are taken from the text section “Litter input to acrotelm”, for precipitation and DOM/DOC export from Table 4, for accretion to the catotelm from Table 3, and for the M/N- and C/N-quotients from Table 2. For N see also the section “Remarks on the nitrogen balance”. The decay loss is calculated from the M/N and C/N quotients according to Equation 2. Measured values in **bold** type, extrapolated values in italics.

Period (Mean annual precipitation)	1953–1960 (680 mm)			1983–1992 (780 mm)			1993–2007 (880 mm)		
Component	Mass g m^{-2} a^{-1}	Carbon g m^{-2} a^{-1}	Nitrogen g m^{-2} a^{-1}	Mass g m^{-2} a^{-1}	Carbon g m^{-2} a^{-1}	Nitrogen g m^{-2} a^{-1}	Mass g m^{-2} a^{-1}	Carbon g m^{-2} a^{-1}	Nitrogen g m^{-2} a^{-1}
Input of organic matter									
Litter input to the acrotelm (M_0 in Equation 1)	214	102	0.86	**214**	**102**	**0.86**	214	102	0.86
Remaining after the decay process									
Accretion to the catotelm (M_A in Equation 1)	*45*	*23*	*0.63*	**38**	**19**	**0.53**	*30*	*16*	*0.42*
DOM/DOC export (M_E in Equation 1)	*17*	*8.8*	*0.21*	*25*	*13*	*0.30*	**32**	**16**	**0.38**
Calculations of the decay loss in the acrotelm (M_D in Equation 1)									
From the decrease in mass	*152*	*70*	-	*151*	*70*	-	*152*	*70*	-
From the M/N or C/N quotient	150	68	-	**150**	**68**	-	150	68	-

CONCLUSIONS

During the last 200 years the autogenic development of the bog on the Åkhult Mire and changes in the climatic conditions have increased the total losses of C from the acrotelm and decreased the rate of C accretion to the catotelm by one third**.** A decrease in the accretion rate during this period has also been found in other bogs in both north-west Europe and North America (Malmer & Wallén 1993). In a shorter time perspective, increases in precipitation may have contributed to increasing the DOC export and decreasing the capacity for net C accumulation in the bog and, indirectly, also increased the release of C to the atmosphere. With regard to productivity and C input to the acrotelm it is evident that changes of similar magnitude have not taken place during the last 200 years, although changes in species abundances may have occurred.

The close connections between climatic variables and the development of ombrotrophic bogs mean that data records covering several decades are desirable to support an understanding of the conditions for peat growth and net C accumulation. At the bog on the Åkhult mire the most recent accretion of C to the catotelm corresponds to 15–20% of the annual C input as litter to the acrotelm. The bog is still a sink for atmospheric C but the time lag between litter input and addition of the decomposed material to the catotelm means it is not certain that the present litter input will result in accretion of that magnitude in the future. In contrast, the C accretion rate around AD 1350 was more than twice the rate 100 years ago or perhaps ~60% of the C in the annual litter input (Malmer *et al.* in prep.).

In the future, it is probable that increased climatic humidity in southern Scandinavia will result in higher inputs of litter and C to the acrotelm in ombrotrophic bogs, as occurs now in more oceanic regions (e.g. Belyea & Clymo 2001, Gunnarsson 2005, Lund *et al.* 2007).The runoff and export of DOM/DOC from bogs is obviously related to the climatic conditions and may be higher in regions with higher precipitation and more oceanic climates than at the Åkhult mire. The reported increase in the total decay loss from the acrotelm of bogs when going from weakly continental through weakly oceanic to hyper-oceanic regions (Malmer & Wallén 1993) may to a great extent result from DOC export increasing with increasing precipitation and climatic humidity.

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