# Effects of climate change and nitrogen deposition on vegetation and decomposition in bog ecosystems.

# Effecten van klimaatverandering en stikstofdepositie op vegetatie en afbraak in hoogveen ecosystemen.

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# Abstract

Ombrotrophic bogs are peat-forming systems and as such they serve as important long-term sinks for atmospheric $CO_2$. A large proportion of northern peatlands consists of *Sphagnum*-dominated ombrotrophic bogs with a sparse vascular plant cover. The different *Sphagnum* species and the vascular plants apparently occur in a stable equilibrium, thereby sustaining the functioning of the bog ecosystem. Global change is expected to have a strong impact on temperature, precipitation and nutrient availability, especially at high northern latitudes where the majority of peat bogs occur. The main question addressed in this study was: how will global change influence the vegetation and functioning of ombrotrophic bogs? We examined the effect of increased temperature, N deposition and water table fluctuations on intact bog vegetation and on competition between different *Sphagnum* species. Furthermore, the effect of temperature and N deposition on decomposition was studied. We performed experiments under controlled conditions and field experiments in four bog sites along a transect from the north of Sweden to north-east Germany, in which both temperature and N deposition increased southwards.

The findings from the greenhouse experiments suggest that a high increase in temperature and N availability would have negative consequences for the production of *Sphagnum* species in bog ecosystems, particularly for the species from wet habitats. The conclusion from the outdoor experiments with intact vegetation is that higher temperature, higher N deposition and lower summer water tables will increase ericoid vegetation in bogs and depress the growth and cover of ‘wet’ *Sphagnum* species. From the decomposition experiment we conclude that the decomposition of vascular plants and *Sphagnum* litter is influenced by different environmental drivers, with enhanced temperatures stimulating mass loss of vascular plant litter, but not of *Sphagnum* litter. Enhanced N deposition increases the loss of N from *Sphagnum* litter.

We conclude that an increase in temperature and N deposition will change the *Sphagnum* species composition and accelerate decomposition of the peat. Since it is mainly the ‘wet’ *Sphagnum* species that will suffer from global change, the proportional cover of ‘dry’ species will increase. Since the ‘dry’ species generally decompose more slowly, it can be expected that carbon sequestration in *Sphagnum* will probably not change immediately as a result of global change. However, in the longer term, the increase in vascular plants could depress *Sphagnum* production and this would increase the proportion of vascular plant litter in peat. As vascular plant litter is much more decomposable than *Sphagnum* litter and its decomposition is accelerated more by an increase in temperature, the litter turnover will accelerate and nutrients will become more readily available – benefiting the vascular plants more than the *Sphagnum*. If the total cover of ericoids and graminoids were to increase, shading from the vascular plants could adversely affect *Sphagnum* production. Consequently, in the long term, global change could have a serious negative effect on *Sphagnum* production and on the capacity of ombrotrophic bogs to sequester carbon.

*Voor Tonny, Ineke, Saskia en Gertjan*

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# CHAPTER 1

# General introduction

Angela Breeuwer

## Ombrotrophic bogs

Ombrotrophic bogs are peat-forming ecosystems and as such they serve as important long-term sinks for atmospheric $CO_2$. In many countries, bogs are protected in conservation areas, not just for their high C sequestration, but also because they provide habitats for many threatened plant and animal species (Rydin and Jeglum 2006). Furthermore, the thick peat deposits formed over thousands of years make bog ecosystems valuable research sites for studying vegetation history and the relationship between vegetation composition, climate change and human impacts (van der Linden 2006).

Although northern peatlands cover only 2% of the total land surface, they store about one-third of the world's soil carbon in the form of peat (Gorham 1991; Rydin and Jeglum 2006). A large proportion of northern peatlands consists of *Sphagnum*-dominated ombrotrophic bogs. Despite their relatively low primary production, the peat mosses (*Sphagnum* spp.) are responsible for the high accumulation of carbon in bogs, because their litter decomposes very slowly (Clymo and Hayward 1982; Coulson and Butterfield 1978; Limpens and Berendse 2003b). The slow decomposition in bogs is mainly caused by three factors: first, the very harsh abiotic conditions (wet, cold, anoxic and acidic); second, the poor quality of the plant litter (Aerts *et al.* 1999; Dorrepaal *et al.* 2005); and third, the secondary plant compounds excreted by *Sphagnum* that hamper fungal and bacterial breakdown (Painter 1991; van Breemen 1995).

Since *Sphagnum* species are often the major primary producers in ombrotrophic bogs and produce very recalcitrant litter, the main part of the peat layer is formed by remnants of *Sphagnum*. Furthermore, *Sphagnum* mosses regulate the hydrological and hydrochemical conditions at the raised bog surface to a high degree (van Breemen 1995; Van der Schaaf 2002). Several studies have revealed differences between *Sphagnum* species in production (Asada *et al.* 2003; Gerdol 1995; Gunnarsson 2005; Lindholm and Vasander 1990) and in decomposition rate (Belyea 1996; Johnson and Damman 1993; Limpens and Berendse 2003b; Rochefort *et al.* 1990). These inter-species differences are often related to differences in preferred microhabitat (Gunnarsson 2005). Within a bog, different *Sphagnum* species occur at different heights above the water table and at different positions along pH and nutrient gradients (Andrus 1986; Limpens *et al.* 2003; Sjörs and Gunnarsson 2002). The most obvious division in microhabitat preference is between the hollow species, which grow in pools and at shallow water levels, and hummock species, which grow in microsites with deeper water levels. Lawn species occur at intermediate water levels. Hummock species can also grow at higher water levels, but they are then usually outgrown by hollow species (Rydin 1986; Rydin 1993; Rydin 1997). However, the competitive ability of species may differ between years, seasons and locations.

The vascular plant cover in bogs is generally low and consists of ericoids, graminoids and a few herbs, some of them carnivorous. Parallel to the distribution of *Sphagnum* mosses, the vascular plant species assemblage varies over the different microhabitats along the water table gradient. Hollows are generally dominated by graminoid species such as *Rhynchospora alba*. Further above the water table (i.e. lawns and hummocks), ericoid species such as *Calluna vulgaris* peak in abundance. The vascular plant species that occur in bogs are also adapted to the harsh conditions – lack of nutrients, wet, partly anoxic and acidic – that result from *Sphagnum* growth and accumulation (Rydin and Jeglum 2006). To avoid being overgrown, the vascular plants have to keep up with the vertical height increment of *Sphagnum* (Backeus 1985; Dorrepaal *et al.* 2006; Malmer *et al.* 1994). On the other hand, the presence of vascular plants is important for *Sphagnum* because they provide a matrix for the *Sphagnum* to grow on (Malmer *et al.* 1994) and reduce evaporation from *Sphagnum* plants (Heijmans *et al.* 2001). However, when the vascular plant cover becomes too dense, the increased shading can adversely affect *Sphagnum* growth (Berendse *et al.* 2001; Bubier *et al.* 2007). In most bogs, the vascular plants and *Sphagnum* apparently occur in a stable equilibrium, thereby sustaining the functioning of the bog ecosystem.

## Global change and bogs

Global change is expected to have a strong impact on temperature, precipitation and nutrient availability, especially at northern latitudes where the majority of peat bogs occur (Gunnarsson 2005; Kivinen and Pakarinen 1980). All global change models predict an increase in temperature and nitrogen (N) deposition (Galloway *et al.* 2004; Solomon *et al.* 2007). Predictions about future precipitation patterns show great variability, but it is likely that summer drought will be more frequent, so water tables will be even lower during summer (Gunnarsson *et al.* 2004). As a result of the lower water tables and the subsequent increase in depth of the oxic layer (Schouten 1992) combined with an increase in temperature, the decomposition of the peat layer and N mineralisation may be stimulated (Hobbie 1996; Rustad *et al.* 2001) and in this way enhance the N availability in bogs.

There is much concern about how the effects of global change will affect the ability of peatlands to sequester carbon and what the feedbacks to climate will be (Aerts 2006; Bragazza *et al.* 2006; Bubier *et al.* 2007; Franzén 2006). Several studies have found a positive relationship between temperature and production of both *Sphagnum* and vascular plants (Backeus 1985; Gunnarsson 2005; Hollister *et al.* 2005; Moore 1989; Sonesson *et al.* 2002). The positive effect that increased temperature might have on carbon sequestration in bogs is, however, often diminished by the positive effect of temperature on decomposition rates (Hobbie 1996). Decomposition in bogs can be affected by temperature and N deposition both directly and indirectly. Higher temperature can increase decomposition rates directly because microbial activity is increased (Dioumaeva *et al.* 2002; Hobbie 1996). Indirectly, an increase in temperature may stimulate aerobic decomposition (Schouten 1992) through its negative effect on the water table and the subsequent increase in the depth of the oxic layer. One direct effect of increased N deposition could be to alleviate N limitation on microbial metabolism in the nutrient-poor bog ecosystems, facilitating the breakdown of litter with low nutrient concentrations (Bragazza *et al.* 2006; Mack *et al.* 2004). As most plant growth in northern bogs is still N-limited, increased N deposition can be expected to decrease the C:N ratios and secondary plant compounds in the litter: this has been shown to enhance decomposition rates (Bragazza *et al.* 2006; Dorrepaal *et al.* 2005; Gerdol *et al.* 2007).

So far, most of the studies dealing with the effects of temperature and N on decomposition have tested their effects separately, often using an experimental approach in which bog vegetation has been subjected to a stepwise increase in temperature and/or N. This has the possible drawback that the microbial community is not adapted to the changed conditions, and therefore any effects on decomposition will be different from what they would be under more gradual global change

Global change influences not only the production and decomposition of individual plant species but also the competitive balance between species. Changes to the current equilibrium between *Sphagnum* species and between *Sphagnum* and vascular plants can have marked effects on the C dynamics and $CO_2$ fluxes of the ecosystem (Ward *et al.* 2007). An important challenge facing ecologists is to predict how climate change will alter species distributions in ecosystems (Mooney 1991). Thus, to generate good predictions of the effects of global change on functioning and carbon sequestration in bog ecosystems, it is necessary to know how the complete vegetation responds to global change. So far, several studies have addressed the separate effects of different aspects of global change, such as temperature and N deposition, on different species. In the research reported in this thesis we set out to investigate the combined effects of several aspects of global change on the production and decomposition of both *Sphagnum* and vascular plants in ombrotrophic bogs.

## Aims and approach

The main question addressed in this study was: how will global change influence the species composition and functioning of ombrotrophic bogs? We examined the effect of increased temperature, N deposition and water table fluctuations on intact bog vegetation and on competition between different *Sphagnum* species. Furthermore, the effect of temperature and N deposition on decomposition was studied. We did this in different experiments: two field experiments over a gradient from the north of Sweden to north-east Germany, in which both temperature and N deposition increased from north to south. Figure 1.1 shows the location of the four field sites. We also performed two greenhouse experiments and one experiment in which peat monoliths from the south Swedish site were kept outdoors in large containers in an experimental field.

First, we focus on the effects of climate change on different *Sphagnum* species. As *Sphagnum* species differ in production and degradability – in general, hollow species are more productive and also more degradable than hummock species, (Gunnarsson 2005; Johnson and Damman 1993; Limpens and Berendse 2003b) – it seems likely that when a species with high production or low decomposition rate increases its relative abundance in a bog, this will increase the carbon-storing capacity of the system.

The predicted increased frequency of dry periods in summer and higher temperature are expected to result in increased water table drawdown in summer. Several studies have examined the effects of water table depth on *Sphagnum* vegetation in peatlands, but most experiments use fixed water tables as an experimental factor, reflecting differences in microtopographical habitat (Robroek *et al.* 2007a; Robroek *et al.* 2007b; Weltzin *et al.* 2001; Weltzin *et al.* 2000). Field studies on the effect of water table on bog vegetation usually use chronosequences of water tables that occur naturally in the field, which are then extrapolated to potential effects of water table drawdown (Fenton and Bergeron 2006; Gunnarsson and Flodin 2007). In our study we set out to elucidate the effect of periodic water table drawdown on species composition; we expected that water table drawdown would depress production of hollow species, so hummock and lawn species would expand.

Although research has been done on the separate effects of temperature (Asada *et al.* 2003; Dorrepaal *et al.* 2003; Gerdol 1995) and N (Aerts *et al.* 2001; Gerdol *et al.* 2007; Gunnarsson and Rydin 2000; Limpens and Berendse 2003a; Press *et al.* 1986) on *Sphagnum* growth, only one other study has examined the combined effects of temperature and N on *Sphagnum* cover (Wiedermann *et al.* 2007). To our knowledge, ours is the first study to examine these combined effects of increased temperature and N addition on different *Sphagnum* species. Since hummock and lawn species grow in drier and therefore also warmer microhabitats than hollow species, we expected the ‘dry’ species to be better adapted to higher temperatures. Within each bog there are different competing species, but the dominant species also differ between bogs, depending on climatic region. In our study, we used species from different sites in Sweden and Germany. In the north of Sweden, *Sphagnum balticum* and *Sphagnum fuscum* are the dominant species; these species also occur in southern Sweden, but here the most abundant species are *Sphagnum magellanicum* and *Sphagnum cuspidatum*. This corresponds with the general distribution of these species in Europe, since both *S. magellanicum* and *S. cuspidatum* occur further south than *S. fuscum* and *S. balticum* (Daniels and Eddy 1985). We expected the southern species to be better adapted to higher temperatures.

Second, changes in temperature, N availability and water level are also likely to influence the current competitive balance between *Sphagnum* and vascular plants. Production in both groups is controlled by the factors temperature, light, wetness and nutrient availability, but the competition between *Sphagnum* and vascular plants is highly asymmetrical (Rydin and Jeglum 2006), In general, climate warming is expected to increase *Sphagnum* productivity, as long as water does not become limiting (Dorrepaal *et al.* 2006; Gunnarsson 2005). The effect of increased N deposition is less clear-cut; it has been shown that a small increase in N can enhance *Sphagnum* production at locations where N is a limiting nutrient (Turunen *et al.* 2004), but when N concentrations exceed a critical threshold value, *Sphagnum* production and cover are reduced (Berendse *et al.* 2001; Bragazza *et al.* 2006; Gerdol *et al.* 2007; Gunnarsson and Rydin 2000). Vascular plant cover and production are stimulated by increased temperature and N availability (Berendse *et al.* 2001; Bubier *et al.* 2007; Wiedermann *et al.* 2007). Changing water tables too can directly affect competition between *Sphagnum* and vascular plants. Low water tables will hamper capillary rise of water to the apical parts (i.e. capitula) of the *Sphagnum* individuals and consequently reduce their growth rate (Rydin and McDonald 1985; Wallén *et al.* 1988). Most vascular plants can avoid drought more easily than *Sphagnum* mosses because their roots can reach the deeper water-saturated layers in the peat. Additionally, in contrast to Sphagna, vascular plants can control water loss via their stomata. Water table drawdown and concomitant low availability of water at the surface may reduce the productivity of *Sphagnum* but stimulate that of vascular plants (Malmer *et al.* 1994). Thus, climate change can generally be expected to favour vascular plants (Berendse *et al.* 2001; Bubier *et al.* 2007; Heijmans *et al.* in press; Wiedermann *et al.* 2007).

The differences in decomposition rates between *Sphagnum* species are smaller than the difference in decomposition rate between *Sphagnum* and vascular plants. Comparative studies on the decomposition of *Sphagnum* and vascular plant in peatlands have shown that vascular plant litter can be decomposed 4 to 10 times faster than *Sphagnum* litter in similar conditions (Bragazza *et al.* 2007; Coulson and Butterfield 1978; Dorrepaal *et al.* 2005; Hobbie 1996), so an increased proportion of vascular plant litter will result in higher turnover rates of the peat.

**Figure 1.1** Location of the 4 research sites: 1= Lappmyran, 2= Åkerlänna Römosse, 3= Saxnäs mosse, 4= Barschpfuhl.

## Thesis outline

**Chapter 2** describes a greenhouse experiment in which we studied the effect of four temperature treatments (11.2 °C, 14.7 °C, 18.0 °C and 21.4 °C) on the growth of 4 *Sphagnum* species: *S. fuscum* and *S. balticum* from the site in northern Sweden and *S. magellanicum* and *S. cuspidatum* from the site in southern Sweden. In addition, three combinations of these species were made to study the effect of temperature on competition during one growing season.

In **chapter 3** another greenhouse experiment is described in which we studied the effect of two temperature treatments (17.5 °C and 21.7 °C) and two N addition treatments (0 and 4 g N $m^{-2}$ $yr^{-1}$) on the growth of four *Sphagnum* species: *S. fuscum* and *S. balticum* from the sites in north and central Sweden and S*. magellanicum* and *S. cuspidatum* from the site in south Sweden. Using four combinations of these species, we studied changes in growth and cover of each species during two growing seasons.

**Chapter 4** describes our first experiment using mesocosms with intact field vegetation. We studied the effects of water table drawdown in summer on the vegetation composition. Mesocosms were collected from the site in southern Sweden, and subsequently transplanted to an experimental field in the Netherlands. Two water table treatments were applied: one with constant water tables at five centimetres below the moss surface, and one in which the water table was allowed to drop, resulting in water tables fluctuating between 5 and 21 cm below the moss surface. *Sphagnum* growth, as well as *Sphagnum* and vascular plant abundance, were assessed for two-and-a-half years.

**Chapter 5** describes the results from the first field experiment in which mesocosms with intact vegetation were transplanted southwards from north Sweden to north-east Germany along the transect of four bog sites. We monitored shifts in abundance of both *Sphagnum* and vascular plants. We measured height increment and production of *Sphagnum* and nutrient concentrations in all plant groups.

In **chapter 6,** our second field experiment, which examined decomposition at the four bog sites along the gradient from north Sweden to north-east Germany is described. We performed two litterbag experiments: one reciprocal experiment with *Eriophorum vaginatum* litter and one experiment using recalcitrant (*S. fuscum*) and more degradable (*S. balticum*) *Sphagnum* litter collected from the northernmost site. We measured mass loss and N release during two years for *Sphagnum* and during three years for *E. vaginatum*.

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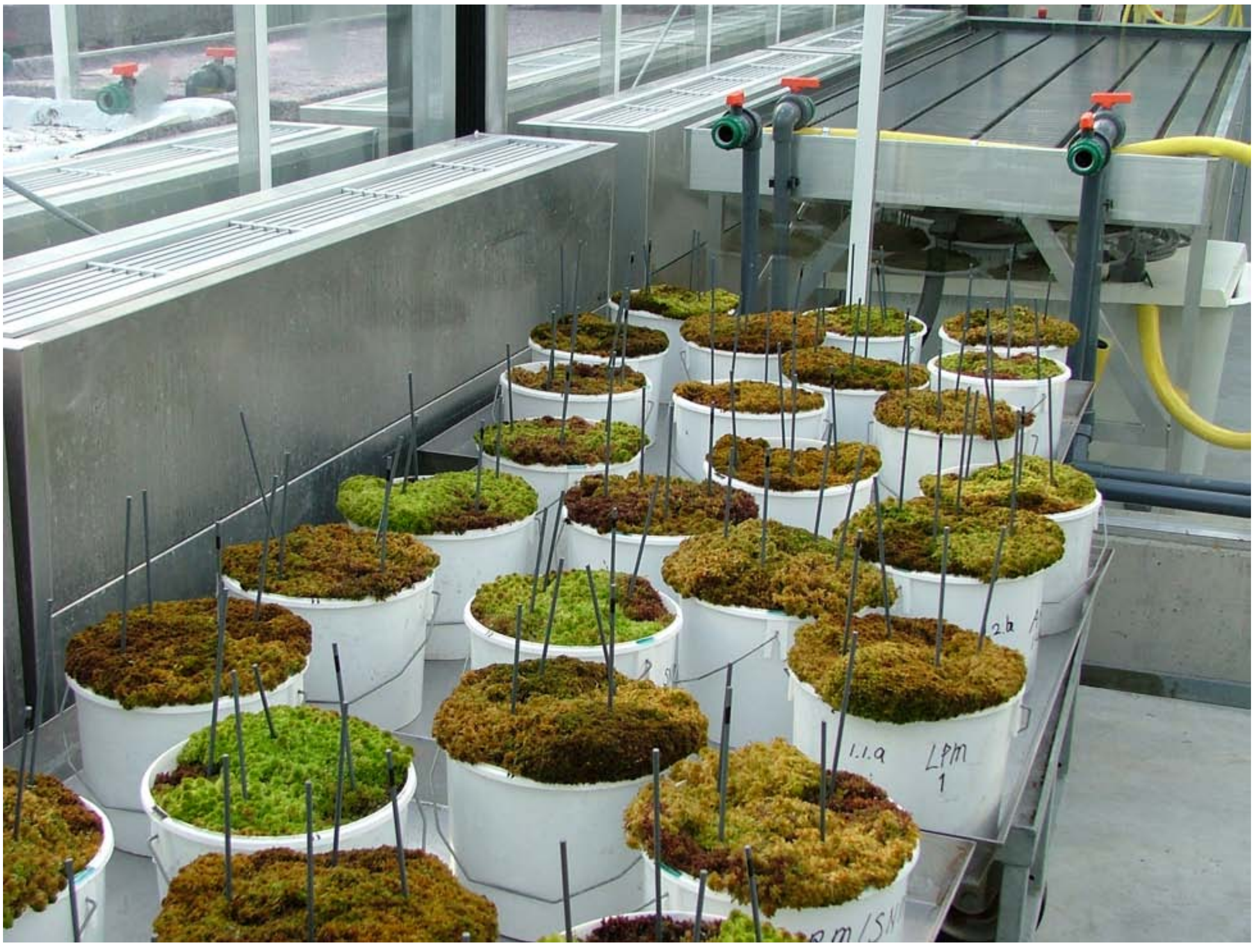
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# CHAPTER 2

# The effect of temperature on growth and competition between *Sphagnum* species.

Angela Breeuwer, Monique MPD Heijmans, Bjorn JM Robroek and Frank Berendse

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## Abstract

Peat bogs play a large role in the global sequestration of carbon and are often dominated by different *Sphagnum* species. Therefore, it is crucial to understand how *Sphagnum* vegetation in peat bogs will respond to global warming. We performed a greenhouse experiment to study the effect of four temperature treatments (11.2 °C, 14.7 °C, 18.0 °C and 21.4 °C) on the growth of 4 *Sphagnum* species: *S. fuscum* and *S. balticum* from a site in northern Sweden and *S. magellanicum* and *S. cuspidatum* from a site in southern Sweden. In addition, three combinations of these species were made to study the effect of temperature on competition. We found that all species increased their height increment and biomass production with an increase in temperature, while bulk densities were lower at higher temperatures. The hollow species *S. cuspidatum* was the least responsive species, whereas the hummock species *S. fuscum* increased biomass production 13 fold from the lowest to the highest temperature treatment in monocultures. Nutrient concentrations were higher at higher temperatures, especially N concentrations of *S. fuscum* and *S. balticum* increased compared to field values. Competition between *S. cuspidatum* and *S. magellanicum* was not influenced by temperature. The mixtures of *S. balticum* with *S. fuscum* and *S. balticum* with *S. magellanicum* showed that *S. balticum* was the stronger competitor, but it lost competitive advantage in the highest temperature treatment. These findings suggest that species abundances will shift in response to global warming, particularly at northern sites where hollow species will lose competitive strength relative to hummock species and southern species.

## Introduction

Peat bogs play a large role in the global sequestration of carbon. Although northern peatlands cover only 2% of the total land surface, they store about one-third of the world soil carbon in the form of peat (Gorham 1991). It is therefore important to know how ombrotrophic bog ecosystems, which form a large part of northern peatlands, will respond to predicted climate changes, especially since the rise in temperature is expected to be above the global average at high latitudes (Christensen *et al*. 2007) where the majority of peat bogs occur (Gunnarsson 2005; Kivinen and Pakarinen 1980).

Vegetation in ombrotrophic bogs is often dominated by different *Sphagnum* species. The *Sphagnum* species account for the bulk of the carbon sequestration in peat because of their recalcitrant litter (Clymo and Hayward 1982; Coulson and Butterfield 1978; Limpens *et al.* 2003). Therefore, it is crucial to understand how *Sphagnum* vegetation in bogs will respond to global warming in order to predict the role of bogs as carbon sinks in the future. Several studies have revealed differences in production (Asada *et al.* 2003; Gerdol 1995; Gunnarsson 2005; Lindholm and Vasander 1990) and in decomposition rate (Belyea 1996; Johnson and Damman 1993; Limpens and Berendse 2003; Rochefort *et al.* 1990) between different *Sphagnum* species. These differences between species are often related to differences in microhabitat preference (Gunnarsson 2005). Within a bog, different *Sphagnum* species occur at different heights above the water table and at different positions along pH and nutrient gradients (Andrus 1986; Limpens *et al.* 2003; Sjörs and Gunnarsson 2002). The most obvious division in microhabitat preference is between hollow species, which grow in pools and at shallow water levels, and hummock species, which grow at deeper water levels. Hummock species can also grow at higher water levels, but they are then usually outgrown by hollow species (Rydin 1986; Rydin 1993; Rydin 1997). However, the competitive ability of species may differ between years, seasons and locations, and as such, competitive replacement occurs very slowly, if at all. This results in a relatively stable competitive balance between species (Rydin 1997).

Several studies found a positive relation between *Sphagnum* productivity and temperature (Gunnarsson 2005; Moore 1989; Sonesson *et al.* 2002). The positive effect that increased temperature might have on carbon sequestration in bogs is, however, often diminished by the positive effect of temperature on decomposition rates (Hobbie 1996). Increased decomposition rates also lead to increased rates of nutrient release from the peat layer, enhancing production rates even further. A change in temperature influences not only the production and decomposition of individual *Sphagnum* species but also the competitive balance that exists between species. An important challenge facing ecologists is to predict how climate change will alter species distributions in ecosystems (Mooney 1991). Robroek *et al*. (2007b) already found different responses in biomass production among species when temperature was increased. It can be imagined that when a species with high production and/ or a low decomposition rate increases its relative abundance in a bog, this will increase the carbon storage capacity of the system.

Not only are there different competing species within a bog, but there are also differences in dominant species between bogs when different climatic regions are compared. In this study, we used species from two different sites. At the site in northern Sweden, *Sphagnum balticum* and *Sphagnum fuscum* are the dominant species while at the site in southern Sweden these species also occur, but *Sphagnum magellanicum* and *Sphagnum cuspidatum* are the most abundant species. This corresponds with the general distribution of these species in Europe since both *S. magellanicum* and *S. cuspidatum* occur further south than *S. fuscum* and *S. balticum* (Daniels and Eddy 1985).

To examine the effect of temperature on the competition between species, we performed a greenhouse experiment in which we studied the effect of four temperature treatments on the growth of the four species: *S. fuscum* and *S. balticum* from a northern Swedish site and *S. magellanicum* and *S. cuspidatum* from a southern Swedish site. Three combinations of species were made to study the effects of temperature on interspecific competition. In our experiment we tried to answer the following questions:

1- What is the effect of increased temperature on the growth of different *Sphagnum* species? We expect all species to show an increase in both height increment and biomass production as a direct result of increased temperature and indirectly through increased nutrient availability.

2- What is the effect of temperature on competition between species? Since *S. fuscum* and *S. magellanicum* grow in drier and therefore also warmer microhabitats than *S. balticum* and *S. cuspidatum* respectively, we expect these species to be better adapted to higher temperatures. *S. magellanicum* grows at more southern sites than *S. balticum*, so we expect this species to be better adapted to higher temperatures. Consequently, we hypothesize that increased temperature will have a positive effect on competitive abilities of the hummock and southern species, leading to a relatively larger increase in height increment and biomass production with temperature than for hollow and northern species.

## Material and methods

### Plant material

In August 2004, *Sphagnum* cores (diameter 16 cm, height 18-22 cm) were collected at 2 different sites in Sweden. From the northern site Lappmyran (64˚09’N, 19˚35'E), 30 *Sphagnum fuscum* (Schimp) H.Klinggr cores and 40 *Sphagnum balticum* (Russ.) C. Jens. cores were collected. This site is a string flark mire or mixed mire with ridges of hummocks and hollows where *S. fuscum* is dominant on the hummocks and *S. balticum* in the dryer parts of the hollows. When identifying the species from this site in the lab, we found specimens of both *S. balticum* and *Sphagnum angustifolium* (Russ.) C. Jens. These species are difficult to distinguish, which both Russow (Smith 1978) and Klinggraff (Daniels and Eddy 1985) recognised when they identified both species as varieties of *Sphagnum recurvum*. In our samples, we were unable to quantify the exact percentages of *S. balticum* and *S. angustifolium*. As result, whenever we mention *S. balticum,* we are referring to a mixture of *S balticum* and *S. angustifolium*.

From the southern site Saxnäs Mosse (56˚51'N, 13˚27' E), 40 *Sphagnum magellanicum* (Brid.) cores and 30 *Sphagnum cuspidatum* (Hoffm.) cores were collected. At this site *S. magellanicum* occurs on the lawns and low hummocks and *S. cuspidatum* in the hollows and pools.

Cores were taken from monospecific stands of each *Sphagnum* species (>95 %) with sparse vascular plant cover (<5 %). The cores were placed in plastic containers (diameter 16 cm, height 22 cm). Vascular plants were clipped flush with the *Sphagnum,* and other *Sphagnum* species were removed with tweezers. The containers were brought to Wageningen and stored outside for 8 weeks before the greenhouse was available. As a result, containers from both sites could acclimate to the same climate to some extent.

### Experimental design

At the start of the experiment, the containers were brought into the greenhouse and randomly divided over the treatments and 5 replicate blocks, with 7 species combinations (4 monocultures and 3 mixtures) and 4 temperature treatments per block. All four species were kept in monoculture and the following three species combinations were made to study interspecific competition: two northern species *S. fuscum* with *S. balticum*, two southern species *S. magellanicum* with *S. cuspidatum* and a northern with a southern species *S. balticum* with *S. magellanicum*. To study competition between a northern and a southern species we chose the combination of *S. balticum* and *S. magellanicum* because they occur at similar water levels. To make the combinations, the cores were cut into four equal quarters and two quarters of both species were placed alternately in an empty container. In potting the species combinations, we made certain that the surface of the mixture was uniform. We did not cut monocultures in four quarters, but another experiment showed no difference in water content between cut and uncut monocultures (Robroek *et al*. 2007a).

The experiment was conducted in four adjacent climate controlled greenhouse compartments from November 2004 till April 2005 for a total of 154 days. Each compartment was assigned one of four temperature treatments. Treatments and containers were switched between compartments every 2 weeks to minimize any effect of the different compartments. The position of the blocks and the position of containers within the blocks were also switched every 2 weeks. The average day temperatures in the four temperature treatments were 11.2 °C, 14.7 °C, 18.0 °C and 21.4 °C, respectively (Table 2.1). During the dark period of 8 hours, the day temperature was lowered by approximately 3 °C to 9.3 °C, 11.6 °C, 15.5 °C and 18.9 °C, resulting in mean temperatures of 10.6 °C, 13.7 °C, 17.2 °C and 20.6 °C in temperature treatments 1, 2, 3 and 4, respectively. In the region of the northern site, the mean temperature in July is 14.7 °C (Alexandersson *et al*. 1991) and in the southern site the mean temperature in July is 17.0 °C (Malmer *et al*. 2003). A light period of 16 hours was applied. If light intensity was low during this period, SON-T AGRO 400 (Philips Powertone 400) lamps were used.

**Table 2.1** Day and night means of temperature (°C), relative humidity (%) and vapour pressure deficit (VPD) (kPa) of the 4 treatments, ±SE, n=154.

| Treatment | Temperature | | Relative humidity | | VPD | |
|---|---|---|---|---|---|---|
| | day | night | day | night | day | night |
| T1 | 11.2 ± 0.04 | 9.3 ± 0.05 | 81.9 ± 0.4 | 86.8 ± 0.4 | 0.24 ± 0.01 | 0.16 ± 0.01 |
| T2 | 14.7 ± 0.03 | 11.6 ± 0.05 | 76.9 ± 0.3 | 81.8 ± 0.5 | 0.39 ± 0.01 | 0.25 ± 0.01 |
| T3 | 18.0 ± 0.02 | 15.5 ± 0.03 | 75.2 ± 0.4 | 76.1 ± 0.4 | 0.51 ± 0.01 | 0.42 ± 0.01 |
| T4 | 21.4 ± 0.03 | 18.9 ± 0.04 | 72.7 ± 0.4 | 73.0 ± 0.5 | 0.70 ± 0.01 | 0.59 ± 0.01 |

Relative humidity during the day was set at 75%. In the greenhouse it was not possible to keep the relative humidity exactly the same with all temperatures. The rise in temperature between treatments corresponded with a decrease in relative humidity, which caused an additional increase in vapour pressure deficit (VPD) with temperature (Table 2.1). The difference in relative humidity only explained 33% of the increase in VPD with the highest temperature. If relative humidity would have been equal in all compartments, VPD would still have been twice as high at temperature 4 as at temperature 1. Our highest VPD of 0.7 kPa with a temperature of 21.4˚C is actually still quite low compared to field conditions. Although not many data on VPD are published for similar ecosystems, Hobbie and Chapin (1998) did find the following values for VPD in Toolik Lake, Alaska, in June and July: in open field sites, 0.02 to 1.71 kPa with temperatures ranging from 5.9 to 22.5 ˚C; and under small plastic greenhouses, 0.08 to 3.83 kPa with temperatures ranging from 6.4 to 31.1˚C. Dorrepaal *et al*. (2003) measured a VPD of 1.54 under normal conditions and 1.41 in open-top chambers with an average temperature of 15 ˚C in June and July in Abisko, Sweden.

The water level was set to 1 cm below capitula at the start of the experiment. All species were subjected to the same water level, so that temperature was the only changing environmental variable. This relatively high water level was used for all species because hollow species cannot grow at low water levels; while hummock species can survive the environmental conditions of hollows quite well; nonetheless, they are absent from these areas because of biotic factors (Rydin and McDonald 1985). Grosvernier *et al*. (1997) found that growth in height and dry weight is equal for *S. fuscum* grown at water levels of 1 cm and 40 cm below moss surface while, for *S. magellanicum* and especially for *Sphagnum fallax,* growth in height and dry weight is much greater with the high water level.

During the experiment an artificial rainwater solution, an 8000-fold dilution of a sea water solution (Garrels and Christ 1965), was added twice a week to bring the water level back to 1 cm below capitula. The amount of water added was used as a measure of evaporation.

The drop in the water table was highest in the highest temperature treatment, but water level never dropped more than 6 cm below moss surface between two water additions. In a number of containers, *Sphagnum* grew higher than 1 cm above the container. To keep the water level at 1 cm below the moss surface, a plastic ridge was glued onto the containers and the crack was filled with silicone kit. Water content was measured using a theta probe (Delta-T Devices, Cambridge, UK) before the final harvest of the experiment. This was done 3 to 4 days after watering the containers for the last time, so the water content would reflect possible differences between treatments.

### Measurements

Height increment of the *Sphagnum* carpet was measured non-destructively every month using a variation of the cranked wire method (Clymo 1970). We used plastic rods that were inserted to a depth of approx. 8 cm and anchored by plastic broom bristles, this method kept the cranked wires firm at the same place so they did not move with *Sphagnum* growth. Two plastic rods were inserted in the monocultures and one plastic rod was inserted in each quarter of the mixtures. The rods had a diameter of 1.5 mm and did not seem to interfere with the growth of the surrounding *Sphagna*.

At the end of the experiment, columns with a diameter of 5 cm were cut around each cranked wire and cut off at 5 cm length. Each column was put in a plastic Ziplock bag and fresh weight was determined. All bags were stored at 1 °C till further measurements could be taken. Capitula were defined as the top 1 cm of each individual plant and stem as the 1-4 cm part. Capitula and stems were separated per column and oven dried at 70 °C for at least 48 hours and then weighed. The weight of the total sample was used to calculate bulk density and the biomass production per squared centimetre to account for changes in capitulum density. For nutrient analyses, samples of capitula were pooled per species for each container. Total N, P and K concentrations were determined by digesting 300 mg of homogeneous, milled material with sulphuric acid, salicylic acid, selenium and hydrogen peroxide. All samples were analysed for total N and P spectrophotometrically using an auto-analyzer (Skalar). K concentrations were measured with an atomic absorption spectrophotometer (Varian AAS). To compare capitulum bulk density and nutrient concentrations with field values, we collected five samples (d= 5cm) from monocultures of the four *Sphagnum* species in the two Swedish sites in August 2006. Measurements on capitulum bulk density and nutrient concentrations were executed as described above.

To measure the change in cover of the species in the mixtures, digital pictures were made at the start and at the end of the experiment. In these pictures we measured the total surface cover per species in each pot with Image J (1.33u, Nat. Inst. Health, USA). The biomass production per unit area (g m-2) was calculated as follows:

height increment (m) * final bulk density total sample (g m-3) * ($\%\text{cover}_{\text{end}}$ / $\%\text{cover}_{\text{start}}$)

### Data analysis

Data were tested for normality and equality of variance. When necessary, data were square-root transformed to achieve homogeneous variances. Block effect was tested as random factor. When no block effect was detected, which was usually the case, block was omitted from the analysis to gain extra degrees of freedom. All analyses were conducted using the SPSS statistical package for Windows (12.0).

One container with a monoculture of *S. balticum* under temperature 4 was heavily affected by a fungal infection, probably *Lyophyllum palustre*. After 4 months, 90% of the plant material had died. This container was further omitted from the analyses.

Height increment in monocultures was tested per species with one-way analysis of variance (ANOVA) with temperature as independent factor. Height increment, biomass production, cover change, bulk density, water content and nutrient concentrations were tested per species. Two-way ANOVAs were performed with temperature and species combination as independent factors. The effect of temperature, species and competition on the concentrations of N, P and K was tested using a 3-way ANOVA. Differences between the treatments were analysed using a Tukey post-hoc test. To test how the environmental variables temperature, N concentration and water content influenced biomass production we performed a stepwise regression analysis per species.

## Results

### Height increment

In the monocultures, the height increment increased with temperature in each species (Fig. 2.1, Table 2.2). For *S. cuspidatum* this effect was least distinct with the lowest height growth at temperature 2 and no difference in growth between temperatures 1, 3 and 4.

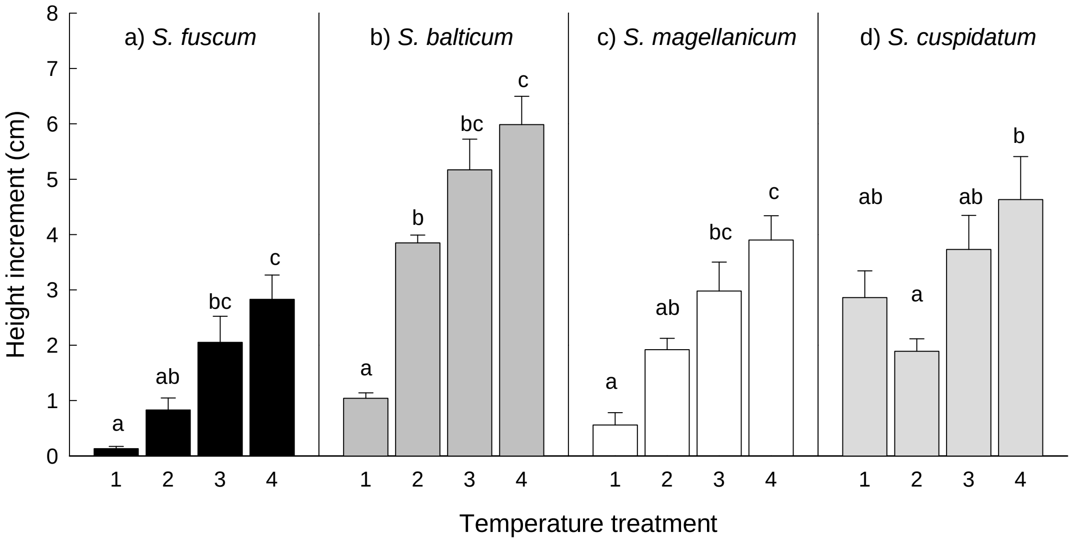

**Figure 2.1** Height increment of species in monocultures (cm). Data are mean values ± SE, n=5 except for *S. balticum* at T4, n=4. Different letters indicate significant differences ($P < 0.05$) between temperature treatments within each species. For temperature treatments, see Table 2.1.

**Table 2.2** *F*-values and *P*-values and direction of main effects influencing height increment and biomass production per species [a], corrected for cover, using a 2-way ANOVA. Number of observations; n=40, except for *S. balticum* n=39.

| | **Temperature** | | | **Combination** | | | **T * Combination** | |
|---|---|---|---|---|---|---|---|---|
| | **F** | ***P*** | **effect** | **F** | ***P*** | **effect** | **F** | ***P*** |
| **Height increment** | | | | | | | | |
| *S. fuscum* (+ *S. balticum*) | 49.31 | **<0.001** | + | 1.17 | 0.288 | + | 0.92 | 0.445 |
| *S.balticum* (+ *S. fuscum*) | 51.19 | **<0.001** | + | 9.13 | **0.005** | - | 0.61 | 0.616 |
| *S.balticum* (+ *S. magellanicum*) | 19.58 | **<0.001** | + | 10.32 | **0.003** | - | 3.24 | **0.035** |
| *S. magellanicum* (+ *S. balticum*) | 28.71 | **<0.001** | + | 8.87 | **0.006** | - | 1.88 | 0.154 |
| *S. magellanicum* (+ *S. cuspidatum*) | 18.53 | **<0.001** | + | 4.86 | **0.035** | - | 1.14 | 0.350 |
| *S. cuspidatum* (+ *S.magellanicum*) | 10.80 | **<0.001** | + | 18.83 | **<0.001** | - | 0.86 | 0.470 |
| **Biomass production** | | | | | | | | |
| *S. fuscum* (+ *S. balticum*) | 20.99 | **<0.001** | + | 18.57 | **<0.001** | - | 2.31 | 0.095 |
| *S.balticum* (+ *S. fuscum*) | 19.41 | **<0.001** | + | 5.48 | **0.026** | - | 2.04 | 0.128 |
| *S.balticum* (+ *S. magellanicum*) | 9.68 | **<0.001** | + | 12.38 | **0.001** | - | 3.47 | **0.028** |
| *S. magellanicum* (+ *S. balticum*) | 17.50 | **<0.001** | + | 44.99 | **<0.001** | - | 1.67 | 0.193 |
| *S. magellanicum* (+ *S. cuspidatum*) | 11.75 | **<0.001** | + | 23.36 | **<0.001** | - | 2.00 | 0.133 |
| *S. cuspidatum* (+ *S.magellanicum*) | 5.15 | **0.005** | + | 2.20 | 0.148 | - | 0.18 | 0.913 |

Only *S. fuscum* showed no difference in height increment between monoculture and mixture. All other species showed a growth reduction in mixtures (Table 2.2). There were no significant interactions between the effect of temperature and competition on height increment, except for *S. balticum* in combination with *S. magellanicum* (Table 2.2). Temperature increased height increment of *S. balticum* in monoculture, while there was no effect of temperature in mixture with *S. magellanicum* (Fig. 2.1b and 2.2b). When we compared height increment between the two species in each mixture, the 'wet' species *S. balticum* and *S. cuspidatum* had higher values than the 'dry' species *S. fuscum* and *S. magellanicum* at temperature treatments 1 and 2 (Fig. 2.2). When temperature increased, the differences in height increment between the two species disappeared.

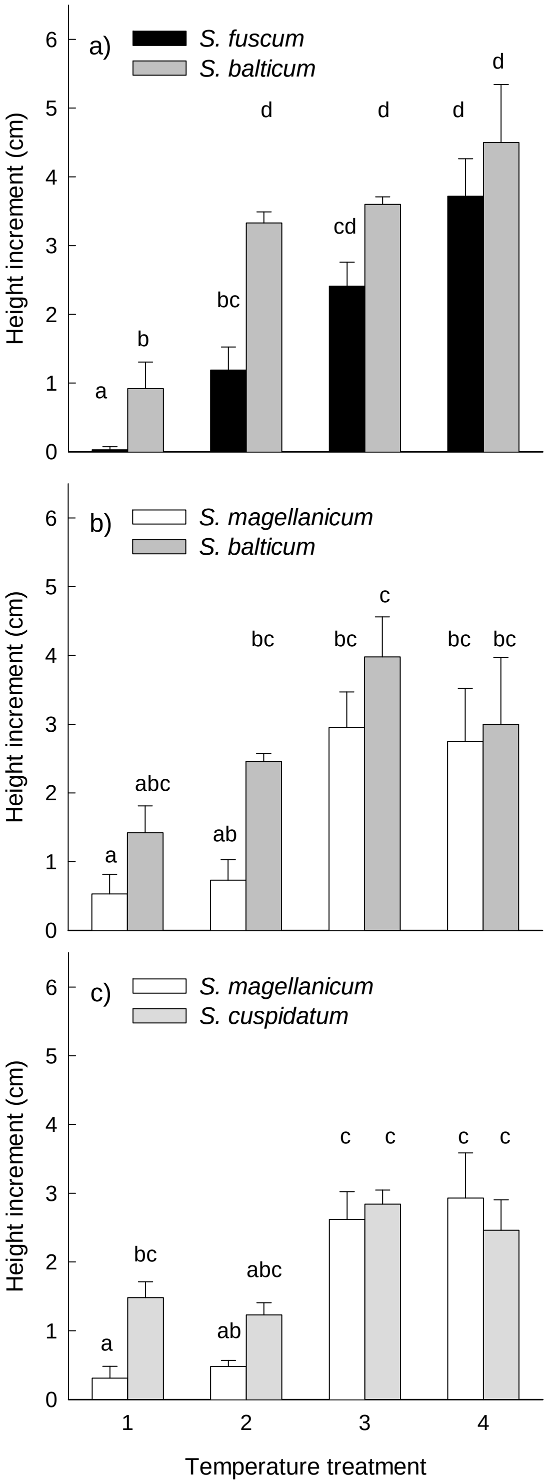

**Figure 2.2** Height increment of the individual species at each temperature treatment (see Table 2.1) within the three mixtures of species: (a) *S. fuscum + S. balticum*, (b) *S. magellanicum + S. balticum* and (c) *S. magellanicum + S. cuspidatum*. Data are mean values ± SE, n=5. Different letters indicate significant differences between treatments (*P* < 0.05).

Cover

The hollow species *S. balticum* and *S. cuspidatum* increased in area in 53 out of 60 containers when growing in the mixtures. In the other seven containers (3 with *S. magellanicum + S. balticum*, 2 with *S. fuscum + S. balticum,* 2 with *S. magellanicum + S. cuspidatum*), cover changed less than 5 %. For *S. balticum* there were significant effects of temperature (F = 3.67, *P* = 0.023) and neighbouring species (F = 4.95, *P* = 0.033) on expansion (Fig. 2.3a and 2.3b). Maximum change in cover was for *S. balticum* in combination with *S. fuscum* with temperature 2 and 3. There was no effect of temperature on expansion of *S. cuspidatum* (Fig. 2.3c, F = 0.88, *P* = 0.470).

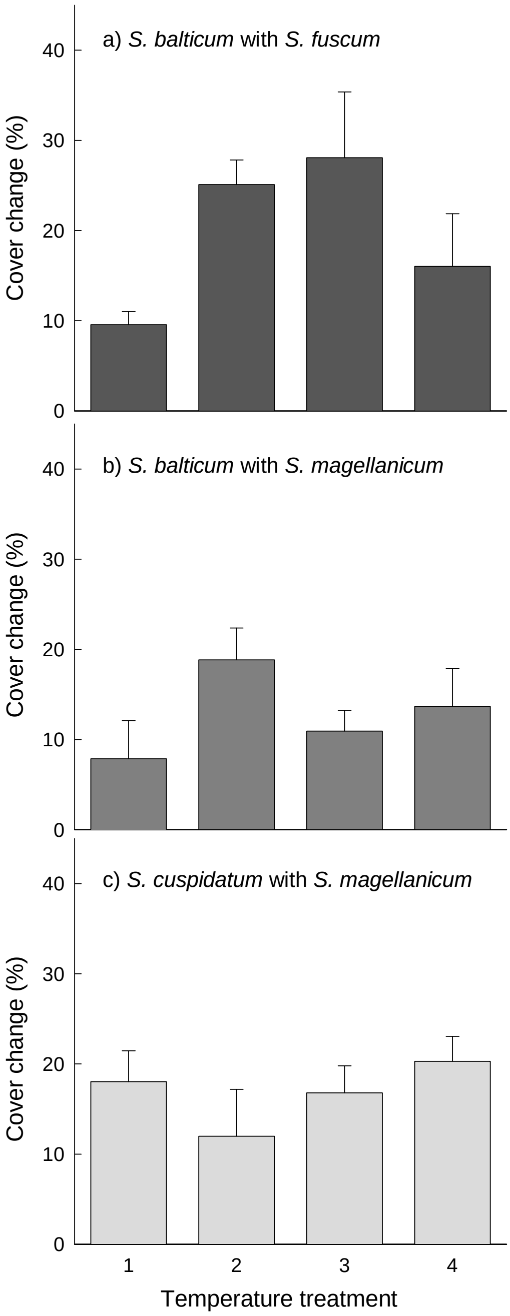

**Figure 2.3** Cover change for hollow species: (a) *S. balticum* in combination with *S. fuscum,* (b) *S. balticum* in combination with *S. magellanicum* and *(c) S. cuspidatum* in combination with *S. magellanicum.* Data are means ±SE, n=5. There were no significant differences between treatments (*P* < 0.05). For temperature treatments, see Table 2.1.

Biomass production

The response of biomass production to the temperature treatments was similar to the response of height increment (Table 2.2). In all species biomass production increased with increased temperature. *S. fuscum* showed the strongest response; this species increased its biomass production 13-fold from the lowest to the highest temperature treatment in monocultures (Fig. 2.4a). Only for *S. balticum* in combination with *S. magellanicum* was there a significant interaction between temperature and species combination in biomass production (Table 2.2). Temperature increased biomass production of *S. balticum* in monoculture and in mixture with *S. fuscum,* while there was no effect of temperature in mixture with *S. magellanicum*.

When differences in biomass production between monocultures and mixtures are compared per temperature treatment, it shows that *S. fuscum* suffered from competition with *S. balticum* at temperature 3 because production was lower in mixture than in monoculture, but it no longer suffered at temperature 4 (Fig. 2.4a). At temperature 4 *S. balticum* does suffer from competition with *S. fuscum,* but not at lower temperatures. In the mixtures of *S. magellanicum* and *S. balticum*, *S. magellanicum* suffers from competition at temperature 1 and 2, whereas *S. balticum* suffers from competition at temperature 3 and 4 (Fig. 2.4b). Biomass production of *S. cuspidatum* did not show any effect of competition with *S. magellanicum*, while biomass production of *S. magellanicum* did suffer from competition at temperatures 1, 2 and 3 (Fig. 2.4c).

In the stepwise regression for biomass production of *S. balticum*, water content was selected as the most explanatory variable ($R^2$=0.36, p<0.001). For biomass production of *S. fuscum* ($R^2$ = 0.52, $P$ < 0.001), *S. magellanicum* ($R^2$ = 0.36, $P$ < 0.001) and *S. cuspidatum* ($R^2$ = 0.12, $P$ = 0.031), temperature was selected as the most explanatory variable.

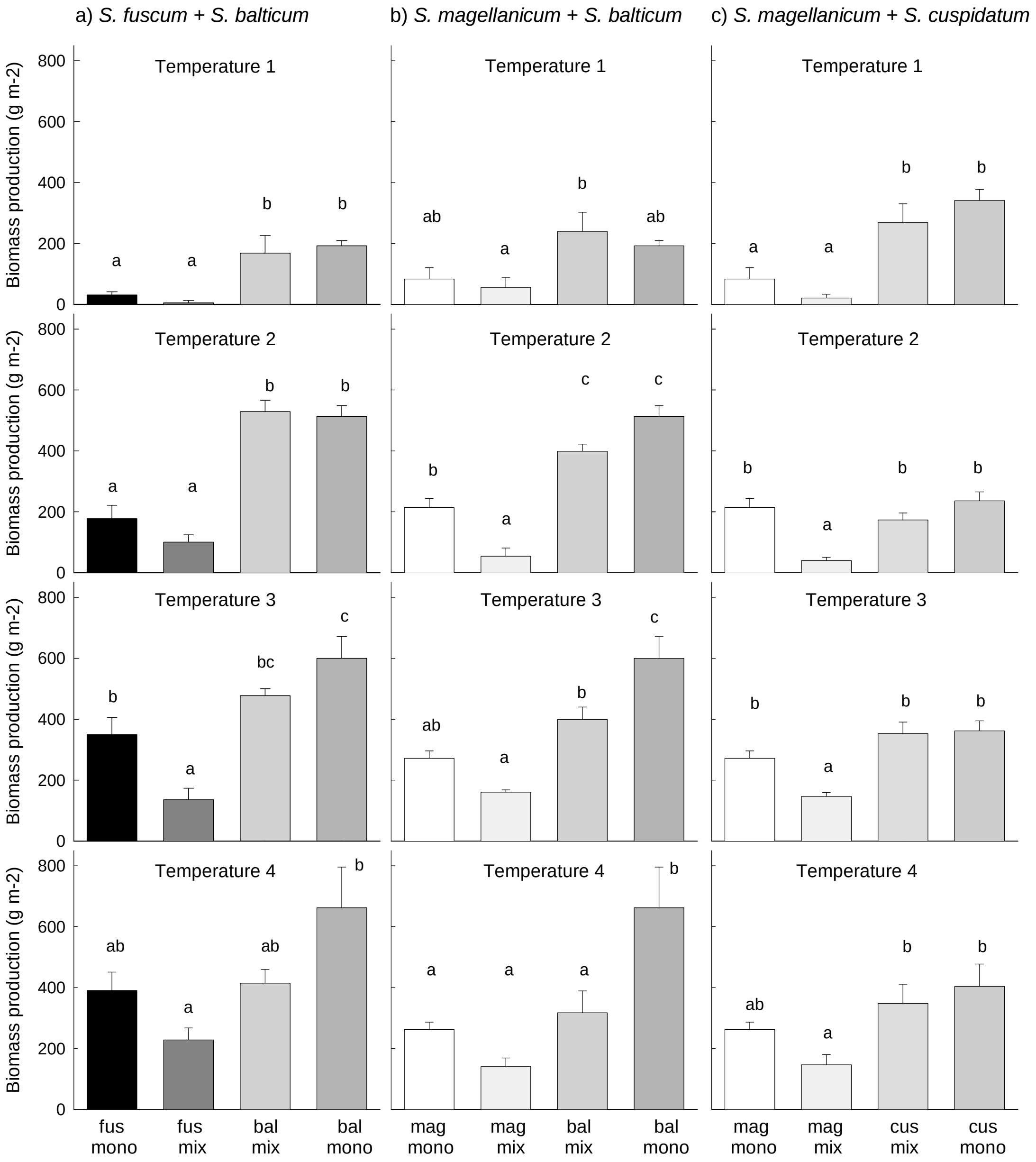

**Figure 2.4** Biomass production corrected for change in cover for species in monocultures (mono) and in mixtures (mix) for each temperature treatment (see Table 2.1) and species combination: (a) *S. fuscum (fus) + S. balticum (bal)*, (b) *S. magellanicum (mag) + S. balticum* and (c) *S. magellanicum + S. cuspidatum (cus)*. Data are mean values ± SE, n=4-5. Different letters indicate significant differences between treatments ($P < 0.05$).

### Bulk density

Bulk densities were lower at higher temperatures for all species, except for bulk density of the capitula and stems of *S. cuspidatum* (Table 2.3). Compared to field values, capitulum bulk density of *S. fuscum* and *S. balticum* decreased with temperature, while capitulum bulk density of *S. magellanicum* and *S. cuspidatum* seemed to increase at low temperatures.

Bulk densities of both capitula and stems were lower in mixtures than in monocultures of *S. fuscum* and *S. balticum*. Similarly, in *S. cuspidatum* the bulk density of the capitula was lower in mixtures than in monocultures. There were no significant interactions between temperature and species combination.

**Table 2.3** Bulk density of capitula section, stem section and total sample. Data are mean values ± SE, pooled within temperature treatment (see Table 2.1) and within competition treatment. Different letters indicate significant differences between treatments within a species ($P < 0.05$). There were no significant interactions between temperature and competition treatments. fus: *S. fuscum*, bal: *S. balticum*, mag: *S. magellanicum*, cus: *S. cuspidatum.* Capitula bulk density values for material from the sites of origin (Field values, n = 5) are given for comparison. Number of observations for each species for each temperature treatment: *S. fuscum* and *S. cuspidatum* = 10; *S. balticum* =14-15; *S. magellanicum*: n =15.
Number of observations for each species for each combination, n=19-20.

| | **Field value** | **Temperature** | | | | **Combination** | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | **T1** | **T2** | **T3** | **T4** | **mono** | **fus-bal** | **mag-bal** | **mag-cus** |
| **Bulk density capitula (mg cm-3)** | | | | | | | | | |
| *S. fuscum* | 38 ± 2 | 35 ± 2$^{b}$ | 37 ± 2$^{b}$ | 21 ± 1$^{a}$ | 17 ± 1$^{a}$ | 30 ± 2$^{b}$ | 25 ± 2$^{a}$ | _ | _ |
| *S. balticum* | 32 ± 1 | 26 ± 1$^{b}$ | 16 ± 1$^{a}$ | 14 ± 1$^{a}$ | 14 ± 1$^{a}$ | 20 ± 1$^{b}$ | 18 ± 2$^{b}$ | 15 ± 1$^{a}$ | _ |
| *S. magellanicum* | 19 ± 1 | 21 ± 1$^{b}$ | 18 ± 1$^{b}$ | 13 ± 1$^{a}$ | 13 ± 1$^{a}$ | 17 ± 1 | _ | 15 ± 1 | 17 ± 1 |
| *S. cuspidatum* | 19 ± 1 | 23 ± 1 | 22 ± 2 | 19 ± 1 | 19 ± 1 | 23 ± 1$^{b}$ | _ | _ | 19 ± 1$^{a}$ |
| **Bulk density stems (mg cm-3)** | | | | | | | | | |
| *S. fuscum* | | 18 ± 1$^{b}$ | 16 ± 1$^{b}$ | 15 ± 2$^{ab}$ | 11 ± 2$^{a}$ | 17 ± 1$^{b}$ | 14 ± 1$^{a}$ | _ | _ |
| *S. balticum* | | 15 ± 1$^{b}$ | 11 ± 1$^{a}$ | 8 ± 1$^{a}$ | 9 ± 1$^{a}$ | 13 ± 1$^{b}$ | 9 ± 1$^{a}$ | 11 ± 1$^{ab}$ | _ |
| *S. magellanicum* | | 11 ± 1$^{c}$ | 9 ± 0$^{bc}$ | 8 ± 1$^{ab}$ | 7 ± 0$^{a}$ | 9 ± 1 | _ | 9 ± 1 | 8 ± 0 |
| *S. cuspidatum* | | 10 ± 1 | 10 ± 1 | 7 ± 1 | 7 ± 1 | 8 ± 1 | _ | _ | 9 ± 1 |
| **Bulk density total sample (mg cm-3)** | | | | | | | | | |
| *S. fuscum* | | 22 ± 1$^{c}$ | 21 ± 1$^{bc}$ | 17 ± 1$^{ab}$ | 13 ± 1$^{a}$ | 20 ± 1$^{b}$ | 16 ± 1$^{a}$ | _ | _ |
| *S. balticum* | | 17 ± 1$^{b}$ | 12 ± 1$^{a}$ | 10 ± 1$^{a}$ | 10 ± 1$^{a}$ | 14 ± 1$^{b}$ | 11 ± 1$^{a}$ | 12 ± 1$^{ab}$ | _ |
| *S. magellanicum* | | 13 ± 1$^{c}$ | 11 ± 0$^{b}$ | 9 ± 1$^{a}$ | 8 ± 0$^{a}$ | 11 ± 1 | _ | 10 ± 1 | 10 ± 0 |
| *S. cuspidatum* | | 12 ± 1$^{c}$ | 12 ± 0$^{bc}$ | 10 ± 1$^{ab}$ | 9 ± 0$^{a}$ | 11 ± 1 | _ | _ | 11 ± 0 |

### Evaporation and water content

Water content decreased with temperature treatment (Table 2.4). Water content was lowest in *S. balticum* in mixture with *S. fuscum*. Evaporation increased with temperature and therefore with VPD for all species (Table 2.4). Evaporation in *S. fuscum* in both monoculture and mixture was lower than in other species.

**Table 2.4** Water content (% volume) at 5 cm depth and evaporation (mm day-1) per temperature treatment (see Table 2.1) and per species combination. Data are mean values ± SE. Different letters indicate significant differences between treatments ($P$ < 0.05). There were no significant interactions between temperature and competition treatments. Number of observations for each temperature treatment: water content = 50, for evaporation = 35. Number of observations for each competition treatment: for water content and for evaporation = 20.

| **Water content** | | **Evaporation** | |
|---|---|---|---|
| **Temperature** | | | |
| 1 | 88 ± 2 $^{c}$ | 1 | 1.2 ± 0.02 $^{a}$ |
| 2 | 79 ± 3 $^{b}$ | 2 | 1.5 ± 0.03 $^{b}$ |
| 3 | 60 ± 3 $^{a}$ | 3 | 1.7 ± 0.04 $^{c}$ |
| 4 | 60 ± 3 $^{a}$ | 4 | 2.0 ± 0.05 $^{d}$ |
| **Monocultures** | | | |
| *S. fuscum* | 83 ± 5 $^{c}$ | *S. fuscum* | 1.3 ± 0.05 $^{a}$ |
| *S. balticum* | 66 ± 6 $^{b}$ | *S. balticum* | 1.7 ± 0.08 $^{bc}$ |
| *S. magellanicum* | 74 ± 4 $^{bc}$ | *S. magellanicum* | 1.8 ± 0.08 $^{c}$ |
| *S. cuspidatum* | 78 ± 4 $^{bc}$ | *S. cuspidatum* | 1.8 ± 0.08 $^{c}$ |
| **Mixtures** | | | |
| *S. fuscum* | 74 ± 5 $^{bc}$ | *S. fuscum* + *S. balticum* | 1.5 ± 0.07 $^{a}$ |
| *S. balticum* | 49 ± 5 $^{a}$ | | |
| *S. magellanicum* | 69 ± 5 $^{b}$ | *S. magellanicum* + *S. balticum* | 1.6 ± 0.07 $^{b}$ |
| *S. balticum* | 68 ± 5 $^{b}$ | | |
| *S. magellanicum* | 82 ± 5 $^{c}$ | *S. magellanicum* + *S. cuspidatum* | 1.7 ± 0.08 $^{bc}$ |
| *S. cuspidatum* | 73 ± 5 $^{bc}$ | | |

### Nutrient concentrations

The concentrations of all nutrients (N, P and K) differed between species and rose with increasing temperature. N concentration was also affected by the interactions of temperature by species (F = 2.66, $P$ = 0.007) and species by combination (F = 3.73, $P$ = 0.006). At temperatures 1 and 2, N concentrations were lower for *S. fuscum* and *S. balticum* than for *S. magellanicum* and *S. cuspidatum,* as was also the case in field values. At temperature 3, only the N concentration of *S. balticum* was lower than that of *S. magellanicum*. At temperature 4, N concentrations of *S. balticum* were lower than those of *S. magellanicum* and *S. fuscum* (Table 2.5). Compared to field values, all species showed an increased N concentration with temperature.

P and K concentrations were affected by temperature (P concentration, F = 9.32, $P$ < 0.001; K concentration, F = 82.77, $P$ < 0.001) and species (P concentration, F = 3.05, $P$ = 0.031; K concentration, F = 3.86, $P$ = 0.011). P and K concentrations were higher at high temperature for all species (Table 2.5). P-values decreased, compared to field values, while K concentration increased compared to field values.

**Table 2.5** N, P and K concentration (mg g-1) of the capitula. Data are mean values ± SE, pooled within temperature treatment (see Table 1) and within competition treatment. Different letters indicate significant differences between treatments within a species ($P < 0.05$). There were no significant interactions between temperature and competition treatments. For abbreviations, see Table 3.

| | **Field value** | **Temperature** | | | | **Combination** | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | **T1** | **T2** | **T3** | **T4** | **mono** | **fus-bal** | **mag-bal** | **mag-cus** |
| **N (mg g-1)** | | | | | | | | | |
| *S fuscum* | 6.5 ± 0.2 | 8.4 ± 0.2 $^{a}$ | 8.6 ± 0.4 $^{a}$ | 11.3 ± 0.6 $^{b}$ | 12.0 ± 0.7 $^{b}$ | 9.8 ± 0.5 | 10.4 ± 0.5 | | |
| *S. balticum* | 5.3 ± 0.1 | 8.4 ± 0.3 | 8.7 ± 0.4 | 9.7 ± 0.5 | 9.6 ± 0.3 | 9.5 ± 0.4 | 8.7 ± 0.4 | 9.0 ± 0.3 | |
| *S. magellanicum* | 11.1 ± 0.5 | 11.7 ± 0.5 | 12.6 ± 0.3 | 12.8 ± 0.3 | 12.9 ± 0.3 | 12.4 ± 0.3 | | 12.3 ± 0.3 | 12.7 ± 0.3 |
| *S. cuspidatum* | 10.0 ± 0.3 | 9.8 ± 0.6 | 11.3 ± 0.6 | 10.5 ± 0.5 | 10.8 ± 0.8 | 11.5 ± 0.4 $^{b}$ | | | 9.7 ± 0.4 $^{a}$ |
| | | | | | | | | | |
| **P (mg g-1)** | | | | | | | | | |
| *S fuscum* | 0.39 ± 0.03 | 0.19 ± 0.07 $^{a}$ | 0.30 ± 0.02 $^{ab}$ | 0.40 ± 0.03 $^{b}$ | 0.41 ± 0.04 $^{b}$ | 0.31 ± 0.04 | 0.34 ± 0.04 | | |
| *S. balticum* | 0.36 ± 0.03 | 0.13 ± 0.09 | 0.26 ± 0.04 | 0.29 ± 0.03 | 0.29 ± 0.02 | 0.32 ± 0.04 | 0.22 ± 0.05 | 0.19 ± 0.05 | |
| *S. magellanicum* | 0.29 ± 0.01 | 0.10 ± 0.06 $^{a}$ | 0.18 ± 0.04 $^{ab}$ | 0.27 ± 0.04 $^{ab}$ | 0.37 ± 0.08 $^{b}$ | 0.26 ± 0.07 | | 0.21 ± 0.05 | 0.21 ± 0.03 |
| *S. cuspidatum* | 0.31 ± 0.03 | 0.10 ± 0.08 | 0.18 ± 0.04 | 0.23 ± 0.02 | 0.26 ± 0.04 | 0.24 ± 0.04 | | | 0.15 ± 0.04 |
| | | | | | | | | | |
| **K (mg g-1)** | | | | | | | | | |
| *S fuscum* | 5.4 ± 0.2 | 4.9 ± 0.2 $^{a}$ | 5.5 ± 0.3 $^{a}$ | 7.1 ± 0.3 $^{b}$ | 7.1 ± 0.2 $^{b}$ | 6.4 ± 0.3 | 5.9 ± 0.3 | | |
| *S. balticum* | 4.7 ± 0.4 | 4.7 ± 0.3 $^{a}$ | 5.2 ± 0.2 $^{a}$ | 6.4 ± 0.3 $^{b}$ | 6.5 ± 0.3 $^{b}$ | 5.6 ± 0.3 | 5.9 ± 0.3 | 5.5 ± 0.3 | |
| *S. magellanicum* | 2.2 ± 0.2 | 3.8 ± 0.1 $^{a}$ | 4.7 ± 0.2 $^{b}$ | 6.6 ± 0.2 $^{c}$ | 6.9 ± 0.2 $^{c}$ | 5.6 ± 0.3 | | 5.3 ± 0.4 | 5.4 ± 0.3 |
| *S. cuspidatum* | 2.2 ± 0.3 | 4.5 ± 0.3 $^{a}$ | 5.0 ± 0.2 $^{a}$ | 6.6 ± 0.3 $^{b}$ | 6.9 ± 0.4 $^{b}$ | 6.1 ± 0.3 $^{b}$ | | | 5.5 ± 0.3 $^{a}$ |

Field values (n = 5) are given for comparison.

Number of observations for each species for each temperature treatment: *S. fuscum* and *S. cuspidatum* = 10; *S. balticum* =14-15; *S. magellanicum*: n =15.

Number of observations for each species for each combination, n=19-20.

## Discussion

Effect of temperature on growth

As expected, all species in monoculture increased height increment with temperature (Fig. 2.1). All species also showed a looser growth form with higher temperatures, which resulted in lower densities (Table 2.3). Despite the lower bulk density at higher temperatures, biomass production still increased with temperature for all species (Table 2.2, Fig. 2.4). The response of height increment to temperature was about a factor 2 larger than the response of biomass production. Growth of *Sphagnum* was probably increased by a higher rate of photosynthesis and a higher N availability. Photosynthesis in *Sphagnum* has been shown to increase with temperature up to an optimum around 20-25 ˚C (Harley *et al.* 1989; Skre and Oechel 1981). When temperature increased, the nutrient concentrations in *Sphagnum* were higher (Table 2.5). Moreover, N and K concentration increased compared to field values (Table 2.5). As biomass production also increased, N and K uptake must have increased considerably with increasing temperature. No nutrients were added with the rainwater solution, so the higher availability of nutrients must have come from *Sphagnum* itself and the peat below. Probably the lower *Sphagnum* parts in the containers decomposed faster when the temperature was higher, making more N and K available for growth. This temperature-induced stimulation of nutrient mineralization is probably larger than it would be in field conditions as the peat soil in the containers is surrounded by warm air on every side, resulting in relatively high soil temperatures in our experiment. However, it can be expected that increased temperature as a result of climate change will also enhance decomposition rates in field situations (Hobbie 1996), thereby increasing nutrient availability for both *Sphagnum* and vascular plants. The lower N concentrations of *S. fuscum* and *S. balticum* compared with *S. magellanicum* and *S. cuspidatum* at temperatures 1 and 2 are probably caused by the different sites of origin. In the northern site, the N deposition is much lower (approx. 0.2 g N m-2 yr-1) than in the southern site (approx. 0.7 g N m-2 yr-1) where *S. magellanicum* and *S. cuspidatum* were collected.

In this experiment we provided near optimal growing conditions for *Sphagnum* with high water level and high humidity, which explains why the *Sphagnum plants* could grow with a lower bulk density and still keep their capitula moist. However, *Sphagnum* water content still decreased with an increase in temperature. In field conditions it would probably not have been possible for the *Sphagnum* plants to change their density so much since it would have led to problems in maintaining the water content of the capitula. The effect of temperature on height increment might therefore also have been less. In a few field studies, no positive or even negative effects of temperature on production were found. However, in these experiments there were other factors besides temperature that could have had a negative effect on biomass production, like drought stress (Gunnarsson *et al.* 2004; Hobbie *et al.* 1999; Weltzin *et al.* 2001) and higher vascular plant cover, which could have resulted in etiolation of the *Sphagnum* plants and reduced biomass production because of increased shading (Gunnarsson *et al*. 2004).

In other studies also positive effects of temperature on height growth and production were found for different species, in both greenhouse (Robroek *et al*. 2007b) and field experiments (Dorrepaal *et al.* 2003; Gerdol 1995; Moore 1989; Sonesson *et al.* 2002). In accordance with our hypothesis, Asada *et al*. (2003) suggested that *Sphagnum* species respond positively to increased temperature and that hollow and lawn species are more sensitive to temperature than hummock species. This, however, does not correspond with the low response of *S. cuspidatum* to temperature in our experiment. Dorrepaal *et al*. (2003) also found a decrease in bulk density with increased temperature. Since the response of height increment and bulk density to temperature were in opposite directions, the dry matter production of *S. fuscum* did not show a significant increase with temperature. Our relatively high height increment and low density of *S. fuscum* compared to the values of Dorrepaal *et al*. (2003) can probably be explained by the much higher water levels in our experiment. Dorrepaal *et al*. used water levels of -20 to -40 cm below moss surface during their measurements. However, the *Sphagnum* densities we measured (Table 2.3) agreed quite well with densities from other studies (Asada *et al.* 2003; Lindholm and Vasander 1990; Moore *et al.* 1998).

From our results, we conclude that the height increment and biomass production of all *Sphagnum* species in bogs can increase with an increase in temperature. However, the literature shows us that, particularly under field conditions, this potential response may not be realized in instances of competition from vascular plants, drought stress or extreme temperature increases.

### Effect of temperature on competition

We hypothesized that increased temperature will have a positive effect on competitive abilities of *S. fuscum* and *S. magellanicum*. This hypothesis was confirmed in the competition with *S. balticum,* since the height increment and biomass production of *S. balticum* at the highest temperature treatment were no longer larger than those of *S. fuscum* and *S. magellanicum* (Fig. 2.2 and 2.4). However, *S. balticum* still increased its cover at the expense of *S. fuscum* and *S. magellanicum* in all mixtures (Fig. 2.3a and 2.3b). This could be expected as the water level we used was relatively high and in the range of the natural habitat of these species. These results correspond to the findings from a field experiment of Rydin (1986), who found an expansion of *S. balticum* at the expense of *S. fuscum* at a water level of -1 cm. At water levels of -5 and -10 cm, he found a small expansion of *S. balticum*, but at a water level of -15 cm *S. fuscum* showed large expansion.

In agreement with the hypothesis, the difference in height increment and biomass production between *S. fuscum* and *S. balticum* disappeared as temperature increased (Fig. 2.2a and 2.4a). *S. fuscum* kept increasing height increment with temperature, but *S. balticum* already reached maximum height growth at temperature 2, which is comparable to the summer temperature in the site of origin of these species. Also, the expansion in cover became lower for *S. balticum* at temperature 4 (Fig.2.3a). As a result, the difference in biomass production between *S. fuscum* and *S. balticum* slowly decreased with an increase of temperature until there was no significant difference at the highest temperature. Apparently, the hummock species *S. fuscum* is better able to profit from a high increase in temperature than *S. balticum*, even at relatively high water levels. This is confirmed by the stepwise regression analysis which shows that biomass production of *S. fuscum* is correlated most to temperature, and biomass production of *S. balticum* to water content. As could be expected, *S. fuscum* as a hummock species has a higher water content than *S. balticum*, also at higher temperatures (Table 2.4), and therefore can profit more from increased temperature, because water does not become limiting for growth. *S. fuscum* also seems to be the better competitor for nutrients. The N and P concentrations in *S. fuscum* tended to be higher in the mixtures than in the monocultures, whereas in *S. balticum* the opposite was the case (Table 2.5). Indeed, *S. fuscum* is known for its high N uptake rate (Jauhiainen *et al*. 1998). Our results show that *S. balticum* loses competitive strength with increasing temperature. With a slight increase in temperature in northern bogs, *S. balticum* may remain the stronger competitor at high water levels, but at higher temperature increases, *S. fuscum* will gain a competitive advantage over *S. balticum*, also because increased temperature may lead to lower water tables in bogs. Recent climate change simulation models predict an increase of 2.5 °C in summer temperature in northern Europe, with increasing precipitation in northern Scandinavia (Christensen *et al*. 2007). This limited rise in temperature, almost similar to the increase from temperature 2 to 3, would not affect competition between *S. balticum* and *S. fuscum* very strongly. However, the effect of a predicted increase in winter temperature of 5.0 °C (Christensen *et al*. 2007) could shift the competitive balance between *S. balticum* and *S. fuscum* further, because increased snow cover and spring temperature have been shown to increase *S. fuscum* production (Dorrepaal *et al*. 2003).

For *S. magellanicum* and *S. cuspidatum*, temperature 3 is comparable to the summer temperature in their site of origin. There was no effect of a temperature increase from temperature 3 to 4 on biomass production and relative performance of the species. This implies that with the predicted increase in temperature of 2.5 °C (Christensen *et al*. 2007), the competitive balance between *S. magellanicum* and *S. cuspidatum* will remain unchanged.

The mixtures of *S. balticum* and *S. magellanicum* show the largest difference in height increment and biomass production at temperature 2, which is comparable to the summer temperature in the site of origin of *S. balticum*. Also the expansion in cover of *S. balticum* was highest at this temperature. When temperature increases, the difference in height growth and biomass production became smaller and then disappeared in mixtures, whereas in monocultures the difference in biomass production between species remained. This implies that *S. balticum* as a northern species can enhance its production with an increase in temperature as long as it grows in monocultures. If *S. magellanicum* expanded its distribution further to the north as a result of global warming, it would be a strong competitor for *S. balticum,* thereby reducing *S. balticum* production. Gunnarsson *et al*. (2004) also showed that *S. balticum* performs less under competition with increased temperatures. They performed a competition experiment in a poor fen, close to the site of origin of the *S. balticum* material. They found that when *Sphagnum papillosum* was transplanted to an area with *S. balticum, S. papillosum* decreased in area by 30 %. However, when temperature was increased by 3.6 ˚C, *S. papillosum* increased by 42 %. This treatment is comparable to the increase from temperature 2 to temperature 3 in our experiment but with lower water tables, ranging from 5 to 17 cm under moss surface.

Generally, we conclude from our experiment that an increase in temperature can favour hummock and lawn species compared to hollow species. This corresponds to the findings of Mauquoy *et al*. (2002), who showed from peat core analyses that in periods with lower temperature, due to decreased solar activity, there was a shift in representation from lawn and hummock species to hollow species in ombrotrophic mires in Denmark and the UK.

## Conclusions

Our findings suggest that production rates can increase and that *Sphagnum* species' abundances can shift in response to global warming, particularly at northern sites. There, hollow species such as *S. balticum* will lose competitive strength relative to hummock species such as *S. fuscum* and southern species such as *S. magellanicum*. What the consequences for the carbon balance of bog ecosystems will be depends not only on the production rates, but also on decomposition. In general, decomposition rates also increase with temperature and increased N availability (Hobbie 1996; Limpens and Berendse 2003) and hummock species decompose slower than hollow species (Johnson and Damman 1993; Limpens and Berendse 2003; Rochefort *et al.* 1990), but virtually nothing is known about the temperature sensitivity of decomposition of bog plant species.

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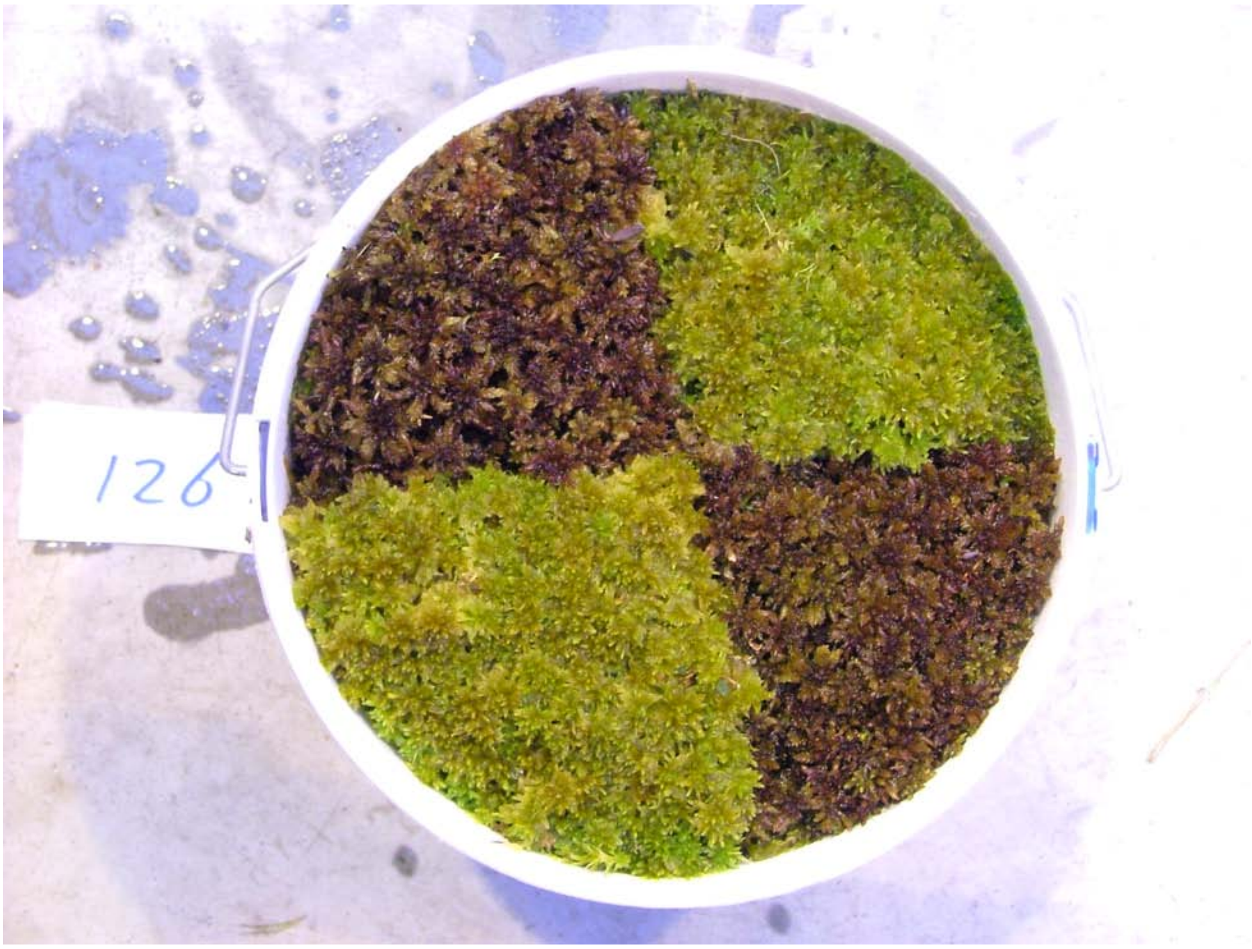
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# CHAPTER 3

# Response of *Sphagnum* mixtures to increased temperature and nitrogen availability

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## Abstract

Ombrotrophic peatlands currently hold a large reservoir of carbon; to predict the role of bogs as carbon sinks in the future, it is crucial to understand how *Sphagnum* vegetation in bogs will respond to global change. We performed a greenhouse experiment to study the effect of two temperature treatments (17.5 °C and 21.7 °C) and two N addition treatments (0 and 4 g N $m^{-2}$ $yr^{-1}$) on the growth of four *Sphagnum* species: *S. fuscum* and *S. balticum* from sites in northern and central Sweden and S. *magellanicum* and *S. cuspidatum* from a site in southern Sweden. Four combinations of these *Sphagnum* species were made, in which we studied the growth and cover of each species during two growing seasons. We found that high temperature and high N addition negatively affected the height increment of the northern species *S. fuscum* and *S. balticum*. For the southern species *S. magellanicum* and *S. cuspidatum,* only high N addition negatively affected height increment. *Sphagnum* production was affected negatively by high temperature and high N addition. However, the northern species were more affected by temperature, while the southern species were more affected by N addition. In all four species combinations, high temperature depressed the cover of the 'wet' species, *S. balticum* and *S. cuspidatum*. Nitrogen concentrations increased with high N addition: in particular the N concentrations of *S. fuscum* and *S. magellanicum* increased greatly compared with their initial values. N:P and N:K ratios indicated P-limited growth in all treatments and co-limitation of P and K in the high N treatments. In the second year of the experiment, several containers suffered from a severe fungal infection, particularly affecting the 'wet' species. A higher percentage of *Sphagnum* died as a result of this infection in the high N treatment. These findings suggest that effects of global change can have negative consequences for the production of *Sphagnum* species in bogs, with important implications for the carbon sequestration in these ecosystems.

## Introduction

Ombrotrophic bogs are peat-forming systems and as such they can serve as important long-term sinks for atmospheric $CO_2$. Although northern peatlands cover only 2% of the total land surface, they store about one-third of the world's soil carbon as peat (Gorham 1991). There is much concern on how global change will affect the ability of peatlands to sequester carbon and what the feedbacks to climate will be (Aerts 2006; Bragazza *et al.* 2006; Bubier *et al.* 2007; Franzén 2006). Global change is expected to have a strong impact on temperature, precipitation and nutrient deposition, especially at northern latitudes (Solomon *et al.* 2007) where the majority of peat bogs occur (Gunnarsson 2005; Kivinen and Pakarinen 1980). Predictions about future precipitation patterns show great variability, but all models predict an increase in temperature and nitrogen (N) deposition (Bouwman *et al.* 2002; Solomon *et al.* 2007).

Vegetation in ombrotrophic bogs is often dominated by *Sphagnum* species which account for the bulk of the carbon sequestration in peat because of their recalcitrant litter (Clymo and Hayward 1982; Coulson and Butterfield 1978; Limpens and Berendse 2003b). Thus, to predict the role of bogs as carbon sinks in the future, it is crucial to understand how *Sphagnum* vegetation in bogs will respond to global change. Several studies have revealed differences between different *Sphagnum* species in production (Asada *et al.* 2003; Breeuwer *et al.* 2008; Gerdol 1995; Gunnarsson 2005; Lindholm and Vasander 1990) and in decomposition rate (Belyea 1996; Johnson and Damman 1993; Limpens and Berendse 2003b; Rochefort *et al.* 1990). Although the effects of temperature (Asada *et al.* 2003; Dorrepaal *et al.* 2003; Gerdol 1995) and N (Aerts *et al.* 2001; Gerdol *et al.* 2007; Limpens and Berendse 2003a; Press *et al.* 1986) on *Sphagnum* growth have been studied and a few studies have examined their separate effects on mixtures of *Sphagnum* species (Breeuwer *et al.* 2008; Gunnarsson and Rydin 2000; Lutke Twenhoven 1992; Robroek *et al.* 2007a), only one other study (Wiedermann *et al.* 2007) has examined the effects of temperature and N on *Sphagnum* cover. To our knowledge, ours is the first study that examines the combined effects of increased temperature and N addition on the growth of different *Sphagnum* species.

In general, climate warming is expected to increase *Sphagnum* productivity, as long as water does not become limiting (Breeuwer *et al.* 2008; Dorrepaal *et al.* 2006; Gunnarsson 2005). One indirect effect of increased temperature can be increased nutrient availability through increased decomposition and N-mineralisation (Hobbie 1996; Rustad *et al.* 2001). The effect of increased N availability is less straight-forward because though a small increase in N can enhance *Sphagnum* production at locations where N is a limiting nutrient (Turunen *et al.* 2004), when N concentrations exceed a critical threshold value, *Sphagnum* production and cover are reduced (Berendse *et al.* 2001; Bragazza *et al.* 2006; Gerdol *et al.* 2007; Gunnarsson and Rydin 2000). Yet any positive effect of increased temperature and N on carbon sequestration in bogs may be counteracted by the positive effect of temperature (Hobbie 1996) and N (Franzén 2006) on decomposition rates. A change in temperature influences not only the production and decomposition of individual *Sphagnum* species but also the competitive balance that exists between species.

An important challenge facing ecologists is to predict how climate change will alter species distributions in ecosystems (Mooney 1991). We have already found different responses in biomass production among species when temperature is increased (Breeuwer *et al.* 2008; Robroek *et al.* 2007b). It seems likely that when a species with high production and/ or a low decomposition rate increases its relative abundance in a bog, this will increase the carbon storage capacity of the system.

Not only are there different competing species within a bog, but there are also differences in dominant species between bogs in different climatic regions. In our study, we used species from three different sites in Sweden situated over a gradient from north to south. At the sites in north and central Sweden, *Sphagnum balticum* and *Sphagnum fuscum* are the dominant species, while at the site in south Sweden these species also occur, but *Sphagnum magellanicum* and *Sphagnum cuspidatum* are the most abundant species. This corresponds with the general distribution of these species in Europe, since both *S. magellanicum* and *S. cuspidatum* occur further south than *S. fuscum* and *S. balticum* (Daniels and Eddy 1985).

To examine the effect of temperature and N on the performance of Sphagnum species, we performed a greenhouse experiment in which we studied the effect of two temperature treatments and two N treatments on the growth of four species originating from three sites: *S. fuscum* and *S. balticum* from two northern Swedish sites and *S. magellanicum* and *S. cuspidatum* from a southern Swedish site. Four combinations of species were made to study the effects of temperature and nitrogen addition on *Sphagnum* growth. We examined how the different *Sphagnum* species from different sites of origin respond to increased temperature and N availability and whether both species in a mixture show the same response. If one species profits more from increased temperature or N availability, it will increase in cover. Since *S. fuscum* and *S. magellanicum* grow in drier and therefore also warmer microhabitats than *S. balticum* and *S. cuspidatum*, we expected them to be better adapted to higher temperatures. *S. magellanicum* grows in more southerly sites than *S. balticum*, so we expected this species to be better adapted to higher temperatures. Consequently, we hypothesised 1) that all four species will show increased growth with increased temperature, 2) that hummock and southern species respond more positively to temperature than hollow and northern species, 3) that high temperature will increase N uptake by *Sphagnum* due to increased N mineralisation and 4) as N concentration in the *Sphagnum* increased (from N addition and increased mineralisation) the growth of all *Sphagnum* species will decline.

**Table 3.1** Treatment codes. Rel. humidity = relative humidity, VPD = vapour pressure deficit, N = nitrogen. Values for temperature, Rel. humidity and VPD are daily (16 hours) and nightly (8 hours) means.

| **Treatment code** | **Temperature** (°C) | | **Rel. humidity** (%) | | **VPD** | | **N** ($g.m^{-2}.yr^{-1}$) |
|---|---|---|---|---|---|---|---|
| | day | night | day | night | day | night | |
| T1N1 | 18.4 | 15.7 | 78 | 84 | 0.47 | 0.29 | 0 |
| T1N2 | 18.4 | 15.7 | 78 | 84 | 0.47 | 0.29 | 4 |
| T2N1 | 22.6 | 20.1 | 71 | 73 | 0.80 | 0.64 | 0 |
| T2N2 | 22.6 | 20.1 | 71 | 73 | 0.80 | 0.64 | 4 |

## Material and methods

### Plant material

In August 2003, *Sphagnum* cores (diameter 22-23 cm, height 16 cm) were collected at three different sites in Sweden, situated along a latitudinal gradient of c. 800 km. All sites were relatively undisturbed, with a peat layer of at least 5 metres deep and vegetation characteristic of ombrotrophic mires. At the northern site Lappmyran (N-Sweden, 64˚09'N, 19˚35'E), we collected 10 *Sphagnum fuscum* (Schimp) H.Klinggr and 10 *Sphagnum balticum* (Russ.) C. Jens. cores. Lappmyran is a string flark mire with ridges of hummocks and hollows where *S. fuscum* is dominant on the hummocks and *S. balticum* in the drier parts of the hollows. The mean temperature in July is 14.7 °C (Alexandersson *et al.* 1991) and mean annual N deposition is about 0.3 g.m$^{-2}$ (Tarrasón *et al.* 2006). When identifying the species from this site in the lab, we found specimens of both *S. balticum* and *S. angustifolium* (Russ.) C. Jens. These species are difficult to distinguish, as Russow (Smith 1978) and Klinggraff (Daniels and Eddy 1985) found: they identified both species as varieties of *S. recurvum*. In our samples, we were unable to quantify the exact percentages of *S. balticum* and *S. angustifolium*. When reporting the results, therefore, whenever we mention *S. balticum* from this site, we are referring to a mixture of *S balticum* and *S. angustifolium*.

At the central Swedish site Åkerlänna Römosse (C-Sweden, 60° 01' N, 17° 22' E), we collected 10 *S. fuscum* and 20 *S.balticum* cores. Here the peatland surface shows a typical microtopography of hollows, lawns and hummocks. *S. fuscum* is the dominant species on the hummocks and *S. balticum* in the hollows and lawns. The mean temperature in July is 16.4 °C (Swedish Meteorological and Hydrological Institute, SMHI) and mean annual N deposition is about 0.6 g.m$^{-2}$ (Tarrasón *et al.* 2006).

At the southernmost site Saxnäs Mosse (S-Sweden, 56˚51'N, 13˚27' E), we collected 20 *Sphagnum magellanicum* (Brid.) and 10 *Sphagnum cuspidatum* (Hoffm.) cores. At this site *S. magellanicum* is the dominant species on the lawns and low hummocks, while *S. cuspidatum* dominates in the hollows and pools. The mean temperature in July is 17.0 °C (Malmer *et al.* 2003) and mean annual N deposition is about 1.1 g.m$^{-2}$ (Tarrasón *et al.* 2006).

Cores were taken from monospecific stands of each *Sphagnum* species (>95 %) with sparse vascular plant cover (<5 %). The cores were placed in plastic containers (diameter 22.3 cm, height 16.2 cm). Vascular plants were clipped flush with the *Sphagnum*, and other *Sphagnum* species were removed with tweezers. The containers were brought to Wageningen and stored outside until March 2004, in order to acclimatise.

### Experimental design

In March 2004, the containers were brought into the greenhouse and randomly divided over the treatments and five replicate blocks, with four species combinations, two temperature treatments (T1: 17.5 °C and T2: 21.7 °C) and two levels of N supply (N1: no N addition and N2: application of 4 g N m$^{-2}$ yr$^{-1}$) per block (Table 3.1). The following four species combinations were made: two combinations of two northern species: *S. fuscum* with *S. balticum* from N-Sweden (combination 1) and C-Sweden (combination 2), one combination of two southern species: *S. magellanicum* with *S. cuspidatum* from S-Sweden (combination 3) and one combination of a northern with a southern species: *S. balticum* from C-Sweden with *S. magellanicum* from S-Sweden (combination 4). To study the relative performance of a northern and a southern species we opted for the combination of *S. balticum* and *S.*

*magellanicum* because they occur at similar water levels. To make the combinations, the cores were cut into four quarters and two quarters of each of the two species in the combination were placed alternately in an empty container. When potting the species combinations, we made certain that the surface of the mixture was uniform.

The experiment was conducted in two adjacent climate-controlled greenhouse compartments from April 2004 until November 2005. Between November 2004 and April 2005 the mesocosms overwintered outside underneath a transparent roof, because it was not possible to maintain low temperatures in the greenhouse. In total, the containers were in the greenhouse for 372 days. Each greenhouse compartment was assigned one of two temperature treatments. Treatments and containers were switched between compartments every 2 weeks to minimise any effect of the different compartments. The position of the blocks and the position of containers within the blocks were also switched every 2 weeks. The average day temperatures in the two temperature treatments T1 and T2 were 18.4 °C and 22.6 °C, respectively (Table 3.1). During the dark period of 8 hours, the day temperature was lowered by approximately 2.5 °C to 15.7 °C and 20.1°C, resulting in mean temperatures in T1 and T2 of 17.5 °C and 21.7 °C respectively. A light period of 16 hours was applied. If light intensity was low during this period, SON-T AGRO 400 (Philips Powertone 400) lamps were switched on. Relative humidity during the day was set at 75%. In the greenhouse it was not possible to keep the relative humidity exactly the same with both temperatures. The rise in temperature between treatments corresponded with a decrease in relative humidity, which caused an additional increase in vapour pressure deficit (VPD) with temperature (Table 3.1). Even if the relative humidity had been equal in both compartments, the VPD would still have been 1.3 times higher at T2 than at T1. Our highest VPD of 0.80 kPa with a temperature of 22.6˚C is actually still low compared to field conditions (Dorrepaal *et al.* 2003; Hobbie and Chapin 1998).

Each year, 4 g N $m^{-2}$ was added to the containers in the N2 treatment. This amount of N was equally distributed over 15 applications in 2004 and 11 applications in 2005 (c. every 2 weeks) by watering with 200 ml of $NH_4NO_3$ solution. The N1 containers received the same amount of demineralised water. These applications preceded the addition of water to top up the water table to the desired level.

The water level was set to 1 cm below capitula at the start of the experiment. All species were subjected to the same water level, so that temperature was the only changing environmental variable. This relatively high water level was used for all species because hollow species cannot grow at low water levels, while hummock species can survive the environmental conditions of hollows quite well; nonetheless, hummock species are absent from the hollows because the hollow species are stronger competitors (Rydin and McDonald 1985). Grosvernier *et al*. (1997) found that growth in height and dry weight is equal for *S. fuscum* grown at water levels of 1 cm and 40 cm below moss surface, while for *S. magellanicum* and even more so for *S. fallax,* growth in height and dry weight is much greater at the high water level. During the experiment an artificial rainwater solution, an 8000-fold dilution of a seawater solution (Garrels and Christ 1965), was added twice a week to top up the water level to 1 cm below capitula. In a number of containers, *Sphagnum* grew higher than 1 cm above the container, so to keep the water level at 1 cm below the moss surface, the height of the container was extended by gluing a plastic rim on the containers and waterproofing the join with silicone sealant.

Measurements

Height increment of the *Sphagnum* carpet was measured non-destructively every month using a variation of the cranked wire method (Clymo 1970; Limpens *et al.* 2003b). One cranked wire was inserted in each quarter of the mixtures. The rods, which had a diameter of 1.5 mm, did not seem to interfere with the growth of the surrounding *Sphagna*.

We calculated biomass production by multiplying height increment over the total experimental period by bulk density at the end of the experiment. We did not use data on biomass production per species because it was impossible to calculate bulk density per species since at the end of the experiment the species were no longer confined to their original quarters and all sub-samples contained a mixture of both species. To determine bulk density at the end of the experiment, columns with a diameter of 5 cm were cut around each cranked wire and cut off at 5 cm length, after which each column was put in a plastic Ziplock bag. All columns were stored at 1 °C until further measurements could be taken. Capitula (0-1 cm) and subcapitula (1-3 cm) were separated per column and oven dried at 70 °C for at least 48 hours and then weighed. Capitulum and subcapitulum dry weight were used to calculate bulk density and biomass production, to account for changes in capitulum density. The biomass production during the experiment per unit area (g $m^{-2}$) was calculated as follows:
height increment (m) * final bulk density cap + subcap (g $m^{-3}$)

For nutrient analyses, samples of capitula were pooled per species for each container. Total N, P and K concentrations were determined by digesting 300 mg of homogeneous, milled material with sulphuric acid, salicylic acid, selenium and hydrogen peroxide. All samples were analysed spectrophotometrically for total N and P, using an auto-analyser (Skalar). K concentrations were measured with an atomic absorption spectrophotometer (Varian AAS). To compare nutrient concentrations with initial values, we collected five samples from monocultures of the four *Sphagnum* species from the containers before they were put in the greenhouse in March 2004. Measurements of nutrient concentrations were conducted as described above.

To measure the change in cover of the species in the mixtures, digital images were made at the start and end of the experiment. From these images we measured the total surface cover per species in each pot, using Image J (1.33u, Nat. Inst. Health, USA). At the end of the experiment, the *Sphagnum* in 37 containers was necrotic, possibly as a result of a fungal infection with *Lyophyllum palustre* (Limpens *et al.* 2003b). Fruiting bodies similar to those of *L. palustre* appeared in several containers, but no molecular analysis was done to confirm the fungus species. The total percentage of dead *Sphagnum* was calculated from the digital images.

## Data analysis

The data were tested for normality and equality of variance. When necessary, data were ln-transformed to achieve homogeneous variances. Block effect was tested as random factor. When no block effect was detected, which was usually the case, block was omitted from the analysis to gain extra degrees of freedom. All analyses were conducted using the SPSS statistical package for Windows (15.0).

Height increment was first analysed with RM-ANOVA, with year as within-subject factor, and species combination, T, N and species as between-subject factors. Since interaction effects appeared of year*species combination, year*N, year*species, year*combination*T*species and combination*species, we then analysed height increment with RM-ANOVA per species combination. Because there were significant interaction effects between year and species, we further analysed the effect of T and N per species and year with ANOVA.

The change in cover of ‘wet’ species was analysed with RM-ANOVA, with year as within-subject factor, T, N and combination as between-subject factors and percentage necrosis as a covariate. Since there was no significant effect of percentage necrosis, the analysis was repeated without covariate.

Biomass production was analysed with ANOVA, with T, N and combination as fixed factors. We further analysed the effect of T and N per combination. N concentration, N:P ratio, N:K ratio and *Sphagnum* necrosis were analysed with ANOVA, with combination, T and N as fixed factors. N concentrations were further analysed with separate ANOVAs per combination with T, N and species as independent factors. Because there were significant interaction effects for species*N treatment, we further analysed the effect of T and N on N concentration per species. For multiple comparisons, Tukey’s a posteriori test was used. We examined the relation between N concentration and percentage necrosis with linear regression analysis.

## Results

### Height increment in *Sphagnum*

With one exception, in all combinations there was a negative effect of both high temperature and high N addition on height increment; the exception was the containers from S-Sweden, which only showed a negative effect of high N addition (Table 3.2). When the effects of temperature and N addition were analysed per species and year, there were different responses to the treatments (Fig. 3.1). In year 1 we found negative effects of high temperature on *S. balticum* from N-Sweden (Fig. 3.1 A) and negative effects of high N addition on the height increment of *S. cuspidatum* (Fig. 3.1 E) and *S. magellanicum* (fig. 3.1 F) in containers from S-Sweden. In year 2, the height increment of all species was negatively affected by high N addition, except for height increment of *S. cuspidatum* and *S. magellanicum* in combination 3, which showed no treatment effects (Fig. 3.1 E and F). In addition, the height increment of *S. fuscum* from N-Sweden and of *S. fuscum* and *S. balticum* in the containers from C-Sweden was also negatively affected by high temperature (Fig 3.1 B-D).

**Table 3.2** Results of RM-ANOVA for height increment per combination. Numbers in bold indicate significant values ($P \leq 0.05$). T = temperature treatment, N = nitrogen treatment.

| | | Combination 1<br>bal+fus N-S | | Combination 2<br>bal+fus C-S | | Combination 3<br>cus+mag S-S | | Combination 4<br>bal N-S + mag S-S | |
|---|---|---|---|---|---|---|---|---|---|
| **Source** | **df** | **F** | ***P*** | **F** | ***P*** | **F** | ***P*** | **F** | ***P*** |
| **Between subjects** | | | | | | | | | |
| T | 1 | 5.906 | **0.021** | 12.526 | **0.001** | 0.071 | 0.791 | 6.865 | **0.013** |
| N | 1 | 11.366 | **0.002** | 8.981 | **0.005** | 10.614 | **0.003** | 19.703 | **<0.001** |
| Species | 1 | 3.201 | 0.083 | 1.896 | 0.178 | 0.120 | 0.732 | 1.203 | 0.281 |
| T x N | 1 | 0.163 | 0.689 | 0.685 | 0.414 | 0.234 | 0.632 | 3.439 | 0.073 |
| T x species | 1 | 1.202 | 0.281 | 0.002 | 0.969 | 0.388 | 0.538 | 0.162 | 0.690 |
| N x species | 1 | 0.031 | 0.862 | 0.290 | 0.594 | 0.001 | 0.977 | 0.392 | 0.536 |
| T x N x species | 1 | 0.096 | 0.758 | 0.819 | 0.372 | 0.017 | 0.899 | 0.126 | 0.725 |
| **Within subjects** | | | | | | | | | |
| year | 1 | 19.468 | **<0.001** | 27.628 | **<0.001** | 9.018 | **0.005** | 1.426 | 0.241 |
| year x T | 1 | 5.106 | **0.031** | 1.378 | 0.249 | 1.832 | 0.185 | 0.430 | 0.517 |
| year x N | 1 | 0.515 | 0.478 | 1.588 | 0.217 | 0.025 | 0.874 | 5.907 | **0.021** |
| year x species | 1 | 3.700 | 0.063 | 1.661 | 0.207 | 0.072 | 0.790 | 9.672 | **0.004** |
| year x T x N | 1 | 1.567 | 0.220 | 0.075 | 0.787 | 0.512 | 0.480 | 0.146 | 0.705 |
| year x T x species | 1 | 24.318 | **<0.001** | 0.051 | 0.823 | 0.111 | 0.742 | 0.088 | 0.768 |
| year x N x species | 1 | 0.001 | 0.976 | 1.333 | 0.257 | 0.058 | 0.811 | 1.540 | 0.224 |
| year x T x N x species | 1 | 6.346 | **0.017** | 0.151 | 0.701 | 0.449 | 0.508 | 0.621 | 0.436 |

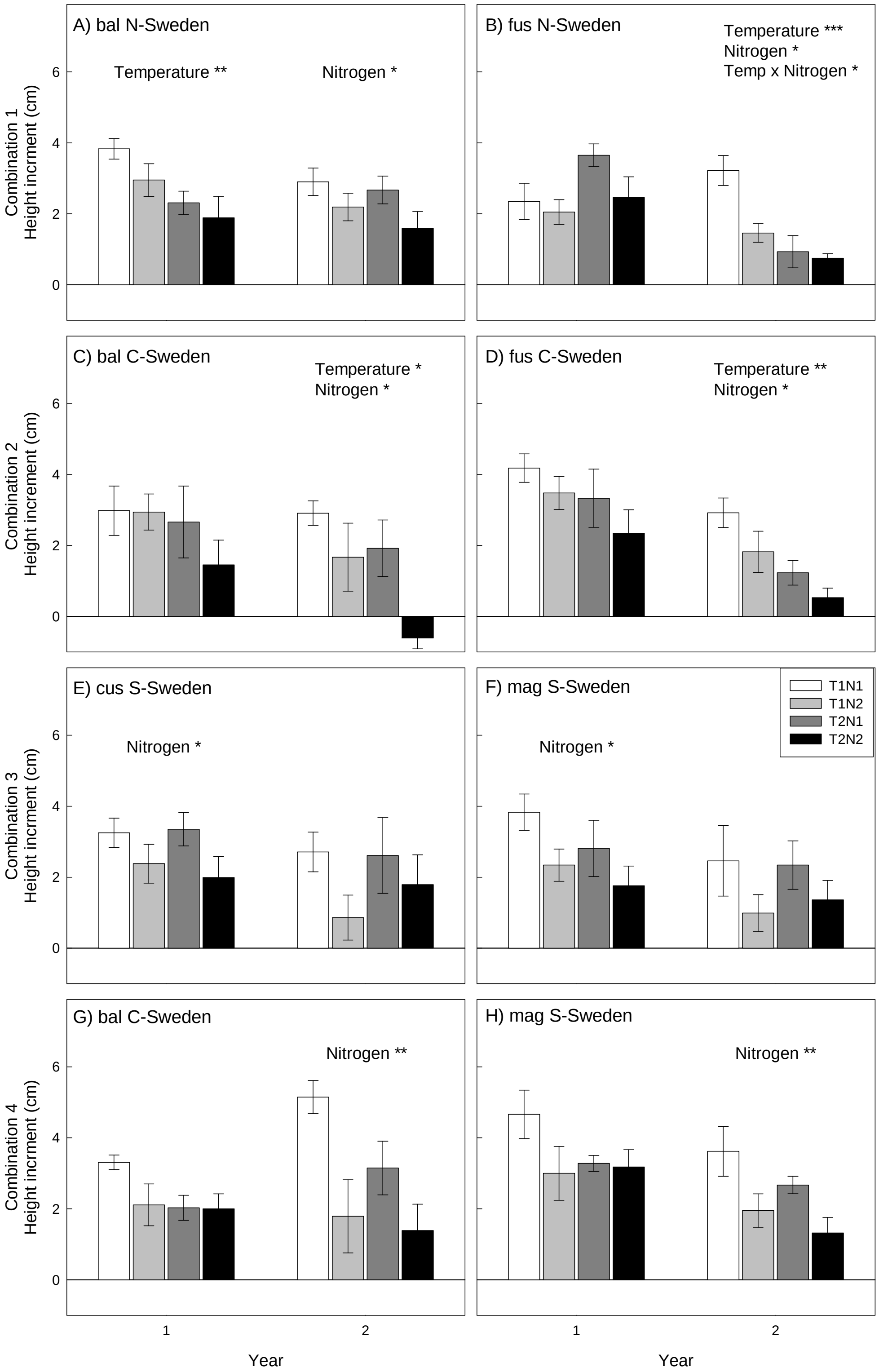

**Figure 3.1** Height increment during the first and second period in the greenhouse. Combination 1: A) *S. balticum* and B) *S. fuscum* from N-Sweden. Combination 2: C) *S. balticum* and D) *S. fuscum* from C-Sweden. Combination 3: E) *S. cuspidatum* and F) *S. magellanicum* from S-Sweden. Combination 4: G) *S. balticum* from C-Sweden and H) *S. magellanicum* from S-Sweden. Data are mean values ± SE, n=5. Significant effects of the temperature and N treatments are indicated: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. For treatment codes see table 3.1.

Species cover

As there were no significant effects of species combination or interaction with species combination on cover change, we pooled the cover change of *S. balticum* and *S. cuspidatum,* which are the 'wet' species in the combinations since their natural habitat is closer to the water table than the habitat of *S. fuscum* and *S. magellanicum*. In the first year, *S. balticum* and *S. cuspidatum* increased their cover at the expense of *S. fuscum* and *S. magellanicum* in all treatments (Fig. 3.2). In the second year, their cover decreased again in all treatments. Both high temperature and N addition seem to have a negative effect on 'wet' species cover, but only the effect of temperature was significant.

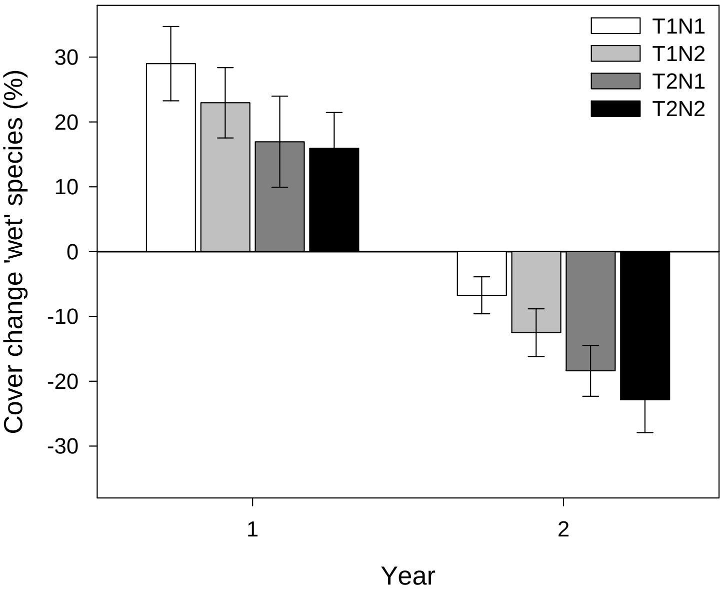

**Figure 3.2** Change in cover of *S. balticum* and *S. cuspidatum*. Year 1: cover change between 23-03-2004 and 19-10-2004. Year 2: cover change between 19-10-2004 and 3-11-2005. Within-subject effect of year: F = 135.608, $P < 0.001$; between-subject effect of T: F = 6.644, $P = 0.012$; between-subject effect of N: F = 1.229, $P = 0.272$. Data are mean values ± SE, n = 20. For treatment codes see Table 3.1.

Production per container

*Sphagnum* production in all combinations was affected negatively by high temperature (F = 17.865, $P < 0.000$) and high N addition (F = 17.209, $P < 0.001$). There was no difference in production between combinations (F = 0.431, $P = 0.731$) and there were no significant interactions between T, N and combination. Production decreased in the combinations in the following order: T1N1, T1N2, T2N1 and T2N2, being 1695 ± 132, 1139 ± 139, 1129 ± 107 and 624 ± 121 g.m$^{-2}$, respectively.

When the effects of temperature and N addition were analysed per combination, we found different responses to the treatments (Fig. 3.3). Production in containers of *S. fuscum* and *S. balticum* showed a negative effect of high temperature (N-Sweden: F = 4.393, $P = 0.052$ and C-Sweden: F = 8.601, $P = 0.010$). In containers from S-Sweden, production was affected negatively by N addition (F = 5.714, $P = 0.029$). Production in containers of *S. balticum* from C-Sweden and *S. magellanicum* from S-Sweden was affected negatively both by high temperature (F = 9.273, $P = 0.008$) and by N addition (F = 6.216, $P = 0.024$).

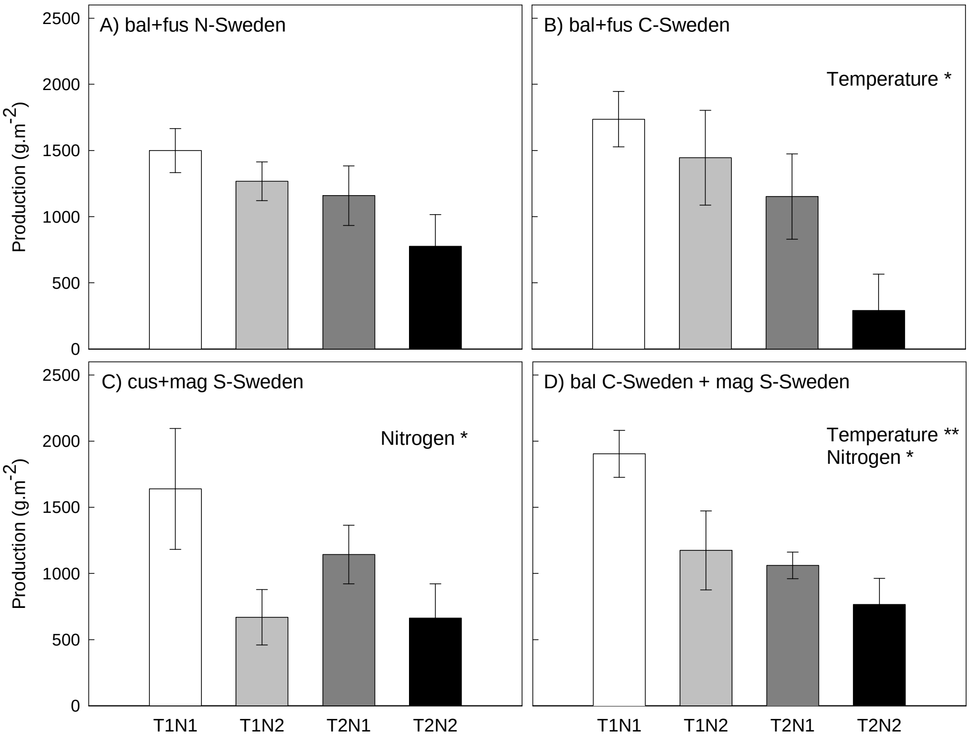

**Figure 3.3** *Sphagnum* production over 2 years per treatment (see Table 3.1) for each species combination: A) combination 1: *S. balticum* + *S. fuscum* from N-Sweden, B) combination 2: *S. balticum* + *S. fuscum* from C-Sweden, C) combination 3: *S. cuspidatum* + *S. magellanicum* from S-Sweden and D) combination 4: *S. balticum* from C-Sweden + *S. magellanicum* from S-Sweden. Data are mean values ± SE, n = 5. Significant effects of the temperature and N treatments are indicated: * $P < 0.05$, ** $P < 0.01$.

### Nitrogen concentration

N concentrations were higher in the high temperature treatment (F = 5.590, $P = 0.019$) and the high N treatment (F = 99.659, $P < 0.001$). The N concentration differed between combinations (F = 6.189, $P = 0.001$), being higher in combinations 2 (C-Sweden) and 4 (*S. balticum* from C-Sweden with *S. magellanicum* from S-Sweden) than in combination 3 (S-Sweden). The N concentration in combination 1 (N-Sweden) had intermediate values. There were no significant interactions between T, N and combination.

N addition increased the N concentration of all species, except for *S. balticum* from C-Sweden (Fig. 3.4). High temperature also increased the N concentration of *S. fuscum* in the absence of N addition (N1) (Fig. 3.4). *S. balticum* and *S. fuscum* from N-Sweden had the lowest initial values: 7.9 and 9.1 $mg.g^{-1}$ respectively. N concentration increased most in *S. fuscum* from N-Sweden with high temperature and high N addition, reaching a concentration of 23.2 $mg.g^{-1}$.

N:P ratios were high in all containers, ranging between 25 and 53 at the start of the experiment, to 35 – 86 at the end of the experiment (data not shown). N:P ratios were higher in the high N treatment (F = 80.999, $P < 0.001$) and differed between combinations (F = 3.726, $P = 0.013$), although Tukey’s a posteriori test did not separate different subsets.

N:K ratios were high in all containers, ranging between 1.7 and 3.8 at the start of the experiment to 1.6 – 5.1 at the end of the experiment (data not shown). N:K ratios were higher in the high N treatment (F = 120.329, $P < 0.001$) and differed between combinations (F =

5.232, $P$ = 0.002), being highest in containers from N-Sweden and C-Sweden and lowest in containers from S-Sweden, N:K ratios in containers with combination 4 had intermediate values.

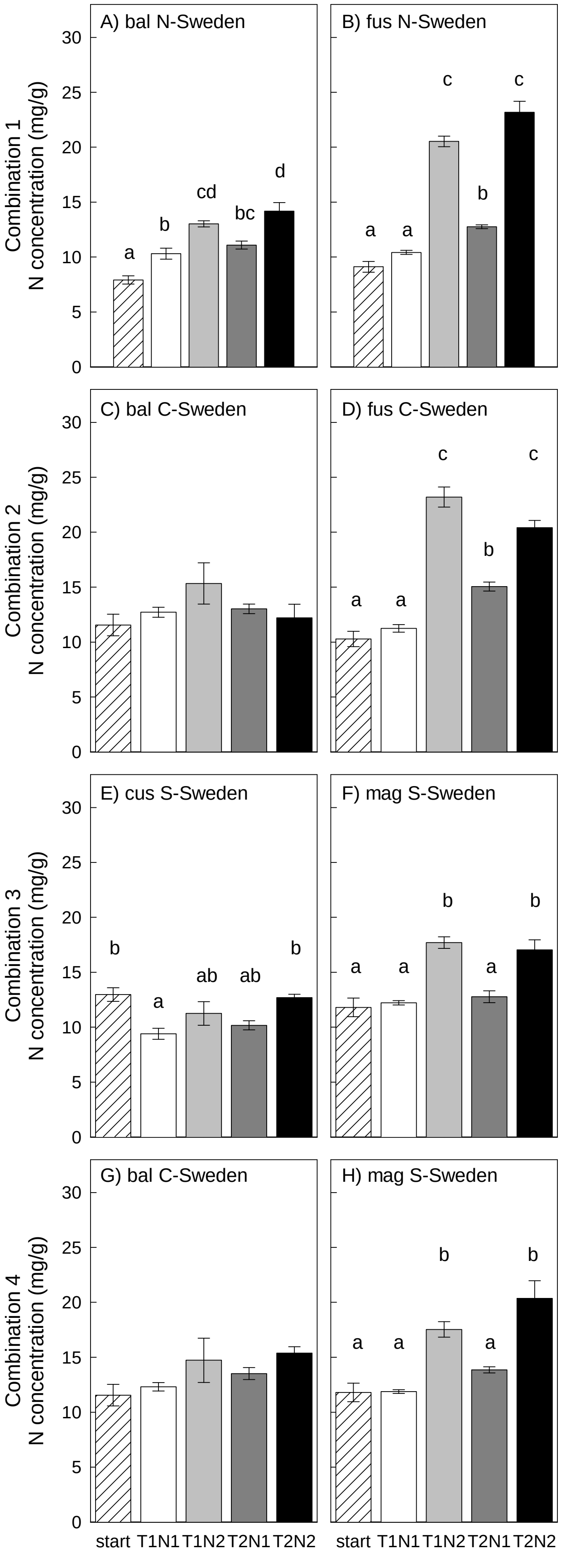

**Figure 3.4** Nitrogen concentrations in capitula of A) *S. balticum* and B) *S. fuscum* from N-Sweden in combination 1; C) *S. balticum* and D) *S. fuscum* from C-Sweden in combination 2; E) *S. cuspidatum* and F) *S. magellanicum* from S-Sweden in combination 3; G) *S. balticum* from C-Sweden and H) *S. magellanicum* from S-Sweden in combination 4. Different letters indicate significant differences between treatments ($P$ < 0.05). Data are mean values ± SE, n = 5. For treatment codes see Table 3.1.

*Sphagnum* necrosis

There were significant differences between sites (effect of combination: F = 4.401, *P* = 0.007) in the percentage of *Sphagnum* that suffered from necrosis due to fungal infection. The percentage necrosis was lowest in containers with *S. balticum* and *S. fuscum* from N-Sweden (Fig. 3.5). N addition increased the percentage necrosis in both temperature treatments (effect of N: F = 23.232, *P* < 0.001). In all containers that suffered from necrosis, a greater proportion of the 'wet' *Sphagnum* species were affected compared with the 'dry' species (personal observation).

We found a positive relationship between N concentration and percentage necrosis (*P* = 0.013), but the relationship is very weak ($R^2$ = 0.040). When the regression analysis is split per species combination, the $R^2$ values are of the same order of magnitude, but models are not significant.

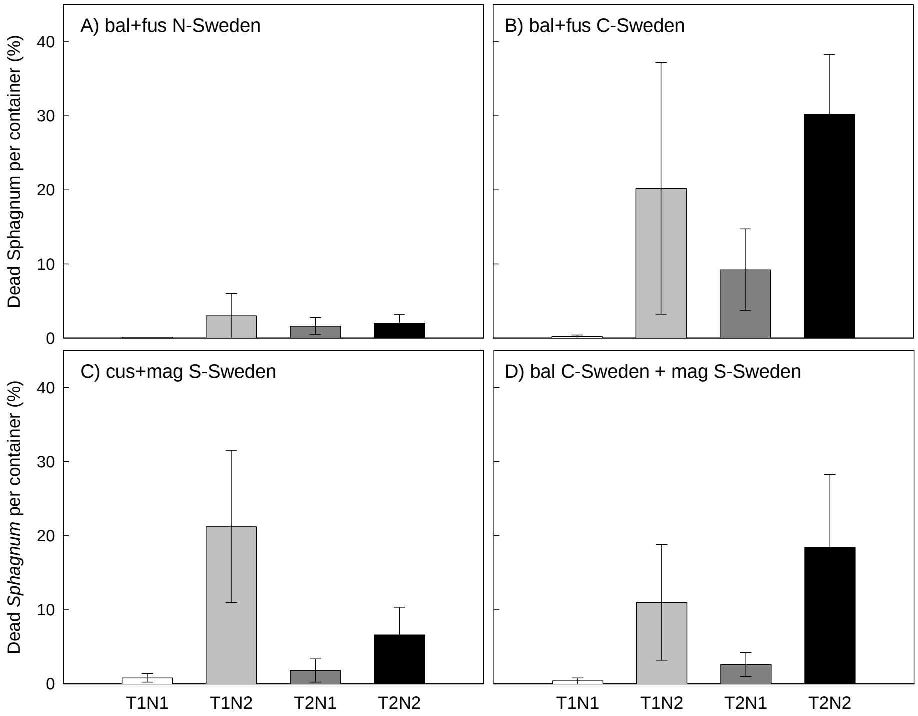

**Figure 3.5** Treatment (see Table 3.1) effect on percentage dead *Sphagnum* per container at the end of the experiment. For combinations, see Figure 3.3. Data are mean values ± SE, n = 5.
Effect of temperature: F = 3.320, *P* = 0.073; Effect of N: F = 23.232, *P* < 0.001; Effect of species combination: F = 4.401, *P* = 0.007; Effect of temperature * species combination: F = 2.377, *P* = 0.078. 3-way ANOVA, only effects with *P* < 0.1 are given

## Discussion and conclusion

To our knowledge, this is the first study on the combined effects of both increased temperature and N deposition on the growth of different *Sphagnum* species. Our findings suggest that temperature and N addition have a cumulative, negative effect on *Sphagnum* growth. However, these effects differ between species and between the sites where the species were collected.

### Temperature

Contrary to our first hypothesis, increased temperature did not have a positive effect on *Sphagnum* growth. Other studies have shown that increased temperature can increase *Sphagnum* production (Asada *et al.* 2003; Dorrepaal *et al.* 2003; Gerdol 1995), but the temperatures used in those experiments were lower and varied between 8 °C and 15 °C. Though Robroek *et al*. (2007b) did find greater height increment and production at 20˚C than at 15 ˚C for several *Sphagnum* species, their experiment lasted for only six months. It seems that the maximum photosynthetic rates of *Sphagnum* were already reached at the average temperatures of 17.4 °C and 21.7 °C we used in our experiment. Harley *et al*. (1989) and Skre and Oechel (1981) showed that photosynthesis in *Sphagnum* increases with temperature up to an optimum around 20-25 ˚C. In another greenhouse experiment we found an increase in height increment and production when temperature increased from 10.6 °C to 17.2°C, but there was no difference in height increment and production between temperatures of 17.2 °C and 20.6°C (Breeuwer *et al.* 2008). That experiment lasted only one growing season and had no N addition, so the results should be comparable to values of the T1N1 and T2N1 treatments in the first year. This proved to be the case, including the small positive effect of high temperature on height increment of *S. fuscum*.

Negative effects of increased temperature have been found in other studies too (Gerdol *et al.* 2007; Weltzin *et al.* 2001), but have usually been ascribed to desiccation. In our experiment desiccation could not have been the cause of the negative effect of temperature, because we saw no desiccated capitula. Moreover, the VPD of 0.80 kPa with a temperature of 22.6˚C is low compared to field conditions. We calculated VPD from mean day temperature and relative humidity in June and July in the three sites of origin of the *Sphagnum* material used in this experiment: at temperatures ranging from 6.5 to 23.7˚C, the VPD ranged from 0.04 – 1.84 kPa. These values are in the same range as found in earlier studies (Dorrepaal *et al.* 2003; Hobbie and Chapin 1998).

In accordance with our second hypothesis, the height increment of northern species was depressed more by increased temperature than the height increment of southern species. Recent climate change simulation models with the A1B scenario for northern Europe predict an increase of 2.7 °C (min-max: 1.4 – 5.0 °C) in summer temperature, an increase of 4.3 °C (min-max: 2.6 – 8.2 °C) in winter temperature and more precipitation in northern Scandinavia (Christensen *et al.* 2007). For the species from the northern site, the temperature treatments simulated an average to very high increase in summer temperature (N-Sweden: T1:+ 2.8 °C, T2: + 7.0 °C). For the species from the central and southern Swedish sites, the temperature treatments simulated a small to large increase in temperature (C-Sweden: T1: + 1.1 °C, T2: + 5.3 °C; S-Sweden: T1: + 0.5 °C, T2: + 4.7 °C). Although the relative increase in temperature was therefore higher for *S. fuscum* and *S. balticum* from the northernmost site than for these species from the central site, their height increment and production did not differ between containers from these sites. On the other hand, there did seem to be a difference between the northern and the southern species, since the height increment and biomass production of *S.*

*balticum* and *S. fuscum* responded negatively to high temperature, while *S. cuspidatum* and *S. magellanicum* showed no response to temperature.

Though there was no difference between height increment in the dry and 'wet' species within containers, the finding that cover of 'wet' species declined in response to high temperature does support our hypothesis, because, all other things being equal, wet habitats are also colder than dry habitats. The increase in cover of the 'wet' species *S. balticum* and *S. cuspidatum* in the first year is not unexpected, as the water level we used was relatively high and in the range of the natural habitat of these species. These results correspond to the findings from a field experiment of Rydin (1986) and the greenhouse experiment mentioned above (Breeuwer *et al.* 2008). The decrease in cover of the 'wet' species in the second year might be related to the % necrosis which mainly affected the 'wet' species, but when % necrosis was tested as a covariate, there was no effect of % necrosis on cover change. Percentage necrosis was not affected significantly by temperature, but there was a trend for increased necrosis with high temperature in combinations with *S. balticum* from C-Sweden.

Our third hypothesis posited that the release of nutrients, and therefore the resulting N concentrations in *Sphagnum,* would be higher with high temperature, but we found no difference in N concentration of the *Sphagnum* capitula between the temperature treatments, except for *S. fuscum* at no N addition (Fig. 3.4). In another greenhouse experiment we did find that N concentration in *Sphagnum* increased with increased temperature up to 17.2 °C, but here too there were no differences in N concentration between the two highest temperatures of 17.2 °C and 20.6°C (Breeuwer *et al.* 2008). We suspect that all the available N from the peat in the containers was mineralised in both temperature treatments during the experiment. Unfortunately, as we did not monitor N concentration in the *Sphagnum* material during the experiment, we could not follow the response curve of N concentration to temperature over time to verify this.

### Nitrogen

Our last hypothesis was confirmed: increased N concentration had a negative effect on height increment and production of all *Sphagnum* species; this was especially evident in the second year of the experiment. Atmospheric N deposition in Europe varies from 0.1 to 2 g $N.m^{-2}.yr^{-1}$ (Bragazza *et al.* 2004), although higher values up to 5 g $N.m^{-2}.yr^{-1}$ are reported for the Netherlands (RIVM 2004). Our N addition of 4 g N $m^{-2}$ $yr^{-1}$ is therefore already relatively high, but actual N availability might have been even higher because of nutrient mineralisation from the *Sphagnum* and peat in containers. The high N concentrations we found were roughly equal to the maximum N concentration in *Sphagnum* of 20 $mg.g^{-1}$ estimated by Berendse *et al*. (2001). Nitrogen concentrations were higher in the high N treatment: the N concentrations of *S. fuscum* and *S. magellanicum* in particular increased compared to initial values. Hummock species are known for their high N uptake rate (Jauhiainen *et al.* 1998). In another greenhouse experiment we performed, N concentrations were also higher in *S. fuscum* and *S. magellanicum* than in *S. balticum* and *S. cuspidatum* (Breeuwer *et al.* 2008).

The negative effect of the high N treatment on height increment in all combinations is probably mainly the result of direct toxic effects of the high N concentration on *Sphagnum,* as found in other studies with N deposition above 4 g $N.m^{-2}.yr^{-1}$ (Gunnarsson and Rydin 2000; Limpens and Berendse 2003a; Limpens *et al.* 2003a; Nordin and Gunnarsson 2000). In studies investigating the effect of increased N on *Sphagnum* and vascular plants, also indirect negative effects of N deposition through increased vascular plant cover were found (Berendse *et al.* 2001; Bubier *et al.* 2007). As the N:P ratios were already relatively high at the start of our experiment, with values of 25 or higher this might indicate that *Sphagnum* was already P limited, since P limitation occurs at high N:P ratios (>15 according to Aerts *et al.* 1992; >30 according to Bragazza *et al.* 2004). Bragazza *et al*. (2004) suggest that the critical load of N deposition in Europe is 1 g N.m$^{-2}$.yr$^{-1}$, above which *Sphagnum* plants change from being N-limited to being P and K co-limited at N : P > 30 and N : K > 3. This would indicate that *Sphagnum* was P-limited in all treatments in our study and co-limited by P and K in the high N treatment. Similar effects were reported by Gerdol *et al*. (2007) who found that *Sphagnum* production was slightly depressed with N addition of 3 g N.m$^{-2}$.yr$^{-1}$ but no concomitant addition of P; nutrient imbalance in the tissues was presumably responsible for this finding. Production in containers with the southern species was affected most by high N addition, but this was not reflected in the N concentrations or N:P and N:K ratios. Perhaps these species were more sensitive to high N concentrations.

Another possible explanation for the negative effect of high N addition, especially in the second year of the experiment, could be decreased *Sphagnum* vitality in the containers that suffered from severe fungal infection. The percentage *Sphagnum* affected by fungal infection also rose in the second year of the experiment, particularly in the 'wet' species. The percentage dead *Sphagnum* as a result of this infection was higher in the high N treatment (Fig. 3.5). Limpens *et al*. (2003b) also found that a high capitulum N concentration increases fungus-induced necrosis in *Sphagnum.* No such relationship was found in our study, but the *Sphagnum* in our study seemed to suffer more from the fungal infection, not only bleaching and defoliating, but also disintegrating, so probably plant cells were broken down and N was no longer retained in the infected plants.

### Implications of global change

Our findings suggest that the production of *Sphagnum* species is negatively affected by an increase in temperature and N deposition and that these negative effects are additive. Decomposition is expected to increase with increased temperature and N deposition (Bragazza *et al.* 2006; Dioumaeva *et al.* 2002; Hobbie 1996; Mack *et al.* 2004), which would mean that global change can reduce the carbon storage capacity of bogs. However, the negative impact from global change might be mitigated to some extent as not all species seem to react equally strongly to increased temperature and nitrogen availability. In this study, the 'dry' species seemed to suffer less from high N and increased in cover with increased temperature. This is an encouraging outcome because some studies have estimated higher carbon sequestration in lawns and low hummocks than in hollows, although this also depends on climatic factors like temperature and moisture availability (Belyea and Clymo 2001; Laine *et al.* 2007). On the other hand, a large amount of carbon is sequestered in northern species, and we found that compared with southern species, their production decreased more as a result of increased temperature. Therefore, when giving quantitative estimates about the effect of global change on the carbon storage capacity of bogs, also the possible effects of climate change on water availability should be taken into account, as well as the effects on and interactions with the vascular plant vegetation (Heijmans *et al.* in press).

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# CHAPTER 4

# Decreased summer water table depth affects peatland vegetation

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## Abstract

Climate change can be expected to increase the frequency of summer droughts and associated low water tables in ombrotrophic peatlands. We studied the effects of periodic water table drawdown in a mesocosm experiment. Mesocosms were collected in Southern Sweden, and subsequently brought to an experimental field in the Netherlands. Two water table treatments were applied: one with constant water tables at five centimetres below the moss surface, and one in which the water table was allowed to drop, resulting in water tables fluctuating between 5 and 21 cm below the moss surface. *Sphagnum* growth, as well as *Sphagnum* and vascular plant abundance, were assessed for two-and-a-half years. Our results show that the abundance of graminoid species increased most in the constant water table treatment. In contrast, ericoid species cover increased when water tables were allowed to fluctuate. Furthermore, *S. cuspidatum* production decreased with fluctuating summer water tables, while *S. magellanicum* responded oppositely. From these results we conclude that increased occurrence of periods with low water tables may effectuate a shift in dominant *Sphagnum* species as well as a shift from graminoid to ericoid vascular plant cover, resembling the shift from hollow to lawn or hummock vegetation. The difference in response within functional groups (vascular plants, *Sphagnum*) may add to the resilience of the ecosystem.

## Introduction

Peatlands play an important role in the global carbon cycle, due to their ability to sequester large amounts of atmospheric carbon (Gorham 1991; Hilbert *et al*. 2000). Additionally, peatlands have the ability to store great quantities of water, making them important water retaining ecosystems (Moore 2002). In ombrotrophic peatlands, such as raised bogs, *Sphagnum* mosses dominate the vegetation, therefore playing a crucial role in these ecosystems. Due to their relatively slow decay rate (Johnson and Damman 1991; Limpens *et al.* 2003b). *Sphagnum* mosses are largely responsible for the formation of peat, and hence the sequestration of carbon. Furthermore, *Sphagnum* mosses regulate the hydrological and hydrochemical conditions at the raised bog surface to a high degree (Van Breemen 1995), but the extent to which these mosses affect their environment may depend on the species identity. Consequently, the *Sphagnum* species composition along the bog's surface and changes therein may affect the functioning of the system.

Water table depth may be a crucial environmental factor controlling the dynamics of *Sphagnum* mosses, due to its influence on the capitulum (i.e. the active, apical part) water content of these mosses (Rydin 1993; Robroek *et al.* 2007a). The ability of *Sphagnum* species to keep their capitula moist is considered to be the most important differentiating factor between species (Titus and Wagner 1984) and determines their occurrence along the water table gradient, from hollows (high water table) to lawns (intermediate water table) and hummocks (low water table) (Andrus *et al.* 1983).

In peatlands, *Sphagnum* mosses and vascular plants co-occur. Parallel to the distribution of *Sphagnum* mosses, the vascular plant species assemblage varies over the different microhabitats along the water table gradient. Hollows are generally dominated by graminoid species such as *Rhynchospora alba* (L.) Vahl. Further above the water table (i.e. lawns and hummocks), ericoid species such as *Calluna vulgaris* (L.) Hull peak in abundance. In concert to its effect on the *Sphagnum* vegetation, changing water tables may affect vascular plant composition in bogs. Moreover, several studies elucidate that cover and production of vascular plant species increase when water tables decrease (e.g. Weltzin *et al*. 2000; Strack *et al.* 2006). Nonetheless, the effect of water table fluctuations on the vegetation in peatlands is less well understood.

Due to the co-occurrence of vascular plants and peat mosses, their relative abundances on peatlands may be crucial to determine the ecosystem functions. Earlier work indicates that increased cover of vascular plants may negatively affect *Sphagnum* growth, due to increased light interception (Heijmans *et al.* 2001; Bubier *et al.* 2007). Apart from the competition for light, changing water tables can directly effect *Sphagnum*-vascular plant competition. Low water tables will hamper capillary rise of water to the apical parts (i.e. capitula) of the *Sphagnum* individuals and consequently reduce their growth rate (Rydin and McDonald 1985; Wallén *et al.* 1988). Most vascular plants can avoid drought more easily than *Sphagnum* mosses because their roots can reach the lower water saturated layers in the peat. Additionally, in contrast to Sphagna, vascular plants can control water loss due to the possession of stomata. Water table drawdown and concomitant low availability of water at the moss surface may reduce the productivity of peat mosses but stimulate that of vascular plants (Malmer *et al.* 1994).

Water table depth, and especially fluctuations therein, are affected by changes in temperature and precipitation patterns (Gunnarsson *et al.* 2004). Climate change is likely to increase the frequency of summer droughts, but leave the winter water tables unaffected. Most studies on the effects of water table on vegetation shifts in peatlands however take fixed water tables as an experimental factor, reflecting differences in microtopographical habitat (e.g. Weltzin *et al.* 2000; Weltzin *et al.* 2001; Robroek *et al.* 2007a; Robroek *et al. 2*007b). Field studies on this topic, on the other hand, examine the full range of water tables which are then translated into potential effects of water table drawdown (e.g. Fenton and Bergeron 2006; Gunnarsson and Flodin, 2007), making it difficult to assess the importance of water table level versus water table fluctuation. With this study we aim to elucidate the effect of periodic water table drawdown on vegetation biomass and species composition. It was hypothesised that summer water table drawdown would favour vascular plant species from drier microhabitats compared to species from moist microhabitats. Similarly, within the *Sphagnum* moss vegetation species from drier habitats were expected to profit more from the increased occurrence of water table drawdown. Furthermore, vascular plants were expected to expand at the cost of *Sphagnum* mosses.

## Methods

### Sampling and experimental design

Late June 2003, 15 intact bog mesocosms (diameter: 45 cm; depth 40 cm) were collected from Saxnäss Mosse (56˚51'N, 13˚27' E), Southern Sweden. The mesocosms were taken from adjacent *Sphagnum* stands, at the transition between hollows and lawns. Vascular plant cover was approximately 25%. The *Sphagnum* layer of the mesocosms consisted of a mix (1:1) of *S. cuspidatum* Ehrh. Ex Hoffm. and *S. magellanicum* Brid. Besides these dominant species, *S. tenellum* (Brid.) Pers. Ex Brid*., S. balticum* (Russow) Russow ex C. Jens. and *S. rubellum* Wils. sparsely occurred. Vascular plant vegetation was dominated by *Andromeda polifolia* L., *Calluna vulgaris*, *Drosera rotundifolia* L., *Erica tetralix* L., *Eriophorum vaginatum* L., *Vaccinium oxycoccos* L. and *Rynchospora alba*. All mesocosms were put into large PVC containers (diameter: 45 cm; depth 40 cm), which were perforated at the bottom. These containers were transported to the Netherlands. During transportation, all mesocosms were kept moist. In an experimental garden in Wageningen (51˚58'N, 5˚40' E), these containers were placed into larger containers (diameter: 80 cm; depth 60 cm), which were sunken down into the soil. These large containers contained an artificial rainwater solution (a diluted seawater solution based on Garrels and Christ 1965). The small containers with the mesocosms were suspended into the large containers by hanging them from a lid. This lid covered the water surface between the small and large container, preventing evaporative water loss via an open water surface. To prevent the water table in the small container to become higher than 5 cm below the moss surface for prolonged periods, all large containers were equipped with an overflow system.

Initially, the containers were randomly assigned three different water regimen treatments (n =5): one constant (constant at –5 cm) and two fluctuating water tables (left to fluctuate between -5 to -15 cm, and left to fluctuate between -5 to -30 cm). If water tables were about to drop below the appointed maximum water table depth, they were raised by adding artificial rainwater to the large container. The constant water table in our experimental set-up corresponds to the water table as measured in the field during collection of the mesocosms. *Sphagnum cuspidatum* generally occurs at higher water tables, but is able to grow at the transition between lawn and hummock, where water table are slightly lower. Water table fluctuation treatments were chosen to reflect potential water table changes induced by climate warming. As both years of the experiment were relatively wet (Table 4.1), maximum water table depths of -30 cm have not been reached. Additionally, fast fluctuations were mitigated by the buffering capacity of the body of water in the large containers. Consequently, mesocosms were categorized into two water table treatments, constant (n = 6) and fluctuating, periodically low water tables (n = 9), based on realized water tables between May and September. From September to May, in both treatments water table depths were approximately at the overflow table (i.e. 5 cm below the *Sphagnum* surface).

**Table 4.1** Weather conditions during the experiment (2003-2005: data for the Netherlands only), compared to long-term averages (1971-2000) at the site of origin of the mesocosms (Sweden) and the Netherlands (NL). Data are averages for temperature and sums of precipitation per season and per year. Autumn =Sep-Nov, Winter =Dec-Feb, Spring = Mar-May, Summer = Jun-Aug.

| | **1971 - 2000** | | **June 2003 - August 2005** | | |
|---|---|---|---|---|---|
| | **Sweden** | **NL** | **2003** | **2003-2004** | **2004-2005** |
| **Temperature (˚C)** | | | | | |
| Autumn | 8.2 | 10.1 | _ | 10 | 10.8 |
| Winter | 0 | 2.9 | _ | 3.9 | 3.3 |
| Spring | 6.6 | 8.8 | _ | 9.5 | 9.9 |
| Summer | 16 | 16.5 | 18.8 | 17.1 | 16.9 |
| Year | 7.6 | 9.6 | _ | 10.1 | 10.2 |
| **Precipitation (mm)** | | | | | |
| Autumn | 358 | 202 | _ | 137 | 202 |
| Winter | 331 | 177 | _ | 317 | 229 |
| Spring | 210 | 159 | _ | 128 | 202 |
| Summer | 302 | 192 | 120 | 248 | 287 |
| Year | 1199 | 728 | _ | 830 | 920 |

### Vascular plants

Vascular plant species composition and their abundance in the mesocosms were measured during the experiment using the point-quadrat method (Jonasson, 1988) with a 150 point frame (25 × 37.5 cm), suspended above the mesocosm. At every point, a needle was vertically lowered untill it touched the moss surface. All contacts with vegetation (further referred to as hits) were noted, specifying species for each hit. Abundance was measured at several dates between July 2003 and September 2005. For data analysis we used the change in abundance for each species between July 2003 and July 2005, since vascular plants had their peak standing biomass in summer.

Total above ground vegetation within the point-quadrat frame was harvested in September 2005. All vascular plants were clipped flush with the moss surface and sorted into species. Per species, dry weight was determined after oven drying for 48 hours at 70°C. We measured light intensity (Skye quantum sensor) just above the moss surface and above the vascular plant vegetation at ten points in each mesocosm early September 2005.

### *Sphagnum*

Parallel to the method used for vascular plants, changes in cover between October 2003 and September 2005 were measured per *Sphagnum* species. Per mesocosm, *Sphagnum* height increment was measured monthly, using four plastic rods with bristles, a variation of the cranked wire method (Clymo 1970; Limpens *et al.* 2004). At harvest, a core (diameter 5 cm) was taken around every rod and separated into a capitulum section (0 - 1 cm) and a subcapitulum section (1-2 cm). Subsequently both sections were sorted onto *Sphagnum* species, after which dry weight was determined by oven-drying for 48 hours at 70°C. For every species, subcapitulum bulk density was expressed as dry weight (g) $cm^{-3}$. Biomass production was calculated by multiplying subcapitulum bulk density with height increment. For each species, production per mesocosm over the 2004 and 2005 growing seasons (May 4th through September 15th) was averaged.

### Analyses

To examine the usefulness of the point intercept data as a proxy for the development of the aboveground vascular plant biomass during the experiment, regressions between the point-quadrat data and the above ground vascular plant biomass at the final harvest were used (Heijmans *et al.* 2001). These regressions were significant for all species ($P < 0.05$; $0.35 \leq R^2 \leq 0.93$; n = 9-15).

Prior to analysis, data were tested for normality and equality of variance and, when necessary, ln-transformed. The effect of the water table treatment on the total production of vascular plants and peat mosses was tested, using ANOVA. Additionally, the effect of species groups (ericoids, graminoids, hollow peat mosses and lawn peat mosses) and water table treatments on the change in production was analysed per functional plant group (vascular plants and *Sphagnum*), using ANOVA. As a proxy for change in biomass production of vascular plants, change in abundance (i.e. change in the number of hits) was used. To test for water table treatment effects on *Sphagnum* production, *Sphagnum* cover change, vascular plant abundance and species responses, multivariate ANOVA models were used with water table treatment and species as fixed factors. Because of significant water table treatment × species interactions, all further analyses on the effects of the water table treatment were performed per species, using univariate ANOVA models. For *Sphagnum*, the effect of species on production and cover change was tested within water table treatment by univariate ANOVA followed by Tukey post hoc tests.

## Results

### Water table treatments

The objective of this study was to delineate the seasonal/periodic water table drawdown on the response of peatland vegetation. Inherent to the chosen experimental set-up, increased occurrence of water table drawdown in the fluctuating water table (FWT) treatment also resulted in decreased modal water table (i.e. the most frequent water table measured between May and September, see Fig. 4.1).

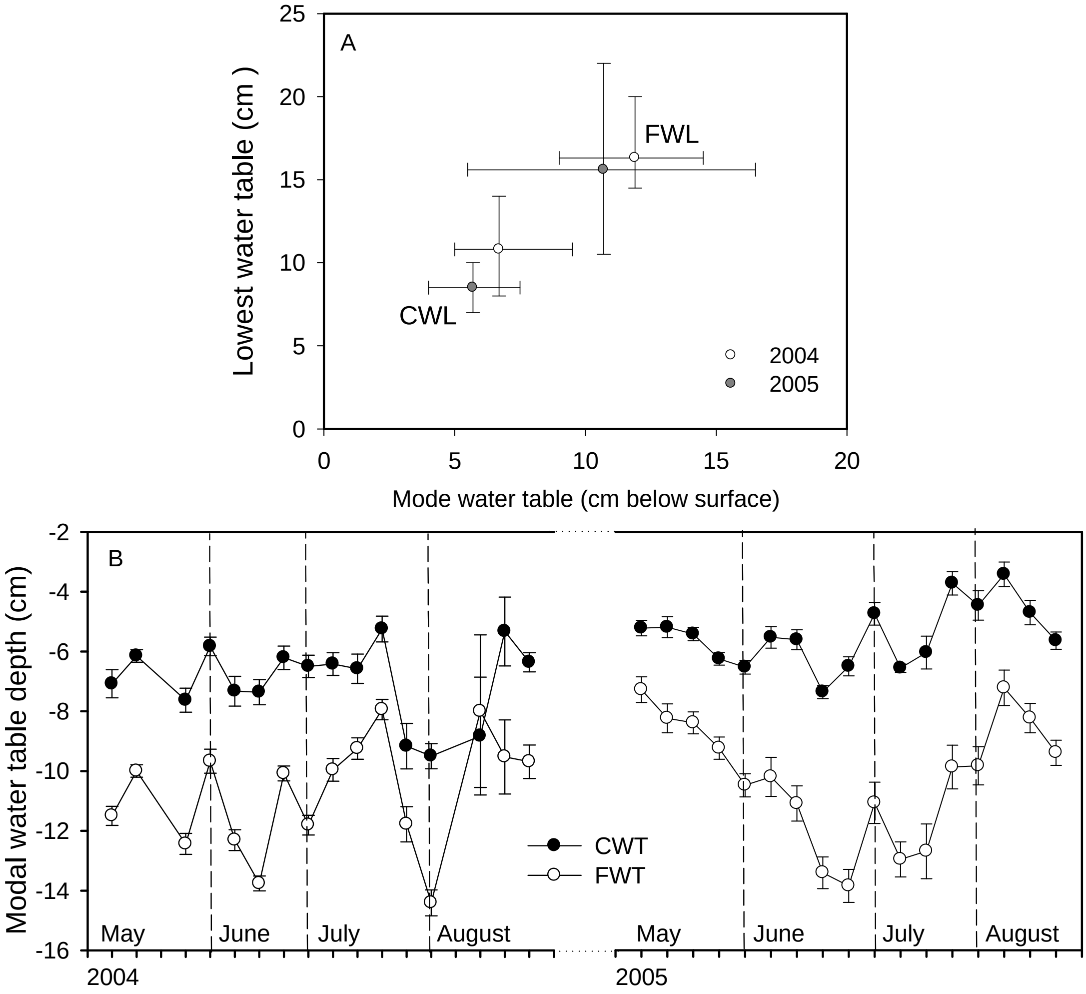

**Figure 4.1** (A) Lowest water table and mode water table from May to September for the two water table treatments: constant water table treatment (CWT) and fluctuating water table treatment (FWT). Error bars indicate minimum and maximum value of mesocosms with constant water table (n=6) and mesocosms with fluctuating water table treatment (n=9). (B) Modal water table depth (± SEM) of the two water table treatments (CWT, n=6; FWT, n = 9) during the summer period (May – September) in two subsequent years.

Vascular plants

Change in hits proved to be a useful proxy for the change in aboveground vascular plant biomass (see analyses), and was not affected by water table treatment (Fig. 4.2A). Total aboveground vascular plant biomass at harvest was 221 ± 16 g $m^{-2}$, corresponding to 37 ± 3 % light interception (data not shown). Vascular plant functional groups (ericoids and graminoids) differed in their response to both water table treatments (F = 3.94, *P* = 0.06), although total biomass remained unaffected (F = 1.91, *P* = 0.19; Fig. 4.2A). Individual species also responded differently to the water table treatments as indicated by the significant interaction between water table treatment and species (Table 4.2). All ericaceous species, except *Erica tetralix*, increased in abundance in the FWT treatment (Table 4.3). As a result, ericoid abundance marginally increased at this treatment (*P* = 0.053; Fig. 4.2A; Table 4.3). Graminoids, generally, showed an opposite response (Fig. 4.2A), which was mostly caused by the increased abundance of *Rynchospora alba* in the constant water table (CWT) treatment (Table 4.3).

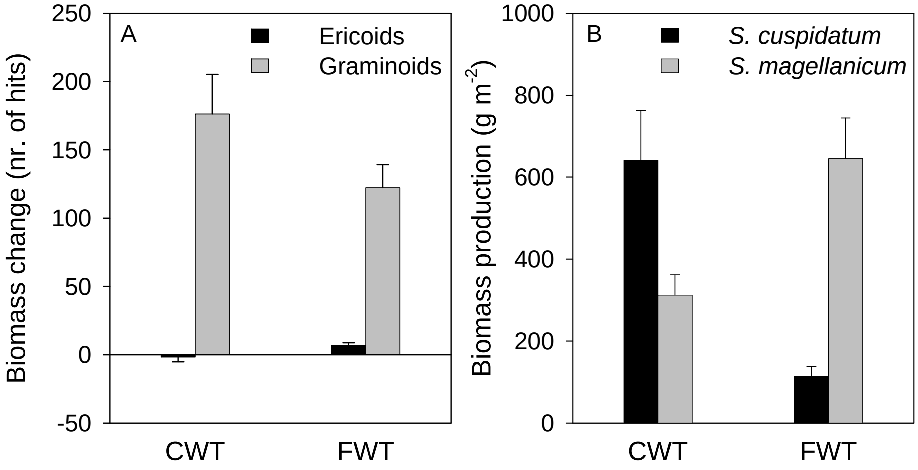

**Figure 4.2** (A) Change in biomass (± SEM) over the experimental period, expressed as the change in number of hits, for the Ericoid and Graminoid functional groups and (B) Summer (May-September) biomass production (± SEM) of the two main peat mosses, *S. cuspidatum* and *S. magellanicum*. For both panels differences in production are separated for the constant water table treatment (CWT) and the fluctuating water table treatment (FWT).

**Table 4.2** Results of two-way ANOVAs for *Sphagnum* production during May-September 2004 and 2005, change in *Sphagnum* cover between October 2003 and September 2005 and change in vascular plant cover between July 2003 and July 2005, testing effects of constant or fluctuating water table treatment with 3 *Sphagnum* species and 6 vascular plant species. df: degrees of freedom.

| **Source** | **df** | **F** | ***P*** |
|---|---|---|---|
| **Vascular plants cover change** | | | |
| WT treatment | 1 | 1.90 | 0.172 |
| Species | 5 | 74.95 | **<0.001** |
| WT treatment x Species | 5 | 4.27 | **0.002** |
| ***Sphagnum* production** | | | |
| WT treatment | 1 | 2.60 | 0.116 |
| Species | 2 | 38.43 | **<0.001** |
| WT treatment x Species | 2 | 12.14 | **<0.001** |
| ***Sphagnum* cover change** | | | |
| WT treatment | 1 | 0.03 | 0.861 |
| Species | 2 | 2.80 | **<0.001** |
| WT treatment x Species | 2 | 2.20 | 0.125 |

**Table 4.3** Change in biomass of vascular plant species, expressed as the change in number of hits, between July 2003 and July 2005. The effect of water table (WT) treatment was tested with separate ANOVAs per species group and per species. Data are mean values ± SE.

| | Change in biomass production (nr. of hits) | | |
|---|---|---|---|
| **species** | **Constant WT** | **Fluctuating WT** | ***P*** |
| Ericoids | -1.7 ± 3.5 | 6.6 ± 2.2 | **0.053** |
| *A. polifolia* | 0.0 ± 2.2 | 2.8 ± 2.0 | 0.385 |
| *C. vulgaris* | -3.2 ± 3.2 | 1.0 ± 1.0 | 0.165 |
| *E. tetralix* | 1.8 ± 1.2 | 0.8 ± 1.0 | 0.519 |
| *V. oxycoccus* | -0.3 ± 1.1 | 2.0 ± 1.5 | 0.290 |
| Graminoids | 176.3 ± 29.0 | 122.3 ± 16.7 | 0.106 |
| *E. vaginatum* | -1.0 ± 8.7 | 9.3 ± 13.3 | 0.573 |
| *R. alba* | 177.3 ± 24.2 | 113.0 ± 15.8 | **0.036** |

### *Sphagnum*

Water table treatment did not affect total biomass production of the *Sphagnum* (F = 0.46, *P* = 0.50), but did affect within-species productivity (Table 4.2). Moreover, the response of biomass production to the water table treatment differed between species (Table 4.2). Production of *S. cuspidatum* was higher in the CWT treatment, while production of *S. magellanicum* was higher in the FWT treatment (Table 4.4, Fig 4.2B). *Sphagnum tenellum* did not respond to the water table treatments (Table 4.4). Although *Sphagnum* species showed different directions in biomass production as a result of water table treatment (Table 4.4, Fig. 4.2B), water table had no effect on *Sphagnum* cover (Table 4.4): irrespective of treatment *S. cuspidatum* decreased, while *S. magellanicum* increased in cover (Table 4.4).

Total *Sphagnum* production was almost three times higher in 2005 (456 ± 65 g.m$^{-2}$) than in 2004 (177 ± 42 g.m$^{-2}$) (F = 13.6, $P < 0.01$). There was no effect of water table treatment (F = 0.8, $P = 0.38$) and no interaction between water table treatment and year (F = 0.0, $P = 0.98$). Although there seemed to be a negative relationship between vascular plant abundance and *Sphagnum* production in 2004 ($P = 0.09$, $R^2 = 0.20$), we found no such relationship in 2005 ($P = 0.75$, $R^2 = 0.01$), when vascular plant abundance had increased even further (data not shown).

**Table 4.4** The effect of two water table (WT) treatments on the summer (May – September) biomass production (g m$^{-2}$) and the change in cover (nr. of hits) hits) of three *Sphagnum* species between October 2003 and September 2005. Data are mean values ± SE. Numbers in bold indicate significant ($P < 0.05$) differences in response to water table, within species. Different letter indicate differences between species (ANOVA with Tukey post hoc test, $P < 0.05$), within water table treatment.

| Species | Constant WT | Fluctuating WT | *P* |
|---|---|---|---|
| **Production** | | | |
| *S. cuspidatum* | 640.7 ± 121.4 $^{c}$ | 113.2 ± 25.1 $^{a}$ | **<0.001** |
| *S. magellanicum* | 312.1 ± 49.5 $^{b}$ | 645.1 ± 99.2 $^{b}$ | **0.016** |
| *S. tenellum* | 47.0 ± 15.3 $^{a}$ | 47.4 ± 11.5 $^{a}$ | 0.781 |
| **Change in cover** | | | |
| *S. cuspidatum* | -20.2 ± 7.0 $^{a}$ | -10.2 ± 3.7 $^{a}$ | 0.192 |
| *S. magellanicum* | 16.3 ± 7.4 $^{b}$ | 11.1 ± 3.0 $^{b}$ | 0.466 |
| *S. tenellum* | 3.5 ± 2.7 $^{b}$ | -3.1 ± 2.5 $^{a}$ | 0.107 |

## Discussion

### Vascular plants

As hypothesised, vascular plants naturally occurring further from the water table, like ericoids, performed slightly better when water table was allowed to fluctuate. In contrast, graminoids, particularly *Rynchospora alba*, performed better at the constantly high water table. Other studies also found a correlation between ericoid biomass and increasing, but stable, depth of the water table (Weltzin *et al.* 2003; Strack *et al.* 2006). These similarities indicate that periodic water table drawdown effectuates changes which parallel the response to constant low water table. Interestingly, *R. alba* not only increased in cover in the constant water table treatment, as expected, but also in the fluctuating treatment. This shallow rooted species may have profited from the increase in temperature and atmospheric nitrogen deposition (Heijmans *et al.* 2002b; Limpens *et al.* 2003a) after transportation from the Southern Swedish site of origin ($T_{1971-2000}$=7.6˚C; 1-2 g N $m^{-2}$ $yr^{-1}$) to the experimental site in Wageningen in the Netherlands ($T_{1971-2000}$=9.6˚C; 4 g N $m^{-2}$ $yr^{-1}$). Nevertheless, it is not likely that increased nitrogen deposition can explain the observed increase, since nitrogen concentrations in *Sphagnum* were relatively low (8.4 ± 0.5 mg $g^{-1}$ in the top 5 cm) and likely not yet saturated with nitrogen, which is assumed to occur only at concentrations above 10-12 mg $g^{-1}$ (Lamers *et al.* 2000). Alternatively, we may have measured the recovery of *Rhynchospora* from the relatively warm and dry period preceding our experiment (the summer of 2003 was exceptionally dry and warm in Northern Europe). Similar lag-effects were reported for *Sphagnum* abundance in bogs in South-Western Sweden by Gunnarsson and Flodin (2007). On account of the above, our results indicate that the increased cover of ericoid species mainly was caused by periodic water table drawdown, reflecting their natural preference along the water table gradient. The most abundant graminoid species, *R. alba*, increased in cover at both water tables, which may be explained by more favourable temperature and precipitation characteristics over the experimental period. Nevertheless, *R. alba* cover peaked at constant high water table, also reflecting its natural preference along the water table gradient.

### *Sphagnum*

Biomass production of the two dominant *Sphagnum* mosses, *S. cuspidatum* and *S. magellanicum*, differed in their response to water table treatment. Similar to vascular plants, these responses corresponded to differences in habitat preferences (Andrus *et al.* 1983; Wallén *et al.* 1988). As hypothesised, *S. cuspidatum* production decreased when water table was allowed to fluctuate, whereas *S. magellanicum* responded oppositely (Table 4.4). The response of the mosses to fluctuating water tables equals that of experiments where *Sphagnum* mosses were grown at constant low water tables (Rydin 1997; Robroek *et al.* 2007b), suggesting that periodic water table drawdown can have a similar effect on *Sphagnum* growth as constant low water tables. Unexpectedly, *S. magellanicum* cover increased in both water table treatments, whereas *S. cuspidatum* decreased in cover. As bulk density for both species did not differ from those measured in the field (unpublished data), competition between both species must have originated from divergent height increments. Although, *S. cuspidatum* and *S. magellanicum* co-occur at water tables of -5 cm in the field, the latter seems to be able to grow better. Possibly, the warmer climate in the Netherlands resulted in increased evaporative water loss, which may have negatively affected *S. cuspidatum*.

Additionally, even at the constant water table water tables sometimes decreased due to warm and dry periods (Fig. 4.1). *S. magellanicum* may have profited from these temporal periods of reduced water availability. These results stress the importance of periodic low water tables and their effects on surface water availability. As such, increased summer drought frequency could lead to an expansion of lawn species at the expense of hollow species. This shift in species composition could be enhanced by the effects of climate change on decomposition rates of *Sphagnum*. By moving the South-Swedish vegetation to the Netherlands, with temperature, nitrogen deposition increased. Both are known to stimulate decomposition of organic litter (Dioumaeva *et al*. 2003; Bragazza *et al.* 2006; Gerdol *et al.* 2007). Litter from lawn and hummock species is known to be intrinsically more resistant to decay than litter from hollow species (Johnson and Damman 1991; Belyea 1996; Moore and Basiliko 2006). Together with the effect of periodic drought, increased decay of the easily decomposing *S. cuspidatum* may have been the key trigger for the change in the *Sphagnum* composition in the mesocosms.

### Implications of water table drawdown on the peatland vegetation

The expected negative relation between vascular plant cover and *Sphagnum* production was observed in the first growing season, yet was absent in the second growing season. This is remarkable since the cover of vascular plants increased with time. In the second year, the potential negative effect of higher vascular plant abundance may have been counteracted by the generally positive effect of higher precipitation, as indicated by the high production values of *Sphagnum* that year. Furthermore, vascular plant abundance may not have been high enough to unambiguously affect *Sphagnum* growth. Total above ground biomass was only 221 g $m^{-2}$, which is relatively low (Chapin *et al.* 1995; Press *et al.* 1998; Heijmans *et al.* 2002a). Only 37 % of the incoming light was intercepted by the vascular plants at the end of the experiment. Earlier it was suggested that cover of vascular plants should at least be 60%, or light reduction exceed 50% in order to negatively affect *Sphagnum* production (Heijmans *et al.* 2002a; Limpens *et al.* 2003a).

From our experiment it remains unclear how vegetation changes due to periodically low water tables would affect carbon sequestration in bog ecosystems. On the one hand, a shift towards lawn *Sphagnum* species at the cost of hollow *Sphagnum* would entail a shift to slower decomposing *Sphagnum* species (e.g. Johnson and Damman 1993). Decomposition rates, on the other hand, will be stimulated because of increased aerobic conditions and higher soil temperatures (Belyea 1996). Moreover, the percentage of more easily decomposable vascular plant material, compared to *Sphagnum*, may increase with periodical low water tables. Additionally, increased water table drawdown affects the composition within the vascular plant vegetation, stimulating the abundance of slower decomposing ericoid species. These findings support the recently published result of Laine *et al.* (2007), who showed that net ecosystem carbon exchange is lowest in wet microforms (hollows) and highest in drier ones (hummocks). It, however, is unclear how production rates of *Sphagnum* will change, regarding climate change induced changes in photosynthetic capacity. *Sphagnum* species differ in photosynthetic efficiency, and these efficiencies are highly influenced by environmental factors such as water and nutrient availability (Schipperges and Rydin 1998; Riutta *et al*. 2007). Consequently, the net effect of water table fluctuations, and parallel periodic drought, on carbon sequestration is difficult to estimate. Riutta *et al.* (2007) show that water table drawdown is much more negative for *Sphagnum* mosses than for vascular plants. In our study, production of *Sphagnum magellanicum*, however, increased at fluctuating water table. The observed shift in species composition towards species better adapted to dry conditions within peat mosses and vascular plants, suggests resilience to increased frequency of prolonged drought, at least at the time scale of several years. This adds to the proposed resilience to water table drawdown with respect to $CO_2$ exchange (Riutta *et al.* 2007), caused by different responses of divergent peatland components (*Sphagnum* mosses, sedges and dwarf shrubs).

Summarised, increased occurrence of periods with low water tables, as a result of climate change, may cause a shift in the dominant *Sphagnum* species and lead to increased ericoid plant cover. On the transition between hollows and lawns, the species assemblage will shift from vegetation dominated by hollow *Sphagna* and graminoids, to vegetation dominated by lawn Sphagna and ericoids. How these changes will influence carbon sequestration and hydrological characteristics of bogs are import questions for future research.

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# CHAPTER 5

# Field simulation of global change: transplanting northern bog mesocosms southwards.

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## Abstract

How global change will affect the species composition of ombrotrophic bog vegetation is still unclear. If vascular plants were to expand at the cost of peat mosses (*Sphagnum*), which are the main constituent of peat, this would significantly reduce long-term carbon sequestration rates. We performed a transplantation experiment in which mesocosms with intact vegetation were transplanted southwards from North-Sweden to North-East Germany along a transect of four bog sites, in which both temperature and N deposition increased from north to south. Our monitoring of shifts in species abundances during three growing seasons revealed that ericoid plant species increased their abundance most when transplanted to the southernmost site. The height increment of *S. balticum* was less when transplanted southwards. Neither incubation site nor site of origin affected *Sphagnum* production, but , as expected, N concentration in *Sphagnum* increased southwards. The lack of a (positive) transplantation effect on *Sphagnum* production can be attributed to other factors, such as P or moisture, becoming limiting. However, vascular plants did become more abundant in bog vegetation when transplanted to warmer sites with higher N deposition. Since global change is expected to have a positive effect on decomposition, we conclude that global change can have serious negative effects on the functioning and the carbon sequestration capacity of ombrotrophic bogs.

## Introduction

Global change is expected to have a strong impact on temperature, precipitation and nutrient deposition, especially at northern latitudes where the majority of peat bogs occur (Gunnarsson 2005; Kivinen and Pakarinen 1980). Predictions about future precipitation patterns show great variability, but all climate models predict an increase in temperature and nitrogen (N) deposition (Bouwman *et al*. 2002; Solomon *et al*. 2007). Ombrotrophic bog vegetation is dominated by peat mosses (*Sphagnum* spp.), which are responsible for the high accumulation of carbon in bogs, due to their low litter decomposition rates (Clymo and Hayward 1982; Coulson and Butterfield 1978; Limpens and Berendse 2003). Furthermore, *Sphagnum* mosses regulate the hydrological and hydrochemical conditions at the raised bog surface to a high degree (van Breemen 1995; Van der Schaaf 2002). The vascular plant cover in bogs is generally low and consists of ericoids, graminoids and a few herbs (some of them carnivorous), that are adapted to the harsh conditions (Rydin and Jeglum 2006). These conditions – lack of nutrients, wet, partly anoxic and acidic – largely result from *Sphagnum* growth and accumulation, forming peat (Rydin and Jeglum 2006). To avoid being overgrown, the vascular plants have to keep up with the vertical height increment of *Sphagnum* (Backeus 1985; Dorrepaal *et al.* 2006; Malmer *et al.* 1994). On the other hand, the presence of vascular plants is important for *Sphagnum* because they provide a matrix for the *Sphagnum* to grow on (Malmer *et al*. 1994) and reduce evaporation from *Sphagnum* (Heijmans *et al*. 2001a). However, when the vascular plant cover becomes too high, the increased shading can adversely affect *Sphagnum* growth (Berendse *et al*. 2001; Bubier *et al*. 2007). In the bog, the vascular plants and *Sphagnum* apparently occur in a stable equilibrium, thereby sustaining the functioning of the bog ecosystem and its high carbon sequestration. Changes to this equilibrium can have marked effects on the C dynamics and $CO_2$ fluxes of the ecosystem (Ward *et al*. 2007). As *Sphagnum* and vascular plant production are both controlled by the factors temperature, light, wetness and nutrient availability, but their competition is highly asymmetrical (Rydin and Jeglum 2006), changes in temperature and N availability are likely to influence the current competitive balance.

In general, climate warming is expected to increase *Sphagnum* productivity, as long as water does not become limiting (Breeuwer *et al.* 2008a; Dorrepaal *et al.* 2006; Gunnarsson 2005). The effect of increased N deposition is less clear-cut; it has been shown that a small increase in N can enhance *Sphagnum* production at locations where N is a limiting nutrient (Turunen *et al*. 2004) but when N concentrations exceed a critical threshold value, *Sphagnum* production and cover are reduced (Berendse *et al.* 2001; Bragazza *et al.* 2006; Gerdol *et al.* 2007; Gunnarsson and Rydin 2000). Vascular plant cover and production are stimulated by increased temperature and N deposition (Berendse *et al*. 2001; Bubier *et al*. 2007; Wiedermann et al. 2007). One indirect effect of higher temperature is increased nutrient availability as a result of enhanced decomposition and N-mineralisation (Hobbie 1996; Rustad *et al*. 2001). As *Sphagnum* litter decomposes much more slowly than vascular plant litter (Bragazza *et al.* 2007; Coulson and Butterfield 1978; Dorrepaal *et al.* 2005; Hobbie 1996), any shift in species composition will have a profound impact on the carbon sequestration function of bog ecosystems.

Though several studies have addressed the response of *Sphagnum* and/or vascular plants to increased temperature and/ or N deposition, little research has been done on the combined effects of the latter on intact bog vegetation (Wiedermann *et al*. 2007). In this study, therefore, we investigated the responses of both vascular plants and *Sphagnum* to expected effects of global change along a transect in which both temperature and N deposition increase. We did this by transplanting mesocosms with intact vegetation southwards from North-Sweden to North-East Germany over a gradient of four bog sites. During the experiment we measured *Sphagnum* height increment and the abundance of vascular plant species. After the final harvest, *Sphagnum* biomass growth, aboveground vascular plant biomass and nutrient concentrations in plant tissues were determined. We expected that southwards there would be an increase in: (1) vascular plant cover, (2) *Sphagnum* growth (for northern species) and (3) nitrogen concentrations in *Sphagnum*.

## Material and methods

### Study Sites

The experiment was executed between May 2003 and August 2006 in four raised bogs, situated along a latitudinal gradient from the north of Sweden to the north of Germany (Fig. 5.1). We selected bog sites that were relatively undisturbed, with a peat layer of at least 5 metres deep and a vegetation characteristic of ombrotrophic mires. However, there are some differences between the sites.

(1) The northernmost site is Lappmyran (N-Sweden), c. 50 km north-west of Umeå , Sweden (64° 10′ N, 19° 35′ E), altitude 300 m a.s.l.. This bog is elongated, being c. 700 m long and 200 m wide, and is surrounded by forest of *Pinus sylvestris* and *Picea abies*. It exhibits a pattern of strings of hummocks and hollows, similar to aapa mires. The hollows are dominated by *Sphagnum balticum* (Russow) Russow ex C. Jens. and *Scheuzeria palustris* L., while the hummock vegetation consists of *Sphagnum fuscum* (Schimp) Klinggr with a vascular plant cover mainly of *Andromeda polifolia* L.*, Calluna vulgaris* (L.) Hull*, Drosera rotundifolia* L., *Empetrum nigrum* L., *Eriophorum vaginatum* L., *Vaccinium oxycoccus* L. and *Rubus chamaemorus* L..

(2) The central Swedish site is Åkerlänna Römosse (C-Sweden), c. 30 km north-west of Uppsala, Sweden (60° 01′ N, 17° 22′ E), altitude 50 m a.s.l.. This bog is more oval: c. 1300 m long and 600 m wide and a belt of *P. sylvestris* and *P. abies* separates it from the surrounding farmland. Towards the bog the vegetation gradually becomes shrubby, dominated by *Ledum palustre*. The peatland surface has a characteristic microtopography of hollows, lawns and hummocks. The dominant species are: *Sphagnum lindbergii* Schimp. in deeper hollows, *S. balticum* in hollows and lawns and *S. fuscum* on hummocks, with vascular plant cover of *A. polifolia*, *C. vulgaris*, *D. rotundifolia*, *E. nigrum*, *E. vaginatum* and *V. oxycoccus.*

(3) The south Swedish site is Saxnäs mosse (S-Sweden), c. 40 km north-east of Halmstad, Sweden (56° 51′ N, 13° 28′ E), altitude 160 m a.s.l.. This bog is elongated, c. 1000 m long and 300 m wide, lies next to a main road and is surrounded by forest consisting mainly of *P. sylvestris* and *P. abies.* Saxnäs mosse has a typical raised bog vegetation with a mosaic of hollows, lawns and small hummocks. The dominant species are: *Sphagnum cuspidatum* Ehrh. Ex Hoffm. in the hollows, *Sphagnum magellanicum* Brid. in lawns and *S. fuscum* on hummocks, with vascular plant cover of *Rhynchospora alba* (L.) Vahl in hollows and *A. polifolia*, *C. vulgaris*, *D. rotundifolia*, *Erica tetralix* L., *E. vaginatum* and *V. oxycoccus* on lawns and hummocks.

(4) The southernmost site is Barschpfuhl (Germany), c. 65 km north-east of Berlin, Germany (53° 03′ N, 13° 51′ E), altitude 80 m a.s.l.. The mire is situated in a restricted-access part of the UNESCO nature reserve Biosphärenreservat Schorfheide-Chorin – a landscape of hills covered with coniferous, mixed and broadleaved forest. Barschpfuhl is a small mire, c. 180

m long and 140 m wide, and is located in a depression. There is no clear distinction between hollows and hummocks and the vegetation is dominated by *S. magellanicum* and *S. fallax* (Klinggr.) Klinggr. with a vascular plant cover of mainly *C. vulgaris, Carex rostrata, D. rotundifolia*, *Eriophorum angustifolium* (Honckeny), *E. vaginatum*, *R. alba* and *V. oxycoccus*.

Differences between the sites in temperature, precipitation, water level and atmospheric nitrogen deposition are described in the Results section.

**Figure 5.1** Location of 4 research sites: 1= Lappmyran (N-Sweden), 2= Åkerlänna Römosse (C-Sweden), 3= Saxnäs mosse (S-Sweden), 4= Barschpfuhl (Germany).

Experimental set-up

At the start of the transplantation experiment in May 2003, we collected peat mesocosms (diameter: 45 cm, depth: 40 cm) with intact vegetation from all four sites. The mesocosms were placed in containers perforated at the bottom to allow water exchange. The containers were then either replaced in their site of origin, or transplanted further southwards (i.e. not reciprocal) with five replicates. As Table 5.1 shows, the final number of containers at each site increased from north to south. We did not transplant mesocosms from south to north because this would not have yielded information on how the vegetation of ombrotrophic bogs responds to the two anticipated environmental changes we were investigating: increased temperature and N deposition.

The mesocosms were taken at the transition from hollow to hummock or hollow to lawn, so that the *Sphagnum* layer consisted of a 1:1 mix of the two dominant *Sphagnum* species in each site. Because the sites differed in their species composition, the dominant *Sphagnum* species also differed between sites. At the two northernmost sites, the mesocosms were taken from the transition between hollows or lawns and hummocks, and consisted mainly of *S. balticum* and *S. fuscum*. At the two southern sites, the mesocosms were taken from the transition between hollows and lawns, and consisted mainly of *S.cuspidatum* and *S. magellanicum* in site 3 and of *S. fallax* and *S. magellanicum* in site 4.

**Table 5.1** The allocation of the mesocosm containers, for location of sites see Figure 5.1.

| Site name | Site no. | Site code | No. of containers |
|---|---|---|---|
| Lappmyran | 1 | N-Sweden | 5 |
| Åkerlänna Römosse | 2 | C-Sweden | 10 |
| Saxnäs mosse | 3 | S-Sweden | 15 |
| Barschpfuhl | 4 | Germany | 20 |

## Measurements

### *Environmental conditions*

To compare the relative deposition of N and P in the four sites, we measured accumulation of $NH_4^+$, $NO_3^-$ and $PO_4^-$ on ion-exchange resins (Bret-Harte *et al.* 2004; Hobbie and Chapin 1998). We constructed resin bags by placing 8 g of ion exchange resins (IONAC ® NM-60 $H^+/OH^-$ Form, type 1 beads 16-50mesh; J.T. Baker, Philipsburg, NJ, USA) in polypropylene mesh litterbags (5 x 5 cm) with a 100 µm mesh size. In May 2005, we placed five resin bags on top of the *Sphagnum* layer in all four sites. In May 2006 we retrieved the resin bags; two resin bags (one in site 1 and one in site 4) were found to be ruptured and so were excluded from the analysis. The remaining resin bags were extracted overnight in 50 ml 2 M NaCl in 0.1 M HCl. The extracts were brought to neutral pH by the addition of NaOH and analysed spectrophotometrically for $NH_4^+$, $NO_3^-$ and $PO_4^-$ using an auto-analyser (Skalar).

Water table depth was measured in each mesocosm during each visit in May and August from 2003 to 2006. Because the sites were so far apart, each time it took about two weeks to visit them all. As the weather conditions varied during this period and between sites, our measurements give only a rough indication of the water table depth in each site.

### *Vascular plants*

Vascular plant species composition and their abundance in the mesocosms were measured during the experiment using the point-quadrat method (Jonasson 1988) with a 150-point frame (25 × 37.5 cm). At every point, a needle was lowered to the moss surface and all contacts with the vegetation were noted, specifying species for each hit. Abundance was measured in August 2003, 2004, 2005 and 2006. For data analysis we used the change in cover between August 2003 and 2006. The total aboveground vegetation within the point-quadrat frame was harvested after the last point quadrat recordings. All vascular plants were clipped flush with the moss surface and sorted into species. Dry weight was determined of all species after oven drying for 48 hours at 70°C. To examine the usefulness of cover change as a proxy for the development of the aboveground vascular plant biomass during the experiment, we used regressions between the point-quadrat data and the aboveground vascular plant biomass at the final harvest (Heijmans *et al*. 2001b). These regressions were significant for all species ($P < 0.001$; $0.68 < R^2 < 0.95$; $13 < n < 70$). For further analyses, we grouped the species into two classes: ericoids, mainly *A. polifolia*, *C. vulgaris*, *E. nigrum*, *E. tetralix* and *V. oxycoccus;* and graminoids, mainly *E. vaginatum, E. angustifolium* and *R. alba.*

Sphagnum

Per mesocosm, *Sphagnum* height increment was measured in May and August of the years 2003 to 2006, using four plastic rods with bristles (a variation of the cranked wire method, (Clymo 1970; Limpens *et al*. 2004). At the end of the experiment, a core (diameter 6.6 cm) was cut around each rod and separated into a capitulum section (0 - 1 cm) and a subcapitulum section (1-3 cm). The sections were stored in ziplock bags and kept cool during transport to the Netherlands. In the lab, all samples were sorted into *Sphagnum* species, after which dry weight was determined by oven-drying for 48 hours at 70°C. For every species, subcapitulum bulk density was expressed as dry weight (g) $cm^{-3}$. Average biomass production in summer was calculated by multiplying subcapitulum bulk density by average height increment between May and August 2004, 2005 and 2006. For data analyses of height increment we used cumulative height increment measured between May 2003 and August 2006.

Per species, changes in *Sphagnum* cover between August 2003 and August 2006 were measured using the abovementioned point-quadrat method. Generally the mesocosm surface consisted completely of *Sphagnum* mosses. For data analysis we used the change in cover between August 2003 and 2006.

*Nutrient concentrations*

For nutrient analyses, samples of aboveground vascular plant parts and *Sphagnum* capitula were pooled per species for each mesocosm. Total N and phosphorus (P) concentrations were determined for ericoids, graminoids, hollow and hummock *Sphagnum* species, by digesting 300 mg of homogeneous, milled material with sulphuric acid, salicylic acid, selenium and hydrogen peroxide. All samples were analysed spectrophotometrically for total N and P using an auto-analyser (Skalar).

### Data analysis

Data were tested for normality and equality of variance. When necessary, data were ln-transformed to achieve homogeneous variances. All analyses were conducted using the SPSS statistical package for Windows (15.0). Differences between sites in nutrient deposition and water table depth in the containers were tested with one-way analysis of variance (ANOVA).

Aboveground vascular plant biomass, *Sphagnum* biomass production and nutrient concentrations of all species groups were analysed with two-way ANOVAs, with incubation site as independent factor and site of origin as random factor. Changes in vascular plant abundance and *Sphagnum* cover were analysed per site of origin, with incubation site as independent factor.

*Sphagnum* height increment was analysed with repeated measures (RM-)ANOVA, with year as the within-subject factor, site of origin, incubation site and species group (wet: *S. balticum, S. cuspidatum* and *S. fallax* or dry: *S. fuscum* and *S. magellanicum*) as the between-subject factors and vascular plant abundance in 2006 as covariate. If Maulchy's test of sphericity revealed that the assumption of homosphericity was violated, we used the Huynh-Feldt epsilon to adjust the degrees of freedom (Potvin *et al*. 1990). We also used RM-ANOVA to investigate cumulative height increment per site of origin and species, with year as the within-subject factor and incubation site as the between-subject factor. For multiple comparisons, Tukey's a posteriori test was used.

## Results

### Environmental conditions

The local official Swedish and German meteorological data for the research period show that mean temperature increases along the transect from north to south (Table 5.2). Precipitation was highest in the South Swedish site (Table 5.2). The summers of 2003 and 2006 were warm, with long dry spells. As Table 5.3 shows, the water table depth was similar in the Swedish sites but was deeper in the German site during our visits in May and August. Within each site, there were no differences in water table depth between mesocosms.

Table 5.3 shows the average N deposition per site from the EMEP model (Tarrasón *et al*. 2006) and availability of $NH_4^+$, $NO_3^-$ and $PO_4^-$ at the moss surface as measured by accumulation on ion exchange resins. Both N deposition and nitrogen availability ($NH_4^+$ and $NO_3^-$), increase from north to south along the gradient. The accumulation of $NH_4^+$ showed a gradual increase along the gradient, whereas the accumulation of $NO_3^-$ increased more sharply: it was four times higher in the southern sites 3 and 4 than in the two northern sites (Table 5.3). There was no significant site effect on $PO_4^-$ accumulation ($F = 2.07$; $P = 0.15$), although $PO_4^-$ was relatively low in sites 1 and 3.

**Table 5.2** Weather conditions in the four sites during the experimental period. For location of study sites, see Figure 5.1. Data from Sveriges Meteorologiska och Hydrologiska Institut (SMHI) and Deutscher Wetterdienst (DWD). Data from weather stations Vindeln, 21 km from N-Sweden (N-S); Uppsala, 27 km from C-Sweden (C-S); Ljungby and Torup, 30 and 26 km from S-Sweden (S-S); and Angermunde, 11 km from Germany. Spring = Mar-May, summer = Jun-Aug, autumn =Sep-Nov, winter =Dec-Feb.

| | | **Temperature (˚C)** | | | | **Sum precipitation (mm)** | | | |
|---|---|---|---|---|---|---|---|---|---|
| **Season** | **Year** | **N-Sweden** | **C-Sweden** | **S-Sweden** | **Germany** | **N-Sweden** | **C-Sweden** | **S-Sweden** | **Germany** |
| Spring | 2003 | 2.9 | 5.7 | 6.1 | 8.8 | 79 | 117 | 199 | 59 |
| | 2004 | 2.6 | 5.5 | 6.6 | 8.8 | 93 | 92 | 182 | 69 |
| | 2005 | 1.2 | 3.7 | 5.0 | 8.1 | 86 | 79 | 130 | 121 |
| | 2006 | 0.6 | 3.1 | 3.8 | 7.4 | 120 | 120 | 223 | 131 |
| Summer | 2003 | 14.6 | 16.8 | 16.4 | 19.1 | 275 | 153 | 283 | 152 |
| | 2004 | 13.1 | 15.4 | 14.8 | 17.1 | 239 | 184 | 408 | 245 |
| | 2005 | 13.9 | 15.7 | 15.1 | 16.9 | 276 | 272 | 328 | 180 |
| | 2006 | 15.4 | 17.7 | 16.7 | 19.3 | 95 | 155 | 223 | 121 |
| Autumn | 2003 | 2.3 | 6.1 | 6.9 | 8.6 | 113 | 129 | 166 | 132 |
| | 2004 | 2.2 | 6.0 | 6.8 | 9.4 | 158 | 150 | 296 | 91 |
| | 2005 | 4.4 | 7.8 | 7.8 | 10.1 | 94 | 87 | 173 | 108 |
| Winter | 2003 | -6.8 | -2.5 | -1.0 | 0.7 | 115 | 147 | 224 | 129 |
| | 2004 | -5.0 | -0.7 | 0.4 | 1.4 | 135 | 120 | 265 | 94 |
| | 2005 | -6.6 | -3.2 | -2.4 | -1.5 | 90 | 88 | 115 | 88 |
| **Average per year** | | **3.9** | **7.0** | **7.4** | **9.6** | **550** | **533** | **907** | **483** |

**Table 5.3** Environmental conditions in the four sites (see Figure 5.1). Nitrogen deposition values are averages from the EMEP model for the period 1994-2004 (Tarrasón *et al*. 2006); accumulation of nutrients between May 2005 and May 2006 on ion-exchange resins placed on the moss surface (n=4-5); average water table depth in container (cm below moss surface) over eight measurements in May and August, n=5-10-15-20. Data are mean values ± SE. Different letters indicate significant differences between sites.

| | **N-Sweden** | **C-Sweden** | **S-Sweden** | **Germany** |
|---|---|---|---|---|
| N deposition (g m$^{-2}$) | 0.3 | 0.6 | 1.1 | 1.5 |
| Exchangeable nutrients (µg g$^{-1}$) | | | | |
| $NH_4^+$ | 10 ± 2 a | 19 ± 6 ab | 20 ± 2 ab | 28 ± 6 b |
| $NO_3^-$ | 31 ± 2 a | 38 ± 5 a | 150 ± 38 b | 126 ± 31 b |
| N total | 41 ± 4 a | 58 ± 10 a | 170 ± 39 b | 154 ± 36 b |
| $PO_4^-$ | 1 ± 1 | 4 ± 2 | 2 ± 1 | 6 ± 1 |
| Water table depth (cm) | 15 ± 3 a | 12 ± 2 a | 13 ± 1 a | 23 ± 1 b |

Vascular plant abundance

At the end of the experimental period, total aboveground vascular plant biomass was similar in all containers within each incubation site. Total vascular plant biomass was greater in incubation site 4 (240 ± 18 g $m^{-2}$) than in sites 1, 2 and 3 (140 ± 19, 170 ± 17 and 109 ± 8 g $m^{-2}$, respectively), (F = 57.068, *P* = 0.004). This was mainly due to the biomass of ericoids: ericoid biomass was higher in incubation site 4 than in the other sites (Table 5.4). For graminoids, there was no overall effect of incubation site on biomass, but graminoid biomass in containers from C-Sweden was higher in site 2 than in site 3 (Table 5.4).

In containers from all sites of origin, the abundance of ericoid species increased most in incubation site 4 (Fig. 5.2). This was mainly due to an increase in *V. oxycoccus* and *C. vulgaris*. There was no significant effect of incubation site on graminoid abundance, although the graminoid increase in mesocosms from the northernmost site was greatest in site 2.

**Table 5.4** Aboveground vascular plant biomass for ericoid and graminoid species (for site locations, see Figure 5.1). Different upper case letters indicate significant overall differences between incubation sites (F = 14.976, P=0.026) for ericoid species. There was no significant effect of site of origin on ericoid biomass (F = 3.010, P=0.195). There were no significant overall effects of incubation site (F = 5.131, P=0.106) and site of origin (F = 4.084, P=0.139) on graminoid biomass. Different lower case letters indicate significant differences between incubation sites per site of origin (P < 0.05).Data are mean values ± SE, n = 5.

| | Site of Origin | Incubation site | | | |
|---|---|---|---|---|---|
| | | 1 | 2 | 3 | 4 |
| Ericoid biomass (g) | N-Sweden | 82 ± 23 ab | 77 ± 17 ab | 68 ± 8 a | 148 ± 25 b |
| | C-Sweden | | 80 ± 13 ab | 60 ± 11 a | 154 ± 36 b |
| | S-Sweden | | | 38 ± 4 a | 140 ± 12 b |
| | Germany | | | | 239 ± 14 |
| | | A | A | A | B |
| Graminoid biomass (g) | N-Sweden | 58 ± 14 | 101 ± 22 | 44 ± 6 | 64 ± 8 |
| | C-Sweden | | 78 ± 13 b | 27 ± 4 a | 56 ± 17 ab |
| | S-Sweden | | | 89 ± 12 | 76 ± 13 |
| | Germany | | | | 77 ± 13 |

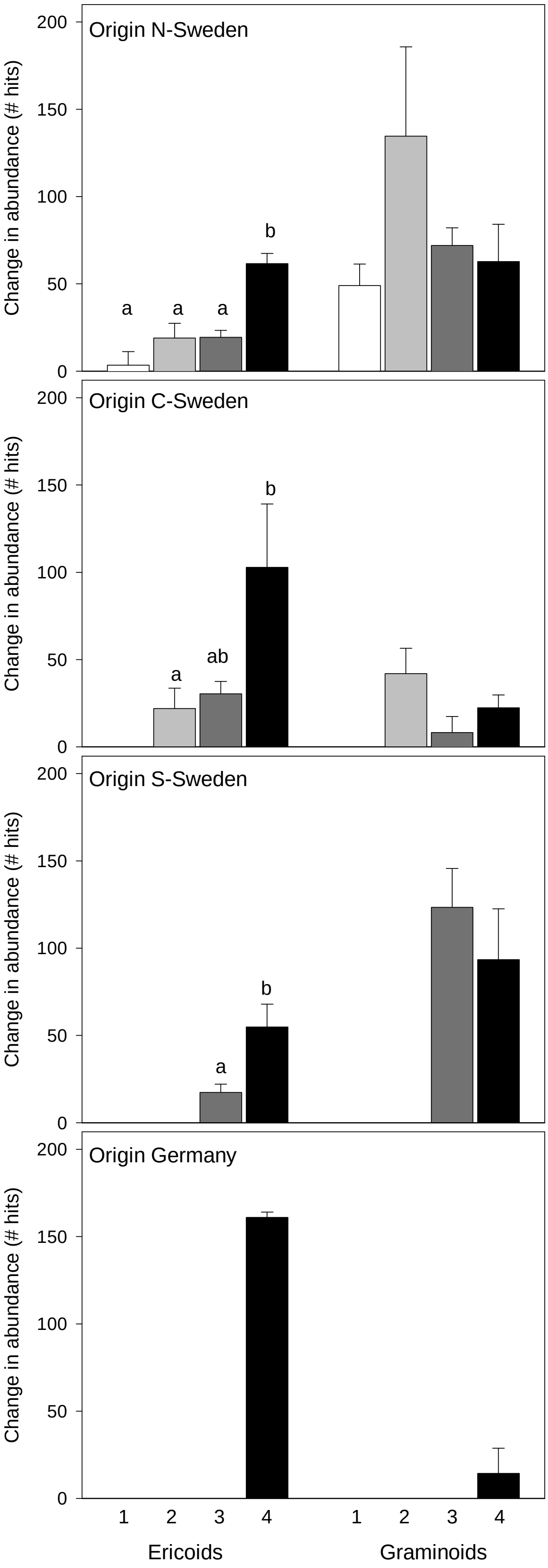

**Figure 5.2** Change in vascular plant cover from August 2003 – August 2006, per site of origin. Different letters indicate significant differences between incubation sites for ericoids. There were no significant effects of incubation site on graminoids. Data are mean values ±SE, n=5. For description of incubation sites, see Table 5.2 and Figure 5.1.

*Sphagnum*

There were significant differences in height increment between different sites of origin and incubation sites (Table 5.5). Height increment was greatest in mesocosms from the two northernmost sites N- and C-Sweden, and least in mesocosms from the south Swedish site (Fig. 5.3). Height increment was least in *S. cuspidatum* and *S. magellanicum* from S-Sweden and *S. fallax* from Germany (Fig. 5.3). There was a significant interaction of time x incubation site x species group (Table 5.5). Height increment of the 'wet' species was affected by incubation site and time x incubation site, but height increment of the 'dry' species was not. The effect of incubation site on the 'wet' species was greatest in the first two years of the experiment. A comparison of total height increment per species and site of origin revealed that the height increment of *S. balticum* from C-Sweden was significantly less in incubation sites 3 and 4 than in C-Sweden (Fig. 5.3). The height increment of *S. balticum* from N-Sweden also decreased southwards, but not statistically significantly (F = 3.022, *P* = 0.060).

**Table 5.5** Results of RM-ANOVA for cumulative *Sphagnum* height increment (cm) over the period May 2003 to September 2006. Site of origin, incubation site and species group (wet or dry) were tested as fixed factors, change in vascular plant cover was tested as a covariate.

| Source | df | F | *P* |
|---|---|---|---|
| **Between-subjects** | | | |
| Vascular plant cover | 1 | 2.86 | 0.095 |
| Site of origin | 3 | 9.63 | **<0.001** |
| Incubation site | 3 | 7.75 | **<0.001** |
| Species group | 1 | 0.03 | 0.869 |
| Origin x Incubation | 3 | 0.50 | 0.687 |
| Origin x Species | 3 | 1.43 | 0.239 |
| Incubation x Species | 3 | 2.63 | 0.055 |
| | | | |
| **Within-subjects** | | | |
| Time | 1.92 | 6.05 | **0.003** |
| Time x Vascular plant cover | 1.92 | 1.05 | 0.351 |
| Time x Origin | 5.76 | 8.75 | **<0.001** |
| Time x Incubation | 5.76 | 2.11 | 0.058 |
| Time x Species | 1.92 | 0.95 | 0.384 |
| Time x Origin x Incubation | 5.76 | 1.07 | 0.379 |
| Time x Origin x Species | 5.76 | 0.90 | 0.494 |
| Time x Incubation x Species | 5.76 | 3.43 | **0.004** |

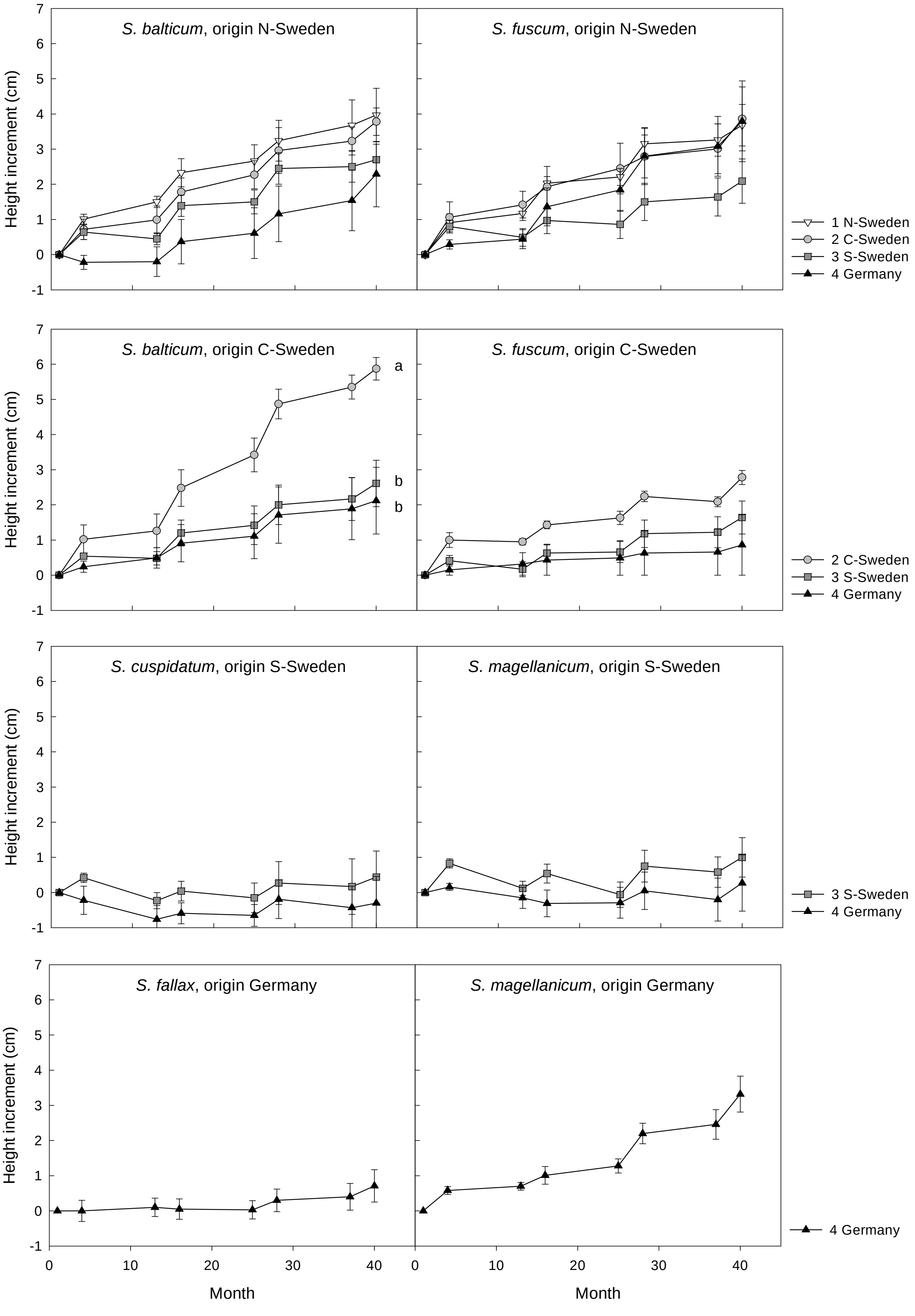

**Figure 5.3** Cumulative height increment *Sphagnum* from May 2003 – August 2006 per species per site of origin. Different letters indicate significant differences between incubation sites, tested with RM-ANOVA per site of origin and species. Data are mean values ±SE, n=5. For description of incubation sites, see Table 5.2 and Figure 5.1.

**Table 5.6** Average *Sphagnum* biomass production between May and September, calculated from height increment in summer 2004, 2005 and 2006, per site of origin and incubation site (see Figure 5.1). There were no significant overall effects of incubation site (F = 0.059, P=0.978) and site of origin (F = 2.224, P=0.264) on *Sphagnum* production. Data are mean values ± SE, n = 5.

| | Site of Origin | Incubation site | | | |
|---|---|---|---|---|---|
| | | 1 | 2 | 3 | 4 |
| Production (g.m$^{-2}$) | N-Sweden | 142 ± 20 | 123 ± 16 | 147 ± 13 | 174 ± 24 |
| | C-Sweden | | 152 ± 15 | 126 ± 12 | 114 ± 13 |
| | S-Sweden | | | 97 ± 13 | 54 ± 31 |
| | Germany | | | | 93 ± 22 |

There were no overall effects of incubation site and site of origin on *Sphagnum* biomass production (Table 5.6). Neither was there any effect of incubation site within containers from each site of origin.

Small shifts in species composition occurred in the *Sphagnum* layer (Fig. 5.4). There were no overall effects of incubation site (F = 0.237, *P* = 0.866) and site of origin (F = 0.512, *P* = 0.702) on 'wet' *Sphagnum* species cover, but there was a significant interaction of incubation site x site of origin (F = 5.412, *P* = 0.003). *S. balticum* increased in mesocosms from N-Sweden transplanted to sites 2 and 3, while *S. balticum* decreased in N-Sweden mesocosms transplanted to site 4 (Fig. 5.4). *S. balticum* in mesocosms from C-Sweden decreased in all incubation sites, but the negative effect was only significant in sites 3 and 4 (Fig. 5.4).

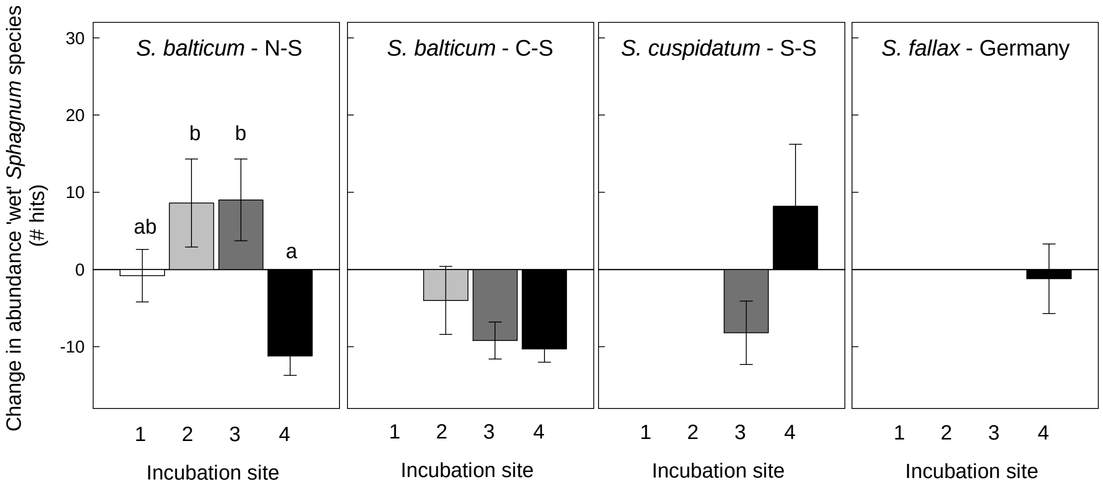

**Figure 5.4** Change in cover of 'wet' *Sphagnum* species per site of origin from August 2003 – August 2006. The response of the 'dry' *Sphagnum* species was the reverse: the total cover of *Sphagnum* did not change. Different letters indicate significant differences between incubation sites (P < 0.05). Data are mean values ±SE, n=5. For description of incubation sites, see Table 5.2 and Figure 5.1.

Nutrient concentrations

N concentration in ericoids and graminoids showed small differences between sites of origin and incubation sites (Fig. 5.5A and 5.5B). There was no significant effect of incubation site on N concentration in ericoids, N concentration in graminoids was higher in incubation site 3 than in incubation sites 1 and 2, and was higher in site 4 was than in site 2. In *Sphagnum*, N concentrations increased southwards, from 5.3 and 6.5 mg $g^{-1}$ in the north of Sweden, to 11.5 and 11.8 mg $g^{-1}$ in Germany, for wet and dry species respectively (Fig. 5.5C and 5.5D).

P concentrations in ericoids and both *Sphagnum* groups were lowest in site 3, and highest in site 4 (data not shown). P concentration in graminoids did not differ between incubation sites. As a result, the N:P ratio in ericoids and both *Sphagnum* groups was highest in incubation site 3 and in material originating from that site (Fig. 5.6A, 5.6C and 5.6D). The N:P ratio in graminoids was higher in site 3 than in site 1 (Fig. 5.6B).

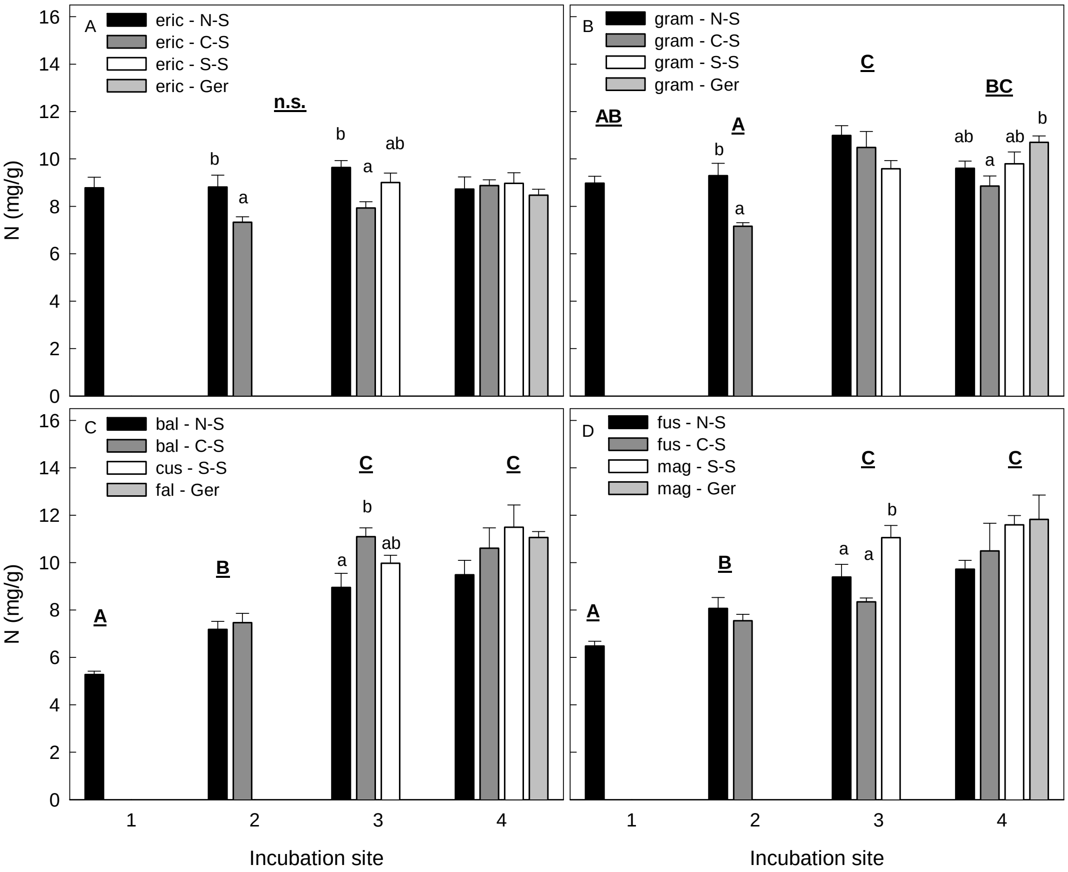

**Figure 5.5** N concentration of A) ericoids, B) graminoids, C) wet *Sphagnum* species (bal: *S. balticum*, cus: *S. cuspidatum*, fal: *S. fallax*) and D) dry *Sphagnum* species (fus: *S. fuscum*, mag: *S. magellanicum*). Data are mean values ±SE, n=5. Capital letters indicate significant differences between incubation sites ($P < 0.05$). Lower case letter indicate significant differences between sites of origin within an incubation site. For description of sites, see Table 5.2 and Figure 5.1.

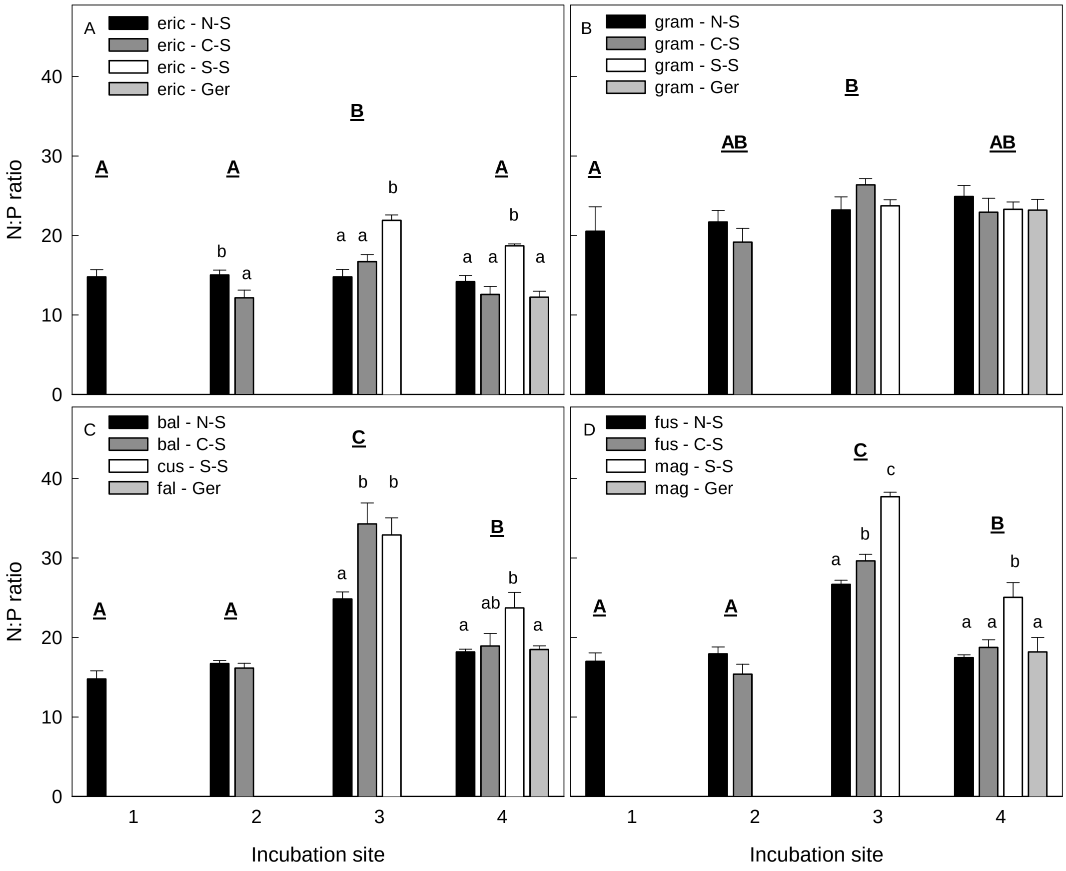

**Figure 5.6** N:P ratio of A) ericoids, B) graminoids, C) wet *Sphagnum* species (bal: *S. balticum*, cus: *S. cuspidatum*, fal: *S. fallax*) and D) dry *Sphagnum* species (fus: *S. fuscum*, mag: *S. magellanicum*). Data are mean values ±SE, n=5. Capital letters indicate significant differences between incubation sites ($P < 0.05$). Lower case letter indicate significant differences between sites of origin within an incubation site. For description of incubation sites, see Table 5.2 and Figure 5.1.

## Discussion

In this study of the expected effects of increased temperature and N deposition on bog vegetation we found that in mesocosms transplanted southwards the cover of ericoids increased, while there was no overall effect on graminoid and *Sphagnum* cover and *Sphagnum* production. *S. balticum* height increment did decrease towards the south. N concentrations in plant tissue increased southwards, especially in *Sphagnum*.

### Vascular plants

As we had expected, the southwards transplantation of bog mesocosms had a positive effect on vascular plant cover. This was mainly attributable to increased cover and biomass of ericoids (Fig. 5.2, Table 5.4). We ascribe this increase in ericoids to the higher temperature and increased N deposition towards the south. However, we expected that graminoids would also profit from being transplanted further south. There are several possible reasons for the difference in response between these two groups. One is the difference in rooting depth between the two species groups: in general, graminoid species have aerenchyma and can therefore root deeper than ericoids, which have more superficial roots (Rydin and Jeglum 2006). So, given that N deposition increased southwards and so did the N concentration in the top layer of the peat, the ericoids could have profited more from the increased availability of N than graminoids. In other experiments is has also been found that shallow-rooting species like *V. oxycoccus* respond more to N addition than graminoid species (Heijmans *et al.* 2001b; Lutke Twenhoven 1992; Wiedermann *et al.* 2007). However, in our study there was no difference in the N concentrations of the graminoids and ericoids (Fig. 5.5). Since the N:P ratios of the graminoids were not only higher than those of ericoids, but also all exceeded the critical value of 15 (Koerselman and Meuleman 1996; Verhoeven 1996) (Fig. 5.6), it seems likely that graminoids are more limited by P availability, whereas ericoids are co-limited by both N and P.

It is known that ericoids respond more to increased temperature than graminoids (Weltzin *et al*. 2000), especially in arctic and subarctic tundra (Dorrepaal *et al.* 2006; Sturm *et al.* 2001). The increased temperature might also have enhanced nutrient mineralisation (Chapin *et al.* 1995, Breeuwer *et al.* 2008b), which makes it likely that the observed increase of ericoids in our bog sites can at least partly be ascribed to the southward increase in temperature and N. However, it cannot be ruled out that the large increase of ericoids in the German site is to some extent caused by the lower water table here (Table 5.3). Higher temperatures also have an indirect effect by increasing potential evapotranspiration and thereby reducing effective precipitation. This seems to have happened in the German site. In this respect, the south Swedish site is somewhat of an outlier due to its high precipitation (Table 5.2); this could explain why the ericoid biomass was relatively small in mesocosms transplanted to this site (Table 5.4).

### *Sphagnum*

Contrary to our hypothesis, we found that transplanting the mesocosms southwards had no positive effect on either the height increment or production of *Sphagnum* (Fig. 5.3 and Table 5.6). In sites 3 and 4, *Sphagnum* biomass production was greatest in mesocosms from the two northernmost sites (Table 5.6). The reason for the relatively small height increment of *S. cuspidatum* and *S. magellanicum* in mesocosms from S-Sweden seems to be the structure of the peat in this site. Palaeoecological research has shown that the site was severely drained in the past, leaving a dark, very decomposed layer at between ca. 19 and 40 cm depth (van der Linden 2006). After 1960 the raised bog vegetation regenerated vigorously, resulting in a very low bulk density in the top 20 to 40 cm. Because of this low density, when the mesocosms (all 40 cm deep) were dug out from this site and placed in the containers they suffered more compaction and damage than those from the other sites. The more fragile species *S. cuspidatum* suffered particularly from this treatment.

The finding that the height increment of *S. balticum* actually decreased southwards (Fig. 5.3) is remarkable, given that the N concentration in *Sphagnum* increased southwards (Fig. 5.5) as did the maximum photosynthetic rate (Granath *et al.*, in review). Higher photosynthetic rates should have been possible, given that the temperatures in the three Swedish sites were below optimum for *Sphagnum*, which is between 20 and 25 ˚C (Harley *et al.* 1989; Skre and Oechel 1981), and that southwards the temperature increased. There are four factors that could be responsible for the sub-optimal biomass production. The first is insufficient availability of water – as suggested by the fact that in mesocosms from the two northern sites the *Sphagnum* height increment was least in 2003 (Fig. 5.3), which had a relatively dry and warm summer (Table 5.2). This factor would also explain the small height increment in the German site, which had the lowest water level during our measurements (Table 5.3), and the stronger negative effect on *S. balticum* than on the hummock species *S. fuscum* when transplanted to the south. The low water availability combined with high summer temperatures caused *Sphagnum* capitula to dry out (personal observations), thereby strongly reducing photosynthesis (Schipperges and Rydin 1998). From the remarkable difference in height increment between *S. fuscum* from N-Sweden and C-Sweden (Fig. 5.3) we infer that *S. fuscum* from N-Sweden was better able to withstand drought, which resulted in the higher total *Sphagnum* production in site 4.

The second factor that could account for the absence of a positive transplantation effect could be that N is not the limiting nutrient, but P is. Indications of P limitation in *Sphagnum* have been found in other studies (Aerts *et al*. 1992; Limpens *et al*. 2004). There is evidence that P limitation is responsible for the relatively low height increment of Sphagnum at site 3, as at this site, $PO_4$ availability was relatively low (Table 5.3) and the N:P ratios were the highest of all sites – well above the critical value of 15 (Fig. 5.6) – indicating that P was limiting growth (Aerts *et al*. 1992; Limpens *et al*. 2003). The N:P ratio of *Sphagnum* from S-Sweden in incubation site 4 was also relatively high, even 3 years after the transplantation, and this too could account – at least partly – for the small height increment and production of *S. cuspidatum* and *S magellanicum* from S-Sweden. In addition, the N deposition in the two southern sites could have had direct negative effects on *Sphagnum*, as it has been found that N deposition values larger than 1-1.5 g $m^{-2}$ depress *Sphagnum* production (Bragazza *et al.* 2004; Gunnarsson and Rydin 2000; Vitt *et al.* 2003). However, the N concentrations we found in *Sphagnum* (Fig. 5.5) are still relatively low and are below the critical threshold of 12 mg $g^{-1}$ mentioned by Lamers *et al*. (2000).

A third possible explanatory factor for the relatively small *Sphagnum* growth – the increased vascular plant cover – was found to be a non-significant co-variable (Table 5.5). The cover of vascular plants was probably too sparse to affect *Sphagnum* growth. Heijmans *et al*. (2002) suggest that the cover of vascular plants has to be at least 60% to negatively affect *Sphagnum* production. The value of 240 ± 17 g $m^{-2}$ we found for total above ground vascular biomass in the German site is not high (Bubier *et al.* 2003; Chapin *et al.* 1995; Heijmans *et al.* 2002). In a comparable experiment we found that this value corresponds to a light interception of approximately 40 % (Chapter 4).

The fourth and final possible reason for the lack of response in *Sphagnum* (and graminoids) to transplantation southwards could be that the duration of the experiment was too short. In other field studies in bogs, the effects of increased temperature and N addition were not visible for the first 4-5 years (Bubier *et al*. 2007; Wiedermann *et al*. 2007) and short-term (3 yr) responses were poor predictors of longer-term (9yr) changes in community composition (Chapin *et al*. 1995).

### Implications of global change for bog ecosystems

Based on our study we conclude that increased temperature and N deposition lead to an increase in ericoid cover. If high N availability through deposition and mineralisation continues, the N concentration in *Sphagnum* will increase, leading to N-enriched peat, which would stimulate ericoids even more. In the longer term, the increase in vascular plants could depress *Sphagnum* production. Since *Sphagnum* production does not profit from global change and will therefore not depress vascular plant growth, the competitive balance between vascular plants and *Sphagnum* will shift to the benefit of vascular plants. This will increase the proportion of vascular plant litter in peat. As vascular plant litter is much more decomposable than *Sphagnum* litter (Bragazza *et al.* 2007; Dorrepaal *et al.* 2005; Hobbie 1996) and its decomposition is accelerated more by an increase in temperature (Breeuwer *et al.* 2008b), the litter turnover will accelerate and nutrients will become more readily available – benefiting the vascular plants more than the *Sphagnum*. In time, more nutrients will become available at deeper levels, and graminoids will also profit. If the total cover of ericoids and graminoids were to increase, shading from the vascular plants could adversely affect *Sphagnum* growth. Consequently, in the long term, global change could have a serious negative effect on *Sphagnum* production and on the capacity of ombrotrophic bogs to sequester carbon.

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# CHAPTER 6

# The effect of increased temperature and nitrogen deposition on decomposition in bogs.

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## Abstract

Despite their low primary production, ombrotrophic peatlands have a considerable potential to store atmospheric carbon as a result of their extremely low litter decomposition rates. Projected changes in temperature and nitrogen (N) deposition may increase decomposition rates by their positive effects on microbial activity and litter quality, which can be expected to result in enhanced mass loss and N release from *Sphagnum* and vascular plant litter. This is the first study that examines the combined effects of increased temperature and N deposition on decomposition in bogs. We investigated mass loss and N release at four bog sites along a gradient from North-Sweden to North-East Germany in which both temperature and N deposition increased from north to south. We performed two litterbag experiments: one reciprocal experiment with *Eriophorum vaginatum* litter and one experiment using recalcitrant (*Sphagnum fuscum*) and more degradable (*Sphagnum balticum*) *Sphagnum* litter collected from the most northern site. We measured mass loss and N release during two (*Sphagnum*) and three (*E. vaginatum*) years. The N concentration and decomposability of the *E. vaginatum* litter did not differ between the sites. Mass loss from *E. vaginatum* litter increased over the gradient from north to south, but there was no such effect on *Sphagnum* litter. N loss of all litter types was affected by collection site, incubation site and time and all interactions between these factors. N release in *Sphagnum* was positively related to N concentration.

We conclude that decomposition of vascular plants and *Sphagnum* litter is influenced by different environmental drivers, with enhanced temperatures stimulating mass loss of vascular plant litter, but not of *Sphagnum*. Enhanced N deposition increases *Sphagnum* litter N loss. As long-term consequences of climate change will presumably entail a higher vascular plant production, overall litter decomposition rates are likely to increase, especially in combination with increased temperature.

## Introduction

Peatlands from the northern hemisphere store about 455 Pg (Pg $=10^{15}$ g) of carbon, which is roughly one third of the total global soil C pool, and currently serve as a net sink for atmospheric carbon (Rydin and Jeglum 2006). A large proportion of northern peatlands consists of *Sphagnum* dominated ombrotrophic bogs. These bogs play an important role in carbon sequestration, despite their relatively low primary production, due to very low litter decomposition rates (Clymo 1984). The slow decomposition in bogs is mainly caused by three factors: first, the very harsh abiotic conditions, being wet, cold, anoxic and acidic. Second, the low quality of plant litter (Aerts *et al.* 1999; Dorrepaal *et al.* 2005) and third, the excretion of secondary plant compounds by *Sphagnum* that interfere with fungal and bacterial breakdown (Painter 1991; van Breemen 1995). Since *Sphagnum* species are the major primary producers in ombrotrophic bogs and produce very recalcitrant litter, the main part of the peat layer is formed by *Sphagnum* remnants.

Global change is expected to have a strong impact on temperature, precipitation and nutrient deposition at northern latitudes (Solomon *et al*. 2007). Global change models predict great variability in future precipitation patterns, but all models predict an increase in temperature and nitrogen (N) deposition (Galloway *et al.* 2004; Solomon *et al.* 2007). When these changes (in temperature and N deposition) alter the current imbalance between net primary production and decomposition responsible for the carbon sequestration in bogs, this can have a serious impact on the global carbon budget. In general, climate warming is expected to increase *Sphagnum* productivity, as long as water does not become limiting (Dorrepaal *et al.* 2006; Gunnarsson 2005; Moore 1989; Robroek *et al.* 2007). The effect of increased N deposition is less straight forward; a small increase in N can enhance *Sphagnum* production at locations where N is a limiting nutrient (Turunen *et al*. 2004). When N concentrations come above a critical threshold value, however, *Sphagnum* production and cover are reduced (Berendse *et al.* 2001; Gerdol *et al.* 2007; Gunnarsson and Rydin 2000). In contrast, vascular plant cover and production are stimulated by both increased temperature and N deposition (Berendse *et al.* 2001; Bubier *et al.* 2007; Wiedermann *et al.* 2007).

Decomposition in bogs can be affected by temperature and N deposition both directly and indirectly. Increased temperature can directly increase decomposition rates due to higher microbial activity (Dioumaeva *et al.* 2002; Hobbie 1996). Indirectly, an increase in temperature may stimulate aerobic decomposition (Schouten 1992) through its negative effect on the water table and the subsequent increase of the oxic layer depth. A direct effect of increased N deposition can be that N limitation on microbial metabolism is alleviated in the nutrient poor bog ecosystems, allowing breakdown of less nutrient rich litter (Bragazza *et al.* 2006; Mack *et al.* 2004). Indirectly, enhanced N deposition and temperature may cause changes in species composition, generally favouring vascular plants (Berendse *et al.* 2001; Bubier *et al.* 2007; Heijmans *et al.* in press; Limpens *et al.* 2003; Wiedermann *et al.* 2007). Comparative studies on the decomposition of *Sphagnum* and vascular plant in peatlands consistently showed that vascular plant litter is decomposed at a higher rate than *Sphagnum* litter (Bragazza *et al.* 2007; Coulson and Butterfield 1978; Dorrepaal *et al.* 2005; Hobbie 1996), so an increased vascular plant fraction in the litter will result in higher turnover rates of the peat. Moreover, as most plant material in northern bogs is still N-limited, increased N deposition can be expected to decrease C:N ratios and secondary plant compounds in the litter, which has been shown to enhance decomposition rates (Bragazza *et al.* 2006; Dorrepaal *et al.* 2005; Gerdol *et al.* 2007).

So far, most of the studies dealing with the effects of temperature and N on decomposition have tested their effects separately , often using an experimental approach, where bog vegetation was subjected to a stepwise increase in temperature an/ or N. A disadvantage from this can be that the microbial community is not adapted to the changed conditions, and therefore effects on decomposition are different from what they would be under more gradual global change. In this study we set out to test the effects of more gradual changes in both temperature and N deposition on mass loss and N loss of vascular plant and *Sphagnum* litter in bog ecosystems, by making use of a latitudinal gradient throughout NW-Europe (Fig. 6.1). In this transect from North-Sweden to North East-Germany, both temperature and N deposition increased from north to south (Table 6.1). We performed two litterbag experiments: one reciprocal experiment with *Eriophorum vaginatum* litter, to separate between the direct and indirect effects of increased temperature and N deposition. We used *E. vaginatum* as a representative species for vascular plants. We chose for *E. vaginatum* because this was the only species that occurred at all four bog sites. In the second experiment we used recalcitrant (*Sphagnum fuscum*) and more degradable (*S. balticum*) *Sphagnum* litter collected from the northernmost site to examine direct effects of increased temperature and N deposition on decomposition of *Sphagnum* litter differing in quality. We tested the hypothesis that (1) increased N deposition would indirectly stimulate mass loss of *E. vaginatum* litter by affecting litter N concentration and C:N ratio. As a result we expected that within each incubation site, decomposition rate would be determined by litter quality, with N enriched litter decomposing at the highest rate. We further tested the hypothesis that (2) as a direct result of increased temperature and N deposition on decomposition environment decomposition rate would increase towards the south, irrespective of litter type and (3) that N release would increase towards the south as well.

**Figure 6.1** Location of 4 research sites. 1= Lappmyran (N-Sweden) 64° 10'N, 19° 35'E, 2= Åkerlänna Römosse (C-Sweden) 60° 01'N, 17° 22'E, 3= Saxnäs mosse (S-Sweden) 56° 51'N, 13° 28'E, 4= Barschpfuhl (Germany) 53° 03'N, 13° 51'E

## Material and Methods

### Study Sites

The experiment was executed between August 2003 and August 2006 in four raised bogs, situated over a latitudinal gradient from the north of Sweden to the north of Germany (Fig. 6.1). Temperature and precipitation over the experimental period are summarized in Table 6.1, together with average N deposition per site. Both the mean temperature and N deposition increase over the gradient from north to south. Precipitation is higher in the South-Swedish site than in the other sites. We selected bog sites that were relatively undisturbed, with a peat layer of at least 5 meters deep and vegetation characteristic for ombrotrophic mires. However, there are some differences between the sites.

The North-Swedish site Lappmyran (N-Sweden) is an aapa mire with strings of hummock and hollow vegetation. The hollows are dominated by *Sphagnum balticum* (Russow) Russow ex C. Jens. and *Scheuzeria palustris* L. while the hummock vegetation consists of *Sphagnum fuscum* (Schimp) Klinggr with a vascular plant cover of mainly *Andromeda polifolia* L.*, Calluna vulgaris* (L.) Hull*, Drosera rotundifolia* L., *Empetrum nigrum* L., *Eriophorum vaginatum* L., *Vaccinium oxycoccus* L. and *Rubus chamaemorus* L..

The peatland surface at the Central-Swedish site Åkerlänna Römosse (C-Sweden) shows a typical microtopographical pattern of hollows, lawns and hummocks. The dominant species are: *Sphagnum lindbergii* Schimp. in low hollows, *S. balticum* in hollows and lawns and *S. fuscum* on hummocks, with vascular plant cover of *A. polifolia*, *C. vulgaris*, *D. rotundifolia*, *E. nigrum*, *E. vaginatum* and *V. oxycoccus.*

The South-Swedish site Saxnäs mosse (S-Sweden) has a typical raised bog vegetation with a mosaic of hollows, lawns and hummocks. The dominant species are: *Sphagnum cuspidatum* Ehrh. Ex Hoffm. in the hollows, *Sphagnum magellanicum* Brid. in lawns and *S. fuscum* on hummocks, with vascular plant cover of *Rhynchospora alba* (L.) Vahl in hollows and *A. polifolia*, *C. vulgaris*, *D. rotundifolia*, *Erica tetralix* L., *E. vaginatum* and *V. oxycoccus* on lawns and hummocks.

The German site, Barschpfuhl (Germany), is a small mire, situated in a mixed forest. There is no clear distinction between hollows and hummocks and vegetation is dominated by *S. magellanicum* and *S. fallax* (Klinggr.) Klinggr. with a vascular plant cover of mainly *C. vulgaris, D. rotundifolia*, *Eriophorum angustifolium* (Honckeny), *E. vaginatum*, *R. alba* and *V. oxycoccus*.

**Table 6.1** Weather conditions in the four sites during the experimental period. N-S = North-Sweden, Lappmyran, C-S = Central-Sweden, Åkerlänna Römosse, S-S = South-Sweden, Saxnäs mosse, Germany= Barschpfuhl. Data from Sveriges Meteorologiska och Hydrologiska Institut (SMHI) and Deutscher Wetterdienst (DWD). Nitrogen deposition values are averages from the EMEP model for the period 1994-2004 (Tarrasón *et al*. 2006).

| | | **Temperature (°C)** | | | | | **Sum precipitation (mm)** | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| **Season** | **Year** | **N-S** | **C-S** | **S-S** | **Germany** | | **N-S** | **C-S** | **S-S** | **Germany** |
| Spring | 2003 | 2.9 | 5.7 | 6.1 | 8.8 | | 79 | 117 | 199 | 59 |
| | 2004 | 2.6 | 5.5 | 6.6 | 8.8 | | 93 | 92 | 182 | 69 |
| | 2005 | 1.2 | 3.7 | 5.0 | 8.1 | | 86 | 79 | 130 | 121 |
| | 2006 | 0.6 | 3.1 | 3.8 | 7.4 | | 120 | 120 | 223 | 131 |
| Summer | 2003 | 14.6 | 16.8 | 16.4 | 19.1 | | 275 | 153 | 283 | 152 |
| | 2004 | 13.1 | 15.4 | 14.8 | 17.1 | | 239 | 184 | 408 | 245 |
| | 2005 | 13.9 | 15.7 | 15.1 | 16.9 | | 276 | 272 | 328 | 180 |
| | 2006 | 15.4 | 17.7 | 16.7 | 19.3 | | 95 | 155 | 223 | 121 |
| Autumn | 2003 | 2.3 | 6.1 | 6.9 | 8.6 | | 113 | 129 | 166 | 132 |
| | 2004 | 2.2 | 6.0 | 6.8 | 9.4 | | 158 | 150 | 296 | 91 |
| | 2005 | 4.4 | 7.8 | 7.8 | 10.1 | | 94 | 87 | 173 | 108 |
| Winter | 2003 | -6.8 | -2.5 | -1.0 | 0.7 | | 115 | 147 | 224 | 129 |
| | 2004 | -5.0 | -0.7 | 0.4 | 1.4 | | 135 | 120 | 265 | 94 |
| | 2005 | -6.6 | -3.2 | -2.4 | -1.5 | | 90 | 88 | 115 | 88 |
| **average (°C)** | | **3.9** | **7.0** | **7.4** | **9.6** | **(mm.year$^{-1}$)** | **550** | **533** | **907** | **483** |
| **N deposition (g.m$^{-2}$)** | | **0.3** | **0.6** | **1.1** | **1.5** | | | | | |

Experimental set up and measurements

We used litter of *E. vaginatum* from all four sites and litter of *S. fuscum* and *S. balticum* from the most northern site (N-Sweden). The *E. vaginatum* material was collected as standing dead leaves and stems in May 2003. All material was oven-dried for at least 48 h at 30°C and then cut into pieces of ca. 3 cm. Samples of 1.3 g were enclosed in litterbags (5 by 5 cm) from polypropylene mesh with a 100 µm mesh size. Mesh of this size allows microfauna and fungi to enter, but excludes macrofauna and prevents loss of dead leaf material (Limpens and Berendse 2003). For each litter type, ten additional litterbags were used to determine initial nutrient concentrations. Litterbags were stored at room temperature and in August 2003 the litterbags were taken to the four field sites. In each site we placed ten poles in lawn or low hummock vegetation. To each pole, we attached four stainless steel rings, each ring holding three litterbags of one of the four litter types. The litterbags were attached to the rings using a ca. 50 cm long wire, and were inserted 5-10 cm below the moss surface. Before placement, all plant litter was rewetted by immersing the litter bags in nearby bog water. In August 2004, 2005 and 2006 we collected a litterbag from each ring on each pole, so ten litterbags from each litter type were retrieved from each site after 1, 2 and 3 years.

*Sphagnum* material was collected as monoculture sods of 10 by 15 cm in August 2003. We extracted *Sphagnum* individuals from the sods and cut off the capitula (0-1 cm) and stem (1-4 cm) section. Decomposition of *Sphagnum* litter is a continuous process which makes it virtually impossible to determine when *Sphagnum* litter begins to decompose (Hogg 1993). So, in accordance with previous studies (Aerts *et al.* 2001; Bragazza *et al.* 2007; Limpens and Berendse 2003), we used the stem section of 1-4 cm as representative of freshly deposited

*Sphagnum* litter which is still stored in the acrotelm. We used the capitulum section to compare *Sphagnum* litter with different nutrient contents. This resulted in four types of material: *S. balticum* capitula, *S. balticum* stem, *S. fuscum* capitula and *S. fuscum* stem. For each litter type the material was mixed thoroughly and oven-dried for at least 48 h at 30°C. Samples of 0.5 g were enclosed in similar litterbags as the *E. vaginatum* material. In May 2004 the litterbags were inserted in the four field sites in the same way as the *E. vaginatum* litterbags. The *Sphagnum* litterbags were collected after 3 months, 1 and 2 years (August 2004, May 2005 and May 2006). We did not continue the experiment with the *Sphagnum* litterbags for three years, like we did for *E. vaginatum*, since other studies have experienced hampered ability to determine *Sphagnum* mass loss after longer term incubation (Dorrepaal *et al.* 2005; Johnson and Damman 1993).

After collection, all litterbags were oven-dried for at least 48 h at 30°C to determine mass loss. Ingrown roots were removed before weighing the content of the litterbags. After weighing the litter, it was oven-dried for 48h at 70°C and then pulverized. C and N concentrations were measured using an elemental analyzer (Fisions Instruments EA 1108, Milan Italy) and used to calculate the C:N ratio. For N, P and K analyses, dried and pulverized material was digested with sulphuric acid, salicylic acid, selenium and hydrogen peroxide. Subsequently, the N and P concentrations were measured colorimetrically, using a continuous flow analyser (SKALAR SAN plus systems, The Netherlands). K was measured by atomic emission flame spectroscopy (Varian AAS).

Calculations and statistical analysis

The percentage remaining mass, after each period of incubation, was calculated as a percentage of the initial mass before incubation. Remaining N was calculated per litterbag from the initial N concentration per litter type and the remaining weight and N concentration after incubation:

$$\text{Remaining N} = \frac{[N]t_x \times Wt_x}{[N]t_0 \times Wt_0}$$

in which $[N]t_x$ is the N concentration in litter after x years, $Wt_x$ is the mass of the litter left after x years , $[N]t_0$ is the average N concentration of the initial litter and $Wt_0$ is the initial mass of the litter. Decomposition constants (i.e. k-values) were estimated by assuming a negative exponential model (Olson 1963; Scheffer *et al.* 2001):

$$\ln\left(\frac{Wt_x}{Wt_0}\right) = -kt$$

in which t is time in years and k is the decomposition constant. For each combination of litter type and incubation site, a regression was performed of the natural logarithm of remaining mass with time, with the intercept of the regression line assumed to go through ln(1) =0 at time 0.

All data analyses were conducted using the SPSS statistical package for Windows (15.0). From the total of 960 litterbags, 24 litterbags with *E. vaginatum* material and 10 litterbags with *Sphagnum* material were omitted from the analyses because these litterbags were damaged during the experiment. The omitted litterbags were almost equally distributed over the material types, sites and years, resulting in 8-10 replicates per treatment.

Data on initial litter quality were compared between litter types by one-way analysis of variance. For multiple comparisons Tukey's a posteriori test was used. Data on remaining mass and remaining N were first analysed separately for *E. vaginatum* material and *Sphagnum* material with a three-way analysis of variance (ANOVA) with litter type, incubation site and time as independent factors. As the litter types differed strongly and had significant interactions with site and time, the data were further analysed with two-way ANOVAs for each litter type separately, with site and time as independent factors. To examine the relation between litter quality parameters and mass and N loss, we used linear regression analyses with N, P, K, CN ratio or NP ratio as independent factors and mass loss per year or N loss per year as dependent factor. We performed linear regression analyses for *E. vaginatum* and *Sphagnum* litter separately.

All data were tested for normality and equality of variances. Data for initial litter quality and remaining mass and N did not meet those requirements for all litter types, even after ln or square root transformation. Since analysis of variance is robust to considerable heterogeneity of variances as long as the sample sizes are nearly equal (Zar 1999), we proceeded with the analyses without transformations.

## Results

### Litter quality

Initial quality of the *E. vaginatum* litter and *Sphagnum* material differed considerably between species, origin site and section (Table 6.2). Nitrogen concentrations in *E. vaginatum* litter exceeded those in *Sphagnum*, irrespective of collection site. For *E. vaginatum*, the N concentration differed among the sites of origin and, surprisingly, was opposite to the N deposition gradient (Germany<C-Sweden<S-Sweden<N-Sweden); N concentration was lowest at the German site, with the highest N deposition, and N concentration was highest at the North-Swedish site. For *Sphagnum* there were no differences between species, but N concentrations were higher in the capitula than in the stem section. Because carbon concentration showed only minor differences between the species, the reverse order was found for C:N ratios.

There was no overall difference in phosphorus (P) concentration between *Sphagnum* and *E. vaginatum*. For *E. vaginatum*, only material from N-Sweden showed a higher P concentration than the other origin sites. P concentration showed the same pattern as N concentration in the *Sphagnum* material. In general, N:P ratios were lower in the initial litter of the *Sphagnum* than of the *E. vaginatum* material.

Potassium (K) concentrations were higher in the initial litter of the *Sphagnum* than of the *E. vaginatum* material. For *E. vaginatum*, the K concentration differed between the origin sites; the K concentration was highest in material from Germany and lowest in material from S-Sweden. Within *Sphagnum* there were no differences between the different types of material.

**Table 6. 2** Initial quality of litter of *Eriophorum vaginatum* collected at 4 sites and of *Sphagnum balticum* and *Sphagnum fuscum* capitula (0-1 cm) and stem (1-4 cm). Different letter indicates significant differences ($P < 0.05$) among the eight types of litter. Data are mean values ± SE, n=10.

| Litter type | N (mg N.g-1) | P (mg P.g-1) | K (mg K.g-1) | N:P ratio | C:N ratio |
|---|---|---|---|---|---|
| *Eriophorum vaginatum* | | | | | |
| N-Sweden | 9.0 ± 0.2 $^{d}$ | 0.33 ± 0.01 $^{d}$ | 1.1 ± 0.0 $^{abc}$ | 28 ± 1 $^{abc}$ | 56 ± 1 $^{a}$ |
| C-Sweden | 7.2 ± 0.1 $^{c}$ | 0.19 ± 0.01 $^{ab}$ | 0.8 ± 0.1 $^{ab}$ | 39 ± 1 $^{d}$ | 69 ± 2 $^{bc}$ |
| S-Sweden | 8.6 ± 0.3 $^{d}$ | 0.23 ± 0.01 $^{bc}$ | 0.6 ± 0.0 $^{a}$ | 37 ± 1 $^{d}$ | 61 ± 1 $^{ab}$ |
| Germany | 6.6 ± 0.2 $^{bc}$ | 0.20 ± 0.02 $^{ab}$ | 1.7 ± 0.1 $^{bc}$ | 35 ± 2 $^{cd}$ | 67 ± 1 $^{bc}$ |
| *Sphagnum balticum* | | | | | |
| capitulum | 6.2 ± 0.1 $^{b}$ | 0.33 ± 0.01 $^{d}$ | 2.9 ± 0.3 $^{c}$ | 19 ± 1 $^{a}$ | 73 ± 1 $^{c}$ |
| stem | 4.0 ± 0.1 $^{a}$ | 0.15 ± 0.01 $^{a}$ | 2.0 ± 0.2 $^{c}$ | 28 ± 2 $^{bc}$ | 104 ± 2 $^{d}$ |
| *Sphagnum fuscum* | | | | | |
| capitulum | 6.2 ± 0.2 $^{b}$ | 0.27 ± 0.02 $^{cd}$ | 2.2 ± 0.4 $^{c}$ | 24 ± 1 $^{ab}$ | 71 ± 1 $^{bc}$ |
| stem | 3.5 ± 0.1 $^{a}$ | 0.13 ± 0.01 $^{a}$ | 3.2 ± 0.4 $^{c}$ | 25 ± 2 $^{ab}$ | 106 ± 3 $^{d}$ |

### Mass loss

*E. vaginatum* mass loss showed similar patterns over time in all sites, i.e. a relatively large initial decrease in the first year, followed by a more gradual decline that continued for two more years (Fig. 6.2). *Sphagnum* litter showed a relatively large initial mass loss in the first 3 months (May - August), but no further decrease in the rest of the first year and only a small decrease in the second year (Fig. 6.3). *S. fuscum* in the German site showed no further decrease or even an increase in mass in the second year. Remaining mass for *Sphagnum* was much higher than for *E. vaginatum* after one year and especially after two years (88 ± 1% for *Sphagnum* and 64 ± 1% for *E. vaginatum*). This was also reflected in the decomposition constants (k-values), which were distinctly lower for *Sphagnum* litter than for *E. vaginatum* litter (Table 6.3).

For *E. vaginatum* the three way analysis of variance showed significant main effects of site of origin (F = 64.180, $P < 0.001$), incubation site (F = 28.702, $P < 0.001$) and time (F = 166.838, $P < 0.001$). Origin types differed strongly in mass loss, and there was a significant interaction term for litter origin x incubation site (F = 4.461, $P < 0.001$). Overall, decomposition rates were highest for material originating from the Central-Swedish site and lowest for material originating from the German site (Table 6.3). Two-way ANOVAs for each litter origin separately showed a significant effect of time for all litter types and of incubation site for all litter types except for litter from Germany (Table 6.4). Mass loss of *E. vaginatum* litter collected from the Swedish sites increased in incubation sites from north to south in the order N-Sweden<C-Sweden<S-Sweden<Germany (Fig. 6.2 and Table 6.3).

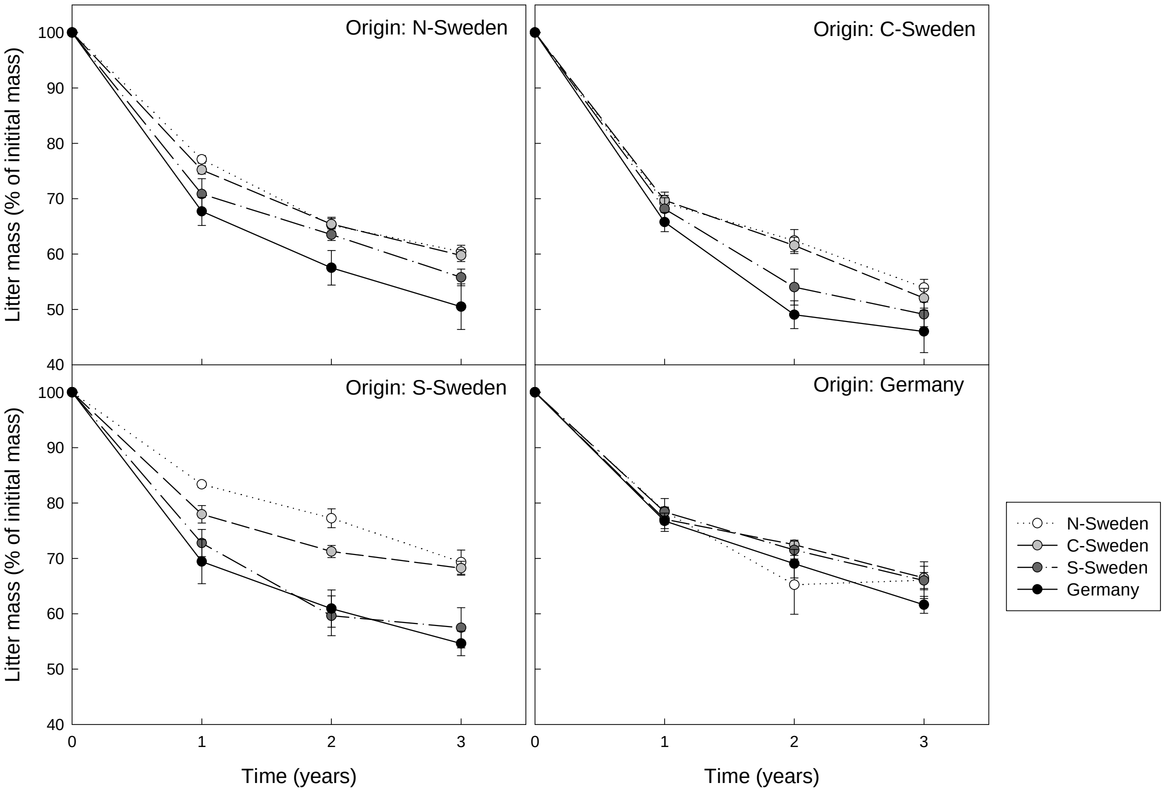

**Figure 6.2** Percentage of initial mass remaining of litter of *Eriophorum vaginatum* collected at 4 sites and incubated at 4 sites after 1, 2 and 3 years after incubation. Graphs indicate a litter type each, with the differently shaded symbols within a graph referring to different incubation sites. Data are mean values ± SE, n =8-10 litterbags.

**Table 6.3** k-values (year$^{-1}$) of *Eriophorum vaginatum* litter from four sites and four *Sphagnum* litter types (see table 2), in four incubation sites.

| | ***Eriophorum vaginatum*** | | | |
|---|---|---|---|---|
| | site of origin | | | |
| Incubation site | N-Sweden | C-Sweden | S-Sweden | Germany |
| N-Sweden | 0.19 ± 0.01 | 0.23 ± 0.01 | 0.13 ± 0.01 | 0.18 ± 0.02 |
| C-Sweden | 0.19 ± 0.01 | 0.24 ± 0.01 | 0.15 ± 0.01 | 0.15 ± 0.01 |
| S-Sweden | 0.22 ± 0.01 | 0.27 ± 0.01 | 0.22 ± 0.02 | 0.16 ± 0.01 |
| Germany | 0.26 ± 0.02 | 0.31 ± 0.02 | 0.23 ± 0.02 | 0.18 ± 0.01 |

| | ***Sphagnum*** | | | |
|---|---|---|---|---|
| Incubation site | *S. balticum* cap | *S. balticum* stem | *S. fuscum* cap | *S. fuscum* stem |
| N-Sweden | 0.15 ± 0.01 | 0.12 ± 0.01 | 0.10 ± 0.01 | 0.05 ± 0.00 |
| C-Sweden | 0.15 ± 0.01 | 0.11 ± 0.01 | 0.09 ± 0.01 | 0.04 ± 0.01 |
| S-Sweden | 0.19 ± 0.02 | 0.15 ± 0.01 | 0.10 ± 0.01 | 0.06 ± 0.00 |
| Germany | 0.15 ± 0.02 | 0.13 ± 0.02 | 0.07 ± 0.02 | 0.01 ± 0.01 |

For *Sphagnum* the three way analysis of variance showed significant main effects of litter type (F = 294.057, $P < 0.001$), incubation site (F = 19.852, $P < 0.001$) and time (F = 65.511, $P < 0.001$). Litter types differed strongly, and there were significant interaction terms for litter type x site (F = 3.898, $P < 0.001$), litter type x time (F = 2.658, $P = 0.015$) and site x time (F = 5.156, $P < 0.001$). Overall, decomposition rates were higher for *S. balticum* than for *S. fuscum* and higher for capitula than for stem section. Two-way ANOVAs for each litter type separately showed a significant effect of site and time for all litter types (Table 6.5). For *S. fuscum* litter, there was also a significant interaction term for site x time. In contrast to the effect of site on *E. vaginatum*, there was no clear order in the site effect on *Sphagnum* litter. For *S. balticum* litter, decomposition rates were highest in the South-Swedish site and did not differ among the other sites (Fig. 6.3 and Table 6.3). For *S. fuscum* litter, decomposition rates were lowest in the German site.

There were no significant correlations between mass loss and the litter quality parameters for both *E. vaginatum* and *Sphagnum* litter (data not shown).

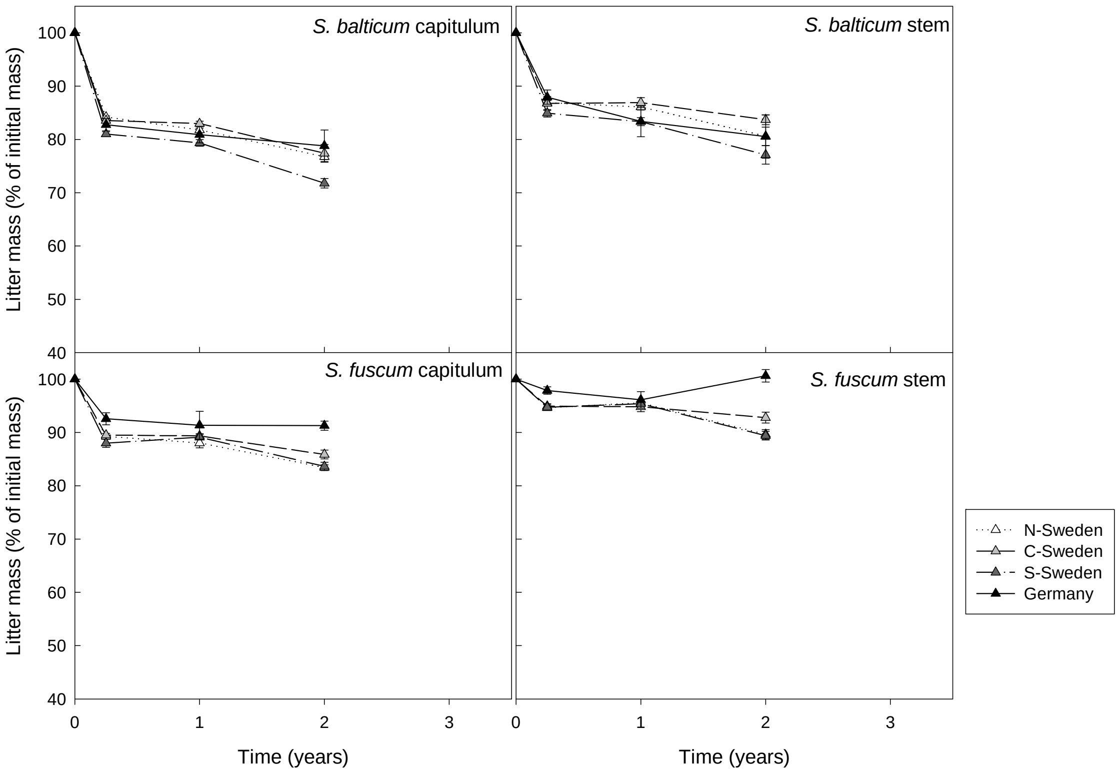

**Figure 6.3** Percentage of initial mass remaining of litter of *Sphagnum balticum* and *Sphagnum fuscum*, divided in capitula (0-1 cm) and stem part (1-3 cm), incubated at 4 sites after 3 months, 1 and 2 years after incubation. Graphs indicate a litter type each, with the differently shaded symbols within a graph referring to different incubation sites. Data are mean values ± SE, n =9-10 litterbags.

**Table 6.4** Results of three-way ANOVA of remaining mass data and remaining N of *Eriophorum vaginatum* material per collection site, with site (incubation site) and time as main effects. df: degrees of freedom.

| | | **litter collection site** | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | **N-Sweden** | | **C-Sweden** | | **S-Sweden** | | **Germany** | |
| | df | F | *P* | F | *P* | F | *P* | F | *P* |
| **Mass loss** | | | | | | | | | |
| Model | 11 | 15.582 | **< 0.001** | 14.882 | **< 0.001** | 10.417 | **< 0.001** | 5.525 | **< 0.001** |
| Site | 3 | 10.441 | **< 0.001** | 7.072 | **< 0.001** | 21.418 | **< 0.001** | 0.993 | 0.399 |
| Time | 2 | 69.241 | **< 0.001** | 65.649 | **< 0.001** | 24.735 | **< 0.001** | 26.129 | **< 0.001** |
| Site x Time | 6 | 0.474 | 0.826 | 1.261 | 0.282 | 0.654 | 0.687 | 0.936 | 0.472 |
| **N loss** | | | | | | | | | |
| Model | 11 | 6.834 | **< 0.001** | 13.954 | **< 0.001** | 8.679 | **< 0.001** | 11.054 | **< 0.001** |
| Site | 3 | 1.158 | 0.330 | 18.317 | **< 0.001** | 4.226 | **0.007** | 7.572 | **< 0.001** |
| Time | 2 | 33.125 | **< 0.001** | 45.278 | **< 0.001** | 41.041 | **< 0.001** | 37.315 | **< 0.001** |
| Site x Time | 6 | 1.067 | 0.387 | 0.993 | 0.434 | 0.378 | 0.892 | 3.948 | **0.001** |

**Table 6.5** Results of three-way ANOVA of remaining mass data and remaining N of *Sphagnum* material per litter type, with site (incubation site) and time as main effects. df: degrees of freedom.

| | | ***S. balticum*** | | | | ***S. fuscum*** | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | **cap** | | **stem** | | **cap** | | **stem** | |
| | df | F | *P* | F | *P* | F | *P* | F | *P* |
| **Mass loss** | | | | | | | | | |
| Model | 11 | 8.227 | **< 0.001** | 3.294 | **0.001** | 10.736 | **< 0.001** | 13.592 | **< 0.001** |
| Site | 3 | 6.807 | **< 0.001** | 2.693 | **0.050** | 18.721 | **< 0.001** | 20.927 | **< 0.001** |
| Time | 2 | 33.022 | **< 0.001** | 12.798 | **< 0.001** | 22.955 | **< 0.001** | 10.609 | **< 0.001** |
| Site x Time | 6 | 1.187 | 0.319 | 0.617 | 0.716 | 2.189 | **0.050** | 9.140 | **< 0.001** |
| **N loss** | | | | | | | | | |
| Model | 11 | 24.772 | **< 0.001** | 30.115 | **< 0.001** | 24.741 | **< 0.001** | 17.376 | **< 0.001** |
| Site | 3 | 7.445 | **< 0.001** | 13.886 | **< 0.001** | 23.251 | **< 0.001** | 3.773 | **0.013** |
| Time | 2 | 83.270 | **< 0.001** | 83.994 | **< 0.001** | 93.467 | **< 0.001** | 40.931 | **< 0.001** |
| Site x Time | 6 | 14.761 | **< 0.001** | 19.254 | **< 0.001** | 7.760 | **< 0.001** | 17.593 | **< 0.001** |

Nitrogen loss

Nitrogen release of both *E. vaginatum* and *Sphagnum* litter differed between litter types, incubation sites and periods ($P < 0.001$) and there were significant interaction terms between all factors ($P < 0.01$), except for site x time in *E. vaginatum* litter (F = 1.551, $P = 0.160$). *E. vaginatum* litter released N from all litter types during the first year, then remaining N stayed relatively constant with only a small decrease or increase in the second year, while N was released again in the third year (Fig. 6.4). The release of N was highest in material from N-Sweden and S-Sweden and lowest in material from Germany. N release of material from C-Sweden was in between, but showed considerable variation between incubation sites. For material from S-Sweden, N release was highest in the South-Swedish site, while there was no effect of site on material from N-Sweden and the effect of site varied over time in material from Germany (Table 6.4). We only found a positive correlation between N concentration and N loss in *E. vaginatum* in the first year ($R^2$=0.41, $P = 0.008$).

Most types of *Sphagnum* litter released N during the first 3 months, then increased in N concentration during the rest of the first year, and subsequently decreased in N concentration over the second year (Fig. 5). Only the stem material in the German site showed a different pattern, with an increase in N during the first 3 months and the first year, followed by a strong release of N in the second year. During the first year, N release was lowest in the German site for all types of *Sphagnum* litter. For *Sphagnum*, we found positive relationships between N and P concentration and N loss ($R^2 = 0.63$, $P < 0.001$ and $R^2 = 0.39$, $P < 0.001$, for N and P concentration respectively), and a negative relationship between C:N ratio and N loss ($R^2 = 0.56$, $P < 0.001$).

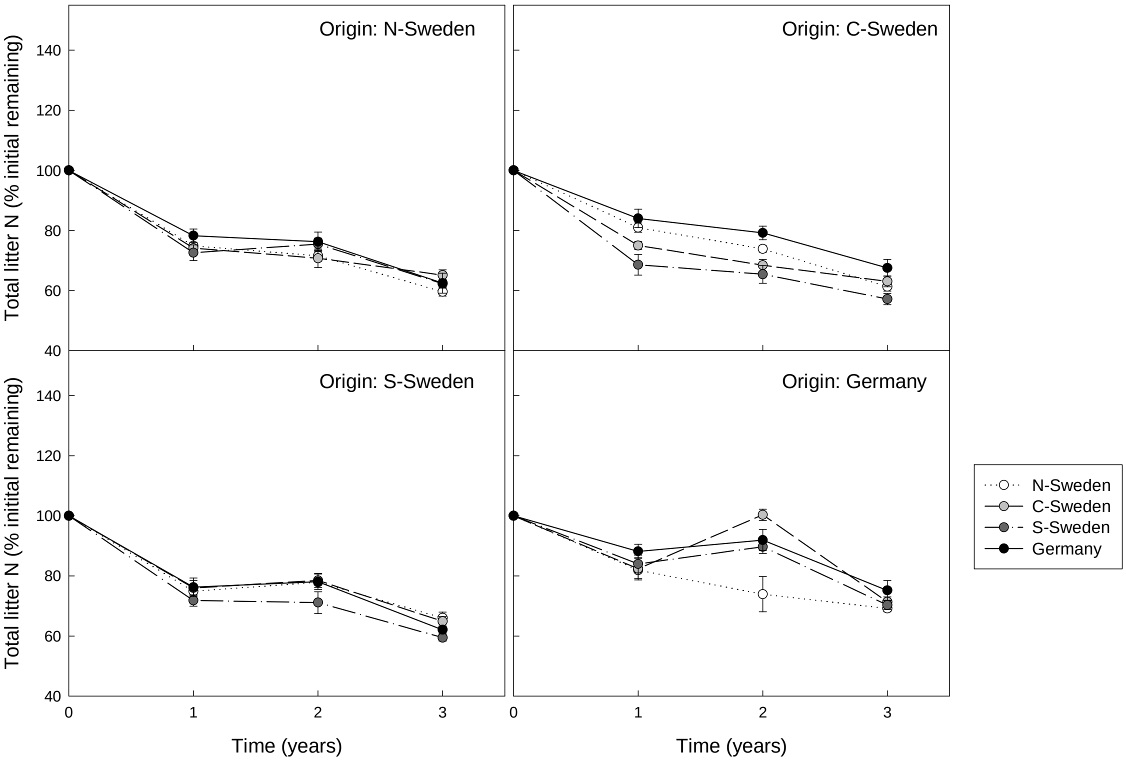

**Figure 6.4** Percentage of initial nitrogen remaining in litter of *Eriophorum vaginatum* collected at 4 sites and incubated at 4 sites after 1, 2 and 3 years after incubation. Graphs indicate a collection site each, with the differently shaded symbols within a graph referring to different incubation sites. Data are mean values ± SE, n =8-10 litterbags.

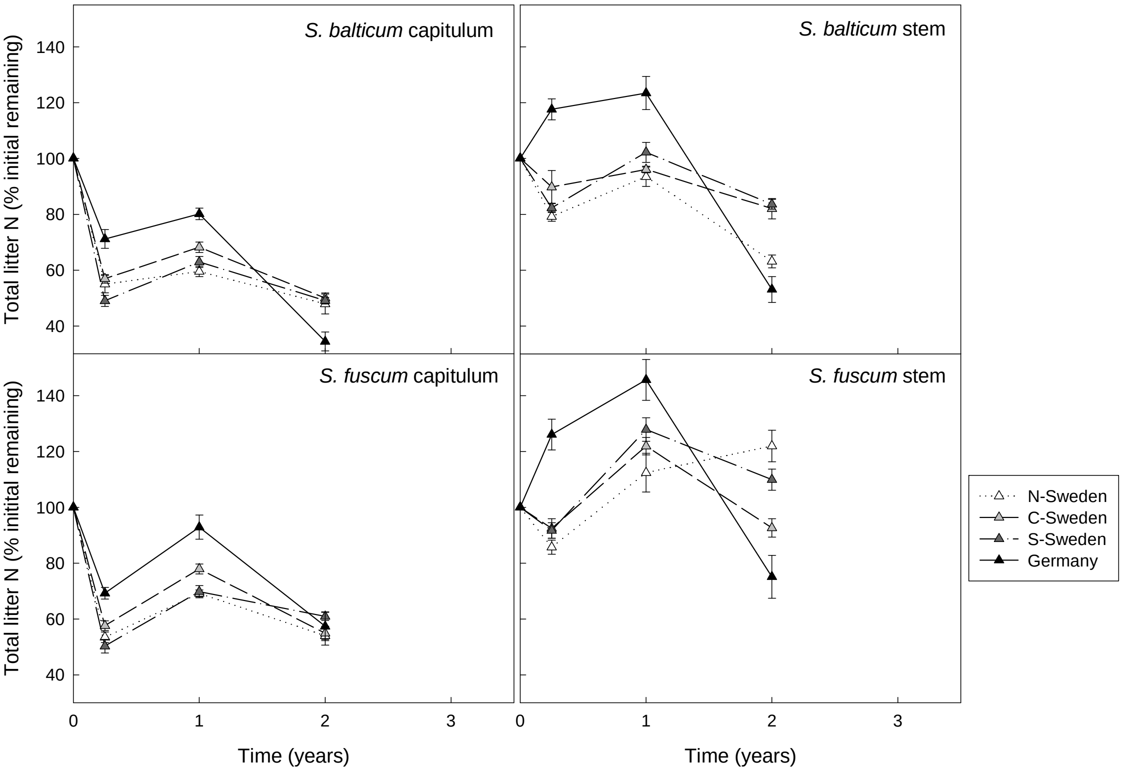

**Figure 6.5** Percentage of initial nitrogen remaining in litter of *Sphagnum balticum* and *Sphagnum fuscum*, divided in capitula (0-1 cm) and stem part (1-3 cm), incubated at 4 sites after 3 months, 1 and 2 years after incubation. Graphs indicate a litter type each, with the differently shaded symbols within a graph referring to different incubation sites. Data are mean values ± SE, n =9-10 litterbags.

## Discussion

### Effect N deposition on litter quality

Contrary to our first hypothesis, N concentration did not increase southwards in *E. vaginatum* material over the N deposition gradient from north to south (Table 6.2). Surprisingly, N concentration in *E. vaginatum* was actually highest in N-Sweden, the site with the lowest N deposition and lowest in Germany, the site with the highest N deposition. Also in the C-Sweden site, N concentration of *E. vaginatum* was much lower than in N-Sweden, while N deposition was slightly higher in C-Sweden. In contrast, in the *Sphagnum* layer we did find a southwards increase in N concentration (unpublished results). This is in contrast with the study by Chapin and Shaver (1996), where N addition lead to higher leaf N concentrations and leaf growth of *E. vaginatum*. Our results are more in line with the study by Wiedermann *et al*. (2007), where *E. vaginatum* has been shown to respond to higher N availability by enhancing biomass growth, while N and C concentrations of the leaves did not change. In the same study, leaf N concentrations of *A. polifolia* decreased as a result of the warming treatment, indicating that a warming induced increase in growth may have diluted leaf N concentrations. Possibly *E. vaginatum* in the German site showed the same dilution effect as a result of enhanced growth, caused by higher temperature and longer growing season compared with the Swedish sites. In addition, vascular plant cover was higher in Germany than in N-Sweden (Chapter 5) suggesting more competition for N with other plant species, especially with other graminoids like *E. angustifolium.* Also other studies showed that increased N supply did not lead to higher N concentrations in the leaf litter of all vascular plant species (Aerts and de Caluwe 1997; van Heerwaarden *et al.* 2003) and that different species in a site, even within the same growth form, can show a large variation in nutrient concentrations (Dorrepaal *et al*. 2005).

The differences in litter quality (Table 6.2) and concomitant differences in mass loss between *Sphagnum* capitula and stems (Table 6.3 and Fig. 6.3) are in accordance with results from other studies (Bragazza *et al.* 2006; Gerdol *et al.* 2007; Limpens and Berendse 2003), in which mass loss increased as a result of higher N concentrations and lower C:N and N:P ratios in *Sphagnum* litter. The lower mass loss in *Sphagnum* compared to *E. vaginatum* litter (Table 6.3) is presumably only partly caused by the lower N concentration of *Sphagnum* (Table 6.2), and mainly a result of the high concentrations of specific secondary compounds such as uronic acids and polyphenols with a strong inhibitory effect on microbial breakdown (Painter 1991; Rudolph and Samland 1985; van Breemen 1995). Within *E. vaginatum,* we found no relation between N concentration, C:N or N:P ratio and mass loss in the different litter types. Other studies have shown that other chemical components besides nutrients, like polyphenols, lignin and non-structural carbohydrates, can have a large effect on decomposition rates in bogs (Bragazza *et al.* 2007; Dorrepaal *et al.* 2005). Bragazza *et al* (2007) found that decomposition of vascular plant litter was not only negatively affected by C:N ratio, but also by lignin:nutrient and polyphenols:nutrient ratio. We have not measured lignin or polyphenol concentrations in this study, so we do not know if the *E. vaginatum* material from the sites of origin differ in this respect, but differences in the chemical parameters mentioned above might be responsible for the lack of effect of N concentration on mass and N loss in *E. vaginatum*.

From these results we conclude that increased N deposition will not necessarily increase the N concentration of *E. vaginatum* and therefore will not necessarily lead to higher decomposition rates by increasing the quality of *E. vaginatum* litter*. Sphagnum* decomposition rates have been shown to increase as a result of increased N concentrations (Aerts *et al.* 2001; Limpens and Berendse 2003; Bragazza *et al.* 2005). However, the high mass loss of *E. vaginatum* litter from Germany (Fig 6.2) compared with the mass loss of *Sphagnum* capitula (Fig. 6.3) shows that even at similar N concentrations*,* decomposition rates of *E. vaginatum* are higher than decomposition rates of *Sphagnum*. This demonstrates that vascular plant litter still decomposes faster than *Sphagnum* that is enriched with N. As it can also be expected that vascular plants will increase at the expense of *Sphagnum* as a result of global change (Berendse *et al.* 2001; Bubier *et al.* 2007; Chapin and Shaver 1996; Wiedermann *et al.* 2007, Chapter 5), and will form a larger fraction of the litter, we expect that peat decomposition rates will increase as a result of increased N deposition.

### Mass loss

Our second hypothesis, in which we expected a positive effect of increasing temperature and N deposition on mass loss, was confirmed for the *E. vaginatum* litter collected from the Swedish sites, as decomposition rates increased over the gradient from north to south (Fig. 6.2 and Table 6.3), but not for *Sphagnum* (Fig. 6.3 and Table 6.3). In this study it is difficult to determine if increased decay towards the south is caused by increased temperature or atmospheric N supply or both, since both variables increased from north to south. In other litterbag experiments, Limpens and Berendse (2003) and Rochefort *et al*. (1990) found that increased N in the incubation environment did not affect mass loss of *Sphagnum* and *E. angustifolium*. In other studies, decomposition rates of vascular plant litter increased with elevated temperature, while decomposition rates of *Sphagnum* litter decreased or remained unaffected (Hobbie 1996; Moore *et al.* 2005; Thormann *et al.* 2004; Trofymow *et al.* 2002). We therefore assume that the increase in mass loss of *E. vaginatum* towards the south is mainly caused by the increase in temperature. As a result, we expect decomposition rates of vascular plant material to increase with increased temperature.

The lack of a north-south effect on mass loss of *E. vaginatum* litter from the German site is difficult to explain. Although N concentration of *E. vaginatum* litter from the German site had the lowest N concentration, it was not much lower than in the litter from the C-Sweden site, furthermore, the N:P and C:N ratio was not different from the litter from the C-Sweden and S-Sweden site. A possible explanation for the different response to incubation site between the Swedish and German litter, might be found in the chemical components that we did not measure, like polyphenol or lignin concentration. To illustrate that these component can differ between climatic regions, Dorrepaal *et al*. (2005) found that the phenolics concentration in *E. angustifolium* in the cool temperate region was twice the concentration of phenolics in *E. vaginatum* in the subarctic region, while N concentration was only slightly higher in *E. angustifolium* (5.5 to 4.8 mgN.g$^{-1}$, respectively).

There are several explanations for the lack of a north-south gradient in mass loss in *Sphagnum* litter. One explanation can be that the largest part of the mass loss occurs in the first three months, and is probably mainly a result of leaching of a labile, water-soluble part of the litter (Scheffer *et al*. 2001). Leaching is probably not so much affected by temperature, but more by the water flow. This would explain why mass and N loss in the first three months are highest in the South-Swedish site for all *Sphagnum* litter types, since rainfall was extremely high in this site in exactly this period (summer 2004, Table 6.1). One explanation for the relatively low decomposition rates of *Sphagnum* litter in the German site might be that decomposition was limited by water. Field measurements show that the mean water level was lower in the German site than in the Swedish site (unpublished data) and that *Sphagnum* at the German site showed more signs of desiccation (personal observation). This corresponds to the results of Gerdol *et al*. (2007) who found that decomposition rates of *Sphagnum* are depressed when litter dries out.

The low decomposition rates of *S. fuscum* litter in Germany might be explained by the characteristics of the microbial decomposer community of this site. Scheffer *et al*. (2001) and Bragazza *et al*. (2007) found that ombrotrophic *Sphagnum* litter decomposes slower in minerotrophic than ombrotrophic habitat. They explained this by suggesting that the minerotrophic microbial community had to face a new litter type which was more decay resistant than it was adapted to, since ombrotrophic *Sphagnum* species generally contain a higher amount of polyphenols compared to minerotrophic *Sphagnum* species (Rudolph and Samland 1985). Litter of hummock species is known to be intrinsically more resistant to decay than litter of hollow species (Belyea 1996; Johnson and Damman 1991; Moore and Basiliko 2006), which was confirmed in our study since decomposition rates of *S. balticum* where greater than decomposition rates of *S. fuscum* in all sites (Table 6.3, Fig. 6.2 and 6.3), while initial nutrient concentrations were similar in both capitula and stems (Table 6.2). We expect that the lack of a north-south effect on mass loss of *S. fuscum* litter, like the lack of response on litter of *E. vaginatum* from the German site, might be explained by a difference in concentration of polyphenolics or lignin between the two *Sphagnum* species. This is in line with the results from Dorrepaal *et al*. (2005), who found higher concentrations of both phenolics and lignin in *S. fuscum* than in *S. balticum*. Given that no hummock *Sphagnum* species occur at the German site, possibly the microbial decomposer community of this site is not adapted to decompose the lower litter quality found in the hummock species, *S. fuscum*, used in this study.

### Nitrogen loss

Our third hypothesis was that higher temperatures and N concentration in the environment in the south would lead to faster N release for both the *Sphagnum* and *E. vaginatum* litter due to higher microbial activity. In other words, we expected the same pattern for N release as for mass loss, but this was not found. Also in other studies there was no positive relation between N mineralisation and decomposition in several litter types, occasionally even an inverse relation was found (Aerts and de Caluwe 1997; Bragazza *et al.* 2007; Scheffer *et al.* 2001; Verhoeven *et al.* 1990). Apparently mass loss and N loss are controlled by different factors, either related to environment or litter chemistry. Verhoeven *et al*. (1990) hypothesized that the low decomposition rates in bogs are due to limitation of the microbial community. Increased temperature and N availability are expected to promote microbial activity, which could subsequently promote mass loss and N release. However, when N concentration in the environment remains relatively low and microbes remain limited by N, the N released from the litter will probably be immobilised by the more active microbes. Therefore N release could respond less to increased temperature and N than mass loss. Only when exogenous N increases further, the N from the decomposing *Sphagnum* litter is no longer immobilised and N release can also increase. Therefore we expected that a greater availability of exogenous N would bring about a faster N release from *Sphagnum* litter, as a result of reduced N immobilisation by micro-organisms (Bragazza *et al*. 2007). However, N release was actually lowest in the German site for all *E. vaginatum* litter and for *Sphagnum* litter during the first year, while N deposition is highest in this site. Also in the comparison of bogs and fens, N mineralisation was higher in bogs, which have a lower availability of exogenous N (Scheffer *et al.* 2001; Verhoeven *et al.* 1990). Moreover, comparison of N mineralisation in different regions revealed no indications of an enhanced rate under high atmospheric N deposition (Verhoeven *et al*. 1990). Temperature also does not seem to affect N mineralisation in both litter types, since N losses did not increase from north to south. Experimental increases in temperature have been shown to stimulate N mineralisation in other studies (Hobbie 1996; Rustad *et al.* 2001), but the effects varied over different biomes and litter types. Hobbie (1996) only found an effect of warming on N release after a period of 5 months, but it was suggested that the litter in the cold treatment lagged behind the warm treatment. No such pattern is visible in our data. Probably intrinsic litter quality is more important than the incubation environment (Belyea 1996; Johnson and Damman 1991; Limpens and Berendse 2003). In our study, N release in *Sphagnum* litter was correlated with N and P concentration and C:N ratio, but showed the strongest relationship with N concentration (Fig. 6.6). Litter quality characteristics that have been reported to determine decomposability in other studies are total N, P, C, polyphenol and lignin concentrations and several of their ratios (Bragazza *et al.* 2007; Coulson and Butterfield 1978; Hobbie 1996).

We conclude that N mineralisation in bogs is not so much affected by environmental conditions such as increased temperature and exogenous N, but more likely by litter quality. As N concentration in *Sphagnum* litter is expected to increase as a result of increased N deposition, this would lead to higher N release and subsequently to more N available for vascular plant growth.

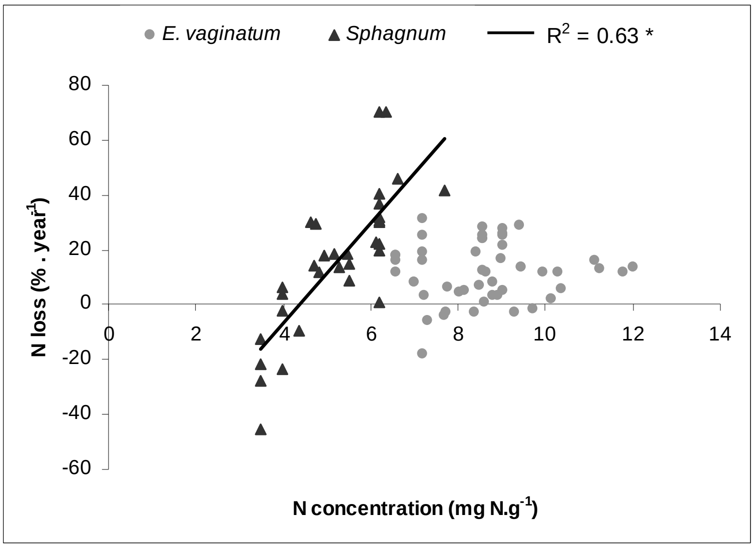

**Figure 6.6** Relationship between the N concentration and N loss per year for *E. vaginatum* and *Sphagnum* litter. * $P < 0.001$.

Conclusions

Increased temperature and N deposition in bog ecosystems affect mass loss and N loss in different ways. Higher temperatures enhance decomposition rates of vascular plant litter, but not of *Sphagnum* litter. There was no effect of temperature on N release. Enhanced N deposition does not seem to affect mass loss of either *Eriophorum* or *Sphagnum*, but does promote N loss from *Sphagnum* litter through increased litter N concentration. However, even at similar N concentrations, decomposition rates of *E. vaginatum* are higher than decomposition rates of *Sphagnum*. If global change would change vegetation composition in favour of vascular plants, such as *E. vaginatum*, at the cost of peat-forming *Sphagnum* species, as has been found in other studies (Berendse *et al.* 2001; Wiedermann *et al.* 2007, Chapter 5), this would likely reduce long-term C accumulation rates. As a result, carbon sequestration in bog ecosystems can be influenced by global change. Since bog ecosystems hold a large reservoir of carbon and are important carbon sequestering systems, a decrease in carbon storage in these systems can have serious consequences for the global carbon budget.

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# Summary

Ombrotrophic bogs are peat-forming systems and as such they serve as important long-term sinks for atmospheric $CO_2$. Although northern peatlands cover only 2% of the total land surface, they store about one-third of the world's soil carbon in the form of peat. A large proportion of northern peatlands consists of *Sphagnum*-dominated ombrotrophic bogs. Despite their relatively low primary production, the peat mosses (*Sphagnum* spp.) are responsible for the large accumulation of carbon in bogs because their litter decomposes very slowly. Several studies have revealed differences in production and in decomposition rate among different *Sphagnum* species. These inter-species differences are often related to differences in preferred microhabitat. Within each bog there are different competing species; the dominant species also differ, depending on the climatic region. In our research, we used species from different sites in Sweden and Germany. *Sphagnum balticum* and *Sphagnum fuscum* are the dominant species in northern Sweden and though they also occur in southern Sweden, here the most abundant species are *Sphagnum magellanicum* and *Sphagnum cuspidatum*. This corresponds with the general distribution of these species in Europe since both *S. magellanicum* and *S. cuspidatum* occur further south than *S. fuscum* and *S. balticum*.

The vascular plant cover in bogs is generally low and consists of ericoids, graminoids and a few herbs (some of them carnivorous), Parallel to the distribution of *Sphagnum* mosses, the vascular plant species assemblage varies over the different microhabitats along the water table gradient. In many northern bogs, the vascular plants and *Sphagnum* apparently occur in a stable equilibrium, thereby sustaining the functioning of the bog ecosystem.

Global change is expected to have a strong impact on temperature, precipitation and nutrient availability, especially at northern latitudes where the majority of peat bogs occur. All global change models predict an increase in temperature and N deposition. Predictions about future precipitation patterns show great variability, but it is likely that the frequency of summer drought will increase, which will result in lower water tables during summer. There is much concern about how the effects of global change will affect the ability of peatlands to sequester carbon and what the feedbacks to climate will be. Changes in the current equilibrium between *Sphagnum* species and between *Sphagnum* and vascular plants might have marked effects on the C dynamics and $CO_2$ fluxes of the ecosystem, especially because vascular plant litter decomposes much faster than *Sphagnum* litter.

The main question addressed in this study was: how will global change influence the vegetation and functioning of ombrotrophic bogs? We examined the effect of increased temperature, N deposition and water table fluctuations on intact bog vegetation and on competition between different *Sphagnum* species. Furthermore, the effect of temperature and N deposition on decomposition was studied. We performed experiments under controlled conditions and field experiments in four bog sites along a transect from north Sweden to north-east Germany, in which both temperature and N deposition increased from north to south.

The first part of this thesis focuses on the experiments under controlled conditions in which the effects of temperature and N deposition on *Sphagnum* growth in monocultures and mixtures of different *Sphagnum* species were examined. **Chapter 2** describes the effect of four temperature treatments (11.2 °C, 14.7 °C, 18.0 °C and 21.4 °C) on the growth of four *Sphagnum*

species in monocultures and mixtures: *S. fuscum* and *S. balticum* from the site in northern Sweden and *S. magellanicum* and *S. cuspidatum* from the site in southern Sweden. All four species increased their height increment and biomass production with an increase in temperature, although the extent of their response differed among species. Competition between *S. cuspidatum* and *S. magellanicum* was not influenced by temperature. The mixtures of *S. balticum* with *S. fuscum* and *S. balticum* with *S. magellanicum* showed that *S. balticum* was the stronger competitor in the experiment, but it lost competitive advantage in the highest temperature treatment. These findings suggest that species abundances will shift in response to global warming, particularly at northern sites where hollow species will lose competitive strength relative to hummock species and southern species.

In **chapter 3,** species mixtures in the two highest temperature treatments (17.5 °C and 21.7 °C) from the experiment described in chapter 2 are examined. We also applied two different N addition treatments (0 and 4 g N m-2 yr-1). In this experiment we found that high temperature and high N addition depressed the height increment and production of the two northern species *S. fuscum* and *S. balticum,* whereas for the southern species *S. magellanicum* and *S. cuspidatum,* we found that only the high N addition depressed height increment and production. As expected, N concentrations of *Sphagnum* were higher in the high N treatment, especially in *S. fuscum* and *S. magellanicum* compared to their initial values. The N:P and N:K ratios indicated P-limited growth in all treatments and co-limitation of P and K in the high N treatments. In the second year of the experiment, several containers, particularly those in the high N treatment, suffered from a severe fungal infection. The ‘wet’ species were the most affected. In addition, the cover of ‘wet’ species was depressed by the high temperature treatment.

**The findings from the greenhouse experiments suggest that a high increase in temperature and N availability can have negative consequences for the production of *Sphagnum* species in bog ecosystems, particularly for the species from wet habitats.**

In the experiments described in the next two chapters we used mesocosms (diameter 45 cm, depth 40 cm) with intact bog vegetation, in order to be able to study the effects of global change on vascular plant composition too. **Chapter 4** describes the effects of periodic water table drawdown in mesocosms collected from the site in southern Sweden. These were transported to an experimental field in the Netherlands, where they were placed in larger containers. Two water table treatments were applied: one with a constant water table at five centimetres below the moss surface, and one in which the water table was allowed to drop, resulting in water tables fluctuating between 5 and 21 cm below the moss surface. *Sphagnum* growth, as well as *Sphagnum* and vascular plant abundance, were assessed for two-and-a-half years. Our results show that the abundance of ericoid species increased when water tables were allowed to fluctuate relative to the constant water table treatment. Furthermore, *S. cuspidatum* production decreased with fluctuating summer water tables, whereas *S. magellanicum* production increased. From these results we conclude that more frequent periods with low water tables may lead to a shift in dominant *Sphagnum* species, again favouring the ‘dry’ species. Lower water tables will also result in a shift from graminoid to ericoid vascular plant cover, similar to a shift from hollow to lawn or hummock vegetation.

In the field experiment described in **chapter 5** we used the same type of mesocosms for a transplantation experiment. The mesocosms with intact vegetation were transplanted southwards from north Sweden to north-east Germany along a transect of four bog sites, in which both temperature and N deposition increased from north to south. For logistic reasons and because we were mainly interested in the effects of climate warming, there was no northward transplantation. Monitoring of shifts in species abundances during three growing seasons revealed that ericoid species increased their abundance most when transplanted to the southernmost site. The height increment of *S. balticum* was less when transplanted southwards. Neither incubation site nor site of origin affected *Sphagnum* production, but, as expected, N concentration in *Sphagnum* increased southwards. The lack of a (positive) transplantation effect on *Sphagnum* production can be attributed to other factors such as P or moisture becoming limiting. However, vascular plants did become more abundant in bog vegetation when transplanted to warmer sites with higher N deposition.

**The conclusion from the mesocosm experiments is that higher temperature, more N deposition and lower water tables will increase ericoid vegetation in bogs and depress the growth and cover of 'wet' *Sphagnum* species.**

**Chapter 6** describes the combined effects of increased temperature and N deposition on decomposition in bogs. We expected that increased temperature and N deposition would have a positive effect on microbial activity and litter quality, and would therefore result in enhanced mass loss and N release of *Sphagnum* and vascular plant litter. We investigated mass loss and N release at the four bog sites along the transect in which both temperature and N deposition increased. Two litterbag experiments were performed: one reciprocal experiment with *Eriophorum vaginatum* litter and one experiment using recalcitrant (*S. fuscum*) and more degradable (*S. balticum*) *Sphagnum* litter collected from the northernmost site. We measured mass loss and N release during two years for *Sphagnum* and during three years for *E. vaginatum*. Neither the N concentration nor the decomposability of the *E. vaginatum* litter differed between the sites where the litter had been collected. Though mass loss from *E. vaginatum* litter increased southwards along the gradient, there was no such effect on *Sphagnum* litter. N release in *Sphagnum* was positively related to N concentration. We conclude that the decomposition of vascular plants and *Sphagnum* litter is influenced by different environmental drivers, with enhanced temperatures stimulating mass loss of vascular plant litter, but not of *Sphagnum* litter. Enhanced N deposition increases the loss of N from *Sphagnum* litter. Given that one of the long-term consequences of climate change will presumably be enhanced vascular plant production, as can also be concluded from our mesocosm experiments, it seems likely that overall litter decomposition rates will increase too, especially in combination with higher temperature.

### Conclusion

From our results we conclude that an increase in temperature and N deposition will change the *Sphagnum* species composition and accelerate decomposition of the peat. Since it is mainly the 'wet' *Sphagnum* species that will suffer from global change, the proportional cover of 'dry' species will increase. Since the 'dry' species decompose more slowly, it can be expected that carbon sequestration in *Sphagnum* will probably not change immediately as a result of global change. However, in the longer term, the increase in vascular plants could depress *Sphagnum* production. Since *Sphagnum* production does not profit from global change and will therefore not depress vascular plant growth, the competitive balance between vascular plants and *Sphagnum* will shift to the benefit of vascular plants. This will increase the proportion of vascular plant litter in peat. As vascular plant litter is much more decomposable than *Sphagnum* litter and its decomposition is accelerated more by an increase in temperature, the litter turnover will accelerate and nutrients will become more readily available – benefiting the vascular plants more than the *Sphagnum*. In time, more nutrients will become available at deeper levels, so that graminoids will profit more. If the total cover of ericoids and graminoids were to increase, shading from the vascular plants could adversely affect *Sphagnum* production. Consequently, in the long term, global change could have a serious negative effect on *Sphagnum* production and on the capacity of ombrotrophic bogs to sequester carbon.

To be able to improve existing models of ombrotrophic bogs in such a way that they can generate better estimates of current and future carbon sequestration in bogs, further research should focus on long time scales and integrate data from vegetation monitoring, field and laboratory experiments, palaeoecological research and climate records.

# Samenvatting

Hoogvenen zijn veenvormende systemen en daardoor functioneren ze als belangrijke opslagplaatsen voor kooldioxide ($CO_2$) uit de atmosfeer. Terwijl slechts 2 % van het totale landoppervlak bestaat uit veengebieden op het noordelijk halfrond, bevatten deze veengebieden wel ongeveer 30% van al het koolstof (C) dat wereldwijd in de bodem opgeslagen is. Een groot deel van de noordelijke veengebieden bestaat uit hoogvenen die worden gedomineerd door veenmossen (*Sphagnum*). Deze veenmossen zijn verantwoordelijk voor de hoge accumulatie van koolstof in hoogvenen, ondanks hun lage primaire productie, doordat hun dode plantmateriaal (strooisel) erg langzaam afbreekt. Andere studies hebben aangetoond dat er verschillen bestaan tussen de verschillende *Sphagnum* soorten in productie en afbraaksnelheid. Deze verschillen tussen soorten zijn vaak gerelateerd aan het microhabitat (droog of nat) waarin de soort bij voorkeur voorkomt. Binnen elk hoogveen vindt er concurrentie plaats tussen verschillende *Sphagnum* soorten, welke soort dominant is verschilt van veen tot veen en hangt onder meer af van de klimaatzone. In ons onderzoek hebben we soorten gebruikt van verschillende lokaties in Zweden en in Duitsland. *Sphagnum balticum* (Baltisch veenmos) en *Sphagnum fuscum* (Bruin veenmos) zijn de dominante soorten in Noord-Zweden maar komen ook voor in Zuid-Zweden, hier zijn echter *Sphagnum magellanicum* (Hoogveen-veenmos) en *Sphagnum cuspidatum* (Waterveenmos*)* de meest voorkomende soorten. Dit komt overeen met de algemene verspreiding van deze soorten in Europa aangezien zowel *S. magellanicum* als *S. cuspidatum* verder zuidelijk voorkomen dan *S. fuscum* en *S. balticum*.

De vaatplantenbedekking in hoogvenen is in het algemeen laag en bestaat uit struiken, grasachtigen en een aantal (al dan niet vleesetende) kruiden. Net zoals bij de *Sphagnum* soorten varieert ook de samenstelling van de vaatplantengemeenschap langs de gradiënt van microhabitats van nat naar droog. In veel noordelijke hoogvenen komen de vaatplanten en *Sphagnum* soorten voor in een stabiel evenwicht, waardoor het functioneren van het hoogveen ecosysteem in stand wordt gehouden.

Er wordt verwacht dat klimaatverandering een grote invloed zal hebben op temperatuur, neerslag en nutriëntenbeschikbaarheid, vooral op de hoge noordelijke breedtegraden, waar ook de meeste hoogvenen voorkomen. Alle klimaatveranderingmodellen voorspellen een toename in temperatuur en stikstof (N) depositie. Voorspellingen over de toekomstige neerslagpatronen vertonen een grote variatie, maar waarschijnlijk zal de frequentie van droge periodes in de zomer toenemen, waardoor waterstanden in de zomer lager zullen worden. Er is veel bezorgdheid over hoe de effecten van klimaatverandering het koolstofvastleggend vermogen van venen zullen beïnvloeden en hoe de terugkoppeling naar het klimaat zal zijn. Veranderingen in het huidige evenwicht tussen *Sphagnum* soorten en tussen *Sphagnum* en vaatplanten kunnen een groot effect hebben op de C dynamiek en de opname en uitstoot van $CO_2$ van het ecosysteem, vooral omdat het strooisel van vaatplanten veel sneller afbreekt dan het strooisel van *Sphagnum*.

De hoofdvraag binnen deze studie was: hoe zal klimaatverandering de vegetatie en het functioneren van hoogvenen beïnvloeden? We hebben onderzocht wat het effect van verhogingen in temperatuur, N depositie en waterstandsfluctuatie op competitie tussen verschillende *Sphagnum* soorten en op de complete hoogveenvegetatie is. Verder hebben we het effect van temperatuur en N depositie op strooiselafbraak onderzocht. We hebben experimenten onder gecontroleerde omstandigheden en in het veld uitgevoerd. De veldexperimenten hebben we gedaan in vier hoogvenen langs een transect van Noord-Zweden naar Noordoost-Duitsland, langs dit transect namen zowel temperatuur als N depositie toe van noord naar zuid.

Het eerste deel van dit proefschrift concentreert zich op de experimenten onder gecontroleerde omstandigheden waarin de effecten van temperatuur en N depositie op de groei van *Sphagnum* in monoculturen (slechts één soort *Sphagnum*) en in mixculturen (combinaties van verschillende *Sphagnum* soorten) werd onderzocht. **Hoofdstuk 2** beschrijft het effect van vier temperatuurbehandelingen (11.2 °C, 14.7 °C, 18.0 °C and 21.4 °C) op de groei van vier *Sphagnum* soorten in mono- en mixculturen: *S. fuscum* en *S. balticum* van de locatie in Noord-Zweden en *S. magellanicum* and *S. cuspidatum* van de locatie in Zuid-Zweden. De hoogtegroei en biomassa productie van alle vier de soorten nam toe bij een toenemende temperatuur, hoewel de mate van respons verschilde tussen de soorten. De competitie tussen *S. cuspidatum* en *S. magellanicum* werd niet beïnvloed door temperatuur. De combinaties van *S. balticum* met *S. fuscum* en van *S. balticum* met *S. magellanicum* lieten zien dat *S. balticum* de dominerende soort was in het experiment, maar dat het zijn overwicht verloor bij de hoogste temperatuurbehandeling. Deze resultaten geven de indruk dat de soortensamenstelling in hoogvenen kan verschuiven als gevolg van klimaatverandering, vooral in de meer noordelijke locaties waar de soorten van natte habitats hun competitieve overwicht zullen verliezen ten koste van zuidelijke soorten en soorten van droge habitats.

In **hoofdstuk 3** hebben we mixculturen onderzocht bij de twee hoogste temperatuurbehandelingen uit hoofdstuk 2 (17.5 °C and 21.7 °C). Daarnaast hebben we twee verschillende N behandelingen toegepast (geen toediening en 4 g N $m^{-2}$ $jaar^{-1}$ toediening). In dit experiment vonden we dat hoge temperatuur en hoge N toediening een negatief effect hadden op de hoogtegroei en productie van de twee noordelijke soorten *S. fuscum* and *S. balticum*, terwijl we voor hoogtegroei en productie van de zuidelijke soorten *S. magellanicum* and *S. cuspidatum,* alleen een negatief effect van hoge N toediening vonden. Zoals verwacht waren de N concentraties in het veenmos hoger bij de hoge N toediening, vooral in *S. fuscum* en *S. magellanicum* in vergelijking met hun oorspronkelijke waarden. De N:P en N:K ratio geven aan dat de groei van het veenmos in alle behandelingen gelimiteerd werd door (fosfaat) P en bij de hoge N toediening gelimiteerd werd door zowel P als kalium (K). Tijdens het tweede jaar van het experiment hadden verschillende bakken met veenmos te lijden van een ernstige schimmelinfectie, vooral bij de behandeling met hoge N toediening. De natte soorten waren het meest aangetast, ook nam de oppervlakte van de natte soorten af bij de hoge temperatuurbehandeling.

**De resultaten van de kasexperimenten doen vermoeden dat een hoge toename in temperatuur en N beschikbaarheid negatieve consequenties zal hebben voor de productie van *Sphagnum* in hoogvenen, vooral voor de soorten van natte habitats.**

In de experimenten die we beschrijven in de volgende twee hoofdstukken hebben we mesocosms (diameter 45 cm, diepte 40 cm) gebruikt met intacte hoogveenvegetatie, zodat we ook de effecten van klimaatsverandering op de vaatplantenvegetatie konden onderzoeken. **Hoofdstuk 4** beschrijft de effecten van periodieke waterstandverlaging in mesocosms afkomstig van de site in Zuid-Zweden. Deze werden vervoerd naar een proefveld in Nederland, waar ze in grotere bakken werden geplaatst. Er werden twee waterstandbehandelingen toegepast: één met een contstante waterstand op 5 cm onder het mosoppervlak en één waarin de waterstand mocht zakkken, met als resultaat dat de waterstanden fluctueerden tussen 5 en 21 cm onder het mosoppervlak. Gedurende twee-en-een-half jaar hebben we de groei van *Sphagnum* en de bedekking van *Sphagnum* en vaatplanten gemeten. Onze resultaten laten zien dat de bedekking van dwergstruiken toeneemt bij de fluctuerende waterstand in vergelijking met de constante waterstand. Verder nam de productie van *S. cuspidatum* af met de fluctuerende waterstand, terwijl de productie van *S. magellanicum* toenam. Uit deze resultaten concluderen we dat het vaker voorkomen van lage waterstanden een verschuiving in dominante *Sphagnum* soorten tot gevolg kan hebben, waarbij opnieuw de 'droge' soorten in het voordeel zijn. Lagere waterstanden zullen ook als gevolg hebben dat de vaatplantenbedekking verschuift van een vegetatie gedomineerd door grasachtigen naar een vegetatie gedomineerd door dwergstruiken, gelijk aan een verschuiving van slenk naar bult vegetatie.

In het veldexperiment dat wordt beschreven in **hoofdstuk 5** hebben we hetzelfde type mesocosms gebruikt voor een transplantatie experiment. De mesocosms met intacte vegetatie werden zuidwaarts getransplanteerd van Noord-Zweden naar Noordoost-Duitsland langs een transect van 4 hoogveenlokaties, langs het transect namen zowel temperatuur als N depositie toe van noord naar zuid. Er was geen transplantatie naar het noorden vanwege logistieke redenen en omdat we voornamelijk geïnteresseerd waren in de effecten van klimaatverwarming. Uit de vegetatieopnames gedurende drie groeiseizoenen bleek dat de bedekking van struiken de hoogste toename liet zien op de meest zuidelijke lokatie. De hoogtegroei van *S. balticum* was lager in de mesocosms die naar het zuiden waren getransplanteerd. Er was geen effect van oorspronkelijke of incubatie-lokatie op de *Sphagnum* productie, maar de N concentratie in *Sphagnum* nam wel toe naar het zuiden, zoals verwacht. Het ontbreken van een (positief) transplantatie-effect op de *Sphagnum* productie kan worden toegeschreven aan het beperkend worden van andere factoren zoals P of vocht. De vaatplanten namen echter wel toe in de hoogveenvegetatie als deze werd getransplanteerd naar warmere lokaties met hogere N depositie.

**De conclusie van de experimenten met de mesocosms is dat als het gevolg van hogere temperatuur, hogere N depositie en lagere waterstanden, de dwergstruikvegetatie in hoogvenen zal toenemen en de groei en bedekking van de 'natte' *Sphagnum* soorten zullen afnemen.**

**Hoofdstuk 6** beschrijft de gecombineerde effecten van een toename in temperatuur en N depositie op strooiselafbraak in hoogvenen. Onze verwachting was dat een hogere temperatuur en N depositie een positief effect zouden hebben op de microbiële activiteit en strooiselkwaliteit, en dat daardoor het massaverlies en stikstofverlies van *Sphagnum*-strooisel en vaatplantenstrooisel zouden toenemen. We hebben het massa- en N-verlies onderzocht op de 4 hoogveenlokaties langs het transect in twee experimenten met litterbags (zakjes van fijnmazig gaas): één experiment met strooisel van *Eriophorum vaginatum* (Eenarig wollegras) dat van alle lokaties naar alle lokaties werd gebracht, en één experiment met *Sphagnum* strooisel van de meest noordelijke lokatie van een moeilijk afbreekbare (*S. fuscum*) en een makkelijker afbreekbare (*S. balticum*) soort. Gedurende twee (*Sphagnum*) en drie (*E. vaginatum*) jaar hebben we het massa- en N-verlies gemeten. Er was geen verschil in N concentratie of afbreekbaarheid van het *E. vaginatum* strooisel afkomstig van de verschillende lokaties. Het massaverlies van het *E. vaginatum* strooisel nam toe langs de gradiënt naar het zuiden, maar dit effect werd niet waargenomen bij het *Sphagnum* strooisel. Het N-verlies in *Sphagnum* was positief gecorreleerd aan de N concentratie. We concluderen dat de afbraak van strooisel van vaatplanten en van *Sphagnum* wordt beïnvloed door verschillende omgevingsfactoren gezien het feit dat een hogere temperatuur het massaverlies van vaatplantenstrooisel wel, maar dat van *Sphagnum* niet stimuleert. Een toename in N depositie veroorzaakt een hoger N-verlies van *Sphagnum* strooisel. Gezien het feit dat één van de lange termijn consequenties van klimaatverandering waarschijnlijk een hogere vaatplantenproductie is, zoals ook geconcludeerd kan worden uit onze experimenten met mesocosms, is het waarschijnlijk dat de afbraaksnelheden van veen in het geheel zullen toenemen, vooral in combinatie met hogere temperatuur.

**Conclusie**

Uit onze resultaten concluderen we dat een toename in temperatuur en N depositie de soortensamenstelling van de *Sphagnum* vegetatie zal veranderen en de afbraak van het veen zal versnellen. Aangezien vooral de soorten van natte habitats te lijden zullen hebben van klimaatsverandering, zullen de soorten van droge habitats in verhouding toenemen. Aangezien het strooisel van de ‘droge’ soorten langzamer afbreekt, kunnen we verwachten dat de koolstofvastlegging waarschijnlijk niet meteen zal veranderen als gevolg van klimaatverandering. Op de lange termijn zou de toename van vaatplanten de *Sphagnum* productie echter kunnen verlagen. Omdat de *Sphagnum* productie niet profiteert van klimaatsverandering, en daardoor de groei van vaatplanten niet verlaagt, zal het competitieve evenwicht tussen *Sphagnum* en vaatplanten verschuiven in het voordeel van vaatplanten. Hierdoor neemt het aandeel vaatplantenstrooisel toe in het veen. Aangezien vaatplantenstrooisel veel makkelijker afbreekbaar is dan *Sphagnum* strooisel en omdat de afbraak van vaatplantenstrooisel veel meer gestimuleerd wordt door een temperatuurstijging, zal de strooiselafbraak veel sneller gaan en zullen nutriënten sneller beschikbaar komen, waarvan de vaatplanten ook weer meer profiteren dan *Sphagnum*. Op termijn zullen ook meer nutriënten beschikbaar komen in diepere lagen en daar kunnen dan ook grasachtigen meer van profiteren. Als de totale bedekking van struiken en grasachtigen toeneemt, kan de beschaduwing door vaatplanten de *Sphagnum* productie negatief beïnvloeden. Zodoende kan klimaatverandering op de lange termijn een ernstig negatief effect hebben op *Sphagnum* productie en op de capaciteit van hoogvenen om koolstof vast te leggen.

Om de bestaande modellen van hoogvenen te verbeteren zodat ze betere schattingen kunnen genereren voor huidige en toekomstige koolstofvastlegging in venen, zou toekomstig onderzoek zich moeten richten op langere tijdsschalen en zouden resultaten van vegetatieopnames, veld- en labstudies, palaeo-ecologisch onderzoek en klimaatdata geïntegreerd moeten worden.

# Dankwoord

Zo, het boekje is af! Hoewel het doen van onderzoek en met name het schrijven soms wel eens een eenzame bezigheid was, had ik dit natuurlijk echt niet alleen kunnen doen en zijn er heel veel mensen die ik moet bedanken voor hun bijdrage.

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Angela

# Curriculum Vitae

Angela Breeuwer werd op 15 april 1979 geboren in het ziekenhuis te Oss. Haar schoolcarrière begon op RK basisschool de Regenboog in Schaijk en werd vervolgd aan het Maaslandcollege te Oss waar zij in 1997 met lof slaagde voor haar eindexamen atheneum. In datzelfde jaar ging zij biologie studeren in Wageningen en koos in het tweede jaar voor de richting ecologie en populatiebiologie. Haar eerste afstudeervak 'Landschapsecologie' voerde zij uit bij Alterra en had als onderwerp de emigratie en dispersie van de Grote Karekiet in noord-west Overijssel. Na dit afstudeervak, waarbij vangst- en terugvangstgegevens werden gebruikt in een ruimtelijk expliciet populatiemodel, ging zij weer colleges en practica volgen met het oog op haar tweede afstudeervak 'Natuurbeheer in de Tropen & Remote Sensing'. Hiervoor ging zij in 2001 naar het Harry Oppenheimer Okavango Research Centre in Botswana waar zij met behulp van een satellietbeeld, vegetatieopnames en videobeelden een vegetatieclassificatie maakte. Deze werd gekoppeld aan GPS-locaties van grote herbivoren om zo uitspraken te kunnen doen over de habitatvoorkeur van deze soorten. Na deze fundamenteel wetenschappelijke afstudeervakken heeft zij nog stage gelopen bij de regiodirectie Oost van het ministerie van LNV waar zij de ervaringen met de regeling Programma Beheer in de provincies Gelderland en Overijssel heeft geëvalueerd. In september 2002 is ze met lof afgestudeerd en daarna is zij als toegevoegd onderzoeker in dienst gekomen bij de leerstoelgroep Natuurbeheer en Plantenecologie in Wageningen. Het betrof een aanstelling voor zes maanden voor een onderzoek naar het effect van agrarisch natuurbeheer op de dichtheden en de aantalsdynamiek van weidevogelsoorten in Nederland, in samenwerking met SOVON. Na dit project begon zij als AIO bij dezelfde leerstoelgroep aan het promotieonderzoek waarvan dit proefschrift het resultaat is.

Sinds december 2007 werkt zij als ecoloog bij Dienst Landelijk Gebied in Tilburg waar zij inrichtingsplannen maakt voor natuur en het landelijk gebied in de provincie Noord-Brabant.

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# CERTIFICATE

The Netherlands Research School for the
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