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Peat Growth and Carbon Accumulation Rates during the Holocene in Boreal Mires

Malin Klarqvist

SWEDISH UNIVERSITY OF AGRICULTURAL SCIENCES

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Abstract

This thesis is based on the analysis of peat stratigraphies to study peat growth and carbon accumulation processes in northern mires. In the first study, problems concerning ^{14}C dating of peat were examined by fractionation of bulk peat samples and ^{14}C AMS dating of the separate fractions. In the following studies, peat cores from twelve Swedish mire sites were investigated. Macrofossil analysis was performed on the sampled cores to describe and classify the plant communities during mire development. Between 6 to 18 ^{14}C AMS datings were performed on one core from each mire in order to estimate the peat growth and carbon accumulation rates for the identified plant communities.

Different fractions within single peat bulk samples gave considerably differing ^{14}C ages. The range in age differed between mire types and depth. For accurate ^{14}C dating, moss-stems, preferably of *Sphagnum* spp. are recommended (Paper **I**). Both autogenic and allogenic factors, e.g. climate and developmental stage, respectively, were identified as important influences on carbon accumulation (Paper **II**). Both peat growth and carbon accumulation rates differed between plant communities. The major factors explaining the variations in accumulation rates of the different plant communities were the amount of *Carex* and *Sphagnum* remains and the geographical position of the mire (Paper **IV**). Carbon accumulation rates decrease along with development in most mires. The results indicate that some mires may have alternated between being carbon sinks and sources, at least over the last several hundred years. The inter-annual variation in carbon accumulation is probably explained by climatic variations (Paper **III**).

Key words: ^{14}C AMS dating, Allogenic, Autogenic, Carbon turnover, *Carex*, Mires, Peatlands, *Sphagnum*.

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Appendix

Papers I-IV

This doctoral thesis is based on studies reported in the following papers, which will be referred to in the text by the corresponding Roman numerals.

I. Nilsson, M., M. Klarqvist, E. Bohlin and G. Possnert. 2001. Variation in ^{14}C age of macrofossils and different fractions of minute peat samples dated by AMS. *The Holocene 11(5)*, 579 -586.

II. Bohlin, E., M. Klarqvist and M. Nilsson. Within-mire variation in peat growth and carbon accumulation rates during the Holocene in boreal mires. (Manuscript.)

III. Klarqvist, M., E. Bohlin and M. Nilsson. Long-term decline in apparent peat carbon accumulation in boreal mires in northern Sweden. (Manuscript.)

IV. Klarqvist, M., E. Bohlin and M. Nilsson. Factors controlling peat growth and carbon accumulation rates in boreal mires during the Holocene. (Manuscript.)

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Introduction

Mires as functional ecosystems

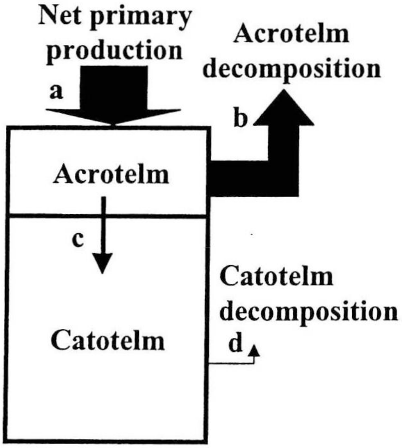

Fig. 1. *Principal model of peat accumulation. Arrows show: a, net primary production of plant material supplied to the acrotelm; b, peat decomposition in the acrotelm, emitted as CO_2 or CH_4; c, transfer of the remaining peat from acrotelm to catotelm; and d, decay of peat in the catotelm emitted as carbonaceous gases.*

Peat formation is a dynamic process, which varies according to the hydrological conditions of the mire, on both large and small scales. The amount of peat accumulating at any given time is mainly determined by the extent of decay occurring in the oxic zone, including the zone with a fluctuating water table of the mire (the acrotelm), before it enters the permanently anoxic zone (the catotelm) and becomes incorporated into the slowly accumulating peat (Fig.1). As new vegetation is produced at the surface of the accumulated peat, the water level rises and consequently the peat accumulation continues. The highest decay rates occur in the acrotelm, and the speed of decay diminishes radically as the plant material enters the catotelm, mainly because the redox conditions are less favourable for decomposition of organic material. The correlation between carbon accumulation and peat accumulation is very strong, although density of the peat is a very important factor influencing the carbon accumulation, whereas its carbon content is of minor importance (see Paper **IV**).

The main gas emitted during decay in the acrotelm is carbon dioxide, CO_2, as most micro-organisms are aerobic, although in the fluctuating water level zone methanogenic micro-organisms are also active. In the catotelm only anaerobic micro-organisms are active, yielding both methane and carbon dioxide as terminal carbon mineralisation end-products. However, some of the CH_4 from deeper peat is converted into CO_2 by aerobic micro-organisms while passing trough the oxic zones. In addition to carbon lost during decomposition, leaching and fires may also contribute to the losses from the mire system.

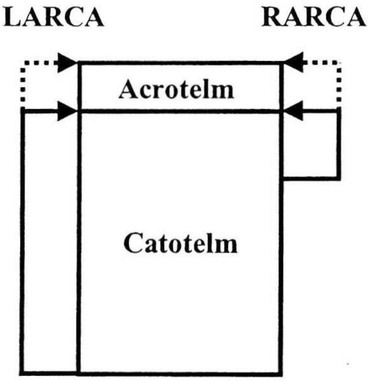

Fig. 2. *Principal model of LARCA (Long-term Apparent Rate of Carbon Accumulation) and RARCA (Recent Apparent Rate of Carbon Accumulation). Solid and dotted arrows illustrate the meaning of these terms as defined in this thesis and in other studies, respectively. Differences in the definitions will affect RARCA relatively more than LARCA.*

The peat-forming processes are important for understanding the long-term rates of peat and carbon accumulation, as well as variations in accumulation rates between and within mires. The interest in mire carbon accumulation has called for accurate terminology. The terms LARCA (Long-term Apparent Rate of Carbon Accumulation), RARCA (Recent Apparent Rate of Carbon Accumulation), and TRACA (True net RAte of Carbon Accumulation) have been suggested by Clymo et al. (1998) (Fig. 2). The differences in these measurements of accumulation are important when comparing different accumulation rates. LARCA is based on the cumulative mass of the peat, the carbon content, and the age of the peat according to basal dating. RARCA is comparable to LARCA, although it only considers the last 1000 years. RARCA is sometimes based on the complete stratigraphy, including the acrotelm, whereas other RARCA estimates are based only on the catotelm. TRACA is based on estimates derived from Clymo's peat accumulation model developed for bogs (Clymo, 1984), and is calculated from the rate at which organic material is added to the catotelm and a decay coefficient to account for decay in the catotelm. To measure TRACA several ^{14}C datings are needed.

Role of mires in global carbon cycles

Mire formation has occurred in the Northern Hemisphere since the last decline of inland ice. The mires store organic carbon and thus act as large terrestrial carbon reservoirs. Through production of mire vegetation together with incomplete decay, the mires have accumulated carbon and hence withdrawn atmospheric carbon from the global carbon cycle. The total amount of carbon stored in mires is estimated to be 230-450 Gt (Gorham, 1991; Immirzi et al., 1992; Lappalainen, 1996). The carbon in mires represents ca. 30% of the global soil carbon (Schlesinger, 1997), which corresponds to about 60% of the carbon currently in the atmosphere in the form of CO_2 (Miller, 1981; Miller et al., 1983). 90% of the mires are located in the temperate and boreal zones in the Northern Hemisphere (Maltby and Proctor, 1996). Consequently, a large percentage of Canada, Finland, Russia, and the Scandinavian countries are covered with mires. According to observations in the Swedish Forestry Inventory, 100000 km^2 (25% of the Swedish land area) is covered by peat or "peaty soils". Open mires, i.e. those with a peat layer exceeding 30 cm in depth and a forest growth of less than 1 $m^3 \times ha^{-1} \times yr^{-1}$ constitute 12% of the total area of Sweden (Hånell, 1988).

Mires act either as a sink for carbon, through the uptake of CO_2 by the vegetation, or as a source of carbon for the atmosphere through degradation of peat and consequent release of carbon into the air, as either CO_2 or CH_4. The most important factors controlling production and decay are climatic (especially hydrological parameters and air temperature), catchment fertility and carbon quality of the organic material. Mires have acted as sinks of carbon from the atmosphere in a long-term perspective. However, questions are now being raised about their role in present-day carbon cycling.

One major issue is how climatic changes might influence the mires, since they affect temperature and precipitation. Besides changing present rates of accumulation, climatic changes could also affect the stability of organic material that has already accumulated, and could thus play an important role in the exchange of greenhouse gases. The Swedish climate research program SWECLIM (SMHI, Norrköping) predicts that in the next 100 years, the Scandinavian climate will become milder, and the average annual air temperature will rise by ca 4°C. It also suggests that precipitation will rise, especially in the northern parts of Sweden. Hence, the relationship between precipitation and evapotranspiration is likely to be strongly affected. The response of peat accumulation is hard to predict, due to regional climatic differences and mire types (Moore et al., 1998). In other areas, climatic models suggest that climate will be warmer and drier. A drier climate implies a lowering of the water level in the wetlands, which would enhance the decay of the mires. In a study by Laine (1996), a lowering of water table decreased CH_4 emissions, and at the same time increased the emissions of CO_2 and N_2O to the atmosphere. A drier climate would also cause more frequent fires on mires and consequently transform organic carbon to atmospheric carbon (Zoltai et al., 1998).

Furthermore, even though a considerable amount of carbon has been withdrawn from the atmosphere and stored in mires as organic carbon, a natural transformation of CO_2 via organic carbon to CH_4 has occurred through anaerobic decay. Thus, large amounts of carbon have been released back to the atmosphere by decay processes. CH_4 is a greenhouse gas, with approximately 21 times stronger warming potential than CO_2. However, the long-term effect of the release of CH_4 from mires back to the atmosphere is highly debatable as the turnover time for CO_2 is considerably longer than for CH_4 (50-200, and 12 years respectively; IPCC, 1995). Today, average methane emissions from different Swedish mire types range between 4-40 g of CH_4 m^{-2} yr^{-1} (Nilsson et al., in press).

Finally, some theories of mire formation suggest that bogs have a maximum growth level (Clymo, 1984). Decay occurs not only in the oxic surface layer, but also in the already accumulated anoxic peat, the catotelm. This suggests that the more mass the peat accumulates, the higher the amount of gases released through decay from the deeper layers will be. At some point the decay of accumulated carbon in the catotelm exceeds the rate of organic material added to the catotelm and the mires become natural sources of carbon to the atmosphere. The mires have then reached an intrinsic limit of growth and are in equilibrium instead of being sinks of carbon gases from the atmosphere.

Mire formation

Mire formation occurs when plant production exceeds decay, and is a result of high precipitation and insufficient evapotranspiration. In a cold climate, low precipitation is sufficient for accumulation, whereas in a warmer climate accumulation requires higher precipitation (Ivanov, 1981).

There are two mechanisms of mire formation: primary and secondary. Primary formation occurs in areas previously unexposed to dry land, e.g. land uplift zones or after the retreat of the inland ice, whereas secondary mire formation occurs on land that is already exposed. Mire formation can be initiated either by the overgrowth of a lake (terrestrialisation), primary formation directly on newly exposed ground in connection with land uplift (primary formation), or changes in hydrology such as waterlogging of a forest (paludification) (c.f. Sjörs, 1983).

Successions of mires are controlled both by allogenic factors (external factors such as climatic conditions or catchment processes) and autogenic factors (internal factors depending on how the vegetation itself influences the growing condition). One common type of development is the transformation from fen to bog. In peat-accumulating ecosystems the nutrient availability is higher in the early development stages as the vegetation is in contact with moving groundwater, and the vegetation is adapted to the environment e.g. fen species are common. As the mire grows, it loses contact with the groundwater and subsequently depends on precipitation. At this stage water and nutrients are supplied solely by precipitation, and vegetation with a greater tolerance to nutrient deficiency and drought appears e.g. *Sphagnum* mosses. There are often diverging patterns of mire development, as shown by the differences in the long-term development between many of the mires described in this thesis (Paper **II**). The dynamic interactions between allogenic and autogenic forces control the succession of mires, although the relative importance of these forces is widely debated. Damman (1996) argues that the water level is the main factor controlling peat accumulation for both bogs and fens. For bogs the autogenic processes determine peat accumulation, whereas for fens the allogenic processes are predominant. Despite this, fens are less sensitive to climatic variations than bogs (Damman, 1996), since a bog is totally dependent on precipitation. Climatic conditions affect the accumulation rates, as both production and decay of the peat-forming vegetation is governed by climatic factors such as hydrology and temperature. Climatic variations should also be reflected in the mire, for instance in changes in its degree of humification, macrofossil composition etc. Using multivariate statistics Barber (1994) demonstrated that macrofossils of *Sphagnum cuspidatum* correlated with wet periods in history, whereas *Ericales* correlated with dry periods. Furthermore, changes in macrofossil composition and known climatic changes during the last 1000 years coincided in a raised bog in northern England investigated by (Barber et al., 1994), and climatic signals interpreted by multi proxy data correlate well with physical and botanical changes in several bogs in the UK (Barber et al., 1999). Oldfield (1997) found that minimum net carbon sequestration rates in a *Sphagnum fuscum* bog with hollows in northern Sweden are consistent with minimum spring and summer temperatures inferred from tree-ring data. Other disturbances that can affect the rates of peat growth and carbon accumulation are permafrost, fire, and changes in hydrology. Consequently, both autogenic and allogenic factors are involved in mire development and, therefore, separating the different factors affecting peat accumulation is difficult.

Production and decay

The two most important peat-forming genera are *Sphagnum* and *Carex*. Ombrotrophic mires are dominated by *Sphagnum* species, whereas minerotrophic mires have a wide range of both *Sphagnum* and *Carex* species. Higher production rates can be expected in minerotrophic fens due to the higher production of *Carex* spp., although the coupling between production for individual species and mire type is not straightforward. Minor differences in production rates were found in a study in Alberta, Canada, of 264-297 g dry weight (dw) m^{-2} yr^{-1} for bogs and 214-360 g dw m^{-2} yr^{-1} for fens (Szumigalski and Bayley, 1996b), whereas production rates were found to be higher in bogs than in the adjacent lagg (1942 and 1631 g m^{-2}, respectively) in a study by Reader and Stewart (1972). Most probably the density of the different species determines the production rates and this blurs the differences between bog and fen. Different peat-forming species have different capacities for production and decay. The intrinsic capability of each species, as well as nutrient availability, controls its rate of production, whereas decomposition is mainly determined by the carbon quality of the litter, together with abiotic factors such as oxygen, moisture, and temperature.

Sphagnum production varies between 10 to 500 g dw m^{-2} yr^{-1}, depending on species and location (c.f. Lindholm and Vasander, 1990). Other studies show similar production rates, e.g. 50-300, 50-200, and 100-200 g dw m^{-2} yr^{-1} for *S. fuscum*, *S. magellanicum* and *S. angustifolium*, respectively (Rochefort et al., 1990); 100-500 and 100-300 dw m^{-2} yr^{-1} for *S. balticum* and *S. magellanicum*, respectively (Aerts et al., 1992b); 100-200 g dw m^{-2} yr^{-1} for *S. fuscum*, and 100-150 g dw m^{-2} yr^{-1} for *S. teres* and *S. angustifolium* (Szumigalski and Bayley, 1996b). Moisture, especially its temporal distribution, is the main factor controlling production (Backeus, 1988), thus both precipitation and distance to groundwater level are important for *Sphagnum* production. However, other climatic factors (e.g. mean annual growing season temperature and growing degree-days) as well as precipitation have been shown to correlate to moss growth (Thormann and Bayley, 1997). The variations of production within individual species are also governed by hydrological factors. Wallén et al. (1988) found that the annual growth in length varied between 16-22 mm for *S. magellanicum* and between 7-23 mm for *Sphagnum* sect. *Acutifolia* during three years with varying precipitation. There are great variations in production and decay between the different peat-forming *Sphagnum* species. Hollow-forming species of *Sphagnum* (sect. *Cuspidata* and *Palustria*) tend to have higher production rates than hummock-forming species (sect. *Acutifolia*) (Rochefort et al., 1990; Malmer and Wallén, 1999), whereas hollow-forming species generally decay faster than hummock-forming species (Johnson and Damman, 1991), although Malmer (1999) found no differences in decay rates between species on lawns and hummocks. The variation in decay rates of *Sphagnum* is more dependent on species than on abiotic factors (Johnson and Damman, 1991; Belyea and Warner, 1996).

The production of *Carex* spp. varies between 50 to above 2000 g dw m^{-2} yr^{-1} (c.f. Aerts et al., 1992a), but this too depends on species and location. However, most studies of *Carex* production focus on aboveground production, and are therefore likely to have generated underestimates. As much as 50% of the annual production for *C. rostrata* and *C. lasiocarpa* has been found to be produced belowground (Bernard and Fiala, 1986), and the proportion found belowground varies between 70 and 97% of the total amount of dry mass (Sjörs, 1991; Aerts et al., 1992a; Saarinen, 1996). For *Carex* spp., the production is mainly determined by the nutrient availability. Decay rates of *Carex* plants correlate to the nutrient content of their different parts (Thormann et al., 2001).

The annual balance between production and decay determines the amount of peat accumulated. For accumulation, decay rates have been shown to play a more important role for accumulation than the production rates (Clymo, 1983). Decay rates are also higher for *Carex* spp. than for *Sphagnum* spp. (Rochefort et al., 1990; Johnson and Damman, 1991; Szumigalski and Bayley, 1996a; Scheffer et al., 2001). Most decomposition occurs in the acrotelm, and when the peat material enters the catotelm, the physical properties of the peat have already been more or less determined. Thus, a limited amount of the original vegetation is deposited as peat in the catotelm. On average 10% of the net primary production is added to the anoxic zone as peat (Reader and Stewart, 1972). In studies focusing on individual species, 70% of *Sphagnum* (both hummock and lawn species) (Malmer and Wallén, 1999) and 40-80% of *Carex rostrata* decomposed in the acrotelm (Ohlson, 1987). Thus, there are great variations in decay, which seem to have a very strong influence on rates of accumulation.

Carbon accumulation rate

The amount of accumulated peat is a result of the differences between production and decay in the different plant communities. Peat accumulation in bogs can be explained by a mathematical model developed by Clymo (1984), which is also widely used for describing other types of mire. The model describes the coupling between primary production, the decay in the oxic surface layer (the acrotelm), and the transport of decayed material into the permanently anoxic underlying peat (the catotelm). Decay in the underlying layers also occurs, but to a much lesser extent due to the anoxic conditions and the lower rates of water movement in the catotelm (Fig. 1). The model presented by Clymo (1984) assumes a constant rate of peat growth, which is highly arguable e.g. Belyea (1996). The model also concentrates on the autogenic processes and does not take into account any possible changes in hydrology caused by allogenic factors. Other models that account for both autogenic and allogenic factors, as well as variable growth rates, have been developed by several authors, including Almquist-Jacobson (1995) and Hilbert (2000).

Both the extent and rate of decay in the anoxic zone have been debated. The most convincing evidence for ongoing decay in the catotelm comes from radiocarbon dating of either CO_2 and CH_4 with ages significantly older than the modern age (Aravena et al., 1993; Charman et al., 1994; Chanton et al., 1995; Charman et al., 1999) and micro-organism specific organic chemical components that are also considerably older than the modern age (Pancost et al., 2000). However, these findings do not yield any information on the rate of decay in the catotelm. Other evidence of decay in the catotelm is provided by the linear decline observed in the C/N ratios of *Sphagnum fuscum*, *Thomentypnum nitens* and *Picea* needles throughout the profile (Kuhry and Vitt, 1996). The use of the C/N ratio as a measure of decomposition of organic material requires the C/N quotient of the material added to be constant, which is probably fulfilled only if plant material of the same tissue and species is used for all the assessments.

The average global carbon accumulation rate in peatlands has been estimated to be 29 g C m^{-2} yr^{-1} by Gorham (1991) and 21 g C m^{-2} yr^{-1} by Clymo et al. (1998). However, the variations are large. Several studies have shown that carbon accumulation varies between mire type and climatic zone. The average accumulation rate of mires examined in Finland varied between 3-89 g C m^{-2} yr^{-1}, with an average in bogs of 24 g C m^{-2} yr^{-1} compared to 15 g C m^{-2} yr^{-1} in fens (Tolonen and Turunen, 1996). Polygonial mires in the former Soviet Union had an average of 12 g C m^{-2} yr^{-1} whereas fens and marches ranged between 72-80 g C m^{-2} yr^{-1} in a study by Botch et al. (1995). Large variations within mires have also been recorded, e.g. 14-35 g C m^{-2} yr^{-1} in a homogeneous *Sphagnum fuscum* peat stratigraphy in Canada, (Kuhry and Vitt, 1996). The variations suggest that accumulation rates are not linear, but reflect differences in plant communities and factors affecting the production and decay of the various communities. Some studies have been done on different vegetation zones within the same peat stratigraphy, most often comparing the lower *Carex*-dominated fen zone with the upper *Sphagnum*-dominated bog zone. The carbon accumulation rate in the upper *Sphagnum* (sect. *Acutifolia*) dominated part was found to be somewhat higher than in the lower *Carex*-dominated part, at 28.65 and 27.5 g C m^{-2} yr^{-1}, respectively, in a Canadian bog (Kuhry et al., 1992), and 23.0 and 21.1 g C m^{-2} yr^{-1}, respectively, in a raised bog in south-eastern Finland (Mäkilä, 1997). However, the opposite relationship has also been seen, e.g. 34.3±22.7 (SD) in the *Sphagnum*-dominated part and 61.5±12.9 in the *Carex*-dominated part of a Finnish bog investigated by Ikonen (1995). Large variations in both peat growth, and carbon accumulation rates are often seen in the topmost part in several mires (Paper **II**). This is most probably due to lack of consolidation of the upper peat. Within the *Sphagnum*-dominated site examined by Kuhry et al. (1992) carbon accumulation rates in the topmost part (0-90 cm) averaged 31.7 g C m^{-2} yr^{-1}, whereas in the lower part (87-154 cm) they averaged just 12.5 g C m^{-2} yr^{-1}. Variations within the different mire types suggest that there are great variations in accumulation rate even within homogenous plant communities, especially at the surface of mires. Therefore, high-resolution studies are needed for examining differences in accumulation rates.

Peat growth rate

The correlation between peat growth rate and carbon accumulation rate is strong. In a study describing one ombrotrophic bog in Finland the correlation was as high as 94% (Ikonen, 1995), whereas in our study, based on eleven different mires in northern Sweden, the correlation was only 57% (Paper **IV**).

Peat growth and carbon accumulation rates differ mainly due to factors related to the climate and vegetation. Another important issue when comparing different accumulation rates is how the estimates have been derived, especially the accuracy of the analysis. The importance of this depends, of course, on the aim of the study. In the studies described in this thesis, the accuracy in all elements has been crucial. For highly accurate results it is imperative to study the stratigraphies by high-resolution. It is also advisable to take several datings within the same peat stratigraphy.

The importance of correct dating and age-depth modelling

An important issue for accurate determinations of peat accumulation and carbon accumulation rates is to minimise the errors of ^{14}C dating of the peat material. In many studies, ^{14}C datings have been performed on the bulk sample of the peat. Bulk samples consist of a mixture of belowground vegetation, aboveground vegetation and vegetation produced at the actual sampled depth as well as dissolved carbon (humic substances), originating either from degradation of the plant material in the bulk sample or by downward transport of carbon compounds within the mire.

Younger roots have been suggested to contaminate the bulk samples e.g. (van Geel and Mook, 1989). Such contamination can have a considerable impact on the dating, e.g. the living roots of *Carex rostrata* have been found to penetrate to a depth of 230 cm (Saarinen, 1996), although most of the roots are found in the uppermost peat. For *Ericaceous* species the highest root densities are found 0 to 10 cm below the mire surface (Wallén, 1986). Plants with perennial root systems, e.g. *Calluna vulgaris*, transport carbon to the root system by active allocation (Wallén, 1983) and consequently tend to make estimated ages of bulk samples younger than true ages. The effect of the aboveground vegetation is more debatable, and its impact on errors among ^{14}C dated ages is not so clear, as most of the mire vegetation collapses during senescence. Thus, carbon from different depths is being dated when bulk samples are ^{14}C dated. The proportion of the different fractions also influences the result of ^{14}C dating of the bulk sample.

Another common method used for dating peat is to fractionate the peat by chemical extraction (e.g. into humin, humic acids, and fulvic acids). Deviations as large as 1000 years between the different fractions have been noted (Shore et al., 1995) and both the humin and the humic acid fraction have been suggested to give accurate dates (Johnson et al., 1990; Bartley and Chambers, 1992). Even though datings are performed on chemical fractions, ages derived using this method depend on the proportions of the fractions in the bulk material.

Accurate dating is important for all approaches, and is highly important when using age-depth models to calculate rates of peat growth and carbon accumulation. Deviations in calibrated ^{14}C ages (which may be as large as hundreds of years) can give misleading accumulation rates, especially when analysing short-term accumulation rates. When modelling age-depth curves, the model has to be very flexible to find the best curve fit and should include calibrated data as well as the uncertainty from the analysis. Most estimates of peat growth and carbon accumulation rates are based only on the calibrated ^{14}C age of the basal peat sample. In some studies linear rates of accumulation are assumed, whereas in others estimates of peat accumulation are based on the accumulated dry mass and a decay constant (Clymo, 1984). However, several datings are necessary since there are large variations in carbon accumulation rates within any mire, depending on variations in peat growth rates, plant composition, and bulk density.

Objectives

The thesis is focused on variations in the peat growth and carbon accumulation rate of eleven different mires in northern Sweden.

The main objectives were to:

- Estimate peat growth and carbon accumulation rates for the mires studied.
- Evaluate the influence of factors controlling peat growth, and carbon accumulation rates for different mire plant communities.
- Compare the development of varying mire types, with trends in peat growth and carbon accumulation rates.
- Evaluate the influence of current apparent rate of carbon accumulation on actual carbon exchange.
- Evaluate possible errors when ^{14}C AMS dating peat.

Outline of papers

Paper I

Paper **I** describes a study in which we investigated possible causes of errors in ^{14}C AMS dating of peat. Different peat fragments from the same depths were dated: *Carex* aboveground, *Carex* belowground, *Sphagnum* stems from various sections, *Bryales* mosses, untreated bulk and treated bulk samples, and the <0.045 mm sieved fraction. These fragments were analysed from two different mire sites and from two different depths.

Paper II

In Paper **II** the botanical remains of peat cores from twelve mires were thoroughly analysed, and 81 different stratigraphical vegetation zones were identified. In total 123 ^{14}C AMS datings were performed, 6-18 on each stratigraphy, and the peat growth, and carbon accumulation rates were estimated for each mire and each plant community. We described the curves for both peat growth, and carbon accumulation rates for each mire in both time and space, and discussed the trends in relation to mire development.

Paper III

In paper **III** we evaluated the relationship between the long-term apparent carbon accumulation rate (LORCA) and recent apparent carbon accumulation rate (RARCA) of ten of the mires discussed in Paper **II**. We discussed the possibility that mires may act as sinks or sources of carbon-containing gases towards the atmosphere, considering both LORCA and carbon flux measurements and their implications.

Paper IV

In Paper **IV** we investigated the different factors that may affect peat growth and carbon accumulation rates. Both biotic and abiotic factors were considered for 59 of the 81 different identified vegetation zones in the stratigraphies from eleven of the mires studied in Papers **II**. The analysis was performed using both univariate statistics (ANOVA) and multivariate methods (PCA and PLS). The factors tested were: botanical content, geographical location defined in terms of latitude × height above sea level and longitude × height above sea level, depth from surface, age from surface, and degree of humification. We discussed the most relevant factors in relation to peat growth and carbon accumulation rates and to mire development.

Material and Methods

Site description

The majority of mires in northern Sweden are soligenous fens and mixed mires (Fig. 3). The most dominant mire plants on fens are *Carex* spp. with varying proportions of *Bryales* (different species of brown mosses), whereas for moss-dominated hummocks, *Sphagnum* is the most dominant species, often in association with dwarf shrubs.

Fig. 3. *Typical mire type in northern Sweden; mesotrophic tall sedge fen.*

Eleven mires in the county of Västerbotten and Norrbotten were sampled (Fig. 4). The mires sampled represent all the most common mire types found in the area. They differ in mire type, age, depth, altitude, development history, and origin, as well as geographical position (Table 1). The mire sites are classified according to Eurola et al., (1984). One supplementary mire from southern Sweden was sampled in order to compare accumulation rates between northern and southern ombrotrophic bogs. The different mires examined showed great heterogeneity with respect to both their mode of formation and their plant community development (see Paper **II**).

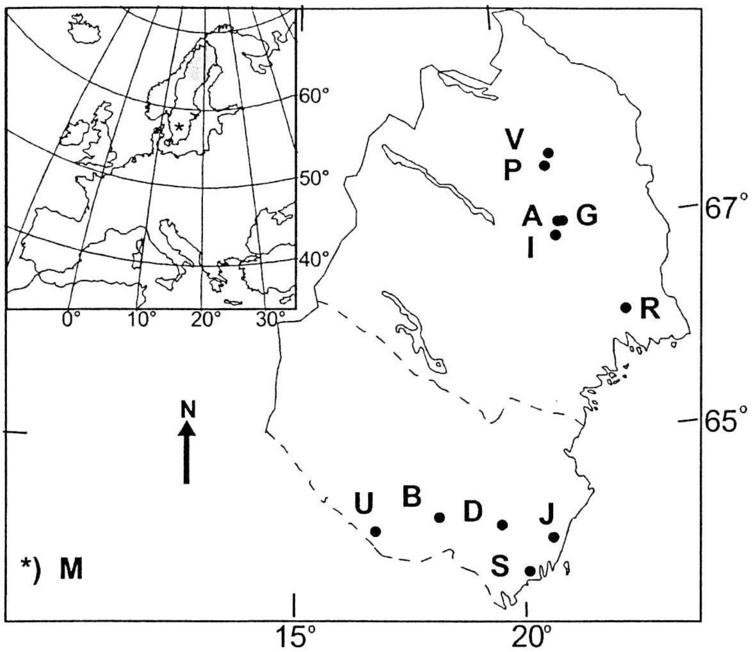

Fig. 4. *Map of mire sites sampled (see Table 1 for details).*

Table 1. *General description of samped sites*

Mire	**Code**[a]	**Miretype**[b]	**Longitude**	**Latitude**	**Height a.s.l. (m)**
Liekovuoma	V	Mesotrophic tall sedge fen	67'39	21'15	300
Pilkkarivuoma	P	Sedge and herb swamp	67'32	21'08	375
Sammakovuoma	G	Swampy sedge fen	67'00	21'27	235
Ala-Vuorkimavuoma	A	Sedge and herb swamp	67'00	21'20	255
Idbäcksträskmyrorna	I	True short sedge fen	66'52	21'15	120
Rismyran	R	True tall sedge fen	66'07	22'45	70
Björnmyran	B	Mesotrophic tall sedge fen	64'17	18'11	350
Svartberget	D	*Vaccinium myrtillus* spruce mire	64'11	19'33	270
Ullsjömyran	U	True tall sedge fen	64'10	16'45	350
Sjulsmyran	J	Poor *Sphagnum papillosum* fen with small flarks	64'02	20'40	60
Stor-Åmyran	S	*Sphagnum fuscum* bog with hollows	63'44	20'06	35
Store Mosse	M	*Sphagnum fuscum* bog with hollows	57'15	14'00	250

[a] Abbreviations used in Fig. 1.

[b] Current mire type according to Eurola et al. (1984).

Historical development

The mires situated in the inland of Norrbotten (Pilkkarivuoma, Liekovuoma, Ala-Vuorkimavuoma, Sammakovuoma and Idbäcksträskmyrorna) and Västerbotten (Ullsjömyran, Björnmyran and Svartberget) differ in age between 3700 years and 9600 years. However, all but Svartberget (2800 years) and Ullsjömyran (3700 years) are older than 8600 years old. The coastal mires (Rismyran, Sjulsmyran and Stor-Åmyran) are younger (2400-4800 years old), as they are situated below the highest shoreline. The results of the analyses of the macrofossils and vegetation zones, obtained from the cluster analysis, are presented in Paper **II** (Fig. 2a-k). The time periods are approximate estimates derived from the age-depth models, presented in Paper **II** (Fig. 3).

The five mires from the inland area of Norrbotten (Pilkkarivuoma, Ala-Vuorkimavuoma, Sammakovuoma, Liekovuoma and Idbäcksträskmyrorna) are all old (initiated between 8600-9600 Cal. Years BP) and their peat stratigraphies are mainly dominated by *Carex* spp. and *Bryales* spp. They originate from lakes (terrestrialisation) and the first plant communities in their stratigraphies were dominated mainly by *Equisetum* spp. Stratigraphies from the Ala-Vuorkimavuoma, Sammakovuoma, Pilkkarivuoma and Liekovuoma mires show similar phases of development and consist of varying percentages of *Bryales* mosses and *Carex* spp. Idbäcksträskmyrorna has a more variable peat stratigraphy, consisting of a mixture of *Bryales* mosses, *Carex* spp., *Eriophorum* spp. and shrubs, with short periods in which *Sphagnum* dominated, especially sect. *Acutifolia* and sect. *Palustria.*

The three coastal mires: Sjulsmyran and Stor-Åmyran in Västerbotten and Rismyran in Norrbotten, are all fairly young (initiated between 2400-4800 Cal. Years BP). Sjulsmyran and Stor-Åmyran are quite shallow (260 and 240 cm respectively) whereas Rismyran is deeper (409 cm). Sjulsmyran appears to have developed from paludification, judging from the high wood content in the deepest layer in its stratigraphy. Stor-Åmyran and Rismyran probably started via primary mire formation with subsequent land uplift with sea shore vegetation and at Rismyran probably floating mats of *Sphagnum*. The difference between the three mires increased as they developed. After the initiation phase, the rest of the Stor-Åmyran profile is mainly *Sphagnum*-dominated. *Eriophorum* spp. and *Graminoides* dominate in the Sjulsmyran profile in the following stage of development while Rismyran has a stage that includes *Sphagnum* sect. *Cuspidata* followed by *Bryales* mosses mixed with *Carex* spp. Towards the surface, *Sphagnum* spp. dominated at Sjulsmyran, whereas *Bryales* mosses and *Carex* spp. continued to dominate in Rismyran.

Three mires were sampled from the inland parts of Västerbotten: Ullsjömyran, Björnmyran and Svartberget. Ullsjömyran and Björnmyran differ in age, length, and botanical development but possess certain similarities, as they are both *Carex*-dominated and were initiated from lakes. The stratigraphy from Ullsjömyran is dominated by *Sphagnum*, which is fairly evenly distributed throughout the profile, while the stratigraphy from Björnmyran reflects a pure sedge mire, with distinct layers of *Bryales* mosses and *Sphagnum* at the bottom. Björnmyran is the deepest site – 625 cm deep and 8900 years old – whereas Ullsjömyran is only 350 cm deep and 3700 years old. Svartberget is the most distinctive of the sites, as it is a forested peat site with peat of high wood content. It is only 70 cm deep and is about 2800 years old. It also shows evidence of fire and has a charcoal layer between 790-850 Cal. Years BP.

The stratigraphy from the mire in southern Sweden, Store Mosse, has an upper bog part that is 650 cm thick and an underlying fen part of ca 100 cm. The bog stage was initiated about 8500 years BP, and consists of different periods of hummock- and hollow-forming vegetation. Also Store Mosse shows evidence of fire.

For further details of the development of the mires studied, see Paper **II** (Result and Fig. 2).

Sample collection and sub-sampling

Peat samples were collected using a peat corer (Jowsey, 1966), the collector being 50 cm long and 5 cm in diameter (Fig. 5). The peat cores were wrapped in plastic film, transported to the lab within at most two days, and stored below +4°C until preparation. Two parallel cores were sampled at each sampling point. The peat cores were sampled from the surface to the bottom, but the uppermost peat was excluded for practical reasons.

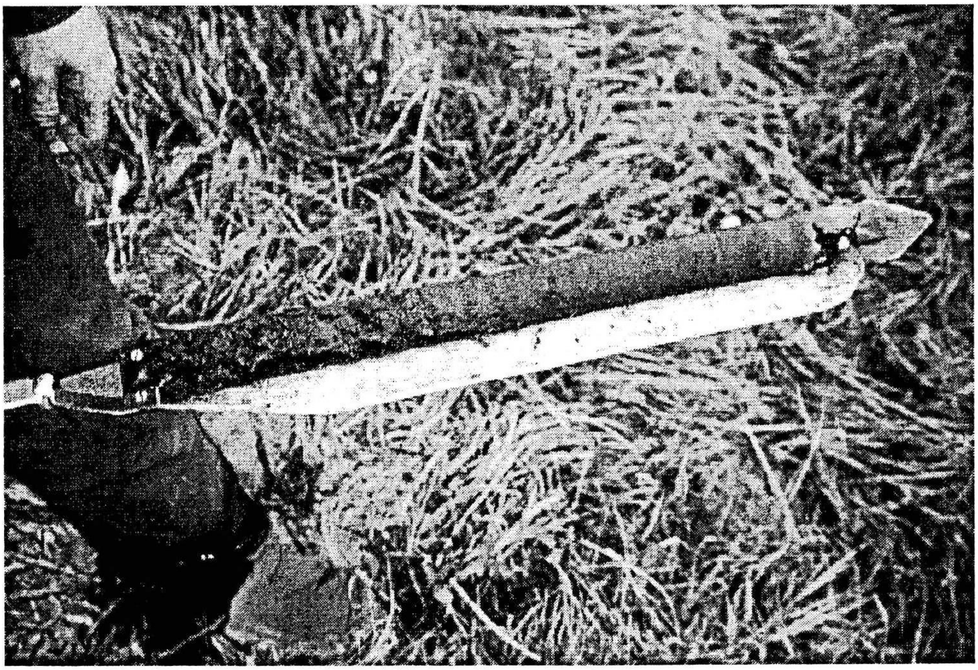

Fig. 5. *Peat sampling, showing the deepest layer of a core.*

One core was used for macrofossil analysis and ^{14}C AMS dating whereas the parallel core was used for bulk density measurements and carbon analysis. The cores were divided into 2 cm subsequent slices (unless this interfered with visually discernible borders) and each slice is hereafter referred to as a subsample. The degree of decomposition was measured (von Post and Granlund, 1926) and a coarse macrofossil analysis was performed on all subsamples.

Macrofossil analysis

In order to determine the duration of the different plant communities present in the stratigraphy, the subsamples selected for macrofossil analyses were irregularly located, i.e. more subsamples were analysed close to the transitions between the plant community zones than in the middle of the zones. Macrofossil analysis was performed using a modified method (Bohlin et al., 1989), originally described by Heikurainen and Huikari (1952). The subsamples were boiled in a 10% KOH solution and then rinsed in a 0.045 mm sieve with water. The rinsed plant fragments were embedded in gelatine glycerine on microscope slides then identified and counted as a percentage of total fragments counted. The fragments were classified in groups of taxa. In addition to the groups defined by Heikurainen (1952), the *Sphagnum* peat constituents were further divided into four sections (*Palustria*, *Acutifolia*, *Cuspidata*, and Eutrophic *Sphagna*). The additional peat fragments, consisting of *Phragmites australis*, *Equisetum fluviatile* and *Polytrichum* spp. remains were also counted as separate constituents. The nomenclature used follows Lid (1985) for phanerogams and Koponen (1977) for bryophytes.

The eighteen determined vegetation zones were separated by cluster analysis, using CONISS software (Grimm, 1987). The vegetation zones were defined using the peat categories suggested by Heikurainen (1973). The zones were divided into three main groups (*Sphagnum* peat, *Carex* peat and wood peat) based on the dominating macrofossils remaining in the peat. Within the three main groups a total of 18 subgroups were further identified (vegetation zones). In Fig. 6 an example of the results obtained for the Idbäckträskmyrorna is shown.

Bulk density measurements and carbon analysis

The bulk density was calculated from the weight of freeze-dried samples, the cross section of the peat sampler and the length of each subsample. For the carbon analysis a minimum of three subsamples were selected from each plant community zone. In zones longer than 30 cm, subsamples were taken every 10 cm. The subsamples from each zone were mixed into one composite sample for each zone. The composite samples were ground and the carbon content analysed using a CHN elemental analyser (Perkin Elmer 2400).

^{14}C AMS dating

^{14}C AMS dating was conducted on selected macrofossil remains from subsamples adjacent to the transitions between stratigraphical plant community zones. From zones with a large vertical extension, additional subsamples between the plant community transitions were ^{14}C dated. Selected macrofossil remains were used to avoid different carbon fractions, particularly roots and dissolved organic carbon

(DOC), distorting the ^{14}C age of the selected stratigraphic layer (c.f. Nilsson et al., 2001). If available, *Sphagnum* stems were selected. As a second choice, stems from other moss species were used and in rare cases other macrofossil remains were dated. A complete list of specific fragments for each dated depth is presented in Paper **II**, Appendix 1. To avoid contamination, the outermost layer of the peat core was removed prior to the removal of the subsamples for ^{14}C dating. The ^{14}C AMS dating was performed at Ångströmslaboratoriet, Uppsala University, Uppsala, Sweden.

The subsamples from which remains were extracted for ^{14}C dating were washed in purified water (deionised, carbon- and millipore-filtered; SuperQ purification system, AKA-filter, Stockholm) and sieved through a 0.14 mm mesh. The selected macrofossils were then boiled in a 10% KOH solution (KOH Proanalysis from Merck, Germany and purified water). The fragments were rinsed thoroughly in excess purified water. All samples were finally dried in a freeze dryer, prior to AMS analysis.

Calculations of accumulation rates

The AMS ^{14}C dates were calibrated using OxCal 3.b2 (Ramsey 1995; 1998). This program gives the calibrated age as a frequency distribution, which usually deviates from a normal distribution, so the median was used as a central value to represent the calibrated age of the sample. A age-depth curve was fitted from calibrated ^{14}C ages against depths using Psimpoll 3.0 (Bennett 1994; 2001). In Fig. 7a the age-depth curve for the Idbäcksträskmyrorna is shown. The models available in the software for interpolation are: Linear interpolation between dates, Cubic spline interpolation, General linear line fitting by weighted least-squares or singular value decomposition and line fitting by Bernstein polynomials. We tested all of these options except linear interpolation for every age-depth relationship. The model giving the highest R^2 value, without yielding negative accumulation rates for each of the age-depth curves was selected. Since one of the main objectives of this thesis was to evaluate the plant community specific peat growth and carbon accumulation rates, the age at each transition between different vegetation zones had to be estimated. This was done by inserting the appropriate depth value into the age-depth model for each peat stratigraphy. To calculate the time interval for each identified stratigraphic zone, the age at each transition was then estimated from the age-depth model. The peat growth rates (mm yr^{-1}) were calculated as the derivative of the age-depth curve. All rates were calculated with a 95%-confidence interval. To calculate accumulation rates (A^c) the following formula was used:

$$A^c = r \times C \times \rho$$

Where A^c is the carbon accumulation rate (g C m^{-2} yr^{-1}), r is the peat growth rate (m yr^{-1}), C is the relative carbon content (0-1), and ρ is the bulk density (g m^{-3}). All carbon accumulation rates were calculated with the sum of standard deviations. The total uncertainty in carbon accumulation rate was calculated by inclusion of the variance of both calibrated ^{14}C age and bulk density according to the standard rules for addition. In Fig. 7b and c peat growth rate and carbon accumulation rate for the Idbäcksträskmyrorna are shown.

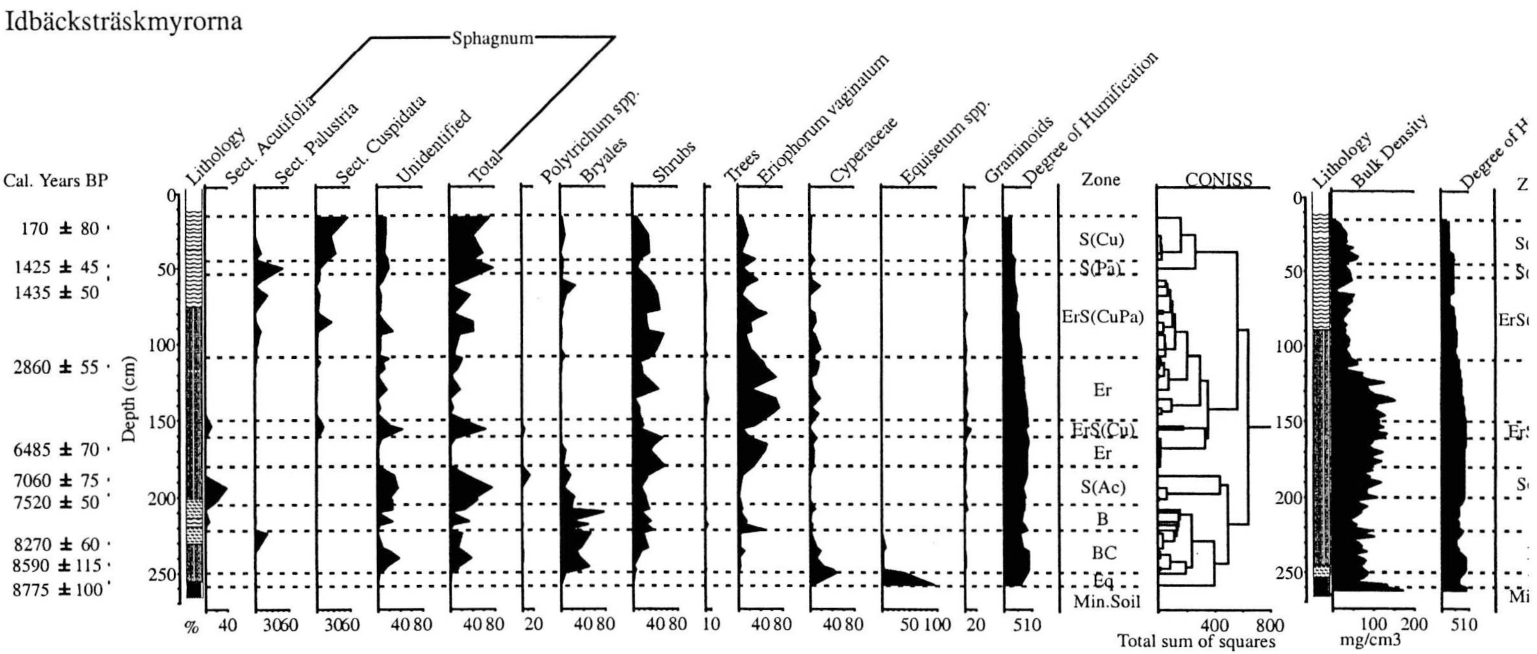

Fig. 6. *Macrofossil analysis of the Idbäcksträskmyrorna site. Diagram showing the principal of using the cluster analysis program, CONISS, which indicates where the largest changes in plant communities occur. CONISS is based on the percentage of the total number of fragment counted. Botanical composition in zones according to (Heikurainen, 1973). Abbreviations: S(X); Sphagnum spp. (Section in brackets), ErS(X); mixture of Eriophorum spp. and Sphagnum (Section in brackets), Er; Eriophorum spp., B; Bryales mosses or Bryales mosses and Carex spp. or Bryales mosses and Sphagnum spp., BC; Mixture of Bryales mosses and Carex spp., Eq; Equisetum spp.*

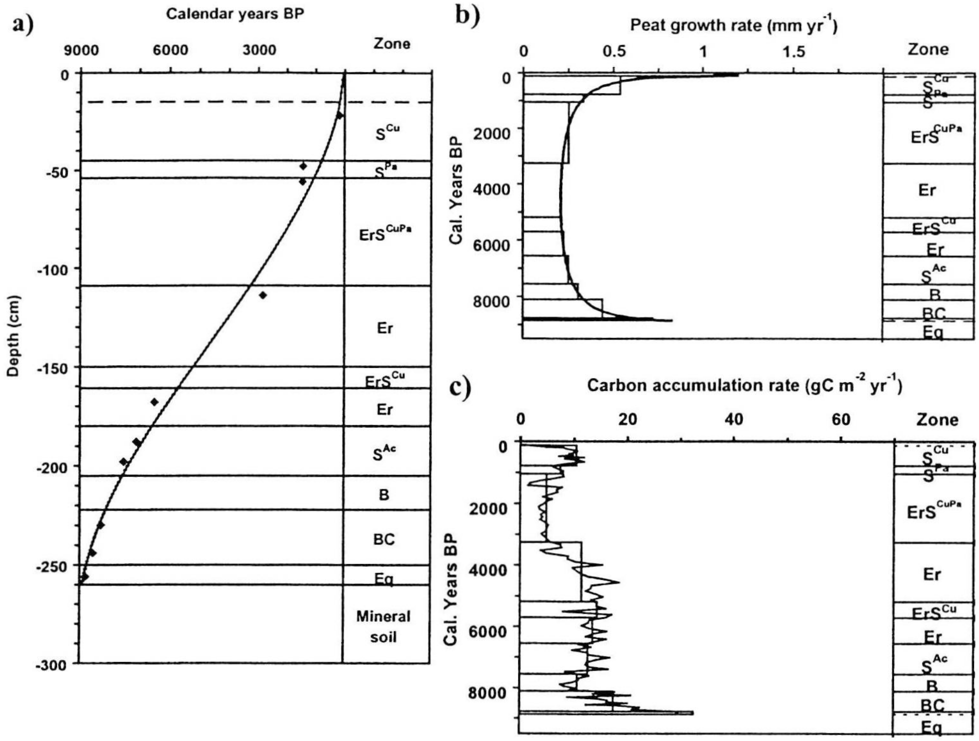

Fig. 7. *Curves showing results from the Idbäcksträskmyrorna site (for abbreviations see Fig. 6). (a) Age-depth curve, fitted using Psimpoll 3.0 ($R^2 = 99.09\%$); (b) Mean peat growth rate for each vegetation zone (bars) and peat growth rate for each sampling point (solid line); (c) Mean carbon accumulation rate for each vegetation zone (bars) and carbon accumulation rate for each sampling point (solid line).*

Statistics

The statistical methods used for analysing the data were ANOVA followed by Tukey's multiple test, multiple linear regression, and the multivariate statistical techniques Principal Component Analysis (PCA) and Partial Least-Square (PLS) regression. PCA and PLS were applied to the data set using SIMCA-P 8.0 (Umetrics AB, Umeå, Sweden). PCA shows the relationship between the samples as well as between the variables, and derived diagrams display a two-dimensional picture of the multi-dimensional objects' or variables' space (Jolliffe, 1986). PLS is a statistical way of examining the relationship between several more or less correlated X-variables and one or several Y-variables. In our analyses, peat growth and carbon accumulation rates were used as response variable (Y-variables) and all other variables were included as independent variables (X-ariables) (Martens and Naes, 1989).

Main results and Discussion

Methodological considerations

^{14}C dating

Peat at a certain depth is a mixture of vegetation that originally grew at the surface (aboveground vegetation), roots penetrating from the peat surface (belowground vegetation), dissolved organic carbon (DOC) and particulate organic carbon (POC) that has been transported, with water, from other parts and depths of the mire. Our study revealed significant differences in the ^{14}C age of various fractions within the peat bulk samples (Paper **I**, Fig. 1a-d). The variations in ages between the different fractions are large within each bulk sample. The extent of variation in ages also differs between mires and between different depths within each mire. Our data suggest that mosses growing at the mire surface yield macrofossils that give the most accurate ^{14}C date for any depth sampled. The different sections of *Sphagnum* currently growing at the mire surface did not show any significant differences in ^{14}C content (Paper **I**, Table 3). We therefore concluded that errors due to variations in the contribution of "old" ^{14}C in the three *Sphagnum* species were not of great significance.

^{14}C AMS dating has the great advantage of allowing small samples (0.1 mg carbon) to be dated, and it is therefore possible to select the amount of specific macrofossils needed, without too much effort. Nevertheless, peat is often ^{14}C dated using the bulk material of the peat. This may be accurate enough for some purposes, but as the demand for sensitivity increases, e.g. for high-resolution studies or discussing historical events (e.g. climatic events) accuracy becomes highly important. For modelling processes, such as peat growth rates in a stratigraphical sequence, accurate dating is extremely important.

Calibrations

The procedure used to calibrate ^{14}C dates to calendar years will also influence the results. There are now several programs available for this purpose on the internet, e.g. BCal, Cal, Calib, and OxCal. We used OxCal 3.b2 (Ramsey 1995; 1998), since it provides the ability to examine the distribution of frequencies as well as calculating 1σ and 2σ values (Fig. 8). Instead of using the midpoint of $\pm 1\sigma$, a common procedure, we used the frequency distribution to estimate the most probable calibrated age, using the full range of calibrated dates for calculating the weighted mean (Papers **II**, **III** and **IV**). The difference between the midpoint derived from $\pm 1\sigma$ and the most probable age based on the frequency curve will not always seriously affect the results, but for certain periods the difference may be large.

Despite the constant decline in ^{14}C isotopes, there are variations in the $^{14}C/^{12}C$ ratio, which cause fluctuations in the calibrating curve. Consequently, the calibrated data are distributed according to a Gaussian rather than a Poisson function. The Gaussian function often produces curves with split peaks, i.e. more than one alternative calibrated age appears. By using calibrating programs providing a wiggle matching option, the uncertainty of the calibrated dates diminishes considerably. However, it requires that several datings are performed within a short time interval, since the wiggle matching uses the small-scale fluctuations in the calibration curve for its analysis. If possible, it is recommended that data should be calibrated using wiggle matching e.g. van Geel and Mook (1989).

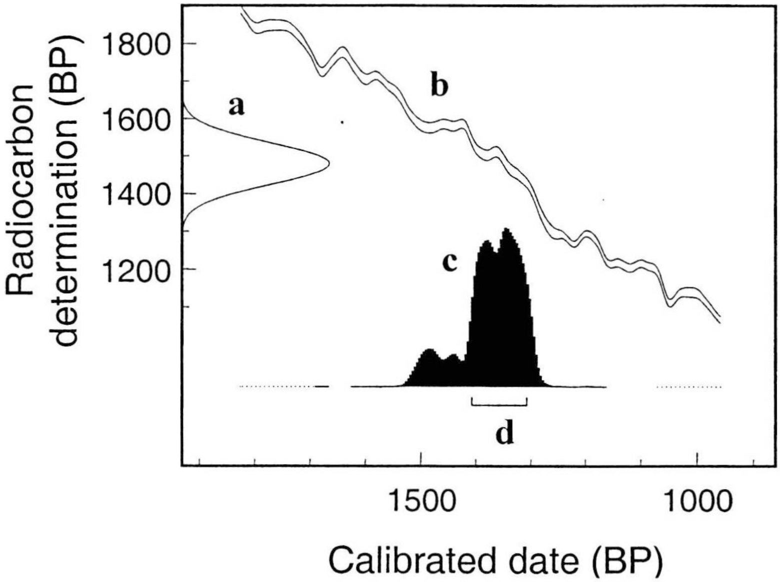

Fig. 8. *Principal for transformation of Radiocarbon-determined into calibrated age. (a) Radiocarbon-determined age; (b) Calibration curve based on M. Stuiver, A. Long and R. S. Kra (eds). 1993. Radiocarbon 35(1); (c) Calibrated dates; (d) The ±1σ range of the calibrated date.*

Curvefit

When evaluating issues concerning age-depth relationships in peat, the accuracy of the dating is utterly important. Even small uncertainties of ages in a sequence may cause large errors in the derived accumulation rates. When estimating rates of accumulation, the model used should be as flexible as possible. We used Psimpoll 3.00 (Bennett 1994; 2001), which provides the possibility of selecting different algorithms to model the age-depth relation as well as providing the opportunity to include the calibrated errors, and reports a 95%-confidence interval (Papers **II**, **III** and **IV**). The different curve-fitting options are Linear interpolation between dates, Cubic spline interpolation, General linear line fitting by weighted least-squares or singular value decomposition and line fitting by Bernstein polynomials. Differences in the different models have been discussed by Bennett (1994) and depending on the type of age-depth model used the accumulation rates derived may vary considerably. We used the model yielding the highest R^2 value without accepting negative accumulation rates. In most cases the Bernstein polynomials were the best option, although in some cases Polynomial line fitting was a better choice. Nevertheless, systematic divergences (Paper **II**, Fig. 3) were found within some of the mires.

For accurate curve-fitting the number of datings is crucial, and both depth and material have to be chosen carefully. We used 6-18 ^{14}C AMS datings for each stratigraphy (Paper **II**, Appendix A). The modelling approach used in this study avoids single deviating ^{14}C dates having a strong, distorting influence on the results. It probably also gives the best description of the general age-depth relationship. Given the limited number of ^{14}C dates available, any of the models used will disregard rapid changes in growth rates. However, the curve-fit still has limitations, and the obvious changes in peat growth rate seen in some of the age-depth curves (Paper **II**, Fig. 3), the curve Stor-Åmyran for example (Paper **II**, Fig. 3k), which shows differences between hollow and hummock communities in the uppermost part of the mire. Similar problems can be seen in Idbäckssträskmyroma (Paper **II**, Fig. 3e) and Björnmyran (Paper **II**, Fig. 3g). However, to allow variations in carbon accumulation rates to be followed in real detail ^{14}C AMS datings would have to be taken at about every 2 cm (Oldfield et al., 1997).

Differences in peat growth and carbon accumulation rates in relation to succession

The macrofossil analysis of the peat stratigraphies (Paper **II**, Fig. 2) revealed major differences in the patterns of development in the mires examined. However, a number of general trends could be observed. The northernmost mires (Liekovuoma, Pilkkarivuoma, Sammakovuoma and Ala-Vuorkimavuoma) have fairly similar temporal patterns. They are all located in the same geographical area and have therefore been exposed to similar climatic conditions. However, they differ in both depth and age. The classical model of mire development, describing a transition from fen- to bog-vegetation as outlined in Mitsch and Gosselink (2000), was only followed at Store Mosse, which is a true raised bog and at Stor-Åmyran, a bog site in a mixed mire. In the more northern latitudes no bog development was found, as low temperatures limit the distribution of bogs (Almquist-Jacobson and Foster, 1995). A large number of different successional pathways for wetlands have been shown, a majority of which progress towards drier plant communities, although regional and local climatic variations can also drive the succession towards wetter plant communities (Tallis, 1983; Klinger, 1996). In this study examples of successions towards both wetter (e.g. Sjulsmyran) and drier plant communities (e.g. Stor-Åmyran) were found. Furthermore, mires with plant communities that appear to have remained fairly constant for more than 5000 years (e.g. Pilkkarivuoma) were common. These results illustrate the complex nature of plant community successions in wetlands.

Thus, the variation in mire plant community succession between mires indicates that both autogenic and allogenic factors, to various extents, control mire development. These factors are also important for peat accumulation. Several studies have shown that rates of peat growth and carbon accumulation differ in different plant communities (Kuhry et al., 1992; Ikonen, 1995; Damman, 1996; Oksanen et al., 2001). In our study, eight out of twelve mires examined showed a decreasing trend in carbon accumulation rates, i.e. accumulation was highest in the bottom layers of the mires and decreased with time (Paper **II**, Fig. 3a, c, d, e, g, h, j and k). However, there was no close connection between different successional stages and the rates of accumulation.

Rates of peat growth and carbon accumulation are determined by the amounts of organic material that are transferred from the acrotelm to the catotelm and the decay processes occurring within the catotelm (Clymo, 1984; Belyea and Warner, 1996; Belyea and Clymo, 2001). The processes determining the amount of organic material that accumulates as peat are affected by both allogenic and autogenic forces, which determine the mire micro-topography and plant community composition. These in turn, regulate the net primary production, decomposition, and redox-conditions in the acrotelm. Therefore we hypothesised that the variation in rates of peat growth and apparent carbon accumulation should be closely connected to plant species composition. However, the differences observed between plant communities dominated by *Carex* spp. and *Sphagnum* spp. could not be distinguished from differences in geographical locations (Paper **IV**, Fig. 6). Since reductions in both peat growth and carbon accumulation rates occur in most mires with time, we suggest that the decline in nutrient availability indicated by the plant succession in some of the mires (meiotrophication; sensu Sjörs, 1983) could be the main reason for the decreasing accumulation. Reductions in nutrient status can be caused by both allogenic and autogenic forces. The most obvious autogenic force is the inflow of mineral-containing groundwater, which diminishes as the mire accumulates, causing the mire to receive successively less groundwater or, ultimately, to lose contact with it completely. An allogenic force which may cause the same effect on net primary production is long-term decline in plant nutrient concentrations in the catchment's mineral soils that are generated by weathering and other soil-forming processes. Evidence for this kind of decline has been observed in boreal lake sediments (Engstrom et al., 2000). A further allogenic force that could be involved is long-term climatic change.

The pattern of high peat growth and carbon accumulation rates being associated with the deepest peat layers was not observed in all mires. Ullsjömyran and Rismyran deviated from this general pattern, as calculated peat growth and carbon accumulation rates increased from the bottom layers to a peak and then diminished again towards their surfaces. Differences in local climate have been suggested to be one cause of variation in the temporal patterns in peat (Lavoie and Richard, 2000), although we find little support for this hypothesis in our data.

The plant composition was analysed with high resolution, and thus provides a good source of information for comparison with the detailed peat growth and carbon accumulation rates. The currently used classification has one disadvantage: since there is no information on individual species within the "*Carex*", "*Bryales*" and "Graminoid" peat constituents, we cannot evaluate changes in nutrient conditions in further detail. Therefore, especially for the sedge fens, no connection between reductions in carbon accumulation rates and diminishing nutrients could be definitively proved in this investigation.

Peat growth rate explains 57% of carbon accumulation rate, whereas the bulk density explains 33% (Paper **IV**, Fig. 4). Part of the unexplained variance probably emanates from the uppermost vegetation layers. Relatively high peat growth rates do not correspond to comparably high carbon accumulation rates (Paper **II**, Fig. 5). This discrepancy most probably results from unconsolidated peat close to the surface.

Differences in peat growth and carbon accumulation rates in relation to plant communities

In theory, *Sphagnum* species ought to have higher potential for accumulation since they are more resistant towards decay than other peat-forming species such as *Carex* spp. (Verhoeven and Toth, 1995; Szumigalski and Bayley, 1996a; Scheffer et al., 2001), and high accumulation rates are determined more by low decay rates rather than high production (Clymo, 1983). However, several external factors affect production and decay e.g. climatic conditions (especially temperature and hydrology). In our study significant differences were found in peat growth rates when comparing different plant communities, but no such differences were found in carbon accumulation rates (Paper **IV**, Fig. 3c and d). The variation of accumulation rates within the plant communities is probably masked by other factors, since objects within specific peat layers originate from different locations, and different developmental phases as well as reflecting differences in climatic conditions during peat formation.

In most of the mires we see a tendency for the rate of carbon accumulation to decrease as their development proceeds, irrespective of the time scale (Paper **II**, Fig. 5). Even though we excluded the first 500-1000 years in the statistical analysis when comparing the accumulation rates in different plant communities, the decreasing trend can still be seen. Hence, the estimated accumulation is higher in the bottom layer than in the layers further up in the stratigraphies. Possible differences in accumulation rates between *Sphagnum*, and *Carex* plant communities (Paper **IV**, Fig. 3c and d), could therefore be masked by decreasing carbon accumulation rates along with succession as well as natural variations in accumulation within each individual plant community. One disadvantage with combining the separate species into specified groups of plant communities according to dominant species is that a lot of information about the original vegetation is lost and the plant communities do not fully reflect the variation in the environment, for instance there are then difficulties in separating oligotrophic fens from bogs.

Therefore, using multivariate analyses, the original constituents, in terms of proportions of the total amount counted in each plant community was used. Furthermore, we added factors that are considered to affect peat growth and carbon accumulation rates e.g. geographical location, depth, and age (see Paper **IV**, Appendix A). The main factors explaining peat growth and carbon accumulation rates in the PLS analysis were the amounts of *Carex* spp. and *Sphagnum* spp., and the geographical parameters Geo1 and Geo2 (Paper **IV**, Fig. 6). In addition to these results, differences in which factors that affect peat growth and carbon accumulation rate respectively was found. Interpreting the PCA (Paper **IV**, Fig. 5a-h), high peat growth rates were correlated to low bulk densities and low wood contents, Whereas high carbon accumulation rates correlated to peat depth and high contents of *Bryales* mosses. Both peat growth and carbon accumulation rate was also correlated to low contents of *Sphagnum* sect *Palustria* and the total amount of *Sphagnum* as well as *Eriophorum* spp.

The strong correlation between species and the geographic locations seen in the PLS might caused by a bias in the stratigraphies sampled. *Carex* spp. and *Bryales* mosses mainly dominate the plant communities of the inland Norrbotten region; whereas the mires more close to the coast have a higher content of different sections of *Sphagnum*. For both PCA and PLS, other factors not included in this study may also affect the accumulation and might be as important as the factors considered. One other possible source of error is that covariation of factors may occur.

Differences in peat growth and carbon accumulation rates in relation to global carbon turnover

The stability of mires is of great concern in today's greenhouse gas debate, and the question of whether mires act as sinks or sources of carbonaceous gases to the atmosphere is crucial. Most assessments of carbon sequestration are based on the apparent rate of carbon accumulation in the mires or flux measurements at the mire surface. The global apparent carbon accumulation rate in mires has been estimated to average 29 g C m^{-2} yr^{-1} (Gorham, 1991), whereas measurements of current flux rates vary between ±100 g C m^{-2} yr^{-1} (Carroll and Crill, 1997; Lafleur et al., 2001; Wickland et al., 2001).

To account for the catotelm decay the calculated long-term apparent rate of carbon accumulation should be reduced by the amount of carbon mineralised in the catotelm. To estimate the amount of carbon mineralised in the catotelm, published values for the decay coefficient were used (Tolonen et al., 1992; Clymo et al., 1998). The true rate of carbon accumulation (TRACA) in the long-term is equivalent to 79% of LARCA, which corresponds to 23 g C m^{-2} yr^{-1}, according to the global carbon accumulation rate estimated by Gorham (1991). Based on data from Finland (Tolonen and Turunen, 1996), Clymo (1998) estimated a corresponding value of 21 g C m^{-2} yr^{-1}. However, due to bias in their dataset, Clymo (1998) suggested that their TRACA values were overestimated. Other studies have supported their suggestion, and presented lower values of TRACA, e.g. 55% (Warner et al., 1991) and 20% (van der Molen and Hoekstra, 1998) of LARCA.

After comparing the measured current flux rates with LARCA several studies have concluded that mires may currently act as either sinks or sources, depending on the large variations in CO_2 measurements. In a two-year study of a boreal peatland in northern Sweden, for instance, the mire seemed to be close to equilibrium and varied between being a source one year and a sink of atmospheric carbon the other year (Waddington and Roulet, 1996).

Based on comparison of current CO_2 fluxes with LARCA it is often stated that the carbon status in boreal mires today is changing, and that the mires are changing from sinks to sources of carbon, i.e. they are starting to emit more carbon than they fix as new biomass. However, our evaluation of carbon accumulation over a long-term perspective show that there has been a gradual reduction in the rates of apparent carbon accumulation in seven out of ten mires studied. Based on the RARCA values we suggest that these mires may have varied between being sources and sinks of CO_2 for several hundreds of years - maybe even thousands of years. Thus, the mires not have acted solely as sinks but have been in equilibrium for a much longer time than commonly suggested.

Decay rates are mainly estimated using the peat bog growth model described by (Clymo, 1984). Estimates of the decay coefficient in the catotelm derived this way normally vary between 5×10^{-4} and 1×10^{-5} (Clymo, 1984; Clymo et al., 1998; van der Molen and Hoekstra, 1988). Using the changes in C/N ratios of selected macrofossils in a stratigraphy, the decay coefficient was estimated to be 1×10^{-4} (Kuhry and Vitt, 1996). However, the rate of proportional decay in mires is far from constant throughout the peat stratigraphy and most probably decreases with depth.

Concluding remarks and future research

This thesis contributes to the knowledge of processes influencing the accumulation of peat. It supplies important information to relevant the areas of ecology, palaeoecology, and biogeochemistry. However, for better understanding the processes, new questions have been raised that remains to be investigated.

Variations in peat growth and carbon accumulation rates between and within mires have been examined in this thesis. The amounts of plant remains from the peat-forming species, *Carex* spp. and *Sphagnum* spp., explained the variation in peat growth and carbon accumulation rate to a high extent. However, a decrease in carbon accumulation rate with development occurred in most of the mires, which suggests that allogenic and autogenic forces interacted. By using time series analysis as used by various authors such as Chambers et al. (1997) on the different mires reported in this thesis, it might be possible to determine the role of large-scale climatic factors and thereby further distinguish between autogenic and allogenic forces influencing peat accumulation. The time series analysis could most probably be interpreted using climatic data from adjacent areas based on organisms such as diatoms and chironomids (Rosén, 2001) or the chemico-physical properties of varved lake sediments (Petterson, 1999).

The question of whether mires act as sinks or sources of carbon-containing gases to the atmosphere remains unresolved. Our results indicates that the boreal mires most probably have been acting both as sinks and sources to the atmosphere during at least several hundreds of years. Nilsson et al. (in press) provides carbon flux results from different mire types in Sweden, which can be used for evaluating the gas exchange between mires and the atmosphere throughout the Holocene. This would add useful information to the discussion about whether mires act as sinks or sources of carbon, and be a valuable tool when estimating the role of mires in global carbon turnover.

Despite the fact that microtopographic features cause ombrotrophic mires to vary in surface height (Okland and Ohlson, 1998), many studies e.g. (Belyea and Clymo, 1998; Malmer and Wallén, 1999) suggest that the effects of this variation on peat growth and carbon accumulation rates are masked by other, stronger factors. In our material there are some sequences where the change between hummock and hollow can be observed within the stratigraphy (e.g. Stor-Åmyran and Store Mosse). A high-resolution study focusing on the differences in peat growth and carbon accumulation rates between hummocks and hollows could be very useful for trying to explain the factors underlying the hollow-hummock accumulation theories. For this purpose, wiggle matching is proposed.

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