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Long-term effects of climate change on vegetation and carbon dynamics in peat bogs

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Abstract

Questions: What are the long-term effects of climate change on the plant species composition and carbon sequestration in peat bogs?

Methods: We developed a bog ecosystem model that includes vegetation, carbon, nitrogen and water dynamics. Two groups of vascular plant species and three groups of *Sphagnum* species compete with each other for light and nitrogen. The model was tested by comparing the outcome with long-term historic vegetation changes in peat cores from Denmark and England. A climate scenario was used to analyse the future effects of atmospheric CO₂, temperature and precipitation.

Results: The main changes in the species composition since 1766 were simulated by the model. Simulations for a future warmer, and slightly wetter, climate with doubling CO₂ concentration suggest that little will change in species composition, due to the contrasting effects of increasing temperatures (favouring vascular plants) and CO₂ (favouring *Sphagnum*). Further analysis of the effects of temperature showed that simulated carbon sequestration is negatively related to vascular plant expansion. Model results show that increasing temperatures may still increase carbon accumulation at cool, low N deposition sites, but decrease carbon accumulation at high N deposition sites.

Conclusions: Our results show that the effects of temperature, precipitation, N-deposition and atmospheric CO₂ are not straightforward, but interactions between these components of global change exist. These interactions are the result of changes in vegetation composition. When analysing long-term effects of global change, vegetation changes should be taken into account and predictions should not be based on temperature increase alone.

Keywords: Carbon cycling; Competition; Ecosystem model; Global change; NUCOM-BOG; Ombrotrophic peatland; Palaeoecology; Species effect; *Sphagnum*; Vegetation composition.

Abbreviations: LVM = Lille Vildmose; NUCOM-BOG = Nutrient cycling and competition model for bog ecosystems; WLM = Walton Moss.

Introduction

Peat bogs are important ecosystems in relation to climate change. Peat forming ombrotrophic bogs serve as important long-term sinks for atmospheric carbon dioxide (CO₂). Although peatlands cover only 2–3% of the global land surface, peat accumulation over thousands of years has resulted in a vast store of carbon of 450–10¹⁵ g C (Gorham 1991), which is at least 20% of the global carbon store in terrestrial ecosystems. Climatic change could bring about changes in these ecosystems that would have important repercussions for global carbon cycling. Typical bog plant communities are comprised of peat mosses (*Sphagnum*) and associated vascular plants. *Sphagnum* species are the main peat-formers, because they decompose very slowly (Clymo & Hayward 1982). Carbon sequestration is expected to increase whenever *Sphagnum* expands at the expense of vascular plants and *vice versa*. Such vegetation changes not only affect carbon cycling, but also exchanges of heat and moisture (Thompson et al. 2004). Thus, changes in vegetation composition could feed back to the climate system through alterations in carbon storage and surface energy balance (McGuire et al. 2002). Therefore, it is of the utmost importance to know how these peatlands will respond to climate change.

Another reason for studying peat bogs in relation to climate change is that the peat contains a natural archive of the history of the vegetation and carbon sequestration. Based on ¹⁴C dated sequences of plant remains, reconstructions of plant species composition through time can be made. Changes in species composition that have been observed in peat cores have been related to past changes in climate (Aaby 1976; Barber 1981; van Geel et al. 1996; Mauquoy et al. 2004). Therefore peat cores contain excellent material to study the long-term effects of historic climatic changes, such as the Little Ice Age.

Future climatic change will very likely affect peat bogs. Experimental studies have been conducted to study the response of *Sphagnum* bog plant communities to components of global change. In these experiments temperature (Bridgham et al. 1999; Weltzin et al. 2000, 2003; Gunnarsson et al. 2004), atmospheric CO₂ (Berendse et al. 2001; Heijmans et al. 2001b), water level (Bridgham et al. 1999; Weltzin et al. 2000, 2003) and N deposition (Berendse et al. 2001; Heijmans et al. 2001b; Gunnarsson et al. 2004; Limpens et al. 2004) have been manipulated during three or four growing seasons. All these studies showed that the main response was a shift in the relative abundance of species. However, three or four growing seasons is still a short time over which to study vegetation responses to changing environmental conditions. For tundra vegetation, Chapin et al. (1995) showed that the response to experimental treatments after nine years was different from that observed after only three years. It takes even longer before changes in the vegetation are reflected in the species composition of the peat, which strongly influences nitrogen mineralisation, decomposition rates and therefore carbon accumulation rates (Laiho et al. 2003).

Models are, therefore, necessary to analyse the long-term effects of climate change on ecosystems. However, many of the models describing the response of ecosystems to global change do not take species composition into account. Bog models, so far, are mostly peat growth models assuming a constant species composition over time (Jones & Gore 1978; Clymo 1978, 1984; Clymo et al. 1998; Hilbert et al. 2000; Wieder 2001). Some recent models (Frolking et al. 2001, 2002; Nungesser 2003; Bauer 2004) acknowledge that *Sphagnum* decomposes more slowly than vascular plants but those models do not simulate changes in the species composition. However, interactions between species and feedbacks through species effects on nutrient and moisture availability (Berendse 1998, 2005; Bridgham et al. 1999) may change the vegetation response to experimental treatments during a longer period (Chapin et al. 1995; Heijmans et al. 2001b). Such feedbacks are particularly important in bogs, where the soil is entirely composed of plant remains and where both soil and vegetation have a large influence on hydrology. Therefore, models that include interactions between species, feedbacks between vegetation, hydrology and soil, and interactions between components of global change are required to predict long-term carbon sequestration rates in peatlands. So far, only Pastor et al. (2002) included plant community dynamics and nutrient cycling in a peatland model, but their theoretical model cannot be related to changes in climate or environment.

The aim of this study is to investigate the effects of climate change on bog ecosystems by developing

a model that simulates long-term vegetation changes and carbon accumulation in peat bogs. The model, named NUCOM-BOG, is derived from earlier NUCOM (nutrient cycling and competition) models describing long-term dynamics in ecosystems (heathland, forest), in which a variable number of plant species compete for light, nitrogen and water (Berendse 1988; van Oene et al. 1999). Our NUCOM-BOG model contains general equations for plant growth, decomposition and other processes involved in carbon, nitrogen and water cycling, but the parameter values are specific for bog plant species. These parameter values were derived from the literature and from our own data. The model was evaluated by comparing model output with palaeoecological data derived from peat cores (reconstructed long-term historic vegetation changes). Finally, the simulated effects of future climate change on plant species composition and carbon sequestration were analysed.

Model description

Model components

Our model describes the vegetation, carbon, nitrogen and water dynamics of undisturbed open bog ecosystems in a temperate to sub-boreal climate. Not included are trees, disturbances such as fire or drainage, and landscape-scale hydrological limitations to peat growth. The bog ecosystem in the model represents an area of one square meter with a flat moss surface. Five groups of plant species are included in the model: two groups of vascular plants and three groups of mosses (Fig. 1). The mosses are represented by hummock *Sphagna*, lawn *Sphagna* and hollow *Sphagna*. Non-*Sphagnum* moss species are not included. The vascular plants are graminoids (e.g. *Eriophorum* species and other *Cyperaceae*) and dwarf shrubs (e.g. *Calluna vulgaris* and other *Ericaceae*). These two groups of species cover almost all of the vascular bog vegetation.

The modelled bog ecosystem is vertically divided into two canopy layers, one living moss layer and two peat layers (Fig. 1). The top canopy layer is assumed to contain only leaves of the graminoids (such as *Eriophorum angustifolium*). The lower canopy layer contains the leaves of the dwarf shrubs. In undisturbed bogs dwarf shrubs do not grow very tall as their lower branches are continuously overgrown by the mosses. To simplify the model, this layer does not contain leaves of graminoids. Although the lower parts of their leaves may be in this layer, they will not intercept much light because of the vertical orientation of the leaves in the lower canopy layer. The moss species make up the living moss layer,

Fig. 1. The bog ecosystem as represented in the model: five species groups and five layers. The vascular plants are divided into leaf, stem and root components. The leaves are used for CO₂ assimilation and the roots are used for N-uptake, so include only fine roots. The category 'stem' includes leaf bases and rhizomes for the graminoids and both above-ground and below-ground (overgrown) stems or branches of dwarf shrubs. The mosses are not subdivided. All species are given a minimum cover of 0.1% so that they are able to establish when conditions become more favourable.

which is assumed to have a maximum thickness of 5 cm. Below the living moss layer is the top peat layer called the acrotelm. In the acrotelm the water table fluctuations take place, so that most of the time this layer is partly oxygenated. The acrotelm contains the roots of the dwarf shrubs, as these species have only roots in partly oxygenated peat (Gimingham 1960). The bottom layer is the catotelm or the deep peat layer. This layer contains older dead plant material and is always water-saturated. For these reasons decomposition rates are considerably lower in the catotelm than in the acrotelm. In order to keep the model relatively simple, the roots of the graminoids are assumed to be only in this deep peat layer (Wein 1973; Heijmans et al. 2002). The model calculates the boundary between acrotelm and catotelm as the yearly deepest mean water level, calculated over the past 10 years, so that the acrotelm depth can respond to climatic changes..

Model equations

The NUCOM-BOG model is based on equations for processes such as plant growth, decomposition, N mineralisation and evapotranspiration. Most equations were from earlier NUCOM models (Berendse 1988; Van Oene et al. 1999). The model follows changes in carbon, nitrogen and water (Fig. 2). To run the model, annual data on atmospheric CO₂ concentration and N deposition and monthly data on mean air temperature, precipitation and reference evapotranspiration are required as input. The model uses a time step of one month, starting with calculating the water level, based on a weekly water balance, followed by decomposition/N mineralisation and plant growth/N uptake. When the acrotelm/catotelm boundary shifts upward (in case of peat growth or wetter conditions), dead mass is transferred from the acrotelm to the catotelm. At the end of each month the amounts of carbon and nitrogen in each pool are updated and the height of the peat layers is calculated. Extensive descriptions of the equations for NUCOM-BOG are shown in App. 1 and the parameter values in App. 2. Below follows a short description of the processes included in the model.

Plant growth requires light, CO₂ and nutrients (N in the model). In addition, growth can be restricted because of unfavourable temperatures or water levels. First, potential growth rate is calculated for each species group, as a function of maximum growth rate, fraction of light intercepted, and modifying functions for CO₂, temperature and water. The actual growth rates depend on the amounts of nitrogen available for each species group. If N uptake is less than N requirement, then actual growth is less than potential growth. If more N is available than is taken up by the plants, then the excess N leaches to a deeper layer.

Decomposition rates are calculated for each organ of each species group in each layer, and depend on temperature. Relative decay rates are different for the acrotelm and catotelm and differ among the species groups and organs within vascular plants (App. 2). Nitrogen mineralisation is dependent on the decomposition rate and the C:N ratio of the dead material. If the C:N ratio of the dead plant parts is lower than the critical C:N ratio for the microbes, a net release of available N takes place.

The height of the water table relative to the moss surface is considered an important factor in bog ecology. *Sphagnum* growth is very sensitive to changes in water level or moisture conditions (Backéus 1988; Wallén et al. 1988) and drought can have deleterious effects (Malmer et al. 1994; Schipperges & Rydin 1998). The model accounts for changes in the water balance in order to calculate the height of the water table. Water is added by precipitation, while evapotranspiration (including

Fig. 2. Carbon, nitrogen and water pools and flows in the model. There are biomass and dead mass pools for each species and each organ. gram = graminoids, eric = dwarf shrubs. See App. 1 for a description of the model equations.

interception) and drainage remove water from the bog ecosystem (Fig. 2).

Evapotranspiration depends on the relative abundance of the mosses and vascular plants, as the peat mosses contribute more to the vegetation's water loss than vascular plants (Bridgham et al. 1999; van der Schaaf 1999; Heijmans et al. 2001a). Vascular plants and mosses both reduce their water losses when water is in short supply. In addition, vascular plants reduce their water losses with increasing CO_2 due to increased stomatal closure (Field et al. 1995). The term 'drainage' represents surface run-off and lateral outflow of water through the living moss layer. Vertical drainage is assumed to be negligible (van der Schaaf 1999).

The model is developed to simulate vegetation and carbon dynamics at timescales of decades to centuries. It is at this timescale that vegetation can respond to anthropogenic climate change and that changes in the relative abundance of the species have repercussions on carbon sequestration. The model is perhaps not detailed enough to capture year-to-year variation. It does not include landscape-scale hydrological limitations to peat growth (Ingram 1983), which would be necessary for simulating peat development over thousands of years (Belyea & Malmer 2004).

Competition

The species compete for light and nitrogen in the model. The model is setup in such a way that competition can be relatively easily modelled by giving the different species groups a monopoly in the different layers. Only the *Sphagnum* groups have to share their resources in the same layer. The top canopy layer is the exclusive domain of the leaves of the graminoids. Therefore, they have full access to light, and what is not absorbed by the graminoids, which depends on their leaf area, becomes available to the dwarf shrubs. Light which is not intercepted by the vascular plants is passed on to the mosses in proportion to their cover. In this way, an increase of vascular plant cover may reduce growth rates of mosses by shading.

For atmospheric nitrogen deposition, the competitive capacities are in reverse order (Malmer et al. 1994; Svensson 1995). Nitrogen from atmospheric deposition is first available to the moss species (Heijmans et al. 2002) and is distributed among the *Sphagnum* in proportion to their cover. Uptake of atmospheric N deposition by leaves of vascular plants is assumed to be negligible (Li & Vitt 1997). What is not captured by the mosses, which depends on their growth rate and maximum N-concentration, leaches to the acrotelm where the roots of the dwarf shrubs have a monopoly on the N available in this layer. If not taken up, this nitrogen leaches further to the catotelm to be available for the graminoids. When

the peat mosses grow well, they absorb most of the atmospheric N and very little of this source is available for vascular plant growth. The other source of available N is mineralised from dead plant parts. Dead leaves fall into the living moss layer and the N mineralised there is available to the mosses, N mineralised in the acrotelm is available to dwarf shrubs and N mineralised in the catotelm is available to graminoids (Fig. 2).

Competition between the moss species is different because the moss species are in the same layer. As both light and N-interception are based on the cover of each moss species, a moss species that increases its cover gains a competitive advantage. In the model, a moss species increases its cover when it grows taller and bends over the other moss species. For each *Sphagnum* group net growth is calculated and differences in height growth among the *Sphagnum* groups result in changes in relative cover. The species may grow at different rates mainly because of differences in maximum growth rate, the range of water levels they can grow at and N-requirement.

Parameter values

Although most equations are valid for ecosystems in general, the parameter values are, as much as possible, specific for bog ecosystems. The parameter values, including an extensive description of how the parameter values were derived, can be found in App. 2. Parameter values were mainly derived from the literature, but in addition, our own data were used, particularly for the vascular plant species. Only a few parameter values are not specific for bog plants or ecosystems. Those are the temperature dependency of decomposition and the CO₂ growth enhancement factor, which is set equal for all species groups.

The resulting sets of parameter values (App. 2) were used for each run of the model. Important parameters for plant growth are maximum growth rate, the range of temperatures and water levels optimal for growth and the minimum N-concentration. The graminoids have a higher maximum growth rate, lower temperature requirements, a broader range of water levels suitable for growth, but a larger requirement for N than the dwarf shrubs. The dwarf shrubs have a lower biomass turnover, represented by smaller mortality fractions. Graminoids decompose faster than dwarf shrubs and leaves decompose faster than stems and roots.

Hummock *Sphagnum* species have superior water conducting capacities because of their morphology and dense packing, which prevent them from drying out at low water tables. The hummock species have the lowest maximum growth rate, but the broadest range of water levels at which they can grow maximally, and the lowest N-requirement. They also have the lowest decomposition

rate. The hollow *Sphagnum* have the largest maximum growth rate and can grow at low temperatures, which gives them the longest growing season. Their growth is restricted by deep water tables and they have the largest N-requirement. For all growth and decomposition parameters, the lawn *Sphagnum* are assumed to be intermediate between hummock and hollow *Sphagnum*.

Initial conditions

The model requires initial values for the amounts of C and N in biomass and the peat layers for all species groups. Initial values for biomass were derived from the species composition in the layer dated nearest to the starting year of the simulation. Initial values for peat mass were derived from the amounts of C and N in the peat cores below that layer. In order to convert volume percentage into biomass, 20 shallow peat cores were cut at the Lille Vildmose site (LVM). Volume percentage in the top 5 cm of peat and biomass for each species group were determined. Using the relationships between both variables (data not shown), initial values for the biomass of each species group were derived from the volume percentages in the layer dated nearest to the starting point. The distribution among organs and the N concentrations were derived from our own measurements (Heijmans et al. 2001b, unpubl.).

Methods

Model evaluation: comparison with peat core data

To evaluate the model, we compared simulated historic changes in species composition and carbon amounts with observations from four peat cores collected at Lille Vildmose, Denmark (LVM) and Walton Moss, England (WLM19, WLM20 and WLM21), both sites are intact ombrotrophic bogs. See Mauquoy et al. (2002a) for detailed descriptions of the sites and methods of peat core analyses. The bottom of the 1m deep cores dates back to AD 1340 (LVM) and AD 795 - 1025 (WLM cores). For each 1 cm thick layer the species composition of the macrofossils was determined and expressed as volume percentages. Many levels were precisely dated using ¹⁴C wiggle match dating (van Geel & Mook 1989; Mauquoy et al. 2004). In addition, the bulk density of each layer, and C and N content of each uneven numbered layer were determined.

Historical climate data were extracted from the Global Historical Climatology Network data set containing long-term monthly temperature and precipitation data for many stations around the world (cdiac.esd.ornl.gov). In addition, central England monthly temperatures, dating back

Table 1. 30-year means of historical temperatures and precipitation for Lille Vildmose (DK) and Walton Moss (UK). Monthly values were used as input for the historic runs. See App. 3 for data sources and methods. Winter = Dec-Feb, Spring = Mar-May, Summer = Jun-Aug, Autumn = Sep-Nov.

		1766- 1789	1790- 1819	1820- 1849	1850- 1879	1880- 1909	1910- 1939	1940- 1969	1970- 1999
Mean temperature (°C)									
Lille Vildmose (DK)	Winter	-1.1	-0.7	-1.3	-1.0	-0.7	0.3	-0.3	0.7
	Spring	5.0	5.1	4.8	4.4	5.0	5.7	5.7	6.4
	Summer	15.9	15.1	14.5	14.5	14.6	14.9	15.2	15.5
	Autumn	8.1	7.9	7.4	7.0	7.2	7.7	8.4	8.6
Walton Moss (UK)	Winter	2.7	3.0	3.2	3.5	3.5	4.1	3.2	4.0
	Spring	7.3	7.4	7.7	7.3	7.5	7.5	7.7	7.8
	Summer	14.4	14.1	14.1	14.1	14.4	14.1	14.1	14.4
	Autumn	8.6	8.7	8.9	8.6	8.9	8.8	9.3	9.5
Precipitation (mm month⁻¹)									
Lille Vildmose (DK)	Winter	37	38	44	39	38	43	44	42
	Spring	41	42	41	39	40	40	39	39
	Summer	64	60	54	54	56	55	62	53
	Autumn	60	58	51	50	52	51	56	64
Walton Moss (UK)	Winter	54	57	55	59	62	68	59	64
	Spring	48	51	47	43	54	48	48	50
	Summer	83	76	79	74	82	79	77	68
	Autumn	76	73	77	72	77	75	81	77

to 1659, and England and Wales monthly precipitation, dating back to 1766, from the Hadley Centre for Climate Prediction and Research were used (www.meto.govt.uk/research/hadleycentre). We used climate data dating back to AD 1766 (when the England and Wales precipitation series starts) for both the Danish and British sites. All peat cores had a dated layer close to this year, which served as a starting point for the simulations. See App. 3 for an extensive description of the historic climate data used.

Annual mean temperatures at Walton Moss were higher than in Lille Vildmose (App. 3), mainly because winter temperatures were much higher (Table 1). In contrast, Lille Vildmose was warmer in summer. Walton Moss had more precipitation than Lille Vildmose throughout the year (Table 1), reference evapotranspiration was also higher (data not shown). Both sites had relatively high precipitation in summer and autumn. Lille Vildmose temperatures were relatively low between 1840 and 1890 (Table 1, App. 3). Temperatures increased during the 20th century, particularly at Lille Vildmose. No clear trends appear from the historic precipitation data.

The environmental input (atmospheric CO₂ and N deposition) used for the historic runs and how it has been derived, is described in App. 4. The global atmospheric CO₂ concentration has increased markedly since 1950 (App. 4). Historic N deposition rates started to increase from 1900 in England, and from 1950 in Denmark to maximum rates of 37 and 29 kg-N.ha⁻¹.a⁻¹ respectively in the 1980s and 1990s (App. 4).

Model analyses: effects of future climate change

The next step was to simulate the effects of future climate change on the species composition and carbon storage in peat bogs. Climate input came from the Hadley Centre climate models. At both sites, the future climate shows a gradual increase in temperature, temperatures at the end of this century being 2°C warmer than at the start (App. 5). The temperatures of all seasons will increase (data not shown). Precipitation is expected to increase in the second half of the century (App. 5). The climate change scenario used assumes a doubling of atmospheric CO₂ concentrations from 375 ppmv in 2000 to 750 ppmv in 2100. Future N deposition is not included in the climate models. We assumed a future total N-deposition of 15 kg-N.ha⁻¹.a⁻¹ for both sites, which is close to recent measurements for the English site.

To further analyse the effects of temperature and precipitation, we added or subtracted 2 °C and 10 mm of precipitation each month, respectively, to the future climate scenario. Reference evapotranspiration was increased/reduced by 7%, together with the temperature increase/reduction. All scenarios included a doubling of the atmospheric CO₂ concentration and were run for Lille Vildmose and Walton Moss at N-deposition levels of 10 kg-N.ha⁻¹.a⁻¹ and 30 kg-N.ha⁻¹.a⁻¹, representing low and high N deposition.

Results

Model evaluation: comparison with peat core data

We compared the species composition as determined for each cm layer in the peat cores with the simulated species composition from 1766 to present. This period is covered by the top 36 - 38 cm of each peat core. The variable in the model best comparable to the volume percentages describing the species composition in the cores is the fraction of light intercepted by each species. The summed fractions equal one, just as the summed volume percentages of each cm layer equal 100. Although light interception fraction and volume percentage are not the same, major changes in the species composition should be visible in both variables. Unfortunately, only a few layers in the top 40 cm of the peat have been dated. The dates of the intermediate layers have been estimated by simple interpolation. This means that the timing of observed changes in the vegetation may be uncertain, but the fluctuations in species abundances are real. Because of the limited number of dated observations, we did not attempt to quantitatively test for goodness of fit between the model and observed data. Instead, we qualitatively

assessed the developments over time in changes in species composition and carbon accumulation.

The peat core from LVM shows two major changes in the vegetation after 1766. Around 1820 there was a peak in vascular plant abundance, particularly of the graminoids, together with a temporary absence of *Sphagnum* species (Fig. 3). This was probably the result of a bog fire, indicated by coarse charcoal fractions found in the same layers (Mauquoy et al. 2002a). This peak in vascular plant abundance was not simulated by our model (Fig. 3), as disturbances such as those by fire were not included. However, the vegetation shifts induced by this disturbance were only temporary and seem to have had no long-lasting consequences for the species composition and carbon accumulation. The simulated low abundance of dwarf shrubs during the relatively cool 19th century was not visible in the peat core.

However, our model did simulate the second change: the replacement of *S. capillifolium* (hummock) by *S. magellanicum* (lawn) at ca. 1860 (Fig. 3). The lawn *Sphagnum* could establish between 1800 and 1820 in a period of high water tables (data not shown). Under these conditions lawn *Sphagnum* grew at a faster rate than hummock *Sphagnum*. The modelled hummock *Sphagnum* are relatively

Fig. 3. Simulated and observed historic species composition and carbon accumulation for peat core LVM (Lille Vildmose, Denmark). Large symbols represent ^{14}C -dated layers; the small symbols represent the species composition of the layers in between, of which the age is estimated by interpolation. gram = graminoids, eric = dwarf shrubs, humm = hummock *Sphagnum*, lawn = lawn *Sphagnum*.

Fig. 4. Simulated and observed historic species composition and carbon accumulation for peat core WLM19 (Walton Moss, UK). Large symbols represent ^{14}C -dated layers; the small symbols represent the species composition of the layers in between, of which the age is estimated by interpolation.

weak competitors (lowest maximum growth rate), which can only remain dominant when water tables drop regularly to levels limiting growth of other *Sphagnum* species, i.e. lower than 15 cm below moss surface. The relatively cool climate of the 19th century (Table 1) and associated reduced evapotranspiration reduced the occurrence of low water tables favourable for the hummock *Sphagnum*, explaining the replacement by lawn *Sphagnum*. Simulated C-accumulation was slightly higher than measured. It is likely that C-accumulation was lower during the time that the graminoids were abundant in the core, as could be shown deeper in the core (Mauquoy et al. 2002a), but the simulation missed the graminoids peak and the peat continued to accumulate C.

There was one major change in WLM19 peat core when hollow *Sphagnum* were replaced by lawn *Sphagnum* between 1780 and 1800. This change of dominant *Sphagnum* species was also simulated by the model (Fig. 4). This simulation starts with a warm and dry period around 1780 (App. 3) which causes the water table to drop to levels limiting growth of hollow *Sphagnum* (data not shown). Lawn *Sphagnum* were already present and could quickly replace the hollow *Sphagnum*.

In addition, the changes in vascular plant abundance

were well simulated (Fig. 4). Simulated changes in the abundance of dwarf shrubs followed fluctuations in the water level. Growth of the dwarf shrubs in the model is reduced when water tables rise higher than 10 cm below the moss surface. The dwarf shrubs were absent when the hollow *Sphagnum* were dominant, but reappeared when the lawn *Sphagnum* took over and water levels became more favourable (data not shown). The simulated abundance of the graminoids decreased when the dwarf shrubs started to increase in abundance. Simulated N mineralisation rates in the 50–70 cm thick catotelm peat (the N source for the deep-rooted graminoids) were very low ($0.1 - 0.4 \text{ g-N.m}^{-2}.\text{a}^{-1}$), therefore the graminoids depended on N mineralised in higher peat layers not taken up by the other species. When the dwarf shrubs expanded, more of this N was used and less leached to the catotelm, thereby increasing N-limitation of the graminoids. The simulated amounts of C were also similar to the measured amounts of C (Fig. 4).

The two replicate peat cores, WLM20 and WLM21, also showed shifts from hollow *Sphagnum* to lawn *Sphagnum*, but in later years (data not shown). The simulation for WLM20 was very similar to the simulation for WLM19, but did not match the observations as well,

Fig. 5. Simulated future species composition at Lille Vildmose and Walton Moss, using the future climate scenario including doubling of CO₂, at atmospheric N deposition of 15 kg N.ha⁻¹.a⁻¹.

because the observed shift in dominant *Sphagnum* species was later, around 1840. In the simulation for WLM21, the replacement of hollow *Sphagnum* by lawn *Sphagnum* took place around 1910, much later than the observed shift around 1810. In this peat core lawn *Sphagnum* were not present at the start of the simulation in 1788. That the observed shifts from hollow *Sphagnum* to lawn *Sphagnum* in the three replicate cores, collected within 50 m from each other, took place in different time periods might be related to their exact position on the peat bog surface, i.e. their proximity to hollow/lawn/hummock microforms (Mauquoy et al. 2002a).

Fig. 7. The effects of temperature and precipitation increase on carbon accumulation at Lille Vildmose (LVM) and Walton Moss (WLM19) under different conditions. The effect is calculated as the difference between the plus scenario (+2 °C or +10 mm month⁻¹) and the minus scenario (−2 °C or −10 mm/month) divided by the mean of the two scenarios times 100%. Temperature changes were accompanied by potential evapotranspiration changes of +/− 7%. Data are mean values for 2050–2099. P+/-10 = future precipitation plus/minus 10 mm month⁻¹, T+/-2 = future temperatures plus/minus 2 °C, N10/30 = N-deposition of 10/30 kg-N.ha⁻¹.a⁻¹.

Fig. 6. The effects of future climate change and CO₂ doubling for the species composition at Walton Moss. Data are mean values for 2050–2099. Simulated light interception fraction represents community composition. Climate change = Had-CM2GSA1 scenario for Walton Moss: 1.9 °C temperature increase and 9% precipitation increase in 2080–2099 relative to 2000–2019 (App. 5). Current climate = climate scenario for 2000–2019 repeated; current CO₂ = 375 ppmv,.

Model analyses: effects of future climate change

According to our simulations, the future bog vegetation will not change much (Fig. 5). The present vegetation at the two sites in Denmark and England, which is dominated by lawn *Sphagnum* accompanied by dwarf shrubs and graminoids with a low cover, seems to be very stable. In the past century, the vegetation remained remarkably stable despite changes in atmospheric CO₂, N deposition and temperature (Figs. 4 and 5). A reason for the lack of species replacements is that climate change and doubling CO₂ concentrations have contrasting effects (Fig. 6). In our simulations, increasing CO₂ favours the peat mosses whose growth is less nutrient limited than that of vascular plants. Because little is known about the response of bog species to elevated CO₂, all species groups are given the same β -value, so that potential growth rates are equally increased. A species can only realise this

Fig. 8. The temperature effect on carbon accumulation (see Fig. 7) is negatively correlated to the effect on vascular plant abundance for both Lille Vildmose (LVM) and Walton Moss (WLM19).

increased potential growth rate if sufficient nutrients are available. This means that the species whose growth is least nutrient limited benefit most from increasing CO_2 concentrations. In contrast, rising temperatures favour the vascular plants by increasing mineralisation rates, resulting in increased nutrient availability in the peat.

To further analyse the effects of temperature and precipitation, we added or subtracted 2°C and 10 mm of monthly precipitation, respectively, to future climate scenarios at N deposition levels of 10 and $30 \text{ kg-N} \cdot \text{ha}^{-1} \cdot \text{a}^{-1}$. These simulations show that there is no straightforward effect of temperature on carbon accumulation because of interactions with other environmental factors. The model simulations suggest that an increase in temperature may still increase C-accumulation at the cooler LVM site at low N-deposition, but not at high N-deposition (Fig. 7). Increased temperatures generally increased both net primary production and decomposition. However, the net effect on C-sequestration depended on the relative effects on *Sphagnum* and vascular plants (Fig. 8). High temperatures, in combination with high N deposition, resulted in a strong increase of vascular plant cover and reduced *Sphagnum* production and C-accumulation rates. In addition, the temperature effect on C-accumulation was less, or more negative, at the warmer WLM site (Fig. 8).

A simulated increase in precipitation had more general effects. It led to higher water tables, reducing growth of the dwarf shrubs. Increased precipitation generally reduced decomposition and N-mineralisation rates because the higher water tables reduced the acrotelm depth. In addition, the proportion of vascular plant material in the peat was reduced. This strong effect on decomposition resulted in a generally positive effect of precipitation increases on carbon accumulation.

Discussion

Model evaluation

For the first time a model for bog ecosystems has been developed which includes vegetation dynamics and carbon and nitrogen cycling. The model is unique because it includes competition between species and species effects on important ecosystem processes such as C sequestration, N mineralisation and evapotranspiration. The model successfully simulated the major changes in the species composition between 1766 and 1999 in two ombrotrophic bogs in Europe as reconstructed from peat cores. There was no exact agreement between observations and simulations, but that cannot be expected as both observations and simulations have associated uncertainties. The exact timing of vegetation changes in the peat cores is unknown as the age of the layers that are not dated has been simply interpolated. The volume percentages in the peat cores are determined from a 2.5-cm diameter section, which is assumed to represent the bog vegetation. The model uses monthly temperature and precipitation input, as daily records are not available for past centuries. As a result, the hydrology module had to be relatively simple. Many parameters have associated uncertainties, which are difficult to quantify (App. 2). Nevertheless, the main changes in species composition were simulated and C-accumulation was in good agreement with observations in the peat cores. This suggests that the ecological processes that determine the vegetation composition and C-sequestration are captured by the model and that the differences between the species which determine the outcome of competition are well described.

The *Sphagnum* species appeared to have a large influence on the model bog ecosystem. Because of their slowly decomposing litter, they affect N-mineralisation rates, thereby controlling vascular plant growth. To some extent they also control the water level, thereby creating conditions favourable for themselves. As long as they maintain a high growth rate, the well-drained living moss layer is 5 cm thick (maximum thickness), preventing the high water tables favourable for hollow *Sphagnum*. On the other hand, by reducing evaporation rates when the water table drops below 15 cm below the moss surface, the lawn *Sphagnum* limit the occurrence of deep water tables that are favourable for hummock *Sphagnum*. Although it is well known that *Sphagnum* mosses exert a great influence on bog ecosystems (see van Breemen (1995) who described *Sphagnum* as an ecosystem engineer), this species effect has now, for the first time, been included in a model.

Long-term effects of climate change on bog vegetation

The current vegetation of lawn *Sphagnum* with a low cover of vascular plants seems to be stable. Despite changes in temperature, CO₂ concentration, N-deposition and precipitation, both for the previous century and for the coming century, major changes in species composition are not anticipated. This can be explained by the bog ecosystem having its own dynamics, as long as the 'ecosystem engineer' grows well (see above), but also by the contrasting effects of increasing temperature and CO₂ and precipitation. Where increasing temperatures favour the more N-limited species (i.e. vascular plants) by increasing N-mineralisation rates, increasing CO₂ concentrations favour the less N-limited species (i.e. *Sphagnum*), because they can realise the increased potential growth rate. Increasing precipitation also favours the peat mosses, because they depend more on high water tables than the vascular plants. The contrasting effects of increasing temperature and CO₂ on vegetation composition could also be important in other nutrient-limited ecosystems.

The simulated effects of temperature and CO₂ concentration generally agreed with results from 3 - 4 year field experiments in bogs. Elevated CO₂ increased *Sphagnum* height growth, but not at the cost of vascular plant growth during the Dutch BERI experiment (Heijmans et al. 2001b). In the Swiss BERI experiment, *Sphagnum* could increase its cover in response to elevated CO₂ (Mitchell et al. 2002). Experimental warming of bog vegetation in North America showed strongly increased above-ground production of ericaceous shrubs, without directly affecting moss growth (Weltzin et al. 2000). A Swedish warming experiment showed reduced *Sphagnum* production which was related to increased vascular plant biomass (Gunnarsson et al. 2004). These studies in intact bog vegetation suggest that *Sphagnum* can gain competitive advantage from increases in atmospheric CO₂ and that the vascular plants benefit from increases in temperature.

Also in agreement with our simulations is the experimental result that shrubs were most productive in the dry treatment, whereas the moss production increased with elevated water tables (Weltzin et al. 2000). However, the water table hardly changed in our simulation with the future climate scenario. The warming did increase potential evapotranspiration rates, but this was compensated by an increase in precipitation and by an increased water use efficiency of the vascular plants due to elevated CO₂. There is, of course, uncertainty about changes in regional precipitation patterns, so that the compensation described here may not take place everywhere. In our simulations, vegetation changes could occur in combinations of relatively cool temperatures and high precipitation (hollow

Sphagnum expand) and in combinations of relatively high temperatures and low precipitation (vascular plants strongly increased cover). However, the future climate, at least in northwestern Europe, is expected to become warmer and slightly wetter.

Although the vegetation composition did not clearly change during the past century in the peat cores in this study, it did change during earlier phases of the Little Ice Age. Changes in solar activity during the Little Ice Age were reflected by simultaneous and similar changes in the vegetation of Lille Vildmose and Walton Moss situated 800 km apart (Mauquoy et al. 2002b). Occurrences of hollow *Sphagnum* in the 13th, 15th and 17th centuries were related to climatic changes (Mauquoy et al. 2004), demonstrating the potential of bog vegetation to respond to natural climatic changes.

Vegetation changes have also been observed in three Swedish mires, where the vegetation has been re-surveyed after 30-50 years (Gunnarsson et al. 2000, 2002; Malmer et al. 2005). However, the vegetation changes were most pronounced in the more minerotrophic fen part of the mires and almost absent in the ombrotrophic bog part of the mires (Gunnarsson et al. 2000, 2002), suggesting that the bog vegetation is relatively stable. The southern Swedish mire, though, showed increased frequencies of tree species, dwarf shrubs and hummock mosses (Gunnarsson et al. 2002). These changes in species abundance were attributed to increased N deposition and/or surface dryness. Using a model similar to NUCOM-BOG could help to unravel the underlying causes of the observed changes. Vegetation changes did occur in the sub-arctic Stordalen mire, where wet sites dominated by graminoids expanded at the cost of hummock sites dominated by dwarf shrubs (Malmer et al. 2005). Here, permafrost degradation is the probable cause of the observed vegetation changes. Such changes cannot be simulated by NUCOM-BOG, as snow and ice are not (yet) included.

Interactions between components of global change

The analysis of the effects of temperature and precipitation on carbon sequestration revealed that precipitation had a positive effect on C-accumulation, but that the effect of temperature depended on the level of N-deposition. The model simulations suggest that an increase in temperature will increase C-accumulation at low N-deposition, but not at high N-deposition. This interaction between components of global change is the result of changes in vegetation composition having long-term effects on C-accumulation. At low N-deposition, both vascular plants and mosses benefit from increases in temperature via increases in nutrient mineralisation rates and growing season length. Although increases in

temperature increase decomposition rates, these are more than compensated by an increased net primary production without changes in vegetation. At high N-deposition, *Sphagnum* production is less limited by N than vascular plant growth. In this situation, the vascular plants benefit from the temperature-induced increases in mineralisation rates. As a result, the vascular plants expand strongly and reduce moss production, resulting in long-term decreases in C-accumulation due to a smaller proportion of recalcitrant *Sphagnum* litter in the peat.

In the absence of vegetation changes, simulated *Sphagnum* production increased in the future climate, due to increased atmospheric CO₂ and increased growing season length. Moss production can be limited by sub-optimal growing conditions or by shading by vascular plants. Sub-optimal growing conditions could be low CO₂, short growing season or deep water tables, but these are not anticipated for the coming century. Therefore, major changes in *Sphagnum* production and C-sequestration have to be the result of major changes in species composition of the vegetation. Such vegetation changes particularly take place in certain combinations of global changes, resulting in interacting effects of components of global change on C-sequestration.

Concluding, the model simulations with varying temperature, precipitation, CO₂ concentration and N-deposition, confirm the importance of including species interactions and feedbacks between vegetation, hydrology and soil. The simulation results also show that caution is needed when analysing the effects of climatic changes on bog vegetation and C-sequestration. The effects of temperature increase (nutrient-limited species gain competitive advantage, increase in potential evapotranspiration) can be compensated by the effects of increases in atmospheric CO₂ (less nutrient-limited species gain competitive advantage, increased water use efficiency) and precipitation (favouring peat mosses). These simulated contrasting effects of temperature and CO₂ in bog ecosystems, certainly play a role in other ecosystems where net primary production is limited by nutrients. Vegetation changes could occur in some combinations of climatic changes, resulting in interacting effects of components of global change. Model results show that increasing temperatures may still increase carbon accumulation at cool, low N-deposition sites, but decrease carbon accumulation at high N-deposition sites. We can conclude that predictions on the effects of global warming should not be based on the effects of temperature increase alone and that it is important to take vegetation changes into account.

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For App. 1-5, see below (online version)
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App. 1. Extensive description of model equations for processes in the carbon, nitrogen and water balance.

Equations for plant growth and decomposition

Plant growth requires light, CO₂ and nutrients (nitrogen in the model). In addition, growth can be restricted because of unfavourable temperatures or water levels. Most equations are from earlier NUCOM versions (Berendse 1988; van Oene et al. 1999, 2000).

First, potential growth rate (G_{pot} in g-C.m⁻².month⁻¹) is calculated for each species group, as a function of maximum growth rate (G_{max}), fraction of light intercepted (LI), and modifying functions for CO₂ ($f_G(\text{CO}_2)$), temperature ($f_G(T)$) and water ($f_G(W)$):

$$G_{\text{pot}} = LI \times G_{\text{max}} \times f_G(\text{CO}_2) \times f_G(T) \times f_G(W) \quad (\text{A1})$$

The fraction of light intercepted (LI) by vascular plants is determined by their leaf area (leaf area, leaf biomass times specific leaf area, m² m⁻²) and light extinction coefficient (k_{ext}):

$$LI_{\text{vasc}} = 1 - \exp(-k_{\text{ext}} \times \text{LeafArea}) \quad (\text{A2})$$

Light not absorbed by the vascular plants reaches the mosses and is distributed over the moss groups in proportion to their cover. Elevated CO₂ concentrations increase potential growth rates:

$$f_G(\text{CO}_2) = 1 + \beta \times \ln(\text{CO}_2 / 350) \quad (\text{A3})$$

It is a descriptive equation for the CO₂ response of crops within a range of 200 - 1000 ppmv atmospheric CO₂ (Goudriaan et al. 1985). Unfavourable temperatures and water levels reduce growth ($f_G(T)$ and $f_G(W)$) following relatively simple functions (only written out for $f_G(T)$):

$$\begin{aligned} f_G(T) &= 0 & \text{if } T < T_{\text{min}} \\ f_G(T) &= (T - T_{\text{min}}) / (T_{\text{opt1}} - T_{\text{min}}) & \text{if } T_{\text{min}} < T < T_{\text{opt1}} \\ f_G(T) &= 1 & \text{if } T_{\text{opt1}} < T < T_{\text{opt2}} \\ f_G(T) &= (T_{\text{max}} - T) / (T_{\text{max}} - T_{\text{opt2}}) & \text{if } T_{\text{opt2}} < T < T_{\text{max}} \end{aligned} \quad (\text{A4})$$

Thus, light, CO₂ concentration, temperature and water level are considered as growth defining factors which determine potential growth in a given environment (Van Ittersum et al. 2003). In this model, the only growth-limiting factor is nitrogen. The actual growth rates (G_{act} in g C m⁻² month⁻¹) are dependent on the amounts of nitrogen available (N_{avail} in g-N.m⁻².month⁻¹) for each species group:

$$\begin{aligned} \text{if } N_{\text{avail}} < n_{\text{min}} \times G_{\text{pot}} & \quad G_{\text{act}} = N_{\text{avail}} / n_{\text{min}} & \quad N_{\text{upt}} = N_{\text{avail}} \\ \text{if } n_{\text{min}} \times G_{\text{pot}} < N_{\text{avail}} < n_{\text{max}} \times G_{\text{pot}} & \quad G_{\text{act}} = G_{\text{pot}} & \quad N_{\text{upt}} = N_{\text{avail}} \\ \text{if } N_{\text{avail}} > n_{\text{max}} \times G_{\text{pot}} & \quad G_{\text{act}} = G_{\text{pot}} & \quad N_{\text{upt}} = n_{\text{max}} \times G_{\text{pot}} \end{aligned} \quad (\text{A5})$$

A minimum concentration of N is required for growth (n_{min}). If available N is less than N demand ($n_{\text{min}} \times G_{\text{pot}}$), actual growth will be less than potential growth because of N limitation. There is also a maximum a plant can take up ($n_{\text{max}} \times G_{\text{pot}}$). If more N is available than is taken up by the plants (N_{upt}) then the excess N leaches to a deeper layer. This set of equations includes N limitation of growth, luxury consumption and saturation of N uptake. Both growth and N uptake are first calculated for the entire plant and then allocated to the organs following fixed allocation schemes. This procedure does not account for changes in allocation in response to nutrient or light limitation (Chapin 1980).

Litter production (CLP and NLP in g-C or g-N.m⁻².month⁻¹) is calculated for each organ for each species group:

$$CLP = k_{\text{mort}} \times \text{CBiomass} \quad (\text{A6})$$

$$NLP = k_{\text{mort}} \times \text{NBiomass} \cdot (1 - k_{\text{reall}}) \quad (\text{A7})$$

The mortality rate of each organ (k_{mort}) is a constant fraction of biomass and is constant over the year. A fixed part of the

N in the dying organ is withdrawn (k_{reall}). Thus, in the model this reallocation of N is not dependent on the N content. In addition to the litter production as a fixed fraction of biomass, there is extra litter production by the leaves of dwarf shrubs as a result of *Sphagnum* height growth. This is because a significant part of the dwarf shrubs may become overgrown by the mosses (own obs.) and the leaves can no longer intercept light. There is additional litter production by mosses if the living moss layer is thicker than 5 cm, because it is assumed that the living moss material deeper than 5 cm below the moss surface dies because of lack of light. Leaf litter produced by vascular plants is added to the living moss layer. Other litter is added to the dead mass in the acrotelm, with the exception of the roots of the graminoids which are already situated in the catotelm when they die.

Decomposition rates (Dec in $\text{g-C.m}^{-2}.\text{month}^{-1}$) are calculated for each organ of each species group in each peat layer (and for leaf litter in the living moss layer), and depend on temperature (T) following Kirschbaum (1995):

$$\text{Dec} = \text{CDeadmass} \times k_{\text{dec}} \times f_D(T) \quad (\text{A8})$$

$$f_D(T) = \exp(-3.764 + 0.204 \times T \times (1 - 0.5 \times T / 36.9)) \quad (\text{A9})$$

Half the temperature dependency is used for the catotelm because the temperature fluctuations will be reduced. Relative decay rates (k_{dec}) are different for the acrotelm and catotelm and differ among the species groups and organs within vascular plants (App. 2). The effect of moisture conditions on decomposition was not separately described because it is assumed that the peat is never too dry for decomposition. The reduction of decomposition because of water-saturated conditions is included in much lower decomposition rates in the catotelm. The acrotelm may also be periodically water-saturated, but this will mainly be in winter when low temperatures already limit decomposition.

Nitrogen mineralisation (N_{min} in $\text{g-N.m}^{-2}.\text{month}^{-1}$) is dependent on the decomposition rate and the N:C ratio of the dead material (NCDeadmass), with NC_{crit} the critical N:C ratio and ε the microbial assimilation efficiency:

$$N_{\text{min}} = (\text{NCDeadmass} - NC_{\text{crit}}) \times \text{Dec} / (1 - \varepsilon) \quad (\text{A10})$$

If the N:C ratio of the dead plant parts is larger than the critical N:C ratio for the microbes, a net release of available nitrogen takes place. Net immobilization occurs when the N:C ratio is below this critical value.

If litter production exceeds decomposition rates, the bog grows both in mass and in height (mass divided by bulk density). This means that the moss surface rises together with the water level and the acrotelm/catotelm boundary, which is defined as the 10 year mean deepest water level. When the acrotelm/catotelm boundary shifts upward (in case of peat growth or wetter conditions), dead mass is transferred from the acrotelm to the catotelm. Thus, when the peat grows quickly, transfer rates will be relatively high and the residence time of the peat in the acrotelm will be relatively short.

Equations for the water balance

The model accounts for changes in the water balance in order to calculate the height of the water table. Water is added by precipitation, while evapotranspiration (including interception) and drainage remove water from the bog ecosystem. The water level is calculated using the depth and water storage capacity of each layer.

Evapotranspiration (ET; in mm.month^{-1}) is calculated for each species group as they contribute differently to total evapotranspiration. When the cover of vascular plants increases, the total evapotranspiration may be reduced, because the presence of vascular plants reduces wind speed and solar radiation at the moss surface, thereby reducing evaporation rates (Heijmans et al. 2001, 2004). However, in dry conditions vascular plants may continue transpiration while moss evaporation is strongly reduced. As solar radiation is the main driving force behind evapotranspiration, the light interception fraction (LI) of each species, calculated in the plant growth part of the model, is used to determine the contribution of each species group to total evapotranspiration:

$$ET_{\text{moss}} = LI \times k_{\text{crop}} \times ET_{\text{ref}} \times f_{\text{ET}}(W) \quad (\text{A11})$$

$$ET_{\text{vasc}} = LI \times k_{\text{crop}} \times ET_{\text{ref}} \times f_{\text{ET}}(W) \times f_{\text{ET}}(\text{CO}_2) \quad (\text{A12})$$

Crop coefficients (k_{crop}) describe the evapotranspiration of each species relative to a reference evapotranspiration rate (ET_{ref} ; open water evaporation in the model), to account for the larger water loss of mosses compared with vascular plants. Both vascular plants and mosses reduce their water losses when water is in short supply ($f_{\text{ET}}(W)$). Vascular plants reduce transpiration when soil moisture content becomes insufficient to meet water demand. For the mosses evaporation is reduced when the water loss can no longer be compensated by water supply through capillary rise. The *Sphagnum*

species groups differ considerably in their water transporting capacities. In the model, evapotranspiration is reduced linearly from a certain threshold water level (W_{opt1}) to a water level where no evapotranspiration takes place (W_{min}):

$$\begin{aligned} f_{ET}(W) &= 0 & \text{if } W < W_{min} \\ f_{ET}(W) &= (W - W_{min}) / (W_{opt1} - W_{min}) & \text{if } W_{min} < W < W_{opt1} \\ f_{ET}(W) &= 1 & \text{if } W > W_{opt1} \end{aligned} \quad (A13)$$

For the vascular plants a function for reducing transpiration at elevated atmospheric CO_2 concentrations ($f_{ET}(CO_2)$) is included, using the CO_2 growth enhancement factor (β):

$$f_{ET}(CO_2) = 1 / (1 + \beta \times \ln(CO_2 / 350)) \quad (A14)$$

It assumes that the CO_2 effect on water use efficiency is the same as on potential growth. Increased water use efficiency (expressed as the amount of water used to produce a unit of plant biomass) is a common response to elevated CO_2 (Arp et al. 1998). Reduced water loss due to increased stomatal closure does not apply to *Sphagnum* plants which lack stomata and do not actively regulate water exchange.

The term 'drainage' represents surface run-off and lateral outflow of water through the living moss layer. Vertical drainage is assumed to be negligible (van der Schaaf 1999). Because the living moss layer has a very small resistance to horizontal water flow and the model bog ecosystem (1 m²) is assumed to be in the centre of a larger bog area, all the water in and on the living moss is drained. As surface run-off and water flow through the living moss layer occur in much shorter time spans than the one-month time step (Ingram 1983), the whole water balance is calculated four times a month, dividing the monthly precipitation into four equal portions. This procedure speeds up drainage and the response of evapotranspiration to water level. The water level after four cycles is used in the plant growth equations.

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App. 2. Extensive description of the parameter values

Parameter values were mainly derived from the literature but, in addition, our own data were used, particularly for the vascular plant species. From the literature, preferably data from field studies in regions with a temperate or sub-boreal climate were used. For the mosses we preferentially extracted data from studies using two or three *Sphagnum* species from the different groups, so that the differences between the species could be well established. For changes in species composition in the model, the differences in parameter values between the species are probably more important than the absolute values. Most values were rounded to prevent the suggestion that characteristics are precisely known. The values in the literature are usually expressed on a dry mass basis, while our model works on a carbon basis. All literature values for biomass or peat mass were assumed to have a carbon concentration of 0.5 g-C.g⁻¹ dry matter.

Parameter values for graminoids and dwarf shrubs were mainly derived from data on *Eriophorum vaginatum* and *Calluna vulgaris*, respectively. The detailed data collected at blanket bog sites at Moor House National Park in northern England (Heal & Perkins 1978) were an important source of information particularly for the vascular plants. The hummock *Sphagna* belong to the Section *Acutifolia*. Literature data on *S. capillifolium* (or *S. rubellum*) and *S. fuscum* were used for the parameter values. These are compact, small-sized plants occurring at relatively dry sites (Daniels & Eddy 1985). The hollow *Sphagna* belong to the Section *Cuspidata*. Literature data on *S. cuspidatum*, *S. fallax* and *S. tenellum* were used for the parameter values. The morphology of these species resembles those of the Section *Acutifolia*, but they are usually less compact depending on the wetness of the site and they occur in consistently wet areas (Daniels & Eddy 1985). The lawn *Sphagna* belong to the Section *Sphagnum*. Literature data on *S. papillosum* and *S. magellanicum* were used for the parameter values. These are coarse, fat-looking species (Daniels & Eddy 1985).

Our own data were from the final harvest of the Dutch BERI (Bog Ecosystem Research Initiative) experiment, examining the effects of elevated CO₂ and increased N deposition on bog vegetation (for details see Heijmans et al. 2001). Data of the control treatment were used, as this closely resembled the field situation. Carbon and nitrogen concentrations were determined in all species and plant parts so that values could be directly expressed on a carbon or nitrogen basis.

Parameter values for vascular plant species characteristics (Gram = graminoids; Eric = dwarf shrubs):

Name	Description (unit)	Value	Gram	Eric
$G_{\max}$	Maximum growth rate ($\text{g-C.m}^{-2}.\text{month}^{-1}$)		70	60
k_{ext}	Light extinction coefficient (-)		0.5	0.8
SLA	Specific leaf area ($\text{m}^2.\text{g}^{-1} \text{C}$)		0.012	0.012
β	CO_2 growth enhancement factor (-)		0.7	0.7
$T_{\min}$	Minimum temperature for growth ($^{\circ}\text{C}$)		2	5
T_{opt1}	Lowest temperature for optimal growth ($^{\circ}\text{C}$)		12	14
T_{opt2}	Highest temperature for optimal growth ($^{\circ}\text{C}$)		20	20
$T_{\max}$	Maximum temperature for growth ($^{\circ}\text{C}$)		30	30
$W_{\min}$	Minimum water level for evapotranspiration and growth (mm)		-1000	-600
W_{opt1}	Lowest water level for optimal evapotranspiration and growth (mm)		-400	-300
W_{opt2}	Highest water level for optimal growth (mm)		0	-100
$W_{\max}$	Maximum water level for growth (mm)		100	-50
$n_{\min}$	Minimum N concentration for uptake ($\text{g-N.g}^{-1}\text{-C}$)		0.020	0.014
$n_{\max}$	Maximum N concentration for uptake ($\text{g-N.g}^{-1}\text{-C}$)		0.030	0.022
C_{alloc}	Fraction of growth allocated to leaves, stems and roots (-)	Leaf	0.40	0.35
		Stem	0.40	0.30
		Root	0.20	0.35
N_{alloc}	Fraction of N uptake allocated to leaves, stems and roots (-)	Leaf	0.45	0.45
		Stem	0.40	0.25
		Root	0.15	0.30
k_{mort}	Mortality rate (month^{-1})	Leaf	0.08	0.04
		Stem	0.06	0.01
		Root	0.10	0.04
k_{reall}	Fraction of N that is reallocated (-)	Leaf	0.45	0.25
		Stem	0.00	0.00
		Root	0.30	0.10
$k_{\text{dec,lvm}}$	Decomposition rate in living moss layer (a^{-1}) ^a	Leaf	0.19	0.14
$k_{\text{dec,acro}}$	Decomposition rate in acrotelm (a^{-1}) ^a	Leaf	0.11	0.07
		Stem	0.11	0.05
		Root		0.06
$k_{\text{dec,cato}}$	Decomposition rate in catotelm (a^{-1}) ^a	Leaf	$1 \cdot 10^{-4}$	$1 \cdot 10^{-4}$
		Stem	$1 \cdot 10^{-4}$	$1 \cdot 10^{-4}$
		Root	0.11	$1 \cdot 10^{-4}$
k_{crop}	Crop coefficient (-)		0.9	0.7
BD_{acro}	Bulk density in acrotelm (g-C.dm^{-3})	Leaf	16	16
		Stem	25	100
		Root	35	70
BD_{cato}	Bulk density in catotelm (g-C.dm^{-3})	Leaf	25	25
		Stem	30	100
		Root	35	70

^a The model uses monthly decomposition rates; here annual values are shown for easier comparison with literature values.

Parameter values for moss species characteristics (Humm = hummock *Sphagna*; Lawn = lawn *Sphagna*; Holl = hollow *Sphagna*):

Name	Description (unit)	Humm	Lawn	Holl
$G_{\max}$	Maximum growth rate (g-C.m ⁻² .month ⁻¹)	45	50	60
β	CO ₂ growth enhancement factor (-)	0.7	0.7	0.7
$T_{\min}$	Minimum temperature for growth (°C)	5	3	0
T_{opt1}	Lowest temperature for optimal growth (°C)	14	14	10
T_{opt2}	Highest temperature for optimal growth (°C)	18	18	18
$T_{\max}$	Maximum temperature for growth (°C)	25	25	25
$W_{\min}$	Minimum water level for evapotranspiration and growth (mm)	-500	-350	-200
W_{opt1}	Lowest water level for optimal evapotranspiration and growth (mm)	-200	-150	-50
W_{opt2}	Highest water level for optimal growth (mm)	-50	-50	0
$W_{\max}$	Maximum water level for growth (mm)	0	0	100
$n_{\min}$	Minimum N concentration for uptake (g-N.g ⁻¹ C)	0.005	0.006	0.008
$n_{\max}$	Maximum N concentration for uptake (g-N.g ⁻¹ C)	0.032	0.036	0.042
k_{mort}	Mortality rate (month ⁻¹)	0.04	0.04	0.08
k_{reall}	Fraction of N that is reallocated (-)	0.40	0.40	0.40
$k_{\text{dec,acro}}$	Decomposition rate in acrotelm (a ⁻¹) ^a	0.017	0.034	0.067
$k_{\text{dec,cato}}$	Decomposition rate in catotelm (a ⁻¹) ^a	1·10 ⁻⁴	1·10 ⁻⁴	1·10 ⁻⁴
k_{crop}	Crop coefficient (-)	1.4	1.3	1.2
BD_{lvms}	Bulk density in living moss layer (g-C.dm ⁻³)	9	7	5
BD_{acro}	Bulk density in acrotelm (g-C.dm ⁻³)	20	13	15
BD_{cato}	Bulk density in catotelm (g-C.dm ⁻³)	40	25	30

^a The model uses monthly decomposition rates; here annual values are shown for easier comparison with literature values.

Other parameter values:

Name	Description (unit)	Value
μ_{lvms}	Water storage coefficient of living moss layer (-)	0.85
μ_{acro}	Water storage coefficient of acrotelm layer (-)	0.70
μ_{cato}	Water storage coefficient of catotelm layer (-)	0.40
NC_{crit}	Critical N:C ratio for net N mineralisation (g N g ⁻¹ C)	0.014
ε	Microbial assimilation efficiency (-)	0.2

Extensive motivation of parameter values:

Maximum growth rate. Maximum growth rates for the vascular plants were derived from total biomass of the graminoids (*Eriophorum angustifolium*, *Rhynchospora alba* and *Eriophorum vaginatum*) and the current-year biomass of the dwarf shrubs (*Vaccinium oxycoccus*, *Erica tetralix*, *Calluna vulgaris*, *Empetrum nigrum* and *Andromeda polifolia*) at the final harvest of the Dutch BERI experiment (Heijmans et al. 2001). It was assumed that half of the fine root biomass of the dwarf shrubs was produced in the current year. For the graminoids, production was calculated from biomass combined with the mortality rates for each organ. These production values were corrected for cover (derived from point-quadrat measurements) and the maximum value (excluding elevated CO₂ treatment) was divided by the length of the growing season, calculated from the temperature function for each species group and the monthly temperature data for the last year of the BERI experiment. The maximum growth rate for dwarf shrubs was slightly increased because secondary stem growth was not measured. Maximum growth rates for the mosses were derived from growth measurements for four species of *Sphagnum* at Moor House in three habitats (Clymo 1970). The maximum yearly growth rate was taken and divided by the length of the growing season, calculated using the temperature function for each species and monthly temperature data from Moor House (Heal & Smith 1978). These values corresponded very closely to maximum monthly values (height increment times density) measured by Overbeck & Happach (1956) in a German mire. Brock & Bregman (1989) measured a very high growth rate for *S. recurvum* in a *Betula* carr, but the value does not seem realistic for growth in an ombrotrophic bog. Also the high value from Overbeck & Happach (1956) for *S. recurvum*, often cited in papers dealing with *Sphagnum* growth, is not used as this value was not measured, but extrapolated.

Light extinction coefficient. The light extinction coefficient for the graminoids was derived from our own measurements of the reduction of light intensity at the moss surface relative to light intensity above the canopy of *E. angustifolium* in combination with leaf biomass data (assuming specific leaf area = 60 cm² g⁻¹). The light extinction coefficient for the dwarf shrubs was derived from

data of light transmittance related to leaf area for *Calluna vulgaris* at a solar angle of 40°, which is near the mean of the observed solar angles in the field (Grace & Marks 1978).

Specific leaf area. The values for specific leaf area were derived from our own measurements on leaves of *Eriophorum angustifolium* and *Vaccinium oxycoccus*, which correspond with values for Alaskan *E. angustifolium* in Shaver et al. (1998) and for *C. vulgaris* in Grace & Marks (1978).

Beta. The value of 0.7 was derived for crops (Goudriaan & Unsworth 1990), but corresponds with responses measured in own CO₂ experiments (Heijmans et al. 2001, 2002). This value is used for all species, although some *Sphagnum* species might be more sensitive to CO₂ concentration than others, because of a greater resistance to CO₂ uptake (Proctor et al. 1992).

Minimum, optimum and maximum temperature. There is little information about the temperature range for growth of the vascular plants. Note that the temperatures in the model are mean monthly temperatures which are lower than maximum daily temperatures. In the British Isles, growth of the graminoids starts in March or April (Philips 1954 (*E. angustifolium*), Wein 1973 (*E. vaginatum*)) whereas growth of the dwarf shrubs starts in April or May (Gimingham 1960 (*C. vulgaris*), Bannister 1966 (*E. tetralix*)). The monthly Moor House temperatures (Heal & Smith 1978) for these months were used as minimum temperature. Optimum temperatures for dwarf shrubs are likely to be higher than for graminoids as the dwarf shrubs often expand in warming treatments (Weltzin et al. 2000). The optimum and maximum temperatures were estimated. Both Overbeck & Happach (1956) and Clymo & Hayward (1982) show that hollow species start growing earlier than the other *Sphagnum* species. In England, *S. recurvum* even continued growth in winter and *S. papillosum* started growing earlier than *S. rubellum* (Clymo & Hayward 1982). The optimum temperatures were derived from Overbeck & Happach (1956) and our own data using monthly growth rates (height increment) and monthly temperature data. Only months in which water was not severely limiting growth were included. The temperature range for *S. magellanicum* and *S. rubellum* was not different, but *S. recurvum* had reached a high growth rate at a lower temperature than the other two species (Overbeck & Happach 1956). The maximum temperatures for growth were estimated and set the same for all moss species.

Minimum, optimum and maximum water level. The graminoids can grow at a large range of water levels because of their deep roots and aerenchymae, so that both low and high water tables should be no problem. The dwarf shrubs have a much more restricted range of water levels to grow at. Their roots are only in the top part of the peat, which is oxygenated for part of the year. In addition, growth can be much reduced in waterlogged soil, particularly for *C. vulgaris* (Gimingham 1960). Dwarf shrubs are therefore most abundant on hummocks. The lowest water levels for the dwarf shrubs represent the water levels where evapotranspiration was reduced and minimized in a Russian dwarf shrub-dominated bog (Ingram 1983). It is assumed that when transpiration is reduced, growth rate will also be reduced. The maximum water levels and the range of water levels for the graminoids were estimated. The values for the *Sphagnum* groups were derived from growth experiments using several water levels by Clymo (1973) and Wallén et al. (1988). The values correspond with observed reductions in evapotranspiration by Schouwenaars (1993). The lowest water levels at which growth or evapotranspiration can occur were derived from Overbeck & Happach (1956) for *S. magellanicum* (lawn) and *S. recurvum* (hollow) from a map of occurrence of these species in relation to water level (recorded when water levels were deepest) and is estimated for the hummock *Sphagna*. The deepest water level at which hummock *Sphagna* can grow or evaporate is certainly lower than for the other *Sphagna* as these species are more drought tolerant (Schipperges & Rydin 1998).

Minimum and maximum N-concentration. The minimum and maximum concentration of N in the plant was derived from own data for the vascular plants. The mean of the three lowest and highest N-concentrations, each for graminoids and dwarf shrubs (whole plants), from all treatments (20 plots) was taken. For the mosses, minimum concentrations were found in Pitcairn et al. (1995) in mosses from Scotland from the 1950s. The N-concentrations were from the top 2 cm of moss and because of reallocation (40%) less N is needed for growth. Therefore, 60% of the values is used as minimum N-concentration. The maximum concentrations were from a polluted area (Ferguson et al. 1984).

Carbon and nitrogen allocation. For vascular plants the allocation patterns were derived from our own data from the final harvest (control treatment) combined with mortality rates for the graminoids. For the dwarf shrubs, current year leaves and stems could be recognized and it was assumed that half of the root biomass was produced in the current year. The parameter value for allocation to stems was slightly increased, because secondary stem growth was not measured. The values for C allocation of graminoids and dwarf shrubs correspond with modelled dry mass allocation patterns in *E. vaginatum* and *C. vulgaris* (Smith & Forrest 1978). The value for C allocation to roots of dwarf shrubs was similar to that measured by Backéus (1990) for a dwarf-shrub dominated hummock vegetation using root-ingrowth cores.

Mortality. Mortality rates for the organs of the vascular plants were derived from models for *E. vaginatum* and *C. vulgaris* (Smith & Forrest 1978). The mortality rate for the leaves was slightly increased because the extensive measurements of Backéus (1985) on mire plants, showed that leaves of *E. vaginatum* died after 6 to 12 months, and leaves of *A. polifolia* in the second year and leaves of *E. nigrum* in the third year. Leaves of *E. tetralix* shed during their second growing season (Bannister 1966, own observations).

Reallocation. Reallocation fractions for our own data were estimated from the difference in N concentration between new and old or dead leaves and stems. These values were lower than measured for *M. caerulea* and *E. tetralix* in Dutch heathlands (Berendse 1988). The mean was taken and for roots and stems of graminoids the values from Berendse (1988) were used. The value for graminoid leaves corresponds with differences in N-concentration between green and brown leaves of *E. vaginatum* and *E. angustifolium* (Heal & Smith 1978). For *Sphagnum*, data were used from a greenhouse experiment in which N deposition was reduced (Heijmans et al. 2002).

Decomposition rates. For the vascular plants, parameter values for decomposition in the acrotelm were calculated from yearly decomposition rates for stems and young shoots (considered as leaves) of *C. vulgaris* and leaves of *E. vaginatum* in a 10-yr study at a blanket bog at Moor House (Heal et al. 1978, Swift et al. 1979) and the monthly mean temperatures from Moor House, England (Heal & Smith 1978). The yearly decomposition rates were calculated from the slope of the logarithm of the mass remaining versus time (years). For the other organs data from a two year decomposition study were used (Heal et al. 1978). For the decomposition rates of leaves in the living moss layer, two year decomposition values were used. For the mosses, parameter values for decomposition were calculated from yearly decomposition rates for hummock and hollow *Sphagnum*, measured in a six year litterbag study in Eastern Canada (Moore & Basiliko 2006). The value for lawn *Sphagnum* was chosen in between and corresponds with best estimates for lawn *Sphagnum* decomposition rates derived from model simulations (Clymo 1978). The decomposition rate in the catotelm is derived from carbon accumulation in peat cores (Clymo 1984) and is not species specific.

Crop coefficient. The crop coefficients for the *Sphagnum* species were derived from Clymo (1973). In his experiment, evaporation from *Sphagnum* in beakers decreased in the order *S. rubellum* (hummock) > *S. papillosum* (lawn) > *S. cuspidatum* (hollow) > open water. The crop coefficients for the vascular plant species were derived from a Dutch literature survey (Spieksma et al. 1996). The value for graminoids was based on *Molinia caerulea* on a bog remnant. The value used for dwarf shrubs was from *Erica tetralix*/*Calluna vulgaris* vegetation on a bog remnant. The crop coefficient is kept constant throughout the year as the species are evergreen.

Bulk density. Bulk densities have been measured for peats, but not for individual species and species composition of the peat is often not given. Bulk density of ericaceous stems is estimated from own data using the largest peat bulk densities measured. Jones & Gore (1978) give values for vascular plant leaves and roots of *E. vaginatum*. Bulk densities of other organs were estimated. Bulk densities for *Sphagnum* species were measured by Overbeck & Happach (1956) and Hayward & Clymo (1982). Values for the acrotelm and catotelm were measured in peats with different *Sphagnum* species on top (assuming that the same species is also dominant in the peat) (Hayward & Clymo 1982; Williams et al. 1999a, b).

Water storage capacity. Values for water storage capacities are from the review in Ingram (1983). The value for the acrotelm is derived from values for surface *Sphagnum* peat (Von Post humification degree 1 or 2) and for the catotelm for peats from several mires of Von Post humification degree 4.

Critical C:N ratio and microbial efficiency. These parameter values were taken from Damman (1988).

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App. 3. Climate input for historic runs: annual temperature and precipitation since 1766.

Historic climate of Lille Vildmose (Denmark) and Walton Moss (UK), reconstructed from measured temperature and precipitation data. The points represent yearly mean temperatures and yearly sums of precipitation. The solid lines represent five year moving means.

For the historic temperature at Walton Moss, we used temperature data from Dumfries (near Walton Moss) from the GHCN database (Vose et al. 1992) and the Central England temperatures from the Hadley Centre (Manley 1974; Parker et al. 1992). The Dumfries data were available for 1871 to 1969. For the overlapping period, the Dumfries temperatures correlated very well with the central England temperatures and this linear relationship ($\text{TempDumfries} = 0.9359 \cdot \text{TempCentralEngland} - 0.1573$, $R^2 = 0.98$, $n = 1188$ monthly mean temperatures 1871-1969) was used to reconstruct the temperatures for the periods 1766-1870 and 1970-1999.

For the historic temperature at Lille Vildmose, temperature data from Ålborg (near Lille Vildmose), Copenhagen (back to 1768), both from the GHCN database, and Walton Moss were used. The Ålborg data were available for 1961 to 1990. The strong relation between temperatures in Ålborg and Copenhagen ($\text{TempÅlborg} = 0.9589 \cdot \text{TempCopenhagen} - 0.7872$, $R^2 = 0.99$, $n = 360$ monthly mean temperatures 1961-1990) was used to calculate temperatures for Lille Vildmose for the period 1768-1960. For the missing periods (Copenhagen data were missing for 1766-1767, 1777-1781, 1789-1797 and 1991-1999) the temperature was derived from the Walton Moss temperature ($\text{TempLVM} = 1.3794 \cdot \text{TempWLM} - 4.3723$, $R^2 = 0.95$, $n = 360$ monthly mean temperatures 1961-1990).

For the historic precipitation at Walton Moss, precipitation data from Carlisle (ca. 15 km southwest of Walton Moss) from the GHCN database and the England and Wales precipitation from the Hadley Centre (Wigley & Jones 1987; Gregory et al. 1991; Jones & Conway 1997) were used. The Carlisle data were available from 1845 to 1987. These data correlated with the longer term series of England and Wales, but not as well as for temperature (as precipitation is much more variable and more a local phenomenon). Precipitation in Carlisle was similar to the England and Wales precipitation from June to September, but much lower in the other months. Therefore two relationships were established to reconstruct the precipitation at Walton Moss (for June to September: $\text{PrecCarlisle} = 0.7568 \cdot \text{PrecEnglandWales} + 18.968$, $R^2 = 0.44$, $n = 572$; for October to May: $\text{PrecCarlisle} = 0.6322 \cdot \text{PrecEnglandWales} + 11.712$, $R^2 = 0.50$, $n = 1144$) for the periods 1766-1844 and 1988-1999.

For the historic precipitation at Lille Vildmose, precipitation data from Ålborg, Copenhagen (back to 1821) and Walton Moss were used. The Ålborg data were available for 1961 to 1990. For the period 1821-1960 the precipitation was related to the data from Copenhagen ($\text{PrecÅlborg} = 0.6728 \cdot \text{PrecCopenhagen} + 14.591$, $R^2 = 0.42$, $n = 360$). For the periods 1766-1820 and 1991-1999 the precipitation was derived from the Walton Moss precipitation (for April to November: $\text{PrecLVM} = 0.5628 \cdot \text{PrecWLM} + 17.188$, $R^2 = 0.36$, $n = 240$; for December to March: $\text{PrecLVM} = 0.5229 \cdot \text{PrecWLM} + 8.2856$, $R^2 = 0.44$, $n = 120$).

For the reference evapotranspiration, evaporation data from the Hadley Centre climate models were used. This source was also used for the simulations of the future. Calculation of Penman open water evapotranspiration requires data for net solar radiation, air temperature, relative humidity and wind speed. Long-term historical data for these variables are not available. Instead, the monthly evaporation for the grid cells representing Lille Vildmose and Walton Moss was chosen and related to the monthly temperatures for the period 1961-1990 to reconstruct historic evaporation rates. The evaporation of the grid cells probably resembles open water evaporation as ca. half of the grid cells consists of sea. There is a strong relationship between monthly temperature and monthly evaporation, but the relationship is not linear. Evaporation in the first half of the year is relatively high, while evaporation in the second half is much lower at the same temperature (as temperature lags behind solar radiation, which is the main driving force for evaporation). The relationship between monthly temperature and evaporation for each cell for the period 1961-1990 is used to reconstruct past reference evapotranspiration rates (for Cell 96-15 representing Walton Moss: for February to June: $\text{Evap} = 5.8556 \cdot \text{Temp} - 0.5798$, $R^2 = 0.71$, $n = 150$; for July to January: $\text{Evap} = 3.173 \cdot \exp(0.2194 \cdot \text{Temp})$, $R^2 = 0.87$, $n = 210$; for Cell 04-15 representing Lille Vildmose: for February to June: $\text{Evap} = 3.9163 \cdot \text{Temp} + 15.765$, $R^2 = 0.62$, $n = 150$; for July to January: $\text{Evap} = 6.1409 \cdot \exp(0.1343 \cdot \text{Temp})$, $R^2 = 0.79$, $n = 210$; Evap in mm month⁻¹, Temp in °C).

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App. 4. Environmental input for historic runs: atmospheric CO₂ and N deposition since 1766.

Historic atmospheric CO₂ concentrations and N deposition rates at Lille Vildmose (Denmark) and Walton Moss (UK), reconstructed from measured data.

The historical CO₂ concentrations were from van Oene et al. (1999), who used measured data from the Siple ice core and from Mauna Loa, Hawaii (1958-1988). The historic N-deposition was also derived from measured data. In England, N-deposition in precipitation has been measured since 1850 in Rothamsted (Goulding et al. 1998). Although Rothamsted is far from Walton Moss, both places are in areas of relatively low N-deposition (map in Pitcairn et al. 1995). Therefore, the Rothamsted data are assumed to be representative for Walton Moss. For total N deposition (wet and dry) the measured bulk N-deposition was doubled (Lamers et al. 2000). To estimate N-deposition back to 1766, the trend of the three earliest measurements was extrapolated. For Denmark, historic measured bulk N deposition data for four stations were available (Risager 1998). Data from Tylstrup were used (near Lille Vildmose) and N deposition from the earliest measurement (1959) was extrapolated to the same starting point as in England. Data from another Danish station confirmed that N deposition did not increase in the first half of the 20th century.

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App. 5. Climate input for future runs for Lille Vildmose and Walton Moss.

Future climate of Lille Vildmose (Denmark) and Walton Moss (UK). The points represent yearly mean temperatures and yearly sums of precipitation. The solid lines represent five year moving means.

Climate input came from the Hadley Centre climate models. Weather data were generated by the HadCM2 model (a global circulation model) for each grid cell of 2.5° by 3.75° (latitude × longitude) for the HadCM2GSa1 scenario. This scenario assumes a yearly increase of atmospheric greenhouse gas concentrations of 1%, in the presence of (cooling) sulphate aerosols according to the IPCC IS92a scenario (Verweij & Viner 2001). Scenario data are from 1960 to 2099. The relationships between grid cell data and measured data for the overlapping period (1960-1999) were used to determine the future climate of Lille Vildmose and Walton Moss.

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