A comparison of two recent 23-year growth periods in Sphagnum dominated hummocks reveals increased vertical growth and carbon accumulation in ombrotrophic bog, SE Norway.

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Preface

Several people have given generously of their time to help support and guide this work. I would like to thank my main supervisor Prof. Mikael Ohlson for tutoring me before and during my field work. His know-how and general experience in the field and in this particular research area has been instrumental for the process of gathering data and making sense of the dynamics of mire ecosystems. I would also like to thank my co-supervisor Prof Rune Halvorsen at Norwegian Natural History Museum for insightful comments throughout and invaluable experience in the statistical aspect of the research process, and not least for knowing how to share this knowledge. In addition I would like to thank Barbro Dahlberg for teaching me how to age-determine trees by counting annual growth rings. Lastly I want to thank my spouse Ida Aasebø for support and valuable feedback during the process.

Abstract

Bogs are important sinks of atmospheric carbon (C) due to their unique ability to accumulate vast amounts of partially decomposed litter as peat, containing up to 25% of the world's soil carbon. Climate change and increases in nitrogen (N) deposition as a result of human activities is expected to affect the dynamics of carbon accumulation and the fate of the carbon sink capacity of peatlands is therefore uncertain. Increased N deposition may alter decomposition dynamics and decrease the carbon sink ability if the layer of peat-forming *Sphagnum* moss becomes N saturated. This study builds on a study by Ohlson and Økland (1998a) who measured peat accumulation variables in an ombrotrophic bog, SE Norway, in 1995. The aim of this study was to collect samples and model peat accumulation in peat that had accumulated since 1995, and compare rates of peat accumulation to those recorded in the previous study. Here I used the exact same location and estimated vertical peat growth, carbon accumulation rate and peat bulk density in *Sphagnum* dominated hummocks. Peat samples were gathered from the top peat layer and dated using small pines. A subset of samples from hummocks and within the same age-range was then derived from Ohlson and Økland (1998a) to acquire a comparable set of samples. Mean vertical peat growth recorded in 2012 (the current study) was 64% higher compared to the previous measurements, while the mean carbon accumulation rate and bulk density was 85% and 11% higher, respectively. Atmospheric N deposition in the region has decreased the last three decades. Despite this, the mean peat N concentration increased from 1.06% in the previous study, to 1.22% in the samples recorded in 2012. This indicates that the *Sphagnum* layer is not currently N saturated, and that beneficial climatic conditions might explain the increase in peat growth rates.

Sammendrag

Økosystemet myr utgjør en viktig lagringskilde for atmosfærisk karbon (C) på grunn av dets unike evne til å akkumulere store mengder av delvis nedbrutt organisk materiale som torv, og lagrer opp mot 25% av jordas jordbundne karbon. Menneskeskapte klimaendringer og økt nitrogen (N) avsetning forventes å påvirke denne dynamikken og framtiden for karbonlagringsevnen i myr er derfor usikker. Økt avsetning av N kan endre nedbrytingsdynamikken og svekke lagringsevnen av karbon hvis laget av torvdannende *Sphagnum* mose blir N-mettet. Denne studien bygger på en studie av Ohlson og Økland (1998a), som estimerte torv- og karbonakkumulering i en myr i sørøst-Norge i 1995. Ved å bruke nøyaktig samme område var målet med denne studien å innhente torvprøver og modellere torvakkumulering i torv som hadde akkumulert siden 1995, og sammenligne torvtilvekstrater med ratene estimert i den tidligere studien. Jeg målte vertikal torvtilvekst, akkumuleringsrate av karbon og tetthetsgrad i *Sphagnum* dominerte tuer. Torvprøver ble innhentet fra det øvre torvlaget og datert ved å bruke små furuer. Et underutvalg av prøver innenfor samme aldersspenn ble deretter filtrert ut fra Ohlson og Økland (1998a) for å danne et sammenlignbart sett med prøver. Jeg viser i denne studien at gjennomsnittlig vertikal torvtilvekst estimert i 2012 (denne studien) var 64% høyere sammenlignet med de tidligere estimatene, mens akkumuleringsraten av karbon og tetthetsgrad var respektivt 85% og 11% høyere. Atmosfærisk N avsetning i regionen har avtatt de siste tre tiårene. På tross av dette økte den gjennomsnittlige nitrogenkonsentrasjonen i torven fra 1.06% i prøvene fra den tidligere studien, til 1.22% i prøvene innhentet i 2012. Dette indikerer at *Sphagnum* laget ikke er N-mettet, og at gunstige klimatiske forutsetninger kan forklare økningen i torvtilvekstraten.

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Introduction

Broadly defined, peatlands are wetlands characterised by organic soil layers of at least 30 cm in depth, with an estimated mean depth for northern peatlands of 1.3-2.3 m (Limpens et al. 2008). Peatlands cover about 4.16 x 10^6 km^2 worldwide, although 80% of this is located in temperate-cold climates in the northern hemisphere (Joosten 2004). Although covering a modest 3% of the Earth's land surface, boreal peatlands constitute substantial carbon pools, storing between 270 and 370 PgC (1 Pg = 10^{12}g) of carbon in the form of peat (Turunen et al. 2002). This is over one third of the amount that is currently held in the atmosphere as CO_2 (IPCC 2007), and is a result of peatlands being a slow, variable but persistent carbon sink since the last glacial retreat. The carbon has thus accumulated at an estimated rate of between 20 and 30 g C m^{-1} yr^{-1} over the last 6–8 thousand years (Gorham 1991; Gorham et al. 2003; Vitt et al. 2000).

The amount of CO_2 that is exchanged between peatlands and the atmosphere is only a small part of the total contemporary exchange (around 0.1 – 0.5 Pg yr^{-1} compared to the net terrestrial exchange of 60 Pg yr^{-1}(Schimel 1995)). However, due to their large carbon (C) storage, boreal peatlands have the potential to significantly influence the atmospheric budget of important greenhouse gases like carbon dioxide, methane and nitrous oxide, and the potential impact on the global climate is assumed to be considerable (Franzén et al. 1996). Recent climate change and elevated deposition levels of nitrogen (N) are thought to influence mire ecology and potentially altering peat accumulation dynamics and carbon sequestration (Dise 2009; Gorham 1991), as northern peatlands are characterised by large interannual and interseasonal variation in C-exchange due to climate variability (Roulet et al. 2007).

The central paradigm in Scandinavian mire ecology suggests that there are three major environmental gradients in the mire vegetation that are connected to variation in ecological conditions; relating to nutrient richness, depth of the water table and proximity to the mire margin (Halvorsen et al. 2009; Malmer 1962; Økland 1989b; Sjörs 1948). A mire system can be divided into components that relate to each other hierarchically from major landscape units to mire microstructures, each associated with hydrological characteristics (Halvorsen et al. 2009; Moen 1983). The mire components, in order of decreasing size, include (1) mire complex, (2) mire synsegments, (3) mire segments, (4) mire features and (5) mire subfeatures (although this is a common classification, other terms are also being used; see Økland 1989a for an overview). Mosaics on one level (e.g., mire synsegments) combine to create components on a higher level (e.g. mire complex). The three local complex-gradients in the mire vegetation (poor-rich, depth to the water table and mire expanse-mire margin) operate on different spatial scales and affect different mire component levels; the mire expanse–mire margin gradient on the segment level, the poor-rich gradient on the segment-to-feature level, and the gradient in depth to the water table at the subfeature level (Økland 1989b).

The characteristics of the nutrient supply to the peatland have important implications for the dynamics of the ecosystem. *Minerogenous* peatlands receive water from the surrounding mineral soil, while *ombrogenous* peatlands receive water mostly by precipitation. The corresponding mineral nutrition regimes are termed minerotrophic and ombrotrophic, respectively, and the corresponding peatland types are referred to as *fens* and *bogs*, respectively (Moen 1973; Rydin & Jeglum 2006). Ombrotrophic, or “raised”, bogs are typically dominated by peat mosses of the genus *Sphagnum*, which may reach a cover of 80–100% (Økland 1989b; Robroek et al. 2008) and that form plant litter that is more resistant to decay than the litter of most vascular plants (Coulson & Butterfield 1978; Dorrepaal et al. 2005; Johnson & Damman 1993).

An important structural feature of peatlands structure is that they have two layers; the *acrotelm* which is the upper aerated and active layer, and underlying *catotelm* which is waterlogged and anoxic (Ingram 1983). However, a substantial variation in the lowermost position of the water table may occur between wet and dry years (Glaser et al. 1996). About 90 – 97 % of the carbon that is fixed by living plants is usually lost by decomposition in the acrotelm, with only a small fraction being incorporated as peat in the anoxic catotelm where low decomposition rates favour accumulation of peat (Francez & Vasander 1995). Slowly decaying plant material is gradually 'bogged down' towards the base of the acrotelm, subsequently becoming immersed into the catotelm and becoming anoxic as microbial communities use up molecular O_2 at a faster rate than oxygen diffuses down from the air through the water (Clymo 1984; Clymo et al. 1998). The slow rate of decomposition in the catotelm is not primarily a result of anaerobic decay but is brought about by easily degraded molecules no longer being present when the matter reaches the catotelm (Rydin & Jeglum 2006).

Due to the highly contrasting conditions in the two bog layers, the residence time of plant material in the acrotelm is very important for the carbon sink capacity of the bog. Average distance to the groundwater table (relative distribution of hummocks and hollows), climate and peat production rate are all important factors influencing residence time in the acrotelm and the time the material is subjected to aerobic decomposition, affecting the amount of material that is stored in the anoxic layers (Belyea & Malmer 2004; Gunnarson et al. 2008). Furthermore, the accumulation of peat may occur at variable rates among and within ombrotrophic bogs as different plant communities may contribute unevenly to the accumulation process (Ohlson & Økland 1998a).

Sphagnum mosses produce nutrient-poor, recalcitrant litter that is enriched in organochemical compounds (e.g. uronic acids) and polyphenols, thus inhibiting microbial activity and depressing vascular plant growth, fundamentally influencing bog biogeochemistry (van Breemen 1995). As such, their success is largely due to their ability to act as ecosystem engineers (Jones et al. 1994), creating and maintaing conditions unsuitable for many potential competitors (Sjörs 1948). The ecological relationship between *Sphagnum* and vascular plants is maintained by the characteristics of the nutrient regime in ombrotrophic bogs, receiving nutrients from atmospheric depositions as the only source of external nutrients. In pristine bogs, N inputs provided by atmospheric depositions and N fixating cyanobacteria are low (<5 kg ha^{-1}yr^{-1}). Plant growth in such bogs is therefore limited by N (Aerts et al. 1992; Verhoeven et al. 1996), and species are typically very economically efficient with regards to N uptake and relocation from older tissue (Lamers et al. 2000; Malmer & Nihlgård 1980).

While *Sphagnum* species utilise nutrients from the atmospheric inputs, vascular plants depend predominantly on the mineralization in decomposing organic material (Malmer et al. 2003; Svensson 1995). In contrast to bryophytes, vascular plants mainly take up N through the roots. *Sphagnum* therefore restrict the supply of nitrogen (N) to vascular plants by intercepting and utilising the atmospheric depositions before they become available for uptake through the roots of vascular plants (Nordbakken et al. 2003; Svensson 1995; Williams et al. 1999), a case of asymmetric nutrient competition that also seems to apply for phosphorus (Malmer et al. 2003). In addition, vascular plants are further restricted by the slow rates of *Sphagnum* decomposition and the low quality of the resulting litter, creating a slow, wet and mineral poor environment for decomposers (van Breemen 1995).

The economical effectiveness with N that has evolved in bog plants suggests that such ecosystems should be sensitive to alterations in N availability. At low levels of N input, growth is limited by lack of N and N is rapidly taken up by *Sphagnum* and used for growth so that the N concentration in the *Sphagnum* layer remains (more or less) constant (Aerts et al. 1992). If N deposition increases (i.e., through anthropogenic supplies), N may stop being the main growth-limiting factor for *Sphagnum*, and start to accumulate in moss tissue. Eventually, under higher inputs, N concentration will no longer increase, indicating that the *Sphagnum* layer is N-saturated (Lamers et al. 2000). In turn, increased N availability for taller and faster-growing vascular plants may gradually reduce the *Sphagnum* species' access to light (Hautier et al. 2009) The dynamics of the interaction between *Sphagnum* and vascular plants in relation to light is therefore an example of amensalism (Burkholder 1952), in which the outcome of the interaction is negative for one interactor (*Sphagnum*) and neutral for the other (vascular plants).

As *Sphagnum* growth becomes restricted by lack of light , a positive feed-back mechanism may create a vegetational shift towards a state more dominated by vascular plants with higher nitrogen demands, increasing the rate of decomposition as these plants have a different litter structure and typically decompose faster (Coulson & Butterfield 1978; Limpens & Berendse 2003). Litter characteristics of *Sphagnum* may also be physiologically affected by increased N availability through a reduction in polyphenol content and hence in the recalcitrant character of *Sphagnum* litter (Bragazza et al. 2006; Bragazza 2007).

As long as N is a limiting resource, N deposition may also enhance *Sphagnum* production and carbon accumulation rates (Aerts et al. 1992; Kuhry & Vitt 1996; Turunen et al. 2004), and increased growth may then act to dilute N concentrations and maintain the filtering function of the moss layer. This suggests the existence of important threshold values for N input that influences bog ecosystem dynamics through the effects on growth, decay and plant interactions – effects that in turn seem to be connected to climatic factors (Limpens et al. 2011).

Although recent studies have suggested that decomposition rates now tend to increase and carbon accumulation rates tend to decrease in Fennoscandian mires (Franzén 2006; Gunnarson et al. 2008), and that *Sphagnum* respond to combinations of climatic factors and nutrient regimes (Breeuwer et al. 2009; Limpens et al. 2011), more research is still needed on the degree of which these ecosystems are currently undergoing a change from N-limited to not N-limited ecosystem dynamics. Because contrasting background rates of nutrient deposition may yield different ecosystem responses to nutrient addition, the effects on carbon exchange dynamics may therefore vary depending on the characteristics of the nutrient regime (Lund et al. 2009).

The purpose of this study is to investigate current peat accumulation rates and associated peat characteristics in an SE Norwegian bog. This study builds on the study by Ohlson and Økland (1998a) who recorded rates of carbon- and nitrogen accumulation as well as other peat growth and vegetational parameters, enabling comparative analysis which was conducted in this study in order to investigate peat accumulation variables over a longer time period. While increased airborne N pollution in recent decades is a serious threat to the function of terrestrial ecosystems (Bobbink et al. 1998; Galloway et al. 2008), recent trends suggest decreased atmospheric nitrogen deposition in Norway in general and within the current study area in particular (Aas 2012). Although several studies have assessed peat growth dynamics in relation to climate and nutrient regimes, few studies have investigated recent changes in peat accumulation variables within a time series in the same location. The use of identical locations grants accuracy in time series studies, controlling for local climatic- and topographic factors. I wanted to measure peat accumulation variables in peat that had accumulated since 1995 under comparable conditions to peat from the previous study (the *119-pine data set*, see Ohlson & Økland, 1998a), and therefore selected pines that had sprouted on hummocks since 1995 when the previous field work was conducted. Vegetation and peat accumulation variables were investigated and values in 2012 were compared to those from 1995. I hypothesised that if the upper *Sphagnum* layer had become N saturated, rates of peat accumulation would have declined from 1995 levels due to one or more negative effects of elevated N levels on *Sphagnum* growth and/ or positive effects on peat decomposition rates.

Materials and methods

Study site

The study was conducted within a 400-m^2 (20 x 20 m) area on the eastern part of the bog expanse of Southern Kisselbergmosen, a multilaterally sloping and eccentric raised bog located 65 km southeast of Oslo, Norway (59°38’ N, 11°38’E), 285 m above sea level (Økland 1989b) (Figure 1). The hydrology of the mire is intact with the exception for a marginal influence of the road along the eastern border and a few old ditches along the margin of the bog, which indicate past drainage activities, although it is unlikely that these have had a significant influence on the hydrology of the bog expanse. The area corresponded exactly to Plot 1 of Ohlson & Økland (1998a), who studied spatial variation in peat, carbon and nitrogen accumulation rates. The peat at the study site was dominated by *Sphagnum* remains and was approximately 4 m deep (M. Ohlson, personal observation). Scattered, more or less stunted individuals of Scots pine (*Pinus sylvestris* L.) typically occurred within the plot and on the bog in general. Among bryophytes, *Sphagnum fuscum* and *Sphagnum rubellum* were dominating hummock species, while *Sphagnum tenellum* and *Sphagnum*

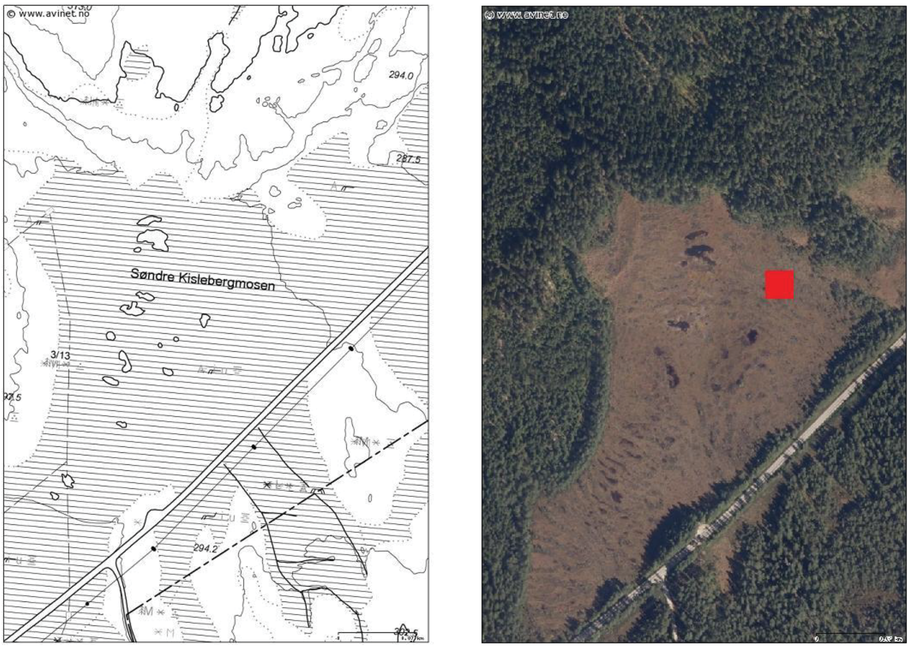
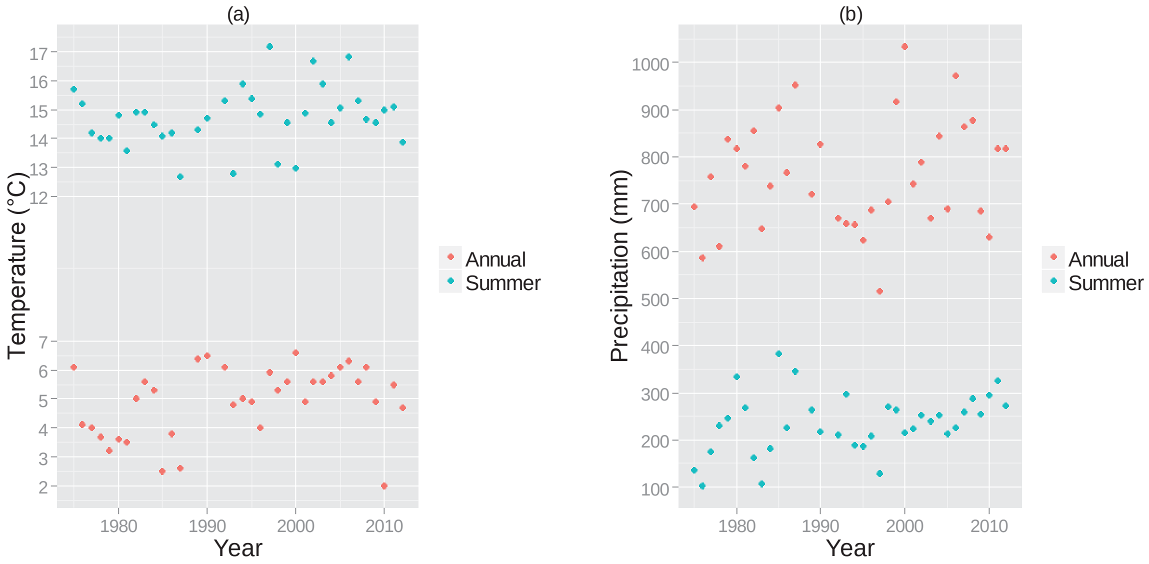


Figure 1 Plot 1 (red square) on the eastern part of Southern Kisselbergmosen. Photo and map extract from The Norwegian Mapping Authority.

cuspidatum dominated in the hollows. *Cladonia rangiferina* was the dominating lichen species, while *Calluna vulgaris* was the most prominent vascular plant species.

Microtopographically, an evenly dispersed and irregular pattern of hummocks and hollows characterised the study area. The slope of the groundwater table was 20 cm from the southwest corner to the northeast corner of the study plot (Ohlson & Økland 1998a). The study plot was located at the mire expanse end of the mire expanse-mire margin gradient. The climate is weakly oceanic (Moen 1998), with an estimated average temperature (1961 – 1990) of 3.7°C [data on climate normal from Magnor, 45 km N-NE of Southern Kisselbergmosen, corrected for altitude following Laaksonen (1976), all data from the Norwegian Meteorological Institute]. Annual mean precipitation (1961 – 1990) at the closest meteorological station was 700mm, but is likely somewhat higher in the study area due to orographic effects (Økland 1989b).

In the period between 1995 and 2012, the mean annual temperature was 5.3°C, while mean year precipitation at the Høland-Fosser (1995 – 2007) and Aurskog II (2007 – 2012) meteorological stations was 771 mm (http://www.eklima.no). Mean summer (June, July, August) temperature was 15 °C, and total summer precipitation increased significantly during the 18-year period (Figure 2 a + c). Historical atmospheric N deposition estimates in the study area (50 x 50 km^2 resolution) as measured in 5 year periods (Aas et al. 2006; Aas 2012; Hole & Tørseth 2002; Pedersen et al. 1990; Tørseth & Pedersen 1994; Tørseth & Semb 1997) show a decreasing trend the last decades (Figure 2 D).



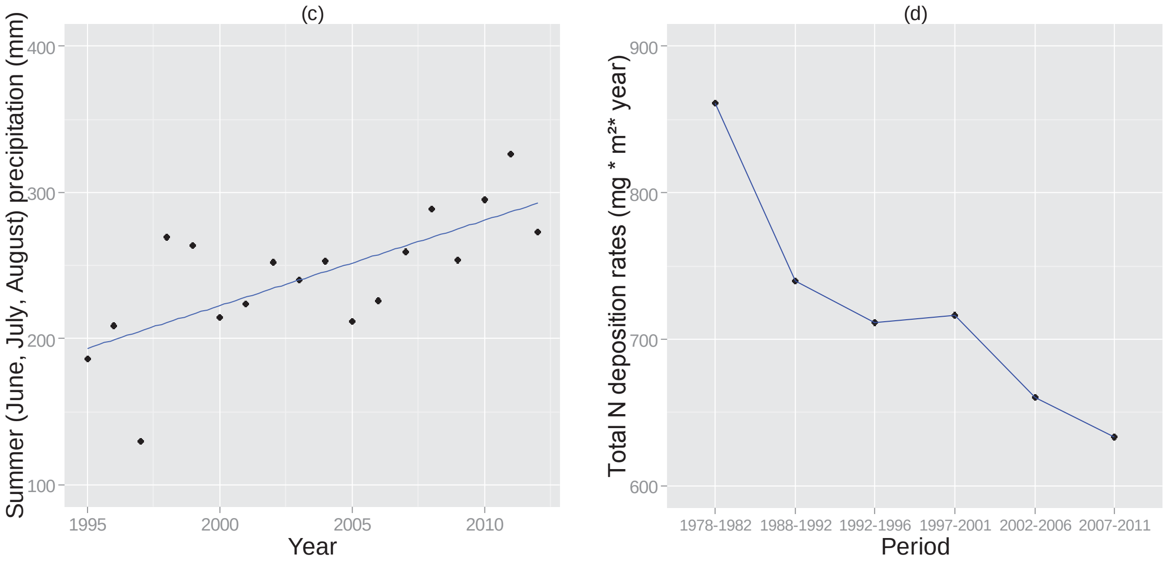


Figure 2 Scatter plots showing temporal variation of annual and summer (June, July and August) temperature (a) and precipitation (b) in the period 1975–2012, in addition to total summer precipitation in the period between 1995 and 2012 (c) (linear regression, total summer precipitation = -11446 + 5.8Year, $p <.01$, $n = 18$) and 5-year interval estimates of atmospheric N deposition in the region of the study area (d).

Peat core sampling and age estimation

All (104) Scots pine saplings (*Pinus sylvestris* L.) growing on hummocks in Plot 1 were collected between 25th of August and 16th of September 2012, and used for dating of surface peat by the so-called pine method, a precise method for dating surface peat layers (Borggreve, 1889; Ohlson & Dahlberg, 1991). The vertical distance from the root collar to the level of the stem where it emerged from the mire surface was measured. The age of each pine was determined in the laboratory by counting growth rings in a stereomicroscope.

Peat cores were sampled immediately adjacent to each of the pines, using a sharp-edged cylindrical corer (50 cm long, 10 cm in diameter). Each core was cut at the level corresponding to the level of the pines' root collars, so that one sample represented the amount of peat accumulated since the adjacent pine germinated. Thus, knowing the age of each pine sapling it is possible with reasonable accuracy to estimate the age of a layer of the adjacent peat (Figure 3).

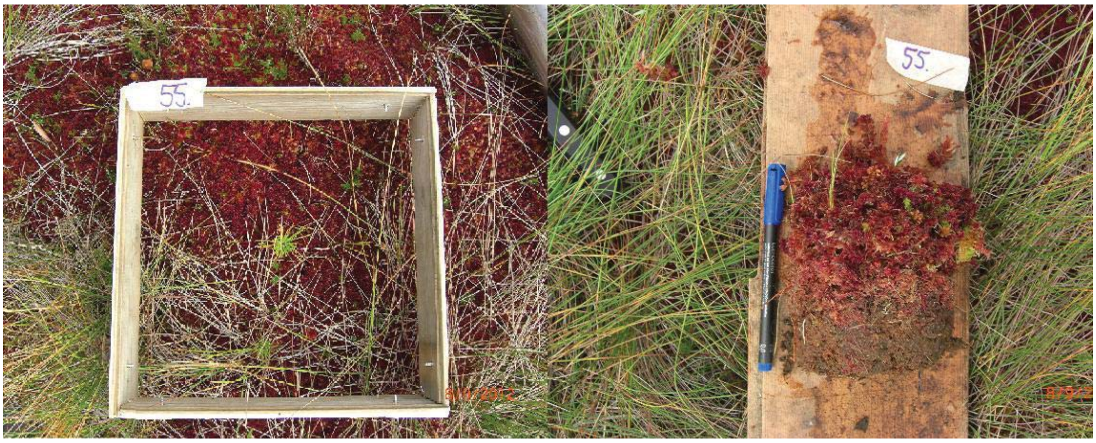


Figure 3 Sample images of pine sampling within a quadrat and the associated peat sample. Peat samples were extracted next to the pine sapling and cut at the position of the pine root collar.

Care was taken not to compact peat cores during the sampling process. All peat cores were dried at 80°C to constant mass. Each core was weighed in order to obtain bulk density. A subset of 20 peat samples was randomly selected for further processing to obtain information on nitrogen and carbon content. These samples were ground to peat powder using a mill before analysed for C and N concentrations in a Leco EC12 Carbon Content Analyser (St. Joseph, Michigan, USA). Total carbon and nitrogen contents were estimated by applying *dry combustion* methods described by Nelson (1982) and Bremner (1982). Peat accumulation variables (Table 1) were estimated using determinations of vertical peat growth, sample volume, dry weight, and peat sample age as well as N and C content.

Table 1 Summary statistics for peat accumulation variables 2012 (n = 102 unless otherwise stated. 2 outliers were removed before statistical analysis).

Variable name	Abbreviation	Unit of measurement	Mean	1 SD	Range
Peat age	YR	Years	8.41	5.30	1 – 23
Vertical peat growth rate	PG	mm/yr	14.06	0.67	0.6–36.7
Mass accumulation rate	MAR	$g \cdot dm^2 \cdot yr^{-1}$	7	3.65	0.67–21.11
Nitrogen concentration (n = 20)	NC	percentage of dry mass	1.22	0.34	0.76–1.94
Nitrogen accumulation rate (n = 20)	NAR	$mg \cdot dm^2 \cdot yr^{-1}$	55.5	30.17	23.23–133.55
Carbon concentration (n=20)	CC	percentage of dry mass	49.5	1.18	47.81–51.94

Carbon accumulation rate	CAR	$g \cdot dm^2 \cdot yr^{-1}$	3.46	1.81	0.33–10.45
Carbon-to-nitrogen ratio (n= 20)	C/N		43.61	11.36	25.97–65.47
Bulk density	BD	g/dm^3	53.18	19.72	18.34–128.35

Analysis of vegetation

Quadrats, 25 x 25 cm with the sampled pine in the centre, were located around each pine. The percentage cover of all *Sphagnum* species, lichens, hepatics and vascular plants within each quadrat was determined. Following Økland (1989b), each quadrat was further characterised as belonging to upper or lower hummock levels along the hydro-topographical gradient (expressing vegetational responses to depth to the water table). Each quadrat was classified to dominance type according to Økland and Ohlson (1998), based on the relative importance of lichen and bryophyte species. Following Ohlson and Økland (1998), six such dominance types were assigned: *Sr*, cover of *Sphagnum rubellum* >25% ; *Sf*, cover of *Sphagnum fuscum* > 25%; *Sm*, cover of *Sphagnum magellanicum* > 25 %; *Cr*, cover of *Cladonia rangiferina* > 25%; *He*, cover of Hepatics (all species) > 25 %; and *Naked peat*, referring to quadrats where living bryophytes and/or lichen cover was below 50%. Several categories could apply to a given plot.

Statistical analysis

GLM modelling of peat growth variables

Vertical peat-growth rate (cm per year), bulk density (g/dm^3) and carbon accumulation rate ($g*dm^2*year$) were used as response variables in this study, while peat age (years), total *Sphagnum* cover (%), hummock zone (upper/lower) and dominance-type category (see description above) were used as predictor variables for the analysis of data collected in 2012.

Initial data exploration revealed that two samples, both 1-year old pines and associated peat, acted as strong outliers in the distributions of both vertical growth rate and carbon accumulation rate. These outliers most likely represent combinations of exceptionally favourable local growth conditions and a favourable climate for growth;

conditions that are not representative for the general growth dynamics of the bog. Pines are expected to be particularly sensitive to variation in growth conditions early in their life cycle. I therefore considered it legitimate to remove these outliers before proceeding with statistical analyses (see Appendix for complete dataset).

Initially, single-variable general linear models (GLM) (Venables & Ripley 2002) were constructed to assess the effect of predictor variables on peat growth variables for the 2012 data-set. For the response variable *vertical peat* growth and *bulk density,* final models were constructed using a forward selection procedure, first including the *peat age* variable and subsequently sequentially adding predictors that explain a significant amount of residual variation to the model. The predictor *peat age* was included first when significant due to the clear and well-documented effects on peat accumulation rates (Ohlson & Økland 1998a; Turunen et al. 2004).For the response variable *carbon accumulation rate*, *peat age* was not a significant predictor and *total Sphagnum cover* was entered first in the sequential models. Nested models (a model M is a submodel of a more complex model M0 if and only if all predictor variables in M are included in M0) were evaluated by use of the F-ratio test, using a significance level of $\alpha = .05$. Casewise diagnostics and normality checking was conducted in order to assess the validity and generalizability of the models.

In order to compare peat growth characteristics between the two sampling years (1995 and 2012), GLMs with a mixture of categorical and continuous predictor variables (analyses of covariance) were conducted for each of the response variables, using sampling year as a categorical factor while controlling for the effect of significant covariates. As measurements of species cover in Ohlson & Økland (1998) were conducted using the Hult-Sernander-Du Rietz cover scale (Du Rietz 1921) subset of the 1995 (n = 63) and 2012 (n = 83) data sets were derived in which total *Sphagnum* cover > 50% . Restriction to these subsets was applied in order to avoid any biases due to differences in measurements between the years. The majority of samples in each of the years did, however, have *Sphagnum* cover of at least 50% (83.2% and 86.74% of the samples from 1995 and 2012, respectively).

In order to compare nitrogen concentration between the sampling years, a subset of the 1995-data was extracted (n = 63) that was within the same age range (1 – 19 years) as the 20 samples from 2012 that were analysed for N content. Potential differences in nitrogen concentrations between the two sampling years were investigated by GLM (ANCOVA) with peat age as covariate.

Significant Levene's test revealed unequal variances of two response variables (bulk density and vertical peat growth) between sampling years. As 2012 samples were slightly younger on average compared to 1995 samples, it is likely that these samples were more sensitive to local differences in growth conditions compared to the 1995 samples. T-tests revealed that the assumption of independence between covariates (*peat age* and *hummock zone*) and treatment (sampling year) was violated. Response variables were log-transformed before the analysis of covariance in order to better meet the assumptions of parametric tests.

Results

Vertical peat growth rate

Single variable GLMs revealed that vertical peat growth rate was significantly related to each of the four predictor variables (Table 2). The effect of peat age on peat growth rates was negative, while the effect of overall *Sphagnum* cover was positive. Affiliation to upper hummock zone positively affected vertical peat growth rates, while quadrats dominated by naked peat had significantly lower growth rates compared to *Sphagnum rubellum*-dominated quadrats. The best two-predictor model included the predictors *peat age* and *total Sphagnum cover*, and no further predictor inclusions significantly improved the final model of vertical peat growth. The assumptions of independent errors, linearity and no multicollinearity between predictors were met and casewise diagnostics revealed no unduly influence from single observations or subset of observations. Visual inspection of residuals vs. fitted values for the regression model as well as quantile-quantile plots revealed slight deviations from the assumption of normally distributed errors.

Table 2 Summary of single predictors' influences on vertical peat growth and the best multiple predictor model. For factor-type predictors (*hummock zone* and *dominance type*) model coefficients are obtained by use of treatment contrasts, the first-mentioned level (for hummock zone: lower) was used as the baseline with which all other levels was compared.

	Predictors	df	*B*	*SE* B	*P*	Residual	ΔR^2	*F* for change in R^2	*P* (F)
Single variable GLMs									
	Constant	100	1.81	0.12	<2e-16				
	Age	1	-0.05	0.01	8.71e-05	0.628	0.14	14.64	8.71e-05
	Constant	100	0.46	0.22	0.037				
	Total *Sphagnum* cover (%)	1	0.01	0.003	1.62e-05	0.618	0.17	20.55	1.62e-05
	Constant	100	1.21	0.11	<2e-16				
	Hummock zone	1	0.297	0.14	0.034	0.663	0.04	4.623	0.034
	Factor Dominance type					0.647	0.13	2.77	0.022
	Constant	90	1.36	0.09	<2e-16				
	Naked peat	5	-0.63	0.26	0.017				
	Sphagnum fuscum	5	0.28	0.19	0.149				
	Sphagnum fuscum/*Clad.* Rangiferina	5	-0.29	0.39	0.45				
	Sphagnum fuscum / *Sphagnum rubellum*	5	0.1	0.18	0.593				
	Sphagnum magellanicum	5	0.39	0.22	0.075				
Best multiple model	Constant	99	0.93	0.25	0.0003	0.5852	0.263	*F* (1,99) = 17.66	2.758e-07
	Age	2	-0.04	0.01	0.006				
	Total *Sphagnum* cover	2	0.01	0.003	0.0001				

Bulk density

Single variable GLMs revealed that peat age, total *Sphagnum* cover and hummock zone were all significantly related to bulk density (Table 3). Bulk density was greater in lower hummocks, and increased with peat age while it decreased with degree of *Sphagnum* cover. The best multiple model included predictors *peat age*, *total Sphagnum cover* and *hummock zone*. The assumptions of independent errors, linearity and no multicollinearity between predictors were met and casewise diagnostics revealed no unduly influence from single observations or a subset of observations. Errors were normally distributed.

Table 3 Summary of single predictors' influences on bulk density, and the best multiple predictor model.

	Predictors	df	*B*	*SE* B	*P*	Residual	ΔR^2	*F* for change in R^2	*P* (F)
Single variable GLMs									
	Constant	100	44.55	3.55	<2e-16				
	Age	1	1.03	0.36	0.005	19.05	0.08	8.248	0.005
	Constant	100	77.83	6.49	<2e-16				
	Total *Sphagnum* cover (%)	1	-0.34	0.09	0.0001	18.43	0.14	15.68	0.0001
	Constant	100	61.25	3.2	<2e-16				
	Hummock zone	1	-12.29	3.95	0.002	18.92	0.09	9.695	0.002
	Factor Dominance type					19.52	0.07	1.424	0.223
	Constant	96	52.11	2.79	<2e-16				
	Naked peat	5	16.13	7.89	0.044				
	Sphagnum fuscum	5	2.55	5.76	0.66				
	Sphagnum fuscum/Clad. rangiferina	5	14.32	11.61	0.22				
	Sphagnum fuscum / Sphagnum rubellum	5	-3.98	5.49	0.47				
	Sphagnum magellanicum	5	-1.52	6.51	0.817				

Best multiple model	Constant	98	70.61	7.43	1.43e– 15	17.58	0.23	*F*(1,98) = 9.61	1.19e-05
	Age	3	0.82	0.34	0.017				
	Total *Sphagnum* cover	3	-0.25	0.09	0.005				
	Hummock zone	3	-9.48	3.78	0.014				

Carbon accumulation rate

Single variable GLMs revealed that carbon accumulation rate was significantly related to total *Sphagnum* cover such that a higher total percentage cover of *Sphagnum* was associated with higher rates of C accumulation (Table 4). Dominance type *Sphagnum fuscum* was significantly and positively related to C accumulation rate, while a negative relationship between dominance type *Naked peat* and C accumulation rate approached significance at the .05 level. Inclusions of additional predictors in the model did not improve model fit (Table 4). The assumptions of independent errors, linearity were met and no subset of observations had unduly influence on the model. Visual inspection of residuals vs. fitted values for the regression model as well as plots revealed slight deviations from the assumption of normally distributed errors.

Table 4 Summary of single predictors' influence on carbon accumulation rate.

	Predictors	df	*B*	*SE* B	*P*	Residual	ΔR^2	*F* for change in R^2	*P*(F)
Single variable GLMs									
	Constant	100	3.918	0.33	<2e-16				
	Age	1	-0.05	0.03	0.11	1.79	0.03	2.596	0.11
	Constant	100	2.1	0.62	0.001				
	Total *Sphagnum* cover (%)	1	0.02	0.01	0.025	1.77	0.05	5.211	0.025
	Constant	100	3.33	0.31	<2e-16				
	Hummock zone	1	0.2	0.38	0.598	1.81	0.003	0.2799	0.598

Dominance type					1.74	0.12	2.595	0.03
Constant	96	3.33	0.25	<2e-16				
Naked peat	5	-1.3	0.7	0.067				
Sphagnum fuscum	5	1.13	0.51	0.03				
Sphagnum fuscum/Clad. rangiferina	5	0.16	1.03	0.875				
Sphagnum fuscum / Sphagnum rubellum	5	-0.26	0.49	0.596				
Sphagnum magellanicum	5	0.89	0.58	0.127				

Comparison between 1995 and 2012

Peat growth

Both peat age and hummock zone were significantly related to peat growth (Table 2). Both variables were included as covariates in a GLM model with sampling year as treatment factor (levels: 1995, 2012) (Figure 4 a + b). This model revealed a significant main effect of sampling year on vertical peat growth after controlling for the effect of the covariates, *F* (1, 145) = 11.571, *p* <.001, an effect that had a medium effect size, partial η^2 = .07. The mean vertical peat growth rate for samples (n = 89) recorded in 2012 was 1.49 cm yr^{-1} (s = 0.66), while the mean vertical growth rate for samples (n = 59) recorded in 1995 was 0.91 cm yr^{-1} (s = 0.44), constituting a mean difference of 64%. The assumption of homogeneity of regression slopes was met, revealing no significant interaction effect between the treatment factor (year) and covariates.

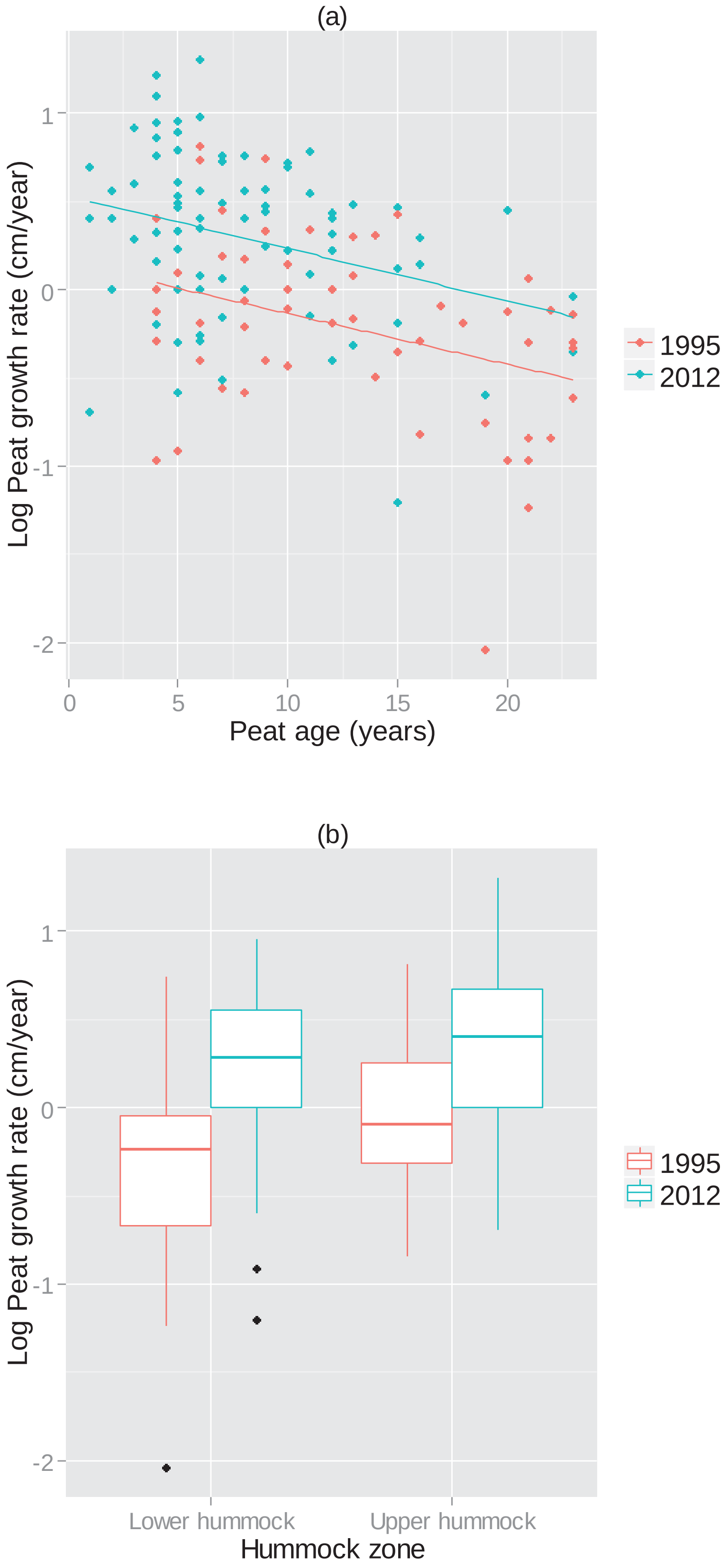


Figure 4 Relationship between (log) peat growth and age (a) and (log) peat growth and affiliation to hummock zone (b) for the two sampling years.

Bulk density

The two-level factor *hummock zone* was significantly related to bulk density (Table 3) and was included as a covariate in a GLM model with sampling year as a treatment factor (levels: 1995, 2012). This model revealed a significant main effect of sampling year on bulk density after controlling for the effect of hummock zone, *F* (1, 145) = 5, *p* = 0.027, an effect that had a small effect size, partial η^2= .03 (Figure 5). Mean bulk density for samples (n = 89) recorded in 2012 was 51.11 g/dm^3 (s = 18.34). The mean for samples (n = 59) recorded in 1995 was 45.12 g/dm^3 (s = 11.54). The assumption of homogeneity of variance was met, revealing no significant interaction effect between year and the covariate.

Figure 5 Relationship between (log) bulk density and hummock zone for the two sampling years showing an overall increase in bulk density in 2012 samples.

Carbon accumulation rate

The variable *peat age* was significantly negatively related to carbon accumulation rate, and was included as a covariate in a GLM model with sampling year as a treatment factor (levels: 1995, 2012). The model revealed a significant main effect of sampling year on accumulation rate of carbon, *F* (1, 145) = 31.51, *p* = 9.79e-08, an effect that had a large effect, size partial η^2 = .18 (Figure 6). The mean carbon accumulation rate for samples recorded in 2012 was 3.62 g dm^{-2} yr^{-1} (s = 1.83), while the mean rate for samples recorded in 1995 was 1.96 g dm^{-2} yr^{-1} (s = 1), constituting a mean difference of 85%. The assumption of homogeneity of variance was met, revealing no significant interaction effect between the treatment factor and the covariate.

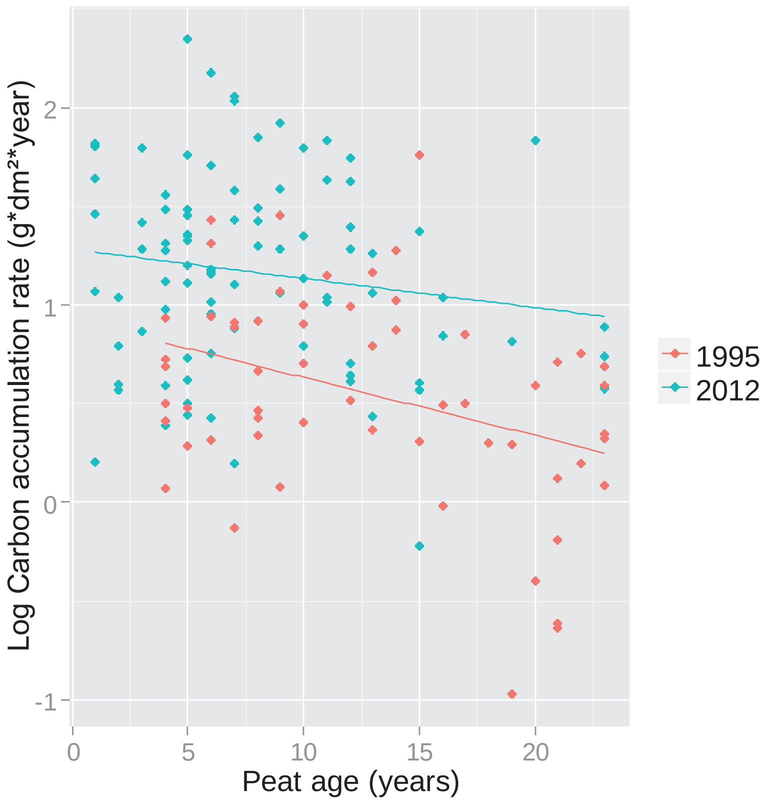


Figure 6 Relationship between (log) carbon accumulation rate and peat age for the two sampling years.

Nitrogen concentration

Peat age was significantly related to nitrogen concentration and was included in a GLM model with sampling year as a treatment factor. The model revealed a significant main effect of sampling year after controlling for the effect of peat age, *F* (1, 80) = 7.69, *p* = .007, an effect that had a large effect size, partial η^2 = .11 (Figure 7). Mean nitrogen concentration in the 20 samples recorded in 2012 was 1.22% (s = 0.34), while mean nitrogen concentration in samples recorded in 1995 was 1.06% (s = 0.23). There was no interaction effect between the treatment factor and the covariate.

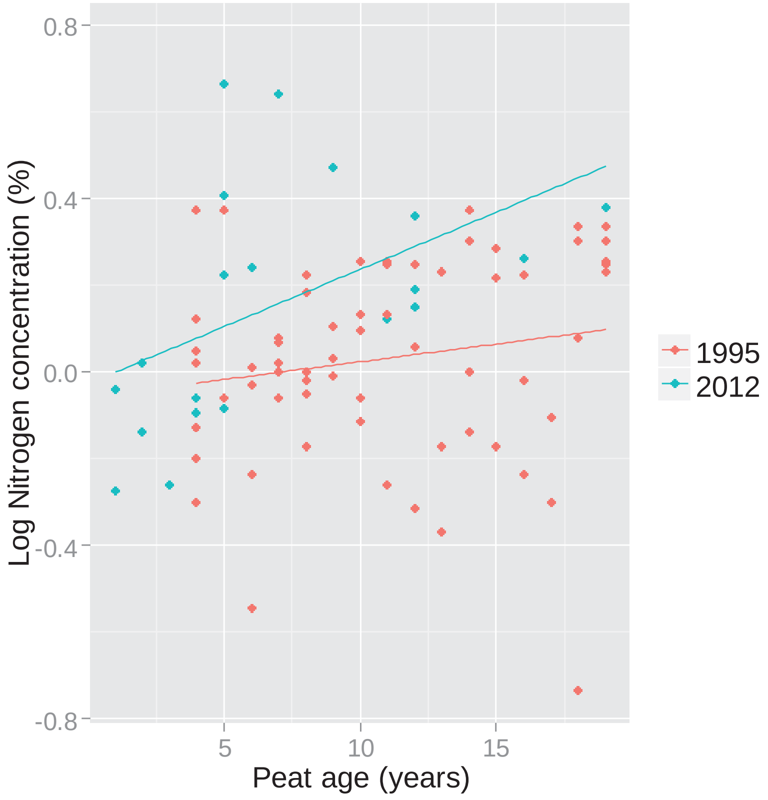


Figure 7 Relationship between (log) N concentration and peat age for the two sampling years.

Discussion

The results show that vertical peat growth is higher in upper hummocks compared to lower hummocks (Table 2), which is similar to the findings of Ohlson and Økland (1998) and supports their conclusion that the carbon budget of the mire ecosystem is highly dependent on the proportion of hummock communities. Whether a peatland ecosystem functions as a source or a sink for carbon depends on the balance between biomass production in the biologically active acrotelm and the loss of carbon from both aerobic and anaerobic decay processes in the entire peat stratigraphy. Methane (CH_4), which is produced by peat decomposition under anaerobic conditions, is spatially variable, dependant on the composition of vegetation and the vertical distance to the groundwater table (Bubier 1995; Bubier et al. 1995; Granberg et al. 1997). Thus, mire areas characterised by high production rates are also characterised by low methane emission, with carbon budgets that are strongly connected to the microtopographical pattern of the mire surface (Ohlson & Økland 1998a; Turunen et al. 2004). The spatial variation in peat accumulation and vertical growth rate has been attributed to faster decomposition rates closer to the water table, where conditions of aeration, water content and nutrient availability are more optimal compared to higher up in the peat profile (Belyea 1996; Turunen et al. 2004). The higher decomposition rate at this level leads to a stronger pore-space collapse which in turn leads to peat compaction and decreasing carbon accumulation rates as well as rates of vertical growth.

Unsurprisingly, total cover of *Sphagnum* species in quadrats was a strong predictor of vertical peat growth in the hummocks in 2012 (Table 2), and vertical peat growth rate was also inversely related with the amount of naked peat in the quadrat, supporting the hypothesis of Malmer (1962) and Økland (1989a) that the typical vegetation gradient from naked peat to dominance by productive *Sphagnum* species in bogs is associated with peat-producing capacity.

Recorded rates of vertical peat growth and carbon accumulation in *Sphagnum* dominated hummocks were significantly higher in 2012 than in 1995 (Figure 4). Compared to 1995 estimates, the mean vertical peat growth measured in 2012 was 64% higher. This is an interesting result given the recent trend of decreasing peat accumulation found in other Fennoscandian mires (Gunnarson et al. 2008).

While both biomass production and decomposition influence overall carbon accumulation and vertical growth rates, the former process is likely to be more influential in the uppermost and recently deposited peat layer. In this study, samples with a maximum age of 23 years were collected, indicating that the increased accumulation rates are a result of comparatively beneficial growth conditions over the last one or two decades. Furthermore, peat samples were denser in 2012 compared to 1995, a difference that was most clearly expressed in the lower hummock zone (Figure 5). Bulk density increases when pore spaces in the upper peat collapses due to eventual litter decay and the weight of the biomass above, and typically increases with the age and in the acrotelm/catotelm transition zone in ombrotrophic peatlands(Ohlson & Økland 1998b). If the increase in accumulation rates were due to decreased decomposition rates, one would expect lower density and not higher as seen here. However, the samples in 2012 were on average 1 cm deeper compared to 1995 samples (10.5 and 9.5 cm, respectively), which might account for some of the difference in bulk density.

I hypothesized that if the *Sphagnum* layer had become nitrogen saturated, the accumulation rate of peat and carbon would decline, as the effect of N saturation is well documented (Gunnarson & Rydin 2000; Tomassen et al. 2003). Over the last 30–40 years, the level of atmospheric nitrogen deposition in the study area has dropped; from estimated amounts of 861 mg $m^{-2}year^{-1}$ in 1979 to current levels of 633 mg $m^{-2}year^{-1}$ (Figure 2). These figures are well below critical threshold values for *Sphagnum* saturation suggested in previous studies (Aerts et al. 1992; Berendse et al. 2001; Lamers et al. 2000; Nordbakken et al. 2003). I therefore hypothesise that the *Sphagnum* layer on Southern Kisselbergmosen has not reached N-saturation, and that it is unlikely to do so if the current trends in N deposition rates continue.

Despite lower N-deposition rates, the peat N concentration recorded in 2012 was higher than the concentration recorded in 1995 (Figure 7). In previous fertilization experiments on Southern Kisselbergmosen, annual N addition of 500 mg m^{-2} $year^{-1}$ (to a background rate of 790 mg N m^{-2} $year^{-1}$) was enough to increase the N concentration in *Sphagnum* mosses and shallow-rooted vascular plants, while annual additions of 4000 mg N per m^2 per year for three years increased the N content in surface peat at depths of 5 and 10 cm but not at depths of 20 and 40 cm (Nordbakken et al. 2003). Such levels of N deposition are significantly higher than currently recorded. However, *Sphagnum* sensitivity to nitrogen deposition may be influenced by climatic factors. The N deposition level at which *Sphagnum* production is negatively affected in hummock communities has been found to be lowered by increases in July temperature and annual precipitation (Limpens et al. 2011). The future development of peat accumulation dynamics in this bog under projected climate change scenarios is therefore uncertain. The climate at S. Kisselbergmosen has shifted towards higher summer precipitation, while summer temperatures have remained stable. Future climate changes may enhance or reduce the sensitivity of *Sphagnum* to nitrogen deposition, depending on the nature of these trends.

It is not clear why peat nitrogen concentrations recorded in 2012 were higher than concentrations recorded in 1995 despite lower deposition levels and higher peat growth rates. The results from N concentration measurements in control plots at peat depths of 0, 5 and 10 cm (mean = 1.17 %) in hummocks in the same mire in a study by Nordbakken et al. (2003), indicate that the current N concentration (mean concentration of 1.22 % at mean peat depth of 9.7 cm) in the upper peat layer has not increased much compared to 1998-levels. The dynamics of nitrogen cycling in relation to peat growth rate and possible interacting climatic factors needs further investigation.

Summer precipitation rates in the study area have increased significantly in the period 1995–2012, while summer temperatures remained variable (Figure 2). The weather is of principal importance for water table fluctuations in mires (Malmer 1962), and a trend towards wetter conditions are expected to have brought about a higher median water table during the growing season towards the end of the period, with a predicted negative impact on the amount of aerobic decay. However, while water table fluctuations undoubtedly affect overall decomposition dynamics in the long-term, Ohlson and Økland (1998a) note that the carbon/nitrogen balance within the peat is not related to age if the peat is less than approximately 40 years old, indicating that little decomposition takes place before peat reaches that age. There is nevertheless a growing consensus that drought is the primary factor controlling inter-annual variation in net ecosystem CO_2 exchange in peatlands (Lafleur 2009; Limpens et al. 2008; Lund et al. 2012).

Increased annual as well as summer precipitation rates may have boosted *Sphagnum* growth, although previous studies on the relationship between *Sphagnum* productivity and precipitation have yielded somewhat contradictory results. While Gunnarson (2005) reported a positive effect of both mean annual temperature and annual precipitation on *Sphagnum* production, Limpens et al. (2011) reported that increased annual precipitation increased *Sphagnum* sensitivity to N, resulting in decreased production. *Sphagnum* growth benefits from the wet and humid conditions that typically occurs during spring and autumn (Brock & Bregman 1989; Lindholm 1990), and increased precipitation rates during June, July and August may therefore have decreased the negative effect of high summer temperatures and drought on *Sphagnum* productivity. Recent studies have shown that the productivity of some *Sphagnum* species is higher close to the water table than further above it (Vitt et al. 2003; Weltzin et al. 2001), as this prevents drought of moss capitula. Typically, however, capillary water transport and a dense growth form allow hummock species to stay moist during extended spells of dry weather conditions, and growth variation between wet and dry periods is therefore typically lower in hummocks than for example in carpets (Moore 1989; Rydin 1985). Indeed, Robroek et al. (2007) found that height increment and biomass growth of the hummock species *S. fuscum* and *S.rubellum* were unaffected by lowered water tables, while the results of a recent study by Robroek et al. (2008) stressed the importance of precipitation, and not a low water tables per se, for CO_2 uptake of *Sphagnum*.

The increased rates of peat growth and carbon accumulation rates recorded at S. Kisselbergmosen in this study indicate that growth conditions for *Sphagnum* are, on average, significantly better by 2012 than by 1995. This is likely due to beneficial climatic changes over the last 18-year period compared to the period before, with longer growing seasons, in turn facilitating and enhancing vertical growth. The level of nitrogen deposition at Southern Kisselbergmosen suggests that the associated reductions in *Sphagnum* production (Breeuwer et al. 2009; Limpens et al. 2011) and carbon accumulation (Bragazza et al. 2012; Gunnarson et al. 2008) found elsewhere at much higher deposition rates should not be expected here. Indeed, as high deposition levels of N are associated with reduced *Sphagnum* growth (Breeuwer et al. 2009), increased recent growth could partly be related to the removal of negative effects of high N deposition.

In the long-term, both the positive and the negative effects of N deposition for net production of *Sphagnum* depend on critical N-deposition loads (Vitt et al. 2003), in concert with climatic factors that govern growth and decomposition. Changes in temperature, precipitation patterns and N deposition as a consequence of global change are expected to vary between and within regions of the world (Christensen et al. 2007), and interactive effects of climate and nutrient regime on peatlands are therefore likely to be variable as well. Moreover, the dynamics of peatland ecosystems is nonlinear, divergent in development and response to climate change (Belyea 2009; Wu 2012). Further investigations into the relevant interactions is therefore important in order to get a better understanding of the fate of the carbon dynamics in boreal peatlands in light of recent and future climate changes.

The aim of this study was to compare rates of peat- and carbon accumulation in a boreal bog recorded in 2012 to the rates at exactly the same location measured for a similar time-period seventeen years ago. This represents a relatively short time of peat accumulation. Results of the study show that rates recorded in 2012 accumulate more rapidly in *Sphagnum*-dominated hummocks in Southern Kisselbergmosen than before, indicating improved growth conditions. While peat-forming processes are highly variable on short-term and small spatial-scales (Alm et al. 1997; Ohlson & Økland 1998a; Wallén et al. 1988), the long-term rates of peat accumulation are typically steady. A feedback mechanism of peat formation has been suggested in which hummocks respond to climate-mediated variations in surface-wetness by vertically expanding and contracting, such that acrotelm thickness compensate for variation in wetness (Belyea & Clymo 2001). Subsequently, both short-term and long-term analysis of carbon sequestration in relation to peatland topography and hydrology is necessary. In order to understand the carbon dynamics of the ecosystem more fully, more comprehensive studies are needed which incorporate the complete carbon budget over a longer time period. Such studies will shed more light on the fate of one of the most significant terrestrial carbon sinks in the world.

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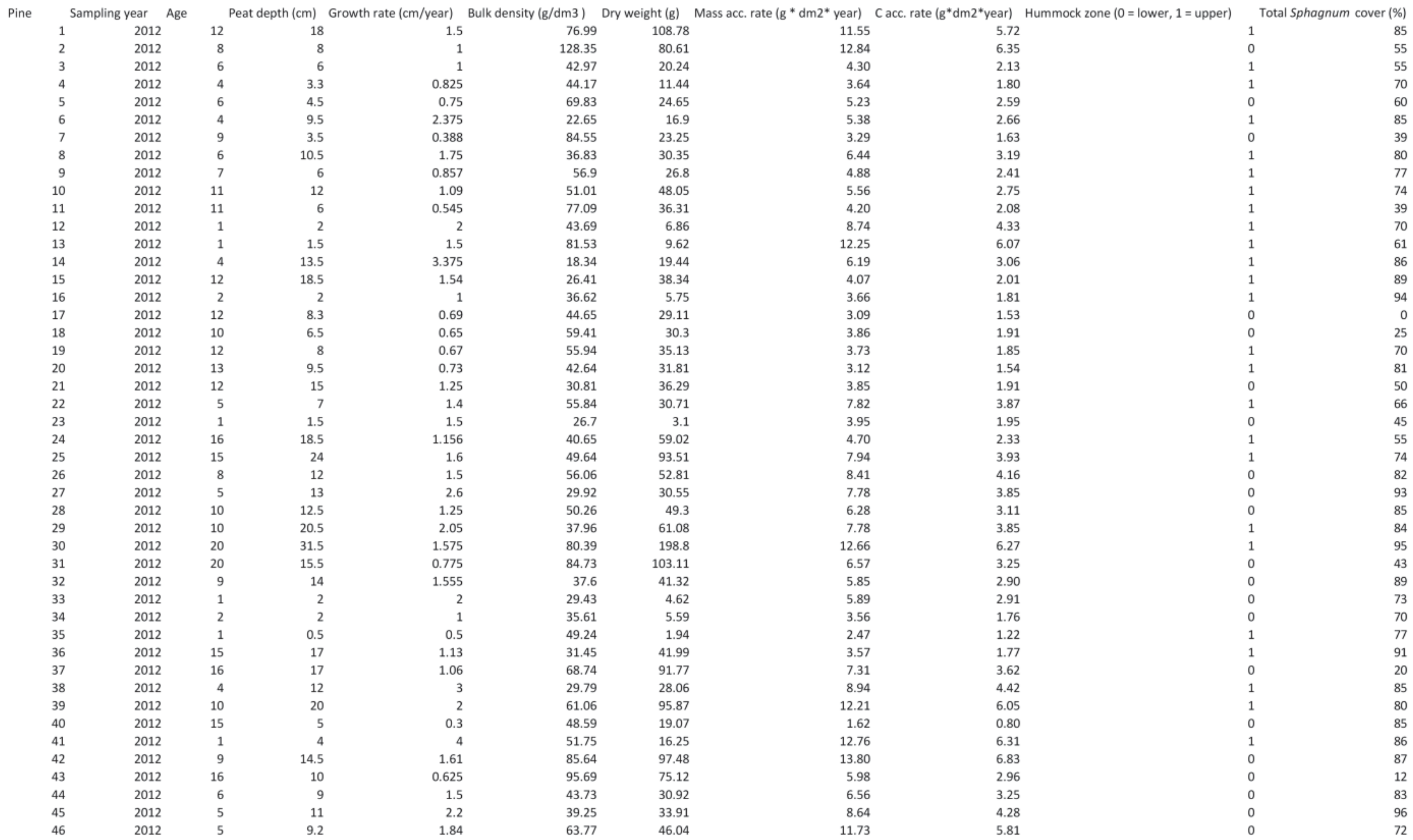
Appendix



Pine	Sampling year	Age	Peat depth (cm)	Growth rate (cm/year)	Bulk density (g/dm3)	Dry weight (g)	Mass acc. rate (g * dm2* year)	C acc. rate (g*dm2*year)	Hummock zone (0 = lower, 1 = upper)	Total *Sphagnum* cover (%)
1	2012	12	18	1.5	76.99	108.78	11.55	5.72	1	85
2	2012	8	8	1	128.35	80.61	12.84	6.35	0	55
3	2012	6	6	1	42.97	20.24	4.30	2.13	1	55
4	2012	4	3.3	0.825	44.17	11.44	3.64	1.80	1	70
5	2012	6	4.5	0.75	69.83	24.65	5.23	2.59	0	60
6	2012	4	9.5	2.375	22.65	16.9	5.38	2.66	1	85
7	2012	9	3.5	0.388	84.55	23.25	3.29	1.63	0	39
8	2012	6	10.5	1.75	36.83	30.35	6.44	3.19	1	80
9	2012	7	6	0.857	56.9	26.8	4.88	2.41	1	77
10	2012	11	12	1.09	51.01	48.05	5.56	2.75	1	74
11	2012	11	6	0.545	77.09	36.31	4.20	2.08	1	39
12	2012	1	2	2	43.69	6.86	8.74	4.33	1	70
13	2012	1	1.5	1.5	81.53	9.62	12.25	6.07	1	61
14	2012	4	13.5	3.375	18.34	19.44	6.19	3.06	1	86
15	2012	12	18.5	1.54	26.41	38.34	4.07	2.01	1	89
16	2012	2	2	1	36.62	5.75	3.66	1.81	1	94
17	2012	12	8.3	0.69	44.65	29.11	3.09	1.53	0	0
18	2012	10	6.5	0.65	59.41	30.3	3.86	1.91	0	25
19	2012	12	8	0.67	55.94	35.13	3.73	1.85	1	70
20	2012	13	9.5	0.73	42.64	31.81	3.12	1.54	1	81
21	2012	12	15	1.25	30.81	36.29	3.85	1.91	0	50
22	2012	5	7	1.4	55.84	30.71	7.82	3.87	1	66
23	2012	1	1.5	1.5	26.7	3.1	3.95	1.95	0	45
24	2012	16	18.5	1.156	40.65	59.02	4.70	2.33	1	55
25	2012	15	24	1.6	49.64	93.51	7.94	3.93	1	74
26	2012	8	12	1.5	56.06	52.81	8.41	4.16	0	82
27	2012	5	13	2.6	29.92	30.55	7.78	3.85	0	93
28	2012	10	12.5	1.25	50.26	49.3	6.28	3.11	0	85
29	2012	10	20.5	2.05	37.96	61.08	7.78	3.85	1	84
30	2012	20	31.5	1.575	80.39	198.8	12.66	6.27	1	95
31	2012	20	15.5	0.775	84.73	103.11	6.57	3.25	0	43
32	2012	9	14	1.555	37.6	41.32	5.85	2.90	0	89
33	2012	1	2	2	29.43	4.62	5.89	2.91	0	73
34	2012	2	2	1	35.61	5.59	3.56	1.76	0	70
35	2012	1	0.5	0.5	49.24	1.94	2.47	1.22	1	77
36	2012	15	17	1.13	31.45	41.99	3.57	1.77	1	91
37	2012	16	17	1.06	68.74	91.77	7.31	3.62	0	20
38	2012	4	12	3	29.79	28.06	8.94	4.42	1	85
39	2012	10	20	2	61.06	95.87	12.21	6.05	1	80
40	2012	15	5	0.3	48.59	19.07	1.62	0.80	0	85
41	2012	1	4	4	51.75	16.25	12.76	6.31	1	86
42	2012	9	14.5	1.61	85.64	97.48	13.80	6.83	0	87
43	2012	16	10	0.625	95.69	75.12	5.98	2.96	0	12
44	2012	6	9	1.5	43.73	30.92	6.56	3.25	0	83
45	2012	5	11	2.2	39.25	33.91	8.64	4.28	0	96
46	2012	5	9.2	1.84	63.77	46.04	11.73	5.81	0	72

Pine	Sampling year	Age	Peat depth (cm)	Growth rate (cm per yea	Bulk density (g/dm3)	Dry weight (g)	Mass acc. rate (g * dm2* year)	C acc. rate (g*dm2*year)	Hummock zone (0 = lower, 1 = upper)	Total *Sphagnum* cover
47	2012	5	12.2	2.44	86.49	82.86	21.11	10.45	0	94
48	2012	5	8	1.6	47.77	30	7.64	3.78	1	85
49	2012	9	11.5	1.277	57.15	51.61	7.31	3.62	1	65
50	2012	4	2	0.5	75.99	11.93	3.80	1.88	1	30
51	2012	13	11	0.85	68.61	59.28	5.81	2.88	1	60
52	2012	8	13.5	1.69	53.25	56.44	8.99	4.45	1	24
53	2012	15	21	1.4	64.68	106.65	9.06	4.48	1	27
54	2012	4	10.3	2.575	37.17	30.07	9.58	4.74	1	92
55	2012	7	14.5	2.07	76.42	86.97	15.83	7.83	1	60
56	2012	12	12	1	72.93	68.7	7.29	3.61	0	77
57	2012	10	6.5	0.65	68.63	35	4.46	2.21	0	80
58	2012	7	15	2.14	71.95	84.76	15.42	7.64	1	70
59	2012	7	4.2	0.6	40.88	13.49	2.45	1.22	1	80
60	2012	3	5.5	1.83	45.42	19.62	8.33	4.12	1	82
61	2012	11	9.5	0.86	65.98	49.22	5.70	2.82	1	80
62	2012	16	1	0.06	106.47	8.35	0.66	0.33	0	0
63	2012	6	6.5	1.08	60.28	30.74	6.53	3.23	0	69
64	2012	9	16	1.77	55.51	69.72	9.87	4.88	1	90
65	2012	5	5	1	41.93	16.48	4.20	2.08	1	85
66	2012	1	2	2	52.23	8.2	10.45	5.17	1	90
67	2012	6	4.6	0.77	40.44	14.6	3.10	1.53	1	85
68	2012	23	22	0.96	44.3	76.51	4.24	2.10	1	87
69	2012	4	5.5	1.38	21.76	9.4	2.99	1.48	1	94
70	2012	14	11	0.79	33.21	28.69	2.61	1.29	1	44
71	2012	3	5.5	1.83	66.48	28.72	12.20	6.04	1	91
72	2012	1	5.5	5.5	73.42	13.62	10.69	5.29	1	90
73	2012	2	3	1.5	29.64	6.98	4.45	2.20	1	62
74	2012	2	3.5	1.75	32.44	8.92	5.68	2.81	1	92
75	2012	5	8.5	1.7	52.46	34.99	8.91	4.41	1	91
76	2012	4	8.5	2.13	35.46	23.65	7.53	3.73	1	86
77	2012	5	2.8	0.56	75.23	16.55	4.22	2.09	0	58
78	2012	3	4	1.33	36.08	11.33	4.81	2.38	0	80
79	2012	5	2	0.4	94.2	14.79	3.77	1.87	0	84
80	2012	1	2	2	62.36	9.79	12.47	6.17	0	60
81	2012	4	4.7	1.175	61.54	22.71	7.23	3.58	1	85
82	2012	8	17	2.13	42.2	56.34	8.97	4.44	1	55
83	2012	6	8.5	1.42	39.49	26.34	5.59	2.77	1	81
84	2012	13	21	1.62	44.23	72.93	7.15	3.54	1	85
85	2012	8	14	1.75	42.14	46.31	7.37	3.65	1	90
86	2012	7	15	2.14	45.78	53.93	9.81	4.86	0	75
87	2012	23	22	0.96	51.4	88.77	4.92	2.43	1	95
88	2012	23	16	0.7	51.8	65.06	3.60	1.78	1	70
89	2012	3	7.5	2.5	29.2	17.2	7.30	3.62	1	80
90	2012	12	18	1.5	68.34	96.57	10.25	5.07	1	71
91	2012	16	21.5	1.34	42.44	71.64	5.70	2.82	1	86
92	2012	6	22	3.67	48.45	83.67	17.76	8.79	1	83

	Sampling year	Age	Peat depth (cm)	Growth rate (cm per yea	Bulk density (g/dm3)	Dry weight (g)	Mass acc. rate (g * dm2* year)	C acc. rate (g*dm2*year)	Hummock zone (0 = lower, 1 = upper)	Total *Sphagnum* cover
93	2012	19	10.5	0.55	82.71	68.15	4.57	2.26	0	85
94	2012	12	16.5	1.375	59.16	76.61	8.13	4.03	0	90
95	2012	15	12.5	0.83	44.36	43.52	3.70	1.83	1	73
96	2012	7	11.5	1.64	51.62	46.61	8.48	4.20	0	81
97	2012	5	6.3	1.26	48.65	24.08	6.14	3.04	1	90
98	2012	11	19	1.73	73.06	109	12.62	6.25	1	86
99	2012	7	7.5	1.07	56.88	33.5	6.10	3.02	1	66
100	2012	5	3.7	0.74	45.05	13.11	3.34	1.65	1	65
101	2012	5	5.5	1.1	28.47	12.3	3.13	1.55	0	93
102	2012	11	24	2.18	47.38	89.27	10.34	5.12	1	94
103	2012	6	16	2.67	41.89	52.61	11.17	5.53	1	94
104	2012	5	8.2	1.64	41.03	26.42	6.73	3.33	1	80
1	1995	4	3	0.75	45.3	10.67	3.40	1.65	0	
2	1995	4	1.5	0.38	58.14	6.85	2.18	1.07	0	
3	1995	4	2	0.5	76.79	12.06	3.84	1.94	0	
4	1995	4	4	1	40.32	12.66	4.03	1.99	0	
5	1995	4	6	1.5	35.5	16.72	5.32	2.55	1	
6	1995	4	3.5	0.88	34.45	9.47	3.01	1.51	0	
7	1995	4	3	0.75	56.11	13.21	4.21	2.07	0	
8	1995	5	2	0.4	66.26	10.4	2.65	1.33	0	
9	1995	5	5.5	1.1	29.2	12.61	3.21	1.61	1	
10	1995	6	4	0.67	78.2	24.55	5.21	2.56	0	
11	1995	6	5	0.83	33.88	13.3	2.82	1.37	0	
12	1995	6	12.5	2.08	41.18	40.41	8.58	4.18	1	
13	1995	6	13.5	2.25	34.06	36.1	7.66	3.71	1	
14	1995	7	11	1.57	31.56	27.26	4.96	2.44	1	
15	1995	7	8.5	1.21	40.97	27.34	4.98	2.49	0	
16	1995	7	3.5	0.5	50.75	13.94	2.54	1.26	0	
17	1995	7	4	0.57	31.64	9.93	1.81	0.88	1	
18	1995	7	7.5	1.07	36.33	21.39	3.89	2.02	1	
19	1995	8	4.5	0.56	53.34	18.84	3.00	1.53	0	
20	1995	8	7.5	0.94	41.3	24.32	3.87	1.94	0	
21	1995	8	6.5	0.81	39.07	19.94	3.17	1.59	1	
22	1995	8	4.5	0.56	50.39	17.8	2.83	1.40	0	
23	1995	8	5	0.63	60.3	23.67	3.77	1.97	1	
24	1995	8	9.5	1.19	42.34	31.58	5.03	2.51	1	
25	1995	9	19	2.11	42.24	63	8.92	4.29	0	
26	1995	9	6	0.67	33.48	15.77	2.23	1.08	0	
27	1995	9	12.5	1.39	42.28	41.49	5.87	2.91	1	
28	1995	10	9	0.9	39.16	27.66	3.52	1.75	0	
29	1995	10	6.5	0.65	47.55	24.26	3.09	1.50	0	
30	1995	10	9	0.9	47.01	33.21	4.23	2.02	0	
31	1995	10	10	1	50.06	39.29	5.01	2.46	1	
32	1995	10	11.5	1.15	48.86	44.11	5.62	2.71	0	
33	1995	11	2	0.18	107.23	16.84	1.95	0.97	0	
34	1995	11	15.5	1.41	45.97	55.94	6.48	3.15	1	

Pine	Sampling year	Age	Peat depth (cm)	Growth rate (cm per yea	Bulk density (g/dm3)	Dry weight (g)	Mass acc. rate (g * dm2* year)	C acc. rate (g*dm2*year)	Hummock zone (0 = lower, 1 = upper)
35	1995	11	4	0.36	70.32	22.08	2.56	1.28	0
36	1995	11	6	0.55	37.6	17.71	2.05	1.01	0
37	1995	12	4	0.33	70.32	22.08	2.34	1.17	0
38	1995	12	12	1	54.75	51.57	5.48	2.69	1
39	1995	12	10	0.83	41.08	32.25	3.42	1.68	0
40	1995	13	14	1.08	41.68	45.81	4.49	2.21	0
41	1995	13	11	0.85	35.06	30.27	2.97	1.44	0
42	1995	13	17.5	1.35	48.58	66.73	6.54	3.20	0
43	1995	14	19	1.36	53.85	80.32	7.31	3.58	0
44	1995	14	8.5	0.61	80.09	53.44	4.86	2.40	1
45	1995	14	4.5	0.32	63.1	22.29	2.03	1.01	0
46	1995	14	19	1.36	41.76	62.28	5.67	2.77	0
47	1995	15	5.5	0.37	39.12	16.89	1.43	0.72	0
48	1995	15	10.5	0.7	39.52	32.57	2.77	1.36	1
49	1995	15	23	1.53	75.76	136.79	11.62	5.79	1
50	1995	16	12	0.75	44.68	42.09	3.35	1.64	1
51	1995	16	7	0.44	45.83	25.18	2.00	0.98	0
52	1995	16	6	0.38	31.32	14.75	1.17	0.58	0
53	1995	17	15.5	0.91	52.75	64.18	4.81	2.34	1
54	1995	17	15.5	0.91	37.33	45.42	3.40	1.65	1
55	1995	18	15	0.83	33.42	39.35	2.78	1.35	1
56	1995	18	6	0.33	51.28	24.15	1.71	0.85	0
57	1995	18	15	0.83	48.91	57.6	4.08	2.08	1
58	1995	18	4	0.22	53.16	16.69	1.18	0.59	0
59	1995	19	6	0.32	49.34	23.24	1.56	0.79	1
60	1995	19	13.5	0.71	59.83	63.4	4.25	2.13	0
61	1995	19	9	0.47	56.56	39.96	2.68	1.34	1
62	1995	19	5.5	0.29	37.75	16.3	1.09	0.56	1
63	1995	19	2.5	0.13	55.75	10.94	0.73	0.38	0
64	1995	20	17.5	0.88	41.55	57.08	3.64	1.80	0
65	1995	20	7.5	0.38	37.12	21.85	1.39	0.67	0
66	1995	20	11	0.55	33.15	28.62	1.82	0.91	1
67	1995	21	22.5	1.07	39.02	68.92	4.18	2.03	1
68	1995	21	15.5	0.74	31.55	38.39	2.33	1.13	1
69	1995	21	8	0.38	29.14	18.3	1.11	0.54	0
70	1995	21	9	0.43	24.89	17.58	1.07	0.53	0
71	1995	21	9	0.43	51.04	36.06	2.19	1.10	1
72	1995	21	6	0.29	58.97	27.77	1.68	0.83	0
73	1995	22	19.5	0.89	48.21	73.8	4.27	2.13	1
74	1995	22	9.5	0.43	55.36	41.28	2.39	1.22	1
75	1995	23	20	0.87	46.37	72.8	4.03	1.99	0
76	1995	23	16.5	0.72	51.1	66.19	3.67	1.81	1
77	1995	23	17	0.74	38.92	51.94	2.88	1.41	1
78	1995	23	16.5	0.72	39.26	50.85	2.82	1.38	1
79	1995	23	12.5	0.54	41.46	40.68	2.25	1.09	0
80	1995	23	5.5	0.24	52.21	22.54	1.25	0.61	0