

# COMPETITION BETWEEN *SPHAGNUM* MOSSES IN EUROPEAN RAISED BOGS

THE EFFECTS OF A CHANGING CLIMATE

CONCURRENTIE TUSSEN VEENMOSSEN IN EUROPESE HOOGVENEN: DE EFFECTEN  
VAN EEN VERANDEREND KLIMAAT

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*Sphagnum* mosses are key-stone species in European raised bogs, and as such play an important role in the functioning of the ecosystem and its response to environmental change. Within *Sphagnum*, species may vary widely in their characteristics, making the identity of the dominant *Sphagnum* species an important factor explaining ecosystem response. We conducted several glasshouse and field studies, aimed at investigating how the main *Sphagnum* species in European raised bog respond to changes in climatic variables such as temperature, water table and precipitation with special focus on their effect on interspecific competition.

Our results showed that *Sphagnum* species differ in their response to water table, although the effect of water table was not as straightforward as hitherto expected. Despite differences in the potential to transport water from the water table towards their apical parts, co-occurring *Sphagnum* species possessed similar water contents. Nevertheless, we found species which naturally occur closest to the water table (hollow) to be ousted by species that naturally occur further from the water table (hummock), indicating that competition is related to interspecific (physiological) differences in the response to capitulum water content. We show that carbon assimilation of hollow species has a narrow optimum at relatively high capitulum water contents, whereas carbon assimilation of hummock species had its optimum under dryer conditions.

Additionally, our results show that precipitation plays an important role in determining the water content of *Sphagnum* mosses. Especially at low water tables, precipitation was found to be an important driver for carbon assimilation. Particularly, the competitive ability of hollow species may largely be determined by precipitation.

A considerable part of the competitive performance of *Sphagnum* mosses may be explained by the size of anisotropic peat moss vegetation. Our results show that the persistence of *Sphagnum* species which are transplanted generally increases with increasing patch size. Our results indicate that with increasing patch size the ability of *Sphagnum* mosses to create their own optimal micro-hydrology increases. Especially, under drier conditions, this ability may increase the competitive strength of species.

Summarizing, competition between *Sphagnum* species is influenced by the photosynthetic capacity at distinct capitulum water content. In turn, the capitulum water content of *Sphagnum* species depends on its capillary system, its water holding capacity (i.e. size of hyaline cells) and on the surrounding vegetation. The results presented in this thesis show that if the availability of water decreases, due to decreasing water tables or prolonged dry periods, hummock species will benefit at the expense of hollow species. Additionally, vascular plants like ericoids will increase. Since *Sphagnum* species differ in their production rates, changes in the species composition in raised bogs may result in changes in the production of the vegetation, and ultimately change the functioning of these ecosystems. It is important that peatland scientist continue to monitor the effects of environmental changes on changes in the species composition of peatlands. Especially long term measurement may provide a lot of information, which will help us to understand the mechanisms of competition between *Sphagnum* species to a higher degree.

remove my hands and feet/watch me crawl/on my stubs/throw me to the  
street/watch me fall/down head first its not that simple/but ive needed it  
from the start/to guide me may/ you will be ok/ it has made life simple/ive  
needed it from the start/to wake up if all else fails/if all turns to dust/set  
sail/on a ship built from trust/if all else fails/when all starts to rust/set sail/on  
a ship buillt for us its time to retreat/i have sawed it down to the bone/the  
canyons are too deep/yeah/i decided to run like a child/then decided to run  
to rescue/it took too long/to wake up

not that simple - dredg

# C

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## RAISED BOGS AND *SPHAGNUM* MOSSES

Raised bogs play an important role in the global carbon cycle because they can sequester large amounts of atmospheric carbon (Gorham 1991; Clymo et al. 1998; Hilbert et al. 2000). It has been estimated that peatlands, including raised bogs, store about 20% - 30% of the world's soil carbon (Clymo et al. 1998; Rydin and Jeglum 2006). This exceeds the amounts stored in tropical rainforests more than three times (Bragg and Lindsay 2003). Apart from being potential carbon sinks, raised bogs have the ability to store great quantities of water, making them important water retaining ecosystems (Moore 2002). Environmental changes (i.e. changes in temperature, water tables, precipitation, nutrient deposition) are believed to impact upon the functioning of raised bog ecosystems (see for example: Moore 2002; Dorrepaal et al. 2003; Belyea and Malmer 2004; Strack et al. 2004; Lafleur et al. 2005), especially since carbon dynamics in peatlands are tightly coupled to temperatures, nutrient inputs and soil moisture content (Rydin and McDonald 1985b; Aerts et al. 1992; Updegraff et al. 2001; Gunnarsson et al. 2004). To understand the effects of environmental changes on a certain ecosystem it is not necessary to study all various parts of the ecosystem. Understanding changes in the dominant species, enables predictions on the ecosystems fate (Grime 2003).

*Sphagnum* species are the key species in the ecology of raised bog systems, since they can influence the hydrochemistry of the bog system by their cations exchange capacity (Van Breemen 1995). Moreover, they can regulate the hydrological conditions at the bog surface to a high extent (Van der Schaaf and Streefkerk 2002). Their morphology and their growth form highly affect the capillarity and the water holding capacity of the moss layer in bogs (Clymo 1983). Recently it has been shown that the living *Sphagnum* layer together with the top peat layer, which consists of poorly decomposed *Sphagnum* remains (i.e. the acrotelm) plays a crucial role in the overall hydrology of raised bog systems (Van der Schaaf 1999; Van der Schaaf 2002). Typically, raised bogs are characterised by a pattern of microtopographical habitats, ranging from wet depressions (hollows) and relatively dry (but regularly inundated) lawns to dry hummocks with a different set of *Sphagnum* species occupying each microhabitat (Andrus *et al.* 1983). Hollow species generally occupy habitats close to the water table, whereas hummock species can occupy habitats further from the water table. The tight correlation between *Sphagnum* species and their position along the hydro-topographical gradient is likely the result of a combination of morphological and physiological constraints. Several studies stress interspecific differences among *Sphagnum* mosses in the efficiency of their external capillary system and their ability to hold water: among species there seems to be a trade-off between maximum growth rate, the ability to transport water to the capitula and the ability to withstand evaporative water loss (Hayward and Clymo 1982; Titus and Wagner 1984; Rydin and McDonald 1985a; Rydin and McDonald 1985b). Furthermore, considerable research has been carried out into the habitat preferences of *Sphagnum* species and there is a good knowledge of hydrological and trophic regimes at which the different species usually occur (e.g. Kelly 1993; Aggenbach and Jalink 1998). However, this information is not sufficient to accurately interpret past changes in the species composition of the moss layer in response to environmental changes or to predict future responses to such changes. A good understanding of the mechanisms



by which different species compete is also required. Since *Sphagnum* mosses lack stomata and roots, their water content in the active apical parts (i.e. capitula) strongly depends on the ability to transport water via an external capillary system and on the capacity to hold water which is supplied by precipitation (Clymo and Hayward 1982). In literature, some factors that influence these abilities have been defined (see for example, Hayward and Clymo 1982; Titus and Wagner 1984; Rydin and McDonald 1985a; Rydin and McDonald 1985b; Rydin and Jeglum 2006). At high water tables, all *Sphagnum* species can perform relatively well, but fast growing hollow species oust the less productive hummock species (Titus and Wagner 1984). At low water tables, the ability to transport water to the capitula is very important, since moisture content strongly determines the ability to assimilate carbon. Hummock species generally are superior in their capillary water transport and water holding capacity and therefore occupy habitats further from the water table. Furthermore, there seem to be interspecific differences in the response of carbon uptake to the capitulum water content but the literature provides inconsistent data (for a review, see Rydin 1993b).

## PEATLANDS IN IRELAND AND ESTONIA

Differences in temperature, annual precipitation and summer water tables are considered to be responsible for the morphological and vegetational differences between sub-oceanic (i.e. North-western European) and continental (i.e. Eastern European) bogs (Schouten et al. 1992). The peatlands of Ireland belong to the most important wetland sites remaining in North-west Europe (IMCG 2007). Due to local and industrial peat cutting, and agricultural activities Irish peatlands have declined dramatically. Exact numbers are difficult to find, but the loss of raised bogs lies between 68% and 92%, while between 46 % and 82% of the blanket bogs has been lost (O'Connell 2002; www.IPCC.ie, 2007). Today only 19% of the peatland resource remains in a relatively intact condition (220,902 ha). Only during the last decades, the importance of Irish peatlands has been acknowledged by the EU. According to the International Mire Conservation Group (IMCG) resolutions, peatland conservation has improved in Ireland the last 20 years. Illustrative are the completion of a survey and evaluation plan for peatlands and the adoption of approximately 225 peatland sites as part of the Natura 2000 network. Despite of this progression, peatland conservation still deserves attention since local activities (e.g. turf cutting), agriculture and plans for renewable energy (e.g. wind farms) remain a threat to Irish peatlands. In 1997 the Irish Peatland Conservation Council identified the main factors that affected peatland biodiversity, among which water table draw down and climate change, and proposed several actions that should promote public awareness of the importance of peatland biodiversity (Foss et al. 2001).

Estonian wetlands (bogs, fens and swamps) cover about 20% of the total land area (Montanarella et al. 2006), but their status has been declining rapidly. Moreover, 70% of all Estonian peatlands have ceased to accumulate carbon, which has been ascribed to drainage, peat extraction, oil shale mining and urban development. On the other hand, Estonia's Nature Conservation laws have led to the conservation of approximately 60% of the country's raised bogs, which are more or less in natural state (Bragg and Lindsay 2003). The adoption of wise use principles and implementation of Natura 2000 legislation might be a powerful tool for further raised bog conservation.

## CLIMATE CHANGE AND THE EFFECTS ON RAISED BOGS

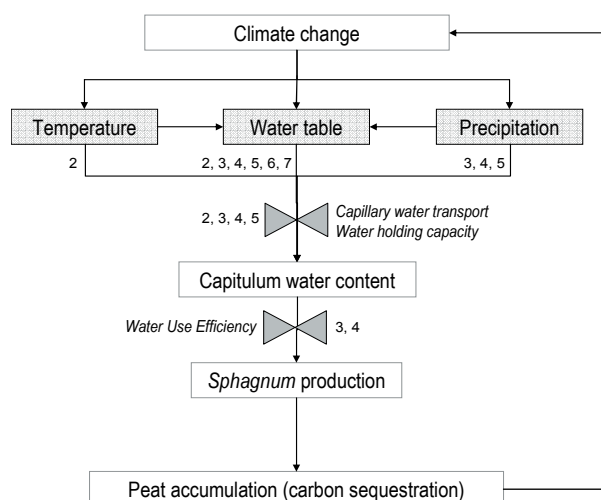
Future climate projections suggest an increase in global temperature together with changes in precipitation patterns (Sweeney and Fealy 2002; Meehl et al. 2007) as a result of increased greenhouse gas ( $\text{CO}_2$ ,  $\text{CH}_4$ ,  $\text{NO}_x$ ,  $\text{N}_2\text{O}$ ) concentrations in the atmosphere. Effects of global changes on the temperature will be above the global average on the Northern high latitudes (Houghton et al. 2001), the area where most European, but also North American, raised bogs are situated. How precipitation patterns will be changing is not fully understood, but projections indicate more intense precipitation events, with longer dry periods in between (Meehl et al. 2007). Global increases in temperature and changes in precipitation patterns are expected to alter the species composition and the species' distribution along the microtopographical gradient (Mauquoy et al. 2002; Bragazza 2006).

Palaeobotanical records show that the contribution of different *Sphagnum* species to the overall peatmos cover of a bog can change in time as a response to the changes in climatic conditions (Middeldorp 1986; Svensson 1988; Van der Molen and Hoekstra 1989; Mauquoy et al. 2001). Relatively dry periods favour the hummock species; in wetter periods the pool and hollow species tend to dominate. Studies in Irish raised bog systems have shown that recent changes in the bog's surface hydrology as a result of drainage and burning have led to changes in the relative cover of the different *Sphagnum* species (Kelly et al. 1995). Additionally, there are indications that temperatures of more than 20°C degrees during the growth season negatively affect at least some of the species (Schouten et al. 1992). It is not clear whether this is due to increased evaporation pressure or to physiological sensitivity to high temperatures. Yet, the lack of extensive and coherent knowledge of the individual and combined effects of environmental changes, like increasing temperatures and changes in the hydrology, on peatland vegetation is a major source of uncertainty in assessing the future role of peatlands in the global carbon cycle. However, it is plausible that changing temperatures, and changes in the amounts and frequency of precipitation and water table will affect the species composition in bogs, and ultimately the functioning of the whole ecosystem. The productivity of different 'functional groups' of *Sphagnum* varies, with productivity of hollow species being highest, that of lawn species intermediate, and productivity of hummock species being lowest (Strack et al. 2004; Gunnarsson 2005). A change of the dominance of a distinct functional group, may therefore affect the carbon sequestration rate of the total system.

Some research has been conducted with respect to competition between *Sphagnum* species (Luken 1985; Rydin 1986; Lütke Twenhoven 1992; Rydin 1993a; Kooijman and Bakker 1995; Rydin 1997a; Rydin 1997b; Heijmans et al. 2002) but no systematic study has been carried out involving all the important species of European raised bogs, and comprising the interactive effects of temperature, water table and precipitation (frequency as well as amount) on interspecific competition.

## AIMS AND OUTLINE OF THIS THESIS

This thesis focuses key environmental factors influencing the function of raised bogs, such as temperature, water table and precipitation, as well as knowledge about their interactive effects on the performance of *Sphagnum* monocultures and on the competition between *Sphagnum* mosses (Fig. 1.1). The most prominent species in European raised bogs, *Sphagnum cuspidatum*, *S. papillosum*, *S. magellanicum*, *S. rubellum*, *S. fuscum* and *S. austinii* (= *S. imbricatum*), are considered. Additionally, attention is paid to which morphological and/or physiological features of the mosses have a bearing on their competitive abilities (Fig. 1.1). The effects of changes in environmental conditions on the competitive abilities of *Sphagnum* species may be used to predict changes in the *Sphagnum* vegetation of raised bogs; changes which may eventually lead to changes in ecosystem services (Fig. 1.1). Furthermore, knowledge about the mechanisms which act in the competition between *Sphagnum* mosses may help to optimize management of peatland reserves.



**Figure 1.1** Schematic overview of the main factors that may influence the sequestration of carbon in raised bogs. The abiotic factors in the grey boxes are considered to be influenced by climate change and are used as experimental factors in the experiments presented in this thesis. The factors in the other boxes may be influenced by these three factors. Hourglass signs indicate interspecific differences for the characteristics written besides them. Numbers refer to the chapter in this thesis.

In this thesis several question are tried to answer:

1. What are the interactive effects of environmental changes, like temperature, water table and changes in precipitation on the performance of the most important European *Sphagnum* species?
2. Do environmental changes affect the competition between *Sphagnum* species, and which mechanisms are important therein?
3. Can we predict changes in the *Sphagnum* vegetation as a result of environmental changes?

The above questions were investigated and reported in this thesis. In chapter 2 we investigated how temperature and water table, and their interactive effects, affect height increment, bulk density and biomass production of four *Sphagnum* species. In this glasshouse experiment we additionally analysed the effects of water table and temperature on capitulum water content and evaporation. Subsequently, in chapter 3 we investigated the effects of water level on the competition between six *Sphagnum* species, in the glasshouse. Thereby we focused on two types of responses: effect responses (cover change) and mechanistic responses (capitulum water content, height increment and subcapitulum bulk density). Under drought, the ability to transport water towards the capitula may become an important factor in determining competitive strength. Therefore, we simulated a situation in which water supply to the capitula was not influenced by precipitation but by the ability of the peat mosses to transport water by capillary rise. We hypothesize on the importance of interspecific differences in the response to moisture content and on the effects of patch size and anisotropy of the peat. In chapter 4 we report on the interactive effects of water table and precipitation on the carbon uptake of a hollow, a lawn and a hummock species. In this chapter we describe a laboratory/glasshouse experiment in which we measured the photosynthetic response over a 23-day period of three *Sphagnum* species grown at high or low water tables, and with or without precipitation. Additionally, after fourteen days of negative CO<sub>2</sub> assimilation, recovery over a period of sixteen days was measured. Furthermore, we disentangle which layers of the *Sphagnum* vegetation are responsible for the bulk carbon uptake.

Chapter 5 elaborates on a short experiment in which we tried to disentangle direct and indirect (via lateral water transport) effects of precipitation on the persistence of hollow *Sphagnum* species in hummock vegetation. In Estonia, we transplanted samples of the hollow species *S. cuspidatum* into two hummocks, differing in height. By eliminating the input of direct precipitation and lateral water transport, we were able to monitor the effects of precipitation and lateral hummock water transport on the water content of the transplanted samples during a period of two weeks with natural precipitation. In chapter 6, we report on the results of two large field studies in which the effects of water table on the persistence of transplanted *Sphagnum* mosses were examined, in two different geographical regions, Ireland and Estonia. We also report on the effect of patch size on the persistence of transplanted species. In Ireland and Estonia, we transplanted large and small intact cores of different *Sphagnum* species into a monospecific matrix vegetation at two different water tables. Height increment of the transplanted samples, as well as that of the surrounding matrix, were measured in April and September. Additionally, change in cover of the transplanted samples was measured. This experiment lasted 3 ½ years. Chapter 7 discusses a (semi-)field experiment in which large monoliths with intact raised bog vegetation were exposed to a constantly high and a fluctuating water table. Changes in the moss cover, species composition and production were followed for two subsequent years.

Finally, chapter 8 gives an overview of the most important results and puts them in the wide context of peatland ecology. The effects of climate change on the composition of the *Sphagnum* vegetation are discussed. Furthermore, we elaborate on the consequences of our results for raised bog management and conservation.

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## EFFECTS OF WATER LEVEL AND TEMPERATURE ON THE PERFORMANCE OF FOUR *SPHAGNUM* MOSSES

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To evaluate the effects of changes in water level and temperatures on performance of four *Sphagnum* mosses, *S. magellanicum*, *S. rubellum*, *S. austinii*, and *S. fuscum* were grown at two water levels, -5 cm and -15 cm, and at two temperatures, 15°C and 20°C. These species differ in their position along the microtopographical gradient and in their geographical distribution. Height increment, subcapitulum bulk density, biomass production, capitulum water content and cumulative evaporation were measured. Height increment and biomass production of *S. magellanicum* was lower at low water table than at high water table, whereas height increment and biomass production of *S. rubellum*, *S. austinii*, and *S. fuscum* were unaffected. Height increment of *S. magellanicum*, *S. rubellum*, and *S. austinii* was higher at high temperature than at low temperature. Biomass production of only *S. magellanicum* and *S. rubellum* was higher at high temperature than at low temperature, corresponding with their more southern distribution. Cumulative evaporation of *S. magellanicum* and *S. rubellum* was lower at low water table and could be explained by hampered water transport towards the capitula. We conclude that changes in water table and temperature may alter the *Sphagnum* composition on raised bogs, which may result in changes to important ecosystem processes. Therefore, it is important that species composition and changes therein are taken into account when evaluating global change effects on raised bog ecosystems.

## INTRODUCTION

Raised bogs play an important role in the global carbon cycle owing to their ability to sequester large amounts of atmospheric carbon (Gorham 1991; Clymo et al. 1998; Hilbert et al. 2000). Apart from being potential carbon sinks, raised bogs have the ability to store great quantities of water, making them important water retaining ecosystems (Moore 2002). Global increases of temperature and changing patterns of precipitation are believed to impact upon the functioning of raised bog ecosystems (Moore 2002; Dorrepaal et al. 2003).

*Sphagnum* mosses are important in the ecology of bogs, since they are the dominant species in these systems. Because of their biomass production and rather slow decay rate (Clymo and Hayward 1982; Moore 2002; Limpens and Berendse 2003b; Rydin et al. 2003), *Sphagnum* species are largely responsible for the peat accumulation. Furthermore, *Sphagnum* mosses regulate the hydrological and hydrochemical conditions at the bog surface to a high degree (Clymo and Hayward 1982; Van der Schaaf 2002; Rydin et al. 2003). Raised bogs show a typical pattern of microtopographical habitats, ranging from wet depressions (hollows) and relatively dry (but regularly inundated) lawns to dry hummocks, with a different set of *Sphagnum* species occupying each microhabitat. The tight correlation between *Sphagnum* species and the position along the hydrological gradient (from hollow to hummock) is likely the result of a combination of morphological and physiological constraints (Andrus et al. 1983). Among species there seems to be a trade off between maximum growth rate, the ability to transport water to the capitula and the ability to minimize evaporative water loss (Titus and Wagner 1984; Rydin and McDonald 1985a; Rydin and McDonald 1985b; Rydin et al. 2003). *Sphagnum* species can differ in growth rate and water holding capacity, implying a different influence on ecosystem functioning (i.e. carbon sequestration and water retention). As such, the impact of environmental changes on the functioning of the ecosystem may depend on species composition and on changes therein.

Numerous papers report on the effects of environmental changes like nutrient deposition and elevated atmospheric CO<sub>2</sub> (e.g. Heijmans et al. 2002; Limpens and Berendse 2003a; Limpens et al. 2003; Bragazza et al. 2004), yet the number of papers reporting on the effects of changes in water level and temperature on the performance of different *Sphagnum* species is limited (e.g. Wallén et al. 1988; Dorrepaal et al. 2003; Gunnarsson et al. 2004) and to our knowledge no study describes the effect of these changes on the performance of the main peat forming species of oceanic Europe. The aim of this study was to investigate the potential effects of temperature and water level on growth of four *Sphagnum* species that are mainly responsible for peat accumulation in raised bogs in Western Europe, *Sphagnum magellanicum* Brid., *S. rubellum* Wils., *S. austinii* Sull. In Aust. (= *S. imbricatum* Hornsch.) and *S. fuscum* (Schimp.) Klinggr. These species differ in their position above the water table in the field and in their distribution across Europe. In the field, *S. magellanicum* occupies microhabitats that are relatively close to the water table (lawns), whereas *S. rubellum*, *S. fuscum* and *S. austinii* occupy microhabitats that range from relatively dry lawns to dry hummocks. Furthermore, *S. magellanicum* and *S. rubellum* extend further southward in Europe than the other two species, which are constrained to more temperate regions (Daniels and Eddy 1990). *S. magellanicum* and *S. rubellum* may be able to profit more from higher temperatures than

*S. fuscum* and *S. austinii*, improving the competitive strength of *S. magellanicum* and *S. rubellum* towards the south.

We hypothesized that (I) productivity of lawn species (*S. magellanicum*) will decrease with decreasing water level, whereas biomass production of hummock species (*S. rubellum*, *S. fuscum* and *S. austinii*) will not be affected. (II) Because of the efficient capillary water transport of hummock species, we expected that capitulum water content and evaporation of hummock species would be less affected by decreased water tables than capitulum water content of lawn species. Furthermore, we expected (III) species that extend further southward (*S. magellanicum* and *S. rubellum*) to perform better at higher temperatures than species with a more northern distribution (*S. fuscum* and *S. austinii*). In order to test these hypotheses, peat cores of the four *Sphagnum* species were placed in a glasshouse under two different temperatures, while keeping the water table at two constant levels.

## METHODS

### *Plant material*

In June 2003, 20 intact peat cores (16 cm diameter and approximately 20 cm depth) of four peat mosses, *Sphagnum magellanicum*, *S. rubellum*, *S. austinii* and *S. fuscum*, were collected from two raised bog in the Irish midlands. *Sphagnum magellanicum* and *S. rubellum* were collected at Clara bog (53°19'N, 007°37'W), whereas *S. austinii* and *S. fuscum* were collected at Mongan bog (53°19'N, 007°58'W), Co. Offaly, Ireland; for detailed site descriptions see Schouten (2002). The two bogs are both classified as true midland raised bogs with a similar age and developmental history. Furthermore, they both have a relatively intact hydrology and an extensive *Sphagnum* cover (Cross 1990; Parkes and Mitchell 2000; Connolly unpublished results summarised in Schouten 2002). Cores were taken from monospecific *Sphagnum* stands (> 95% of one species) with a sparse vascular plant cover (< 5%). The peat cores were cut with a sharp knife and put into PVC pipes (16 cm diameter) for transport. Aboveground vascular plant parts were removed (seedlings were pulled out and older specimens were clipped) before storing the peat cores in the PVC pipes for three months at 1°C. To prevent drying out, the pipes were covered with plastic. The mosses were not visibly affected by the storage period.

### *Experimental design*

Late September 2003, the PVC pipes containing the peat cores were placed in the glasshouse in 50 l containers (25 cm diameter and 100 cm height), containing an artificial rainwater solution (Garrels and Christ 1965). The area between the PVC pipes and the containers was covered by a tight fitting lid. We applied four treatment combinations which comprised two temperature regimens (15°C and 20°C) and two water table regimens (-5 cm and -15 cm below the top of the capitula). The water tables in this experiment represented average water tables at lawn and hummock microhabitats in Clara bog (Kelly and Schouten 2002). Temperatures represented Irish mean summer temperature (15°C to 16.7°C; Met Éirann – The Irish Meteorological Service) and a hypothetical temperature increase of 5°C; the rounded upper limit of temperature increase for the

next century as projected by the IPCC (1996). This study was conducted as a nested randomised block design with four treatments for every species in five replicated blocks. The four treatments were arranged in a  $2 \times 2 \times 4$  nested arrangement (i.e. two adjacent temperature compartments). The weekly mean humidity in the glasshouse ranged from 68% to 80%, but did not differ between the two compartments (paired sample t-test:  $t = 2.36$ ,  $P = 0.11$ ). Light conditions in both glasshouse compartments were assumed to be similar; natural light was supplemented with high pressure sodium lamps (Philips MASTER SON-T PIA Agro 400W E E40 SLV; Luminous flux EM [Lm] 55000,  $1 \text{ lamp} \cdot 4\text{m}^2$ ), to induce a 16 hour photoperiod. Water level in the containers was adjusted to the experimental height below the moss surface once a week, using the same artificial rainwater solution as described above. To avoid complete, chronic (i.e. detrimental) drying out, the capitula in all containers were moistened once every two weeks to simulate natural rain events by adding 8.75 mm (= 175 ml) rainwater solution. This corresponds with 234 mm precipitation per year. During the experiment, regrowth of vascular plants was regularly removed. The mosses were harvested after 6 months.

### *Sphagnum growth and biomass production*

Once a month, height increment of the *Sphagnum* species was measured using a method slightly modified after the one described by Limpens and Berendse (2003a). Two metal rods were placed at fixed points on the PVC pipes edge. A bar fitted between the rods was used as a stable horizontal benchmark above the *Sphagnum* carpet. At 5 fixed points we measured the distance between the *Sphagnum* surface and the traverse, using a ruler. Subsequently, the two metal rods and the benchmark were rotated  $90^\circ$ , after which we repeated the measurements. Before statistical analysis, the measurements for the ten distances were averaged. At final harvest we cut a vertical *Sphagnum* slice ( $3 \times 9 \text{ cm}$  and  $1.5 \text{ cm}$  deep) from the middle of each peat column. Next, every slice was cut into two sections: a capitulum ( $0 - 0.5 \text{ cm}$ ) section and a subcapitulum ( $0.5 - 1.5 \text{ cm}$ ) section (c.f. Dorrepaal et al. 2003). After determining fresh weight, the two sections were oven dried at  $70^\circ\text{C}$  for a least 48 h. Hereafter, we were able to calculate capitulum water content ratios and subcapitulum bulk density. Biomass production (P) per column was calculated by multiplying the subcapitulum bulk density ( $\text{BD}_{\text{Subcap}}$ ) with the height increment (L) of the *Sphagnum* carpet:  $P = L \times \text{BD}_{\text{Subcap}}$ . Since at harvest, capitulum dry weight within species did not differ significantly between the treatments (Table 2.1), we assumed that capitulum dry weight also was not different at the start and did not change over the experimental period as a response to treatment. Consequently, we did not correct for changes in the capitulum dry weight when calculating biomass production.

In the course of the experiment, liverworts (*Mylia anomala* and *Odontoschisma sphagni*) appeared on the peat moss surface. To correct for possible effects of liverwort presence on *Sphagnum* performance, we measured liverwort cover using a transparent sheet that was placed over the *Sphagnum* layer. This sheet had a grid, which constituted 710 intersections. Liverwort cover was expressed as follows:

Liverwort cover = (nr. of intersections coinciding with liverworts/710)  $\times$  100%

**Table 2.1** Mean capitulum dry weight ( $\pm$  SEM) in  $\text{g m}^{-2}$  at harvest for all treatments and species. Unless indicated,  $n = 5$ . Four data points were omitted from the analyses because the containers were leaking and as a consequence constant water levels could not be guaranteed. Treatment effect was tested with every species using PROC GLM in SAS 9.1. Within species, we did not find any treatment effects.

Treatment	code <sup>†</sup>	Species			
		<i>S. magellanicum</i>	<i>S. rubellum</i>	<i>S. fuscum</i>	<i>S. austinii</i>
15°C, -5cm	15; HWT	248.0 $\pm$ 46.8 *	321.7 $\pm$ 37.2	407.9 $\pm$ 118.5 *	470.9 $\pm$ 42.4
15°C, -15cm	15; LWT	209.5 $\pm$ 24.6	382.0 $\pm$ 11.4	539.5 $\pm$ 77.8	511.2 $\pm$ 57.7
20°C, -5cm	20; HWT	222.6 $\pm$ 12.1	305.1 $\pm$ 43.7	342.7 $\pm$ 35.5 *	384.8 $\pm$ 35.9
20°C, -15cm	20; LWT	301.1 $\pm$ 40.1 *	292.0 $\pm$ 18.2	448.0 $\pm$ 51.4	508.4 $\pm$ 71.1

\*  $n = 4$

<sup>†</sup> This code will be used as an abbreviation for treatment in Figure 1 and Figure 2

### *Sphagnum* water loss

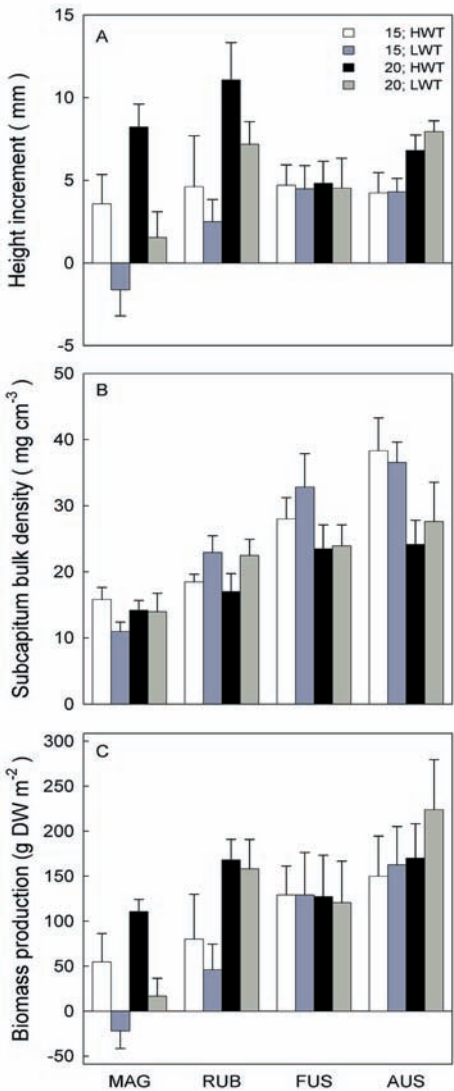
To assure that water loss could only take place from the *Sphagnum* surface, the area between the PVC pipes that contained the peat cores and the containers was covered with a tight fitting lid. The cumulative amount of water, lost during the experiment, was used as a proxy for the evaporative water loss. As a measure for the capitulum water content at harvest, we used the capitulum fresh weight  $\cdot$  dry weight<sup>-1</sup> (FW  $\cdot$  DW<sup>-1</sup>) ratio.

### Data analysis

Data were tested for normality (Shapiro-Wilks W test) and equality of variance (Levene's test) prior to further analysis. Our data did not always meet the assumptions of homogeneity of variances (subcapitulum bulk density:  $F = 1.95$ ,  $P = 0.034$ ; capitulum water content:  $F = 2.03$ ,  $P = 0.027$ ), even after  $\ln$ -transformation. Since analysis of variance appears not to be greatly influenced if the assumptions of equality in variances or normal distribution are not met, as long as sample sizes are more or less equal (Heath 1995), we proceeded our analyses without transformations. The effects of the fixed factors Species (S), Temperature (T) and Water table (W) on the variables height increment, subcapitulum bulk density, biomass production, cumulative evaporation and capitulum water content were analysed using GLM multivariate analysis of covariance. We included liverwort cover as a co-variable in the model. Since we did not find an effect of block, we omitted block from the model. After omitting liverwort as a co-variable from the analyses, overall differences between the *Sphagnum* species were determined by multiple LSD post-hoc tests.

As we often found interactions between species and temperature or species and water table, these overall analyses were followed by ANOVA's for each *Sphagnum* species. Temperature and water table were included in the model as fixed factors. Since liverwort cover affected subcapitulum bulk density, we included liverwort as a co-variable if testing the effects of our variables on subcapitulum bulk density. Liverwort cover was omitted from the analyses not dealing with subcapitulum bulk density. We tested the effects of the fixed factors Species (S), Temperature (T) and Water table (W) on the liverwort cover using GLM univariate analysis.

All statistical analyses have been carried out using SAS 9.1 (SAS Institute, Windows version 5.1.2600). Four data points were omitted from the analysis, because of leaking containers.



**Figure 2.1.** The effects of temperature and water table treatment on A) height increment, B) subcapitulum bulk density at harvest and C) biomass production (means  $\pm$  SEM) on *S. magellanicum* (MAG), *S. rubellum* (RUB), *S. fuscum* (FUS) and *S. austinii* (AUS). For treatment codes, see Table 2.1.

## RESULTS

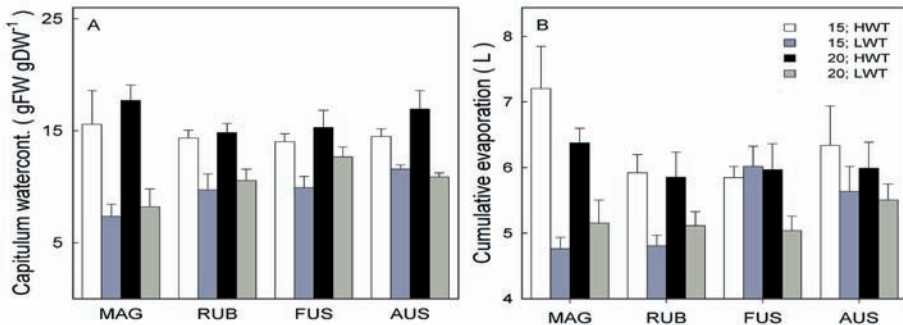
### Overall effects

We found main effects of species, temperature and water on height increment and of species and temperature on subcapitulum bulk density and biomass production. Overall height increment was highest for *S. austinii*, *S. fuscum* and *S. rubellum* and lowest for *S. magellanicum* (LSD post-hoc test; Fig. 2.1A, Table 2.2). Furthermore, subcapitulum bulk density and biomass production of *S. austinii* and *S. fuscum* exceeded that of *S. magellanicum* and *S. rubellum* (LSD post-hoc test; Fig. 2.1B,C; Table 2). Overall capitulum water content and cumulative evaporation did not differ between species (LSD post-hoc test; Fig. 2.2A,B; Table 2.2).

**Table 2.2** Values for the overall effects of the fixed factors species, water table and temperature treatment and the co-variable liverwort cover on height increment, subcapitulum bulk density, biomass production, capitulum water content and cumulative evaporation. Values in bold indicate significant P-values (<0.05).

Source	d.f.	Height increment		Subcap. bulk density		Biomass production		Cap. water content		Cum. evaporation	
		F-value	P-value	F-value	P-value	F-value	P-value	F-value	P-value	F-value	P-value
LW cover	1	0.39	0.533	27.71	<b>&lt;0.001</b>	2.09	0.153	1.22	0.274	0.25	0.617
Species	3	3.58	<b>0.019</b>	6.36	<b>0.001</b>	4.26	<b>0.009</b>	1.30	0.284	1.62	0.196
Water	1	5.76	<b>0.020</b>	0.14	0.713	1.84	0.180	64.58	<b>&lt;0.001</b>	25.74	<b>&lt;0.001</b>
Temperature	1	14.75	<b>&lt;0.001</b>	7.71	<b>0.007</b>	6.35	<b>0.014</b>	3.83	0.055	1.32	0.256
S × W	3	3.40	<b>0.023</b>	1.23	0.306	1.33	0.275	4.07	<b>0.011</b>	3.34	<b>0.025</b>
S × T	3	2.06	0.115	2.81	<b>0.047</b>	1.11	0.353	0.21	0.887	0.47	0.703
W × T	1	0.14	0.714	0.59	0.446	0.11	0.745	0.32	0.573	0.24	0.627
S × W × T	3	0.17	0.917	0.21	0.889	0.17	0.916	0.56	0.641	1.90	0.139

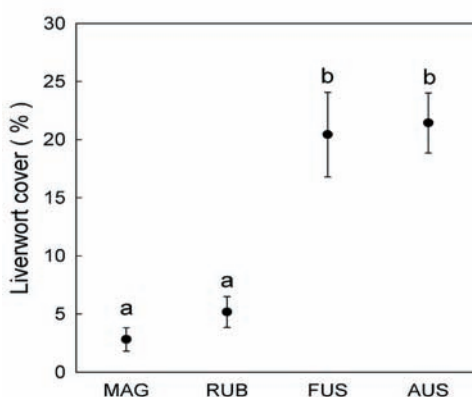
Cover of *Mylia anomala* and *Odontoschisma sphagni* was more pronounced in *S. fuscum* and *S. austinii* than in *S. magellanicum* and *S. rubellum* ( $F = 16.25$ ,  $P < 0.001$ ; Fig. 2.3). Overall, liverwort cover was an important factor explaining subcapitulum bulk density (Table 2.2). Higher liverwort cover resulted in higher bulk density only in *S. fuscum* and *S. austinii* (Table 2.3). Liverwort cover was affected by the water table, resulting in higher cover at low water tables ( $F = 4.33$ ,  $P = 0.04$ ). Nonetheless, these liverworts had no effect on *Sphagnum* height increment, dry weight production, capitulum water content and cumulative evaporation (Table 2.2).



**Figure 2.2** The effect of temperature and water table treatments on (A) capitulum water content and (B) cumulative evaporation (means  $\pm$  SEM). For treatment codes and replicate numbers, see Table 2.1. For statistics, see Table 2.2 and 2.3

### Within species response to water table

Height increment and biomass production of *S. magellanicum* were depressed at low water table, whereas height increment and production of *S. fuscum*, *S. rubellum* and *S. austinii* remained unaffected (Fig. 2.1A,C; Table 2.3). Subcapitulum bulk density was not affected by water table for any of the species. Capitulum water content was lower at the – 15 cm treatment than at the – 5 cm treatment for all *Sphagnum* species (Fig. 2.2A; Table 2.3), but the response of *S. magellanicum* to water level exceeded that of the other three species (Table 2.2). Cumulative evaporation was lower at the – 15 cm treatment than at the – 5 cm treatment for *S. magellanicum* and *S. rubellum*, whereas cumulative evaporation was similar between water table regimens for *S. fuscum* and *S. austinii* (Fig. 2.2B; Table 2.3).



**Figure 2.3** Mean liverwort cover ( $\pm$  SEM) in % at harvest on *S. magellanicum*, *S. rubellum*, *S. fuscum* and *S. imbricatum*. Means with the same letter do not significantly differ.

### Within species response to temperature

Height increment of *S. magellanicum*, *S. rubellum* and *S. austinii* was larger at high temperature, whereas height increment of *S. fuscum* remained unaffected (Fig. 2.1A; Table 2.3). Subcapitulum bulk density of *S. magellanicum* and *S. rubellum* was not affected by temperature, whereas subcapitulum bulk density of *S. austinii* was lower at high temperature. *S. fuscum* subcapitulum bulk density showed a similar, albeit weaker, response to temperature (Fig 2.1B; Table 2.3). As a result increased temperature enhanced biomass production of only *S. magellanicum* and *S. rubellum*. The combination of low temperature and low water table was detrimental to *S. magellanicum* production; this species lost 21.8 g DW m<sup>-2</sup> under these circumstances (Fig. 2.1C). In general, capitulum water content at harvest was higher at high temperature, but within species this effect was masked by the effects of water table (Table 2.2 and 2.3). Cumulative evaporation did not change as a response to increased temperature for any *Sphagnum* species (Fig. 2.2B; Table 2.3).



**Table 2.3** Values for the effects of water table and temperature treatment on height increment, subcapitulum bulk density, biomass production, capitulum water content and cumulative evaporation within every species separately. We included liverwort as a co-variable only if testing the effects of our variables on subcapitulum bulk density. Numbers in bold indicate significant *P*-values (<0.05).

Source	Height increment		Subcap. bulk density		Biomass production		Cap. water content		Cum. evaporation	
	<i>F</i> -value	<i>P</i> -value	<i>F</i> -value	<i>P</i> -value	<i>F</i> -value	<i>P</i> -value	<i>F</i> -value	<i>P</i> -value	<i>F</i> -value	<i>P</i> -value
<i>S. magellanicum</i>										
LW cover *	-	-	0.08	0.776	-	-	-	-	-	-
Water	14.07	<b>0.002</b>	1.68	0.218	16.20	<b>0.001</b>	24.36	<b>&lt;0.001</b>	26.06	<b>&lt;0.001</b>
Temperature	6.10	<b>0.027</b>	0.12	0.737	4.94	<b>0.043</b>	0.70	0.418	0.367	0.555
W × T	0.22	0.648	0.76	0.401	0.16	0.698	0.13	0.727	2.89	0.111
<i>S. rubellum</i>										
LW cover	-	-	2.95	0.106	-	-	-	-	-	-
Water	2.00	0.177	3.79	0.070	0.40	0.536	18.64	<b>0.001</b>	11.70	<b>0.004</b>
Temperature	6.83	<b>0.019</b>	0.29	0.600	8.22	<b>0.011</b>	0.43	0.519	0.19	0.667
W × T	0.17	0.692	0.39	0.543	0.12	0.735	0.03	0.864	0.49	0.496
<i>S. fuscum</i>										
LW cover	-	-	7.66	<b>0.016</b>	-	-	-	-	-	-
Water	0.03	0.954	0.14	0.714	0.01	0.940	9.57	<b>0.008</b>	1.793	0.202
Temperature	0.00	0.952	2.64	0.128	0.01	0.910	3.39	0.087	2.285	0.153
W × T	0.00	0.984	0.04	0.838	0.01	0.941	0.45	0.513	3.8	0.072
<i>S. austinii</i>										
LW cover	-	-	11.15	0.004	-	-	-	-	-	-
Water	0.41	0.531	0.54	0.473	0.53	0.477	23.61	<b>&lt;0.001</b>	1.93	0.183
Temperature	10.96	<b>0.004</b>	6.95	<b>0.019</b>	0.80	0.384	0.93	0.350	0.32	0.582
W × T	0.33	0.572	0.55	0.470	0.20	0.658	2.86	0.110	0.06	0.807

\* Liverwort cover had effect only on subcapitulum bulk density and was therefore omitted from the other analyses.

## DISCUSSION

### Water level

As hypothesised, a low water level resulted in depressed height growth and biomass production for the lawn species *S. magellanicum*, whereas the three hummock species remained unaffected (Fig. 2.1A,C). This implies that hummock species are less sensitive to changes in water level than lawn species. Although Lindholm (1990) found that *Sphagnum* growth in hummocks is strongly related to moisture conditions, it is believed that hummock species are less subject to interseasonal changes in the moisture regime than lawn and hollow species (Hayward and Clymo 1982; Gerdol 1995; Asada et al. 2003). In our glass house study, *S. magellanicum* had lower biomass production than *S. austinii* and *S. fuscum* (Fig. 2.1C), even at the favourable water level for this species. These results contradict with mean productivity values derived from field studies or from outdoor field-like studies, which revealed that differences in average productivity rates between *S. magellanicum* (257 g m<sup>-2</sup> year<sup>-1</sup>), *S. rubellum* (237 g m<sup>-2</sup> year<sup>-1</sup>) and *S. fuscum* (170 g m<sup>-2</sup> year<sup>-1</sup>) were positively correlated to the height of the water table in the field (Gunnarsson 2005). Thus, hummock species had lower productivity than hollow or lawn species in their respective microhabitats. In our experiment, overall *S. magellanicum* productivity was extremely low. Yet, under natural circumstances water levels are subject to some fluctuations and precipitation events may occur more frequently. Hollow and lawn species may have a higher production during wet periods when the water table is close to the

moss surface. Since water tables in our experiment were kept constant, the low production of *S. magellanicum* can be explained by its deficiency to keep a positive capitulum water balance, when both water table and frequency of precipitation are low (c.f. Gerdol 1996). This suggests that *S. magellanicum* is sensitive to periods of prolonged drought.

In accordance with our second hypothesis, a decrease in water table depressed capitulum water content of the lawn species *S. magellanicum* more than that of the hummock species *S. fuscum*, *S. austinii* and *S. rubellum*. Surprisingly, the decrease in capitulum water content was not reflected in decreased height increment and biomass production for hummock species. Apparently, the decrease in capitulum water content was not enough to trigger a reduction in height increment and biomass production in these peat mosses. For the lawn species *S. magellanicum*, however, the decrease in capitulum water content seems to have hampered height increment and biomass production. *Sphagnum* plants depend more or less on water supply via capillary rise (Clymo and Hayward 1982). The dense growth form (i.e. high subcapitulum bulk density) of the hummock species, *S. fuscum*, *S. austinii* and, to a lower extent, *S. rubellum* (Fig. 2.1B) is often associated with an efficient capillary system (Clymo and Hayward 1982; Grosvernier et al. 1997; Asada et al. 2003), making them less sensitive to changes in the water table. At the lowest water table, capitula of *S. magellanicum* were often observed to be dry, which indicates a poor capillary water transport. At low water tables, this poor capillary system probably resulted in the stronger decrease of the capitulum water content of *S. magellanicum* than the capitulum water content of *S. fuscum*, *S. austinii* and *S. rubellum* (c.f. Wallén et al. 1988). On account of the latter, height increment and biomass production of *S. magellanicum* decreased. For *S. fuscum* it has been shown that changes in water supply to the capitula can lead to changes in bulk density (Dorrepal et al. 2003). This implies that, given enough time, *Sphagnum* can adapt its morphology to some extent, if faced with a decrease in capitulum water content. In our experiment, however, *S. magellanicum* subcapitulum bulk density did not change. Perhaps the constant low water level and the inability of *S. magellanicum* to transport water to its capitula resulted in hampered growth. Consequently, *S. magellanicum* has been unable to adapt its morphology to cope with low capitulum water content. Additionally, we did not find changes in subcapitulum bulk density as a response to water table in any of the other species. Since height increment and biomass production of *S. rubellum*, *S. fuscum* and *S. austinii* were not affected by water table, even though capitulum water content decreased, we assume that there was no necessity for these species to change their subcapitulum bulk density.

### Temperature

In accordance with our hypothesis, biomass production of the widely distributed species, *S. magellanicum* and *S. rubellum* increased with temperature (Fig. 2.1C), whereas biomass production of the two species with a more northern distribution, *S. fuscum* and *S. austinii*, remained unaffected by temperature (Fig. 2.1C). Nevertheless, the response of *Sphagnum* to temperature does not seem as straightforward as the above would imply. Other studies may show none, or even an opposite response to the one we are reporting (Gerdol 1995; Gerdol et al. 1998; Weltzin et al. 2001;

Sonesson et al. 2002; Dorrepaal et al. 2003; Gunnarsson et al. 2004). This stresses the importance of environmental conditions (precipitation, temperature, etc.) under which the experiments have been carried out (Sonesson et al. 2002). In our experiment, increased temperature did stimulate *S. austinii* height increment (Fig. 2.1A), although, this effect was not reflected in biomass production because of a decrease in bulk density (Fig. 2.1B). For the widely distributed species *S. magellanicum* and *S. rubellum*, height increment did not occur at the expense of biomass production. Our results raise the question whether the positive response to increased temperature reflects physiological adaptations or is an effect of changes in nutrient availability caused by increased decomposition and N mineralization (Bergman et al. 1999; Rustad et al. 2001). We found increased growth as a response to increased temperature at both water tables. If nutrients would be limiting then we would have found a temperature effect only at high water table, because growth is not hampered by water here. Consequently, a direct physiological response to increased temperature may be the most plausible explanation for our findings.

In general, we observed a small increase in capitulum water content in response to increased temperature (Table 2.2). This implies that increased temperature increases capillary water flow. Under these circumstances, evaporation rates can be higher (Gunnarsson et al. 2004). Within species, however, we did not find an effect of temperature on cumulative evaporation. We applied water to the capitula only once every two weeks, and water lost by evaporation was only filled up weekly. This may have resulted in higher evaporation at high temperatures just after application. Water tables may have dropped slightly. As a result capitulum water content decreased. Subsequently, evaporation rates at high temperature may have dropped faster than at low temperature, resulting in no difference in cumulative evaporation between the two temperatures.

### *Liverworts*

Although higher liverwort cover resulted in higher subcapitulum bulk density, it did not affect the water balance and the performance of *Sphagnum*. We found that low water tables had a positive effect on the cover of these liverworts. Water level, however, may not directly affect the growth of liverworts. A more likely explanation for our results is that the actively growing *Sphagnum* inhibits the growth of liverworts, whereas liverworts can rapidly overgrow *Sphagnum* that is hampered in growth (Duckett and Clymo 1988). In our experiment, liverworts (*M. anomala* and *O. sphagni*) were more abundant in the hummock species, *S. fuscum* and *S. austinii* than in *S. magellanicum* and *S. rubellum* species (Figure 2.3). Field observations support these results: liverwort abundance is higher in hummock species than in lawn and pool species, suggesting that *M. anomala* and *O. sphagni* prefer drier hummock habitats over the relatively moist lawn habitats.

### *Implications of climate change*

We show that water table draw down and temperature increase can have contrasting effects on peat moss growth and evaporative water loss. Since we did not find interactions between temperature and water table, we conclude that these two factors cause independent responses.

Changes in temperature and water table had differential effects on the four peat mosses.

We show that increased temperature will favour the species with a wide geographic range (*S. magellanicum* and *S. rubellum*), whereas lower water tables will be advantageous for hummock species. In time, changes in temperature and raised bog water level might alter the competitive balance between *Sphagnum* mosses, resulting in a change in the species composition of raised bogs. Ultimately, changes in the *Sphagnum* vegetation can have implications on important ecosystem processes. Our results indicate that when temperatures increase, *S. magellanicum* and *S. rubellum* will gain competitive strength whereas *S. rubellum* will likely become dominant when increased temperature would coincide with decreased precipitation.

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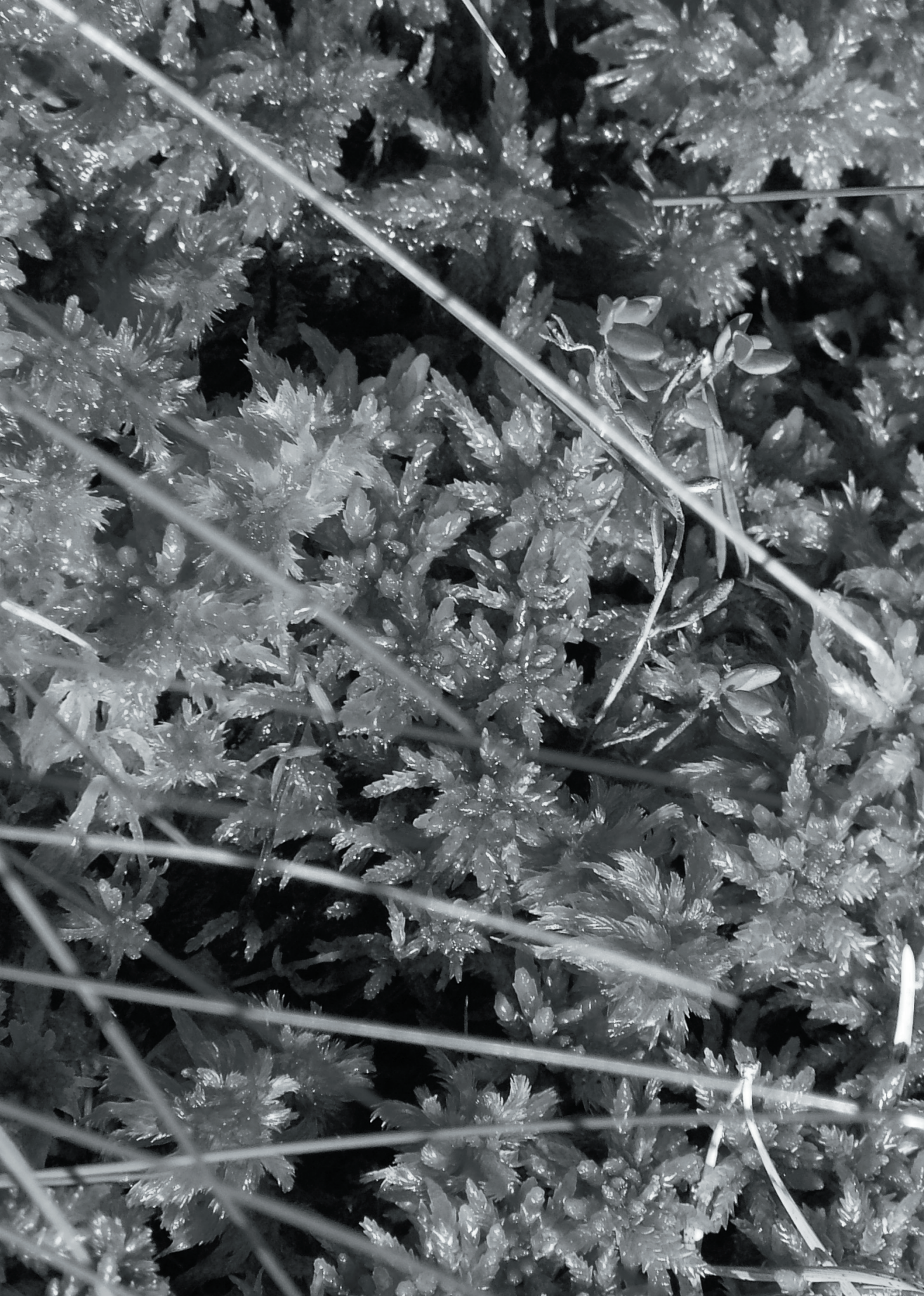
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# 3

## INTERSPECIFIC COMPETITION BETWEEN *SPHAGNUM* MOSSES AT DIFFERENT WATER TABLES

Robroek BJM, Limpens J, Breeuwer A, Crushell PH and Schouten MGC (2007)  
*Functional Ecology* 21: 805-812

Effects of climate change may affect the *Sphagnum* species composition in bogs, and ultimately the functioning of the whole ecosystem. We investigated the effect of different water tables on the competition between six *Sphagnum* species, in the glasshouse. The amount of precipitation (234 mm yr<sup>-1</sup>) and the precipitation frequency (every two weeks) were kept low to encourage water table effects. Relevant species combinations and monocultures were grown at different water tables for a 16-month period. We studied changes in cover, height increment and capitulum water content to understand competitive responses. Species naturally occurring further above the water table generally showed higher competitive strength than species naturally occurring closer to the water table. Surprisingly, this effect was irrespective of the water table, indicating a minor role for capillary water transport. Cover change seemed to be related to differences in length growth, but not to water table or capitulum water content ( $WC_{cap}$ ).  $WC_{cap}$  of species within a mixture did not differ, but was lower than the  $WC_{cap}$  of the individual species growing in monoculture, indicating differences in the ability to supply water to the capitula between mono- and mixed cultures. Subcapitulum bulk density between mono- and mixed cultures did not differ, or were even lower in monocultures, but did differ between species within mixed cultures. Our results indicate that structural heterogeneity of the peat in mixed cultures has a negative effect on the capitulum water content of both species. Furthermore, we show that sustained periods of drought causes species that naturally occur further above the water table to oust species that naturally occur closer to the water table, even if the water table remains high. Ultimately, the *Sphagnum* vegetation in raised bogs may shift from hollow to hummock species, evening out the natural microtopography of raised bogs.

## 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, playing a crucial role in these ecosystems. Due to their considerable biomass production and relatively slow decay rate (Johnson and Damman 1991; Limpens and Berendse 2003), *Sphagnum* mosses are largely responsible for the formation of peat and hence, the sequestration of carbon. Furthermore, *Sphagnum* regulates the hydrological and hydrochemical conditions at the raised bog surface to a high degree (Van Breemen 1995; Van der Schaaf 2002). To what extent *Sphagnum* mosses affect their environment may depend on the identity of the dominant species. Consequently, the *Sphagnum* species composition and changes therein may affect the functioning of the bog ecosystem.

Species composition seems to be mainly determined by differences in water table, with different sets of *Sphagnum* species occupying specific positions above the water table. The distribution of species along the hydrological gradient is thought to be related to differences in growth rate (as reviewed by Gunnarsson 2005), the efficiency of their capillary system and their ability to hold water (Hayward and Clymo 1982; Titus and Wagner 1984; Rydin and McDonald 1985a). Because *Sphagnum* species lack stomata or roots, the ability to keep their active apical parts (i.e. capitula) moist is related to the efficiency to transport water from the water table to the capitula and to avoid water loss. Because of their dense growth (Clymo and Hayward 1982), hummock species are believed to be efficient in transporting and holding water by their capillary system, which enables them to supply water to the capitula even at relatively low water tables (Hayward and Clymo 1982). Water transport to the capitula, however, may also be related to physical properties other than bulk density, such as porosity and carpet structure. Interspecific differences in physical properties, which affect water transport, may result in differences in height increment and in horizontal expansion, and may ultimately influence the outcome of interspecific competition.

Much of the above has been deduced from experiments with monocultures or field measurements (Hayward and Clymo 1983; Schipperges and Rydin 1998; Dorrepaal et al. 2003), but has not yet been tested in mixed cultures under controlled conditions. In order to predict how bogs will respond to environmental change, we need to know the underlying mechanisms that determine the outcome of interspecific competition. Studies that focus on the response of *Sphagnum* species to water table and temperature changes, which are a logical consequence of the dryer and warmer summer conditions as predicted for large parts of North-western Europe (Houghton et al. 2001) are scarce (e.g. Gunnarsson and Rydin 2000; Dorrepaal et al. 2003; Dorrepaal et al. 2006). Moreover, there is a lack of knowledge about the competitive interactions among bryophytes (Mulligan and Gignac 2002), and to our knowledge no study describes the effect of environmental changes on the competition between the main peat forming *Sphagnum* species of (sub-)oceanic raised bogs in Europe.

The aim of this study is to elucidate the effects of water table on the competition between peat mosses. Thereby we focus on two types of responses: effect responses and mechanistic responses. We define cover change as an effect response, whereas capitulum water content, height increment and subcapitulum bulk density were defined as mechanistic responses. Under drought, the ability to transport water towards the capitula may become an important factor in determining competitive strength. Therefore, we mimicked a situation where water supply to the capitula was not influenced by precipitation but by the ability of capillary water transport. Species which naturally occur further above the water table (hummock) are superior in maintaining water supply to the capitula than species which occur closer to the water table (hollow). As a result, hummock species were expected to be less negatively affected in their water content and growth response by low water tables than hollow species. We expected that, (I) in a mixture decreased water table would lead to increased cover of species that naturally occur further above the water table, and (II) we expected these changes in cover to be associated with differences in height increment, subcapitulum bulk density and capitulum water content between competing species.

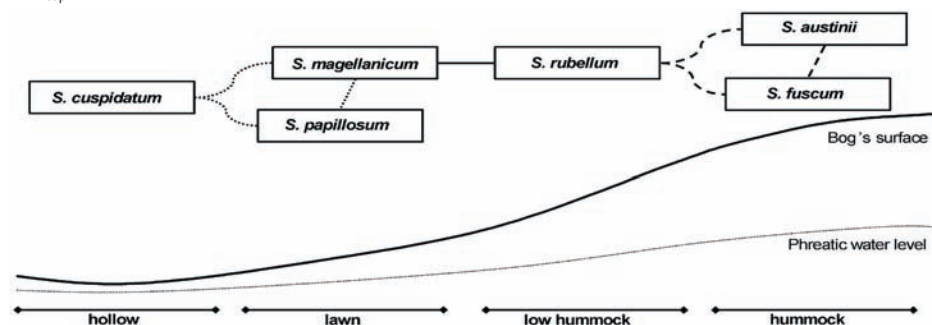
## METHODS

### *Experimental design and sampling*

In May 2004, 135 intact peat cores (diameter: 16 cm; depth 30 cm) of six peat mosses (*S. cuspidatum* Ehrh. Ex. Hoffm., *S. papillosum* Lindb., *S. magellanicum* Brid., *S. rubellum* Wilson, *S. fuscum* (Schimp.) H.Klinggr. and *S. austinii* Sull. in Aust. were collected at Clara bog (53°19'N, 007°58'W), an Irish midland raised bog with a relatively intact hydrology and an extensive *Sphagnum* cover (Cross 1990). Cores were taken from monospecific stands (95% of one species) with sparse vascular plant cover (< 5%), at the natural microsites of the species. The natural occurrence along the water table of these species in Clara bog is as follows: *S. cuspidatum* < *S. papillosum* ≤ *S. magellanicum* < *S. rubellum* < *S. fuscum* ≤ *S. austinii*. Thereafter, the peat cores were put into PVC cylinders and enclosed in plastic bags. Care was taken to avoid disturbance of the natural packing density of the species. The cylinders were placed in large boxes and transported to Wageningen, The Netherlands. Before storing the peat cores at 1°C for three weeks, the few aboveground vascular plants were cut flush with the *Sphagnum*. Drying out of the peat cores was prevented by covering the cylinders with plastic. The mosses were not visibly affected by the storage period.

In early June, the peat cores were transported to the glasshouse facilities. The peat cores were randomly assigned to the mixture and water level treatments, which were arranged in a randomized block design with 5 replicates per treatment. Mixture treatments consisted of two levels: monocultures of each species as well as mixed cultures of species that co-occur in the field, comprising hollow-lawn, lawn-lawn, lawn-low hummock, low hummock-hummock and hummock-hummock combinations (Fig. 3.1). Mixed cultures were made by inserting two equally sized half-cores of two species into one PVC cylinder. Care was taken to minimize disturbance of the moss and underlying peat structure and to ensure that the surfaces of both species made uniform connection. Water table treatments consisted of two or three levels (Fig. 3.1). Monocultures of *S. cuspidatum*, *S. papillosum* and *S. magellanicum* were grown at water levels of -5 cm and -15

cm below the *Sphagnum* surface, whereas *S. rubellum*, *S. fuscum* and *S. austinii* were grown at -15 cm and -25 cm. Mixtures of hollow-lawn and lawn-lawn species were grown at -5 cm and -15 cm, mixtures of lawn-low hummock species at -5 cm, -15 cm and -25 cm, and mixtures of low hummock-hummock and hummock-hummock were grown at -15 cm and -25 cm (Fig. 3.1). These water levels are comparable with the field water levels at which species can (co-) occur (Rydin et al. 1999). In order to analyse the effect of cutting on the capitulum water content, in an additional experiment monocultures of *S. magellanicum* and *S. rubellum* where either left intact or cut in halves and put together again ( $n = 5$ ). Samples were grown at intermediate water level (-10 cm).  $WC_{cap}$  was analysed 15 days after applying the water table treatment, which corresponds to one cycle of rain water addition in the competition experiment. Moreover, the effect of cutting on the  $WC_{cap}$  was expected to be immediate.



**Figure 3.1** Schematic view of the experimental set-up, representing the position of the *Sphagnum* species at their natural habitat along the hydrological gradient from hollow to hummock. Connecting lines indicate species combinations at the applied experimental water tables: -5cm and -15cm (···); -5cm, -15cm and -25 cm (—) and; -15cm and -25cm (---) below the *Sphagnum* surface.

All cylinders, which were closed at the bottom and perforated from the sides to facilitate water movement, were suspended into 50 litre containers (diameter: 25 cm; depth 100 cm), containing an artificial rainwater solution (Garrels and Christ 1965), by hanging them from a lid. This lid also covered the water surface between the large and small container, preventing evaporative water loss via the open water surface. Water tables were kept by weekly addition of artificial rainwater below the *Sphagnum* surface, thereby mimicking prolonged rainless periods. To avoid complete chronic drying out, the capitula in all containers were moistened once every two weeks by sprinkling approximately 9 mm ( $234 \text{ mm yr}^{-1}$ ) of artificial rainwater over the capitula. The last addition of water to the moss capitula was applied one week before harvest.

The experiment lasted from early June 2004 until early October 2005. Temperature in the glasshouse was  $20^{\circ}\text{C}$  day/ $15^{\circ}\text{C}$  night and relative humidity ca. 80%. Natural light was supplemented by high pressure sodium lamps (Philips MASTER SON-T PIA agro 400W E E40 SLV, Luminous flux EM [Lm] 55000), to induce a 16 hour photoperiod. During the winter period (October 2004 through April 2005), the cores were kept in an open greenhouse with a transparent roof and walls of coarse shade mesh, as an earlier experiment had shown that in the glasshouse in winter, when natural

light is reduced but temperature remains relatively high, liverworts overgrow *Sphagnum* (Robroek et al. 2007).

### Measurements

To estimate the competitive strength of the species within a mix, we calculated the change in cover during the experiment. At the end of the experiment, a photograph was taken of the moss surface. The area of each species in the mixed culture was analysed using an image processing and analysis program (ImageJ 1.33u; National Institutes of Health, USA, <http://rsb.info.nih.gov/ij/>).

*Sphagnum* height increment was measured, using a variation on the cranked wire method (Clymo 1970). Plastic rods were inserted to a depth of roughly 10 cm into every species in a combination and in the monocultures. In the monocultures, two rods were anchored so that the treatment resembled that of the mixed cultures. The rods were anchored in the *Sphagnum* substrate by broom bristles and did not visibly interfere with *Sphagnum* growth.

To measure capitulum water content ( $WC_{cap}$ ) and subcapitulum bulk density ( $BD_{subcap}$ ), cores with a diameter and depth of five centimetres were cut around every cranked wire, at harvest. Every core was separated into a capitulum section (0 – 0.5 for species with small capitula or 0–1.0 cm for species with large capitula) and a subcapitulum section, defined as the centimetre directly under the capitulum section (c.f. Dorrepaal et al. 2003), after which fresh weight was measured. Next, dry weight was determined by oven drying both sections for 48h. at 70°C.  $WC_{cap}$  was expressed as the fresh weight · dry weight<sup>-1</sup> ratio.  $BD_{subcap}$  was expressed as the amount (g) of dry weight · cm<sup>-3</sup>.

### Statistical analysis

Data were tested for normality and equality of variance prior to further analysis. Some data of capitulum water content, height increment and cover change did not meet the assumptions of homogeneity of variances. Transformations did not improve the homogeneity of variances. However, analysis of variance appears not to be greatly influenced if the assumptions of equality in variances or normal distribution are not met, as long as sample sizes are more or less equal (Heath 1995). Since sample sizes were equal in our experiment, we decided to perform our analyses without transformations.

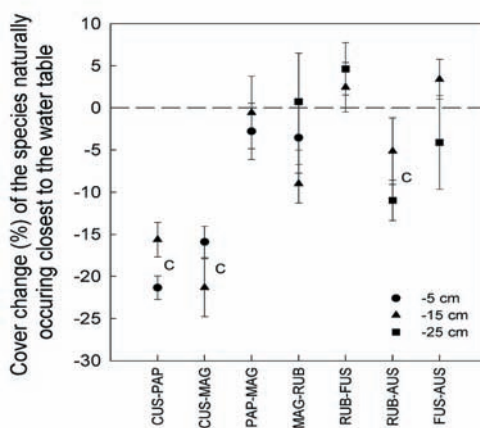
The overall effect of water table and mixture type (i.e. the identity of the species combination) on cover change was tested by two-way ANOVA models. In our analysis, we only used the data of the species within the mixture that naturally occur closest to the water table. Although the interaction between water table and mixture type was not significant ( $F = 1.75$ ,  $P = 0.126$ ), further analyses of the effect of water table on the cover change of species were done within each mixture, in order to be able to analyse whether cover change differed to zero (one-way ANOVA). Two-way ANOVA was used to test the effects of competing species and water table on the height increment of every individual species, and to test the effects of species and water table on the capitulum water content and the subcapitulum bulk density of the species within a mixture. One-way ANOVA was used to test the effect of cutting on the capitulum water content of *S. magellanicum* and *S. rubellum*. Pearson correlation analysis was used to outline the relationship between differences in

height increment and change in cover of the fastest growing species. Paired sample t-tests were used to test for differences in capitulum water content and subcapitulum bulk density between monocultures and the corresponding species in a mixture.

## RESULTS

### Cover change

Over all treatments, water table did not affect cover change of species growing in a mixture ( $F = 0.04$ ,  $P = 0.97$ ), but there was an effect of mixture type ( $F = 10.73$ ,  $P < 0.001$ ). Among the seven species mixtures examined in this study, three showed overall shifts in relative cover, all at the expense of the species naturally occurring lower on the hummock-hollow gradient (Fig. 3.2, Table 3.1). Cover change seemed to be most pronounced when hollow and lawn species were grown in competition (Fig. 3.2). Water table did not play an important role in determining the outcome of competition; it only affected cover change in the CUS-PAP combination, but counterintuitively *S. cuspidatum* cover decrease was largest at the highest water table (Table 3.1).



**Figure 3.2** Cover change at different water tables within the experimental species combinations. Values are mean cover change ( $\pm 1$  SEM) for the species that naturally occurs closest to the water table (see Fig. 3.1). C indicates an overall change in cover (ANOVA,  $P < 0.05$ ). For statistics see Table 3.1.

### Sphagnum height increment, capitulum water content and subcapitulum bulk density

Cumulative height increment was relatively small and varied between -2.20 cm and 2.28 cm over the experimental period, but was smaller than 1 cm in 76% of the observations. In some species (especially *S. cuspidatum*) we found negative height increment (data not shown), possibly caused by the slight subsidence of the peat material. Despite the low height increment we did find



differences in height increment between species growing together. Only in the CUS-PAP mixture, difference in height increment between the species in the mixture was affected by water table ( $F = 5.41$ ,  $P < 0.05$ ). In all cases, but one, cover change of the fastest growing species was significantly correlated to the difference in height increment (Table 3.2).

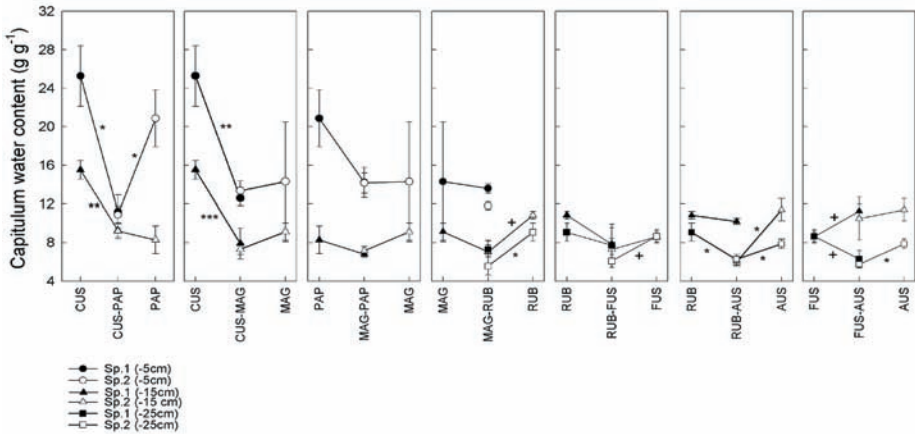
**Table 3.1** Values for the effects of water table on the cover change within each mixture (one-way ANOVA). For the analysis we only used data of the species within the mixture that naturally occur closest to the water table (first mentioned in table). CUS = *S. cuspidatum*, PAP = *S. papillosum*, MAG = *S. magellanicum*, RUB = *S. rubellum*, FUS = *S. fuscum*, and AUS = *S. austini*.

Mixture	Source	Type III SS	df	MS	F-value	P-value
CUS - PAP	Intercept	3411.668	1	3411.668	223.211	< <b>0.001</b>
	Water	81.447	1	81.447	5.329	<b>0.050</b>
	Error	122.276	8	15.285		
	Corrected Total	203.724	9			
CUS - MAG	Intercept	3464.028	1	3464.028	90.284	< <b>0.001</b>
	Water	73.057	1	73.057	1.904	0.205
	Error	306.945	8	38.368		
	Corrected Total	380.002	9			
PAP - MAG	Intercept	27.636	1	27.636	0.373	0.558
	Water	12.522	1	12.522	0.169	0.692
	Error	592.896	8	74.112		
	Corrected Total	605.418	9			
MAG - RUB	Intercept	231.265	1	231.265	2.485	0.141
	Water	238.516	2	119.258	1.282	0.313
	Error	1116.553	12	93.046		
	Corrected Total	1355.068	14			
RUB - FUS	Intercept	125.741	1	125.741	2.742	0.136
	Water	11.964	1	11.964	0.261	0.623
	Error	366.807	8	45.851		
	Corrected Total	378.771	9			
RUB - AUS	Intercept	647.140	1	647.140	12.107	< <b>0.01</b>
	Water	85.328	1	85.328	1.596	0.242
	Error	427.598	8	53.450		
	Corrected Total	512.926	9			
FUS - AUS	Intercept	1.184	1	1.184	0.013	0.912
	Water	141.263	1	141.263	1.546	0.249
	Error	730.913	8	91.364		
	Corrected Total	872.176	9			

**Table 3.2** The correlation between the difference in height increment between two species in a mixture and cover change of the fastest growing species (Pearson correlation analysis).

Mixture	Water table	Corr. coeff.	P-value
CUS - PAP	-5cm	0.781	0.119
	-15cm	0.905	< 0.005
CUS - MAG	overall	0.821	< 0.005
PAP - MAG	overall	0.934	< 0.001
MAG - RUB	overall	0.880	< 0.001
RUB - FUS	overall	0.746	< 0.05
RUB - AUS	overall	0.862	< 0.005
FUS - AUS	overall	0.940	< 0.001

The capitulum water content ( $WC_{cap}$ ) of individual species in a mixture was affected by water table (two-way ANOVA;  $P < 0.1$ ). Lower water tables resulted in lower  $WC_{cap}$ , especially for the hollow and lawn species (Fig. 3.3). Interestingly,  $WC_{cap}$  between individual species in a mixture did not differ, the RUB – AUS combination at -15 cm excepted (two-way ANOVA, species  $\times$  water,  $F = 27.54$ ,  $P < 0.001$ ; Fig. 3.3). Furthermore, for individual species in a mixture  $WC_{cap}$  generally was lower than when growing in a monoculture (paired sample t-tests; Fig. 3.3). It is unlikely that this could be attributed to the different handling of the cores, as an additional experiment with cut and uncut *S. magellanicum* and *S. rubellum* monocultures showed no difference in  $WC_{cap}$  (one-way ANOVA: *S. magellanicum*,  $F = 1.51$ ,  $P = 0.235$ ; *S. rubellum*,  $F = 2.07$ ,  $P = 0.167$ ).



**Figure 3.3** Capitulum water content ( $WC_{cap}$ ) of the individual species in a mix at the applied water tables compared with the  $WC_{cap}$  of the monocultures. Mean  $\pm$  SEM for each species in monoculture and in a mix ( $n = 5$ ) are indicated. Differences in  $WC_{cap}$  between species in monocultures and similar species in a mix at definite water tables are indicated (Paired sample t-tests: +  $P < 0.1$ ; \*  $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$ ).

Sp. 1 = first species on the X-axis; Sp. 2 = second species on the X-axis.

Subcapitulum bulk density ( $BD_{\text{subcap}}$ ) between individual species in a mix was different (Table 3.3). In general,  $BD_{\text{subcap}}$  of species was not affected by growing alone or in a mixture (paired sample t-test). In those cases where we did find differences in  $BD_{\text{subcap}}$  ( $\Delta \text{CUS/CUS}_{\text{-MAG}}^{-15}$ ,  $t = -4.12$ ,  $P < 0.05$ ;  $\Delta \text{CUS/CUS}_{\text{-PAP}}^{-15}$ ,  $t = -2.97$ ,  $P < 0.05$ ;  $\Delta \text{AUS/AUS}_{\text{-FUS}}^{-15}$ ,  $t = -2.97$ ,  $P < 0.05$ ;  $\Delta \text{RUB/RUB}_{\text{-AUS}}^{-15}$ ,  $t = -3.23$ ,  $P < 0.05$ ; and  $\Delta \text{RUB/RUB}_{\text{-AUS}}^{-25}$ ,  $t = -3.17$ ,  $P < 0.05$ ) monocultures had lower  $BD_{\text{subcap}}$ . Surprisingly, we did not find a relation between  $WC_{\text{cap}}$  and  $BD_{\text{subcap}}$ , irrespective of the water table treatments (-5cm, Pearson correlation = -0.110,  $P = 0.43$ ; -15cm, Pearson correlation = -0.078,  $P = 0.44$ ; -25cm, Pearson correlation = -0.055,  $P = 0.69$ ).

**Table 3.3** Subcapitulum bulk density ( $\text{g cm}^{-3}$ ) for the individual species within every species combination. All values are means  $\pm$  SEM ( $n = 5$ ). Within every species combination, two-way ANOVA models were used to test for the effect of species (S) and water table (W) on the subcapitulum bulk density. Sp. 1 = data for the species first mentioned in the species combination, Sp. 2 = second species in the species combination.

+  $P \leq 0.1$ ; \*  $P \leq 0.05$ ; \*\*  $P \leq 0.01$  and \*\*\*  $P \leq 0.001$ .

Species	Subcapitulum bulk density						
	Species combination						
	CUS - PAP	CUS - MAG	MAG - PAP	MAG - RUB	RUB - FUS	RUB - AUS	FUS - AUS
1	-5 0.023 $\pm$ 0.001	0.018 $\pm$ 0.001	0.018 $\pm$ 0.002	0.024 $\pm$ 0.003	-	-	-
	-15 0.034 $\pm$ 0.006	0.024 $\pm$ 0.004	0.022 $\pm$ 0.003	0.015 $\pm$ 0.001	0.022 $\pm$ 0.002	0.027 $\pm$ 0.002	0.023 $\pm$ 0.002
	-25 -	-	-	0.015 $\pm$ 0.002	0.029 $\pm$ 0.003	0.026 $\pm$ 0.001	0.019 $\pm$ 0.001
2	-5 0.024 $\pm$ 0.004	0.014 $\pm$ 0.002	0.018 $\pm$ 0.003	0.026 $\pm$ 0.005	-	-	-
	-15 0.017 $\pm$ 0.002	0.016 $\pm$ 0.002	0.020 $\pm$ 0.002	0.020 $\pm$ 0.001	0.022 $\pm$ 0.001	0.043 $\pm$ 0.006	0.037 $\pm$ 0.002
	-25 -	-	-	0.024 $\pm$ 0.003	0.025 $\pm$ 0.004	0.049 $\pm$ 0.007	0.030 $\pm$ 0.002
S	+	*	ns	*	ns	***	***
W	ns	ns	ns	+	+	ns	**
S $\times$ W	**	ns	ns	ns	ns	ns	ns

## DISCUSSION

### *Competition between Sphagnum species: effect responses*

According to our hypothesis, species that naturally occur further above the water table generally increased in cover at the expense of species that naturally occur closer to the water table. Contrary to our expectations, water table did not seem to be an important factor in influencing cover change. Within species mixture, in general water table did not affect the outcome of the competition between species. Mixture type, and thus species identity, seems to be much more important. In particular, differences in 'functional types' seemed crucial in determining cover change. The effect was largest when a hollow species was involved. A similar conclusion was drawn from a reciprocal transplantation experiment in the field, where three *Sphagnum* species were transplanted to each other's habitat. Hummock species increased in cover at the expense of hollow species, whereas the competitive advantage among more closely related species seemed to be much more variable (Rydin 1993). Our results, however, have to be treated with some caution because our set-up complicates the disentanglement of water table and species mixture effects, since species identity and water table are more or less confounding.

### *Competition between Sphagnum species: mechanistic responses*

Compared to field values (reviewed by Gunnarsson 2005), height increment was relatively small in our experiment, which was probably a result of the low precipitation rates. Nevertheless, species in a mixture differed in height increment and in most mixtures this difference was positively correlated to the increase in cover of the faster growing species. Contrary to our expectations, water table did not seem to play a major role. The competitive outcome seemed to be related to differences in height increment, irrespective of the water table.

Since water supply to the capitula becomes more difficult with decreasing water table (Rydin et al. 1999; Lafleur et al. 2005), the efficiency of the capillary system and interspecific differences therein may become very important in keeping the capitula moist under periodic drought. However, in our experiment,  $WC_{cap}$  between the species in a mixture were not different. Therefore, interspecific differences in height increment cannot be straightforwardly explained by differences in  $WC_{cap}$ . This suggests that the competitive outcome may be related to differences in the ability of species to cope with low water availability, either low water tables or low amounts of precipitation. There are indications that species differ in their ability to photosynthesise when water is scarce, yet consensus about differences in physiological response to  $WC_{cap}$  between 'functional types' is not evident. Silvola and Aaltonen (1984) found no great differences between *S. fuscum* (hummock) and *S. angustifolium* (hollow). At reduced water contents, *S. fuscum* maintained higher photosynthesis than did *S. angustifolium*, whereas at increased water contents the opposite was found. Titus et al. (1983) found an opposite effect when comparing *S. nemoreum* (hummock) and *S. fallax* (hollow) and Rydin and McDonald (1985b) found that *S. balticum* (lawn), *S. tenellum* (hollow) were more sensitive to reduced water content, compared to *S. fuscum*.

Individual species in mixed cultures generally had lower  $WC_{cap}$ , and concomitantly lower height increment (data not shown), than in monoculture.  $BD_{subcap}$  did not differ for a species growing in mono- or mixed culture, or was even lower in monocultures. Contrary to our assumptions, the above suggests that bulk density may not be a good predictor of the *Sphagnum* vegetation's ability to supply water to the capitula. Other physical properties, such as texture and structure, may play a more important part in the efficiency of the capillary system. An interesting outcome of our experiment was that in a larger volume of isotropic peat material water supply to the capitula was more efficient than in a smaller volume. Since  $WC_{cap}$  did not differ between cut and uncut monocultures, it is unlikely that the lower  $WC_{cap}$  of a species in mixed culture compared to monoculture can be explained as an effect of cutting. Probably the structural heterogeneity of the peat in mixed cultures has a negative effect on the water supply to the capitula of both species. These findings are in accordance with those of Kellner and Halldin (2002) who found anisotropy of peat material to be unfavourable for the hydrological conditions at a bog surface. Our data also suggest that patch size has an effect on competitive strength. The ability of a *Sphagnum* species to supply its capitula with water seems to increase with increasing patch size. More research is required to explain the mechanism(s) involved but these findings imply that a species growing in a peat moss mosaic gains in competitive strength when its patch size enlarges.

*Effect of long-term changes in climate*

It has been shown that *Sphagnum* species are able to co-occur for prolonged periods (Rydin and Barber 2001; Gunnarsson et al. 2002), yet changes in the global climate can cause the species composition to change (Mauquoy et al. 2001). Rydin and Barber (2001) stated that competition may be intense among species, but as there is no consistent competitive hierarchy over time, competition is not a structuring force that eliminates species from the community. However, this only applies if there are no linear changes in environmental conditions. Investigations of future climate scenarios suggest a slight increase in temperature (Houghton et al. 2001; e.g. Sweeney and Fealy 2002). Changes in precipitation cannot yet be accurately predicted, but reductions in summer rainfall are likely to occur (e.g. Sweeney and Fealy 2002). In addition, higher summer temperatures could increase evaporation rates (Gunnarsson et al. 2004), and if the increased evaporation rates are not balanced by precipitation this will result in decreased water tables in raised bogs (Schouten et al. 1992). Recently, it has been shown that increased temperature can have a direct positive effect on biomass production of *S. magellanicum* and *S. rubellum*, but not on *S. fuscum* and *S. austini*, irrespective of the water table, whereas of the four species only *S. magellanicum* was negatively affected by decreased water table (Robroek et al. 2007).

Here we show that under sustained periods of drought the competitive balance between species seems to shift towards *Sphagnum* species that naturally occur higher on the hummock-hollow gradient, irrespective of the water table depth. These shifts are largest in hollow-lawn species combinations, which indicates that hollow species will not be able to compete with more drought resistant species, when sustained periods of drought will occur more frequently. Eventually this could lead to species loss and the evening out of the typical hollow-hummock pattern of raised bogs.

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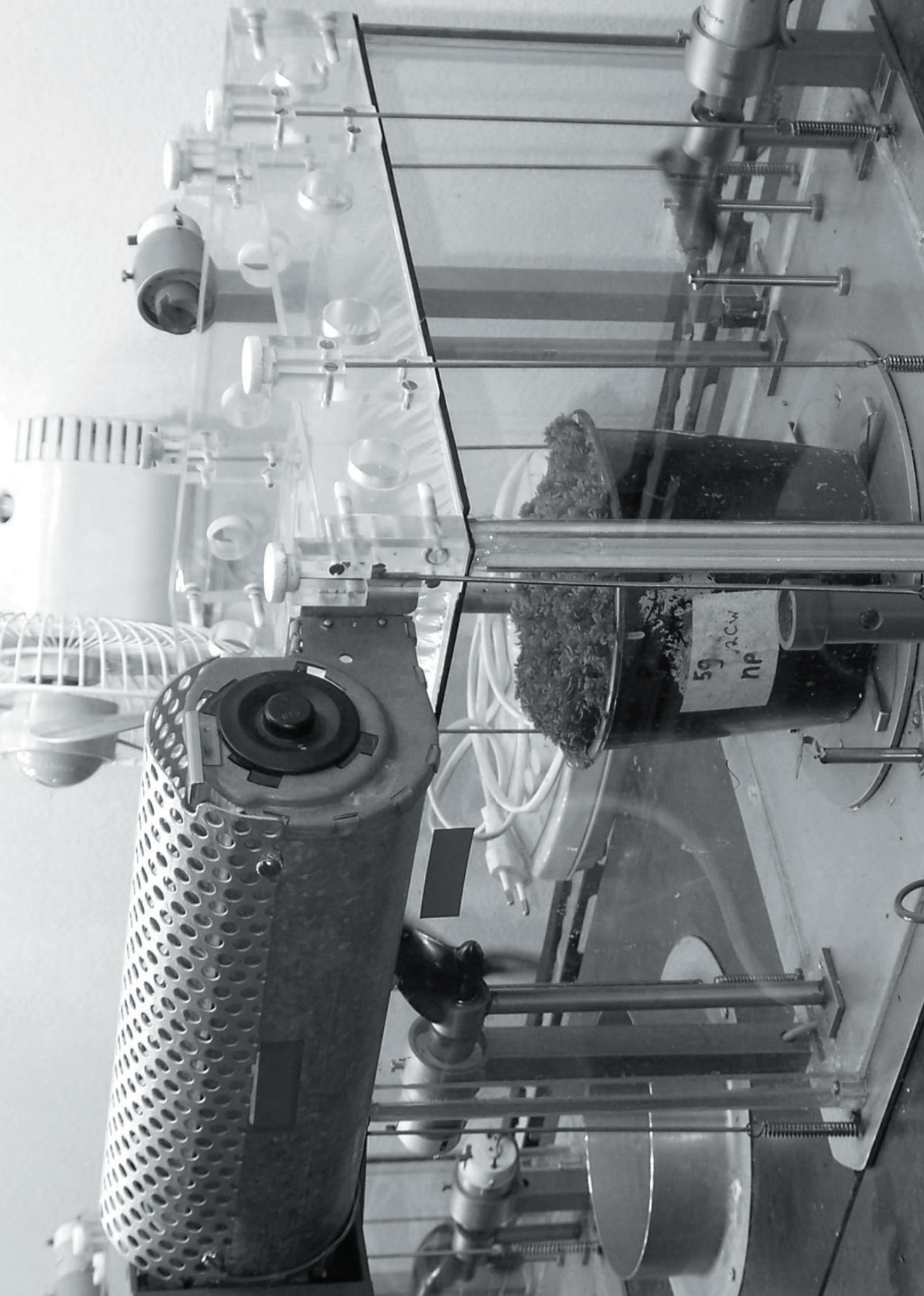
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# INTERACTIVE EFFECTS OF WATER TABLE ON NET CO<sub>2</sub> ASSIMILATION OF THREE CO-OCCURRING *SPHAGNUM* MOSSES DIFFERING IN DISTRIBUTION ABOVE THE WATER TABLE

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*Submitted*

*Sphagnum cuspidatum*, *S. magellanicum* and *S. rubellum*, are three co-occurring peat mosses, which naturally have a different distribution along the microtopographical gradient along the bogs surface. We set out an experiment to assess the interactive effects of water table (low and high) and the presence or absence of precipitation on the CO<sub>2</sub> assimilation and evaporation of these species over a 23 day period. Additionally, we measured which sections of the moss layer were responsible for light absorption and bulk carbon uptake. Thereafter, we investigated the recovery of CO<sub>2</sub> assimilation after prolonged drought. At high water table, CO<sub>2</sub> assimilation of all species gradually increased over time, irrespective of precipitation. At low water table, net CO<sub>2</sub> assimilation of all species declined over time, with the earliest onset and highest rate for *S. cuspidatum*. Precipitation compensated for reduced water tables and positively affected net carbon uptake of all species. Cumulative carbon uptake over the experimental period was lowest for *S. magellanicum*, but stayed positive over the longest period. In addition, CO<sub>2</sub> assimilation of *S. magellanicum* was the slowest to recover after prolonged drought. Almost all light absorption occurred in the first one or two centimeters of the *Sphagnum* vegetation and so did net CO<sub>2</sub> assimilation. CO<sub>2</sub> assimilation rate showed species-specific relationships with capitulum water content. Assimilation for *S. cuspidatum* showed a narrow optimum at relatively high capitulum water content, whereas C assimilation for *S. rubellum* had its optimum at dryer conditions. In contrast, C assimilation of *S. magellanicum* stayed constant at a relatively low rate over a broad range of capitulum water contents. Interspecific differences in the response to precipitation and water table and in the speed of recovery after prolonged drought indicate that environmental changes will alter the competitive balance between species, and concomitantly will affect carbon sequestration rates in peatlands.

## INTRODUCTION

Raised bogs are generally dominated by bryophytes from the genus *Sphagnum* that may reach a cover of 80-100%, thereby substantially contributing to the aboveground biomass production. Productivity varies among peatland types and regions and is in the range of 17 - 380 g m<sup>-2</sup> yr<sup>-1</sup> (Moore et al. 2002). Additionally, *Sphagnum* mosses influence the hydrological and hydrochemical conditions at the raised bog surface to a high degree (Van Breemen 1995; Van der Schaaf 2002), playing an invaluable role in the functioning of the ecosystem. Typically, raised bogs are characterized by a pattern of microtopographical habitats, ranging from wet depressions (hollows) and relatively dry but regularly inundated lawns to dry hummocks. Mosses that occur in the hummocks can rely less on capillary water supply (Ingram 1983), implying increased reliance on precipitation as a source of water. Each microhabitat is occupied by a different set of *Sphagnum* species (Andrus et al. 1983). The relation between *Sphagnum* species and their position along the microtopographical gradient is likely to be the result of a combination of morphological and physiological characteristics. Several studies have stressed interspecific differences among *Sphagnum* mosses in the efficiency of the external capillary system to conduct water and the ability to hold water. There seems to be a trade-off between growth rate and morphological characteristics which influence the ability to conduct water to the capitula on the one hand and the ability to withstand water loss on the other (Hayward and Clymo 1982; Titus and Wagner 1984; Rydin and McDonald 1985a; Rydin and McDonald 1985b).

Earlier, we studied the effect of prolonged absence of precipitation on the competition between six *Sphagnum* species at different water tables (Robroek et al. 2007a). Although height increment was low, it differed between competing species, and was generally larger for those species that naturally occur farther from the water table, indicating that these species are better able to cope with drought. Interestingly, capitulum water content of species which grew together did not differ, from which we concluded that differences in growth may be explained by different physiological responses (e.g., photosynthesis) to water content. However, studies of differences between *Sphagnum* species in physiological response to capitulum water content have yielded inconsistent data, which may be caused by differences in the methods employed (for a review see Rydin 1993). Generally, water content in *Sphagnum* is measured in bulk samples. However, for light interception and the concomitant carbon fixation, only the top layer of the *Sphagnum* will likely be important. There is no consensus in the literature, however, on the depth of this layer. Titus et al. (1983) state that 99% of the carbon fixation in *S. fallax* and *S. capillifolium* carpets takes place in the upper five centimeters. Wallén et al. (1988) show light penetration to be density dependent, and Rydin and Jeglum (2006) suggest that light penetrates only a few centimeters, or even only 1 cm in the case of dense *Sphagnum* carpets.

Habitat preferences are generally determined by the ability of species to withstand or avoid desiccation (Titus and Wagner 1984), and therefore it is expected that hummock species are better able to maintain a water content high enough for photosynthesis than hollow species. As a result, the relative period during which net photosynthesis is positive may be longer for hummock species than for hollow species. Recovery after desiccation may also be important for



species performance. Schipperges & Rydin (1998) found hummock species to display a better rate of recovery during several drying and rewetting periods, compared to hollow and lawn species. Strikingly, hummock species generally show lower recovery after complete desiccation than hollow species (Clymo and Hayward 1982; Wagner and Titus 1984; Schipperges and Rydin 1998). From these results it was concluded that not recovery itself, but interspecific differences to avoid desiccation may be important to withstand longer periods of droughts. Species may differ in their ability to avoid desiccation; environmental conditions, like precipitation and water table are likely to play an important role in maintaining optimal conditions for *Sphagnum* growth. Decreased water tables and increased temperatures are shown to have different effects on different *Sphagnum* mosses (Robroek et al. 2007b), yet how prolonged periods without precipitation affect performance of *Sphagnum* species at different water tables, has to our knowledge never been assessed. In this study we set out to test the interactive effects of water table and precipitation on the ability of *Sphagnum* species to assimilate CO<sub>2</sub>. First, we non-destructively determined the effects of water table (high or low) and the presence or absence of precipitation, on the net CO<sub>2</sub> assimilation of *Sphagnum cuspidatum* (hollow), *S. magellanicum* (lawn) and *S. rubellum* (hummock) microcosms. Moreover, interspecific differences in the ability to recover from prolonged drought were investigated. Secondly, we determined to what extent light penetrates into the *Sphagnum* carpet and which part of the *Sphagnum* layer is important for carbon uptake. Finally, relationships between water content and photosynthesis were assessed destructively

## METHODS

### *Sampling*

In September 2006, intact cores (diameter 12.5 cm, depth 11 cm) of *S. cuspidatum* Ehrh. ex Hoffm., *S. magellanicum* Brid. and *S. rubellum* Wilson were collected at Clara bog (53°19'N, 007°58'W), Ireland. Detailed descriptions of this raised bog are given in Schouten (2002). All samples were taken from monospecific stands at their natural habitat along the bogs surface (i.e. *S. cuspidatum* was taken 2 – 7 cm from the water table, *S. magellanicum* 4 – 20 cm and *S. rubellum* 9 – 27 cm from the water table). Different species were taken from adjacent stands. Care was taken to avoid disturbance of the natural density of the species, before putting them into pots (hereafter referred to as microcosms). The microcosms were transported to the Netherlands where the sparse vascular plant shoots were clipped to the *Sphagnum* surface.

### *Experimental set-up*

At the end of September, two water table treatments low (-10 cm) and high (-1 cm) were randomly assigned to half of the microcosms of each species by means of an overflow. From late September 2006 through December 2006, all mosses were kept outdoors, where natural precipitation kept the mosses moist. At the beginning of January, the mosses were transported to a greenhouse (Average temperature: 19.4°C; average RH: 45%), where two precipitation treatments were assigned within each water table treatment: microcosms received either 2 mm day<sup>-1</sup> (≈ 25 ml) precipitation (c.f. Sweeney and Fealy 2002) or no precipitation at all. We used a Garrels & Christ (1965) solution

as rainwater, which was sprinkled over the capitula, by which we tried to apply the solution evenly over the surface. All treatments were replicated four times, resulting in 48 microcosms. Natural light was supplemented by high pressure sodium lamps, to induce a 12 hour photoperiod. As a result, microcosms were subject to light conditions which were at least around  $200 \mu\text{mol m}^{-2} \text{s}^{-1}$ . Treatments will further be abbreviated as follows: high water table without precipitation, HWT-; high water table with precipitation, HWT+; low water table without precipitation, LWT- and low water table with precipitation, LWT+. Precipitation treatments were applied at the end of every day. High water tables were maintained by adding water  $\approx 1\text{cm}$  below the capitulum layer. If a low water table was applied, no extra water was added to the microcosms. Net  $\text{CO}_2$  assimilation, as well as fresh weight, of all microcosms was measured every two days.

After 23 days all microcosms, except LWT- (which were used to measure recovery), were separated into three sections: capitulum layer (0–2 cm), subcapitulum layer (2–4 cm) and bulk layer (4–10/11cm). A PVC ring was used to prevent deformation of the layer, by disabling potential pressure by handling the section. Light absorbance of each layer was measured by placing the layer on a clean glass plate, under which a sensor (Skye Instruments Quantum sensor) was attached. Light intensity at the canopy surface varied between 442 and  $552 \mu\text{mol m}^{-2} \text{s}^{-1}$ . After absorbance measurements, net  $\text{CO}_2$  assimilation was measured for every layer at similar intensities, in order to elucidate each layer's potential contribution to the total samples carbon uptake. Additionally, light absorption in the capitulum layer was further investigated by removing an extra centimeter (i.e. the 1–2 cm layer). Finally, fresh weight: dry weight ratios ( $\text{fw dw}^{-1}$ ) were calculated for all layers.

Two weeks after net  $\text{CO}_2$  assimilation of the mosses which were grown at low water table without precipitation (LWT-) had become negative, the mosses were rewetted. Rainwater solution was added to the microcosms until the water level remained at the moss surface. Recovery was assessed by measuring net  $\text{CO}_2$  assimilation just before rewetting, as well as 2.5 hours, 2, 6 and 16 days after rewetting. Per individual microcosm, recovery was defined as net  $\text{CO}_2$  assimilation after rewetting compared to the maximum net  $\text{CO}_2$  assimilation of that microcosm. Prior to these measurements, interstitial water was drained from the pots, in order to be able to compare the measured values with the values as measured during the  $\text{CO}_2$  assimilation experiment.

### *Data collection*

The microcosms were placed in 18 l cuvettes made of stainless steel and glass where  $\text{CO}_2$  and  $\text{H}_2\text{O}$  partial pressures in the air entering were controlled by mixing  $\text{CO}_2$  with  $\text{CO}_2$ -free air by means of flow controllers (air flow  $\approx 0.08 \text{ l s}^{-1}$ ) and by dehumidifying moistened air at a preset dew point, respectively. For a detailed description of the cuvettes, see Poorter & Welschen (1993). Net assimilation was measured at a light intensity of  $410 - 470 \mu\text{mol m}^{-2} \text{s}^{-1}$  and a  $\text{CO}_2$  concentration of  $360 - 390 \text{ ppm}$ . The plants were enclosed in the cuvettes for at least 35 minutes before measurements started. Differences in  $\text{CO}_2$  and  $\text{H}_2\text{O}$  partial pressures between cuvettes with and without plants were measured using an Infrared gas analyzer (LI-6262  $\text{CO}_2/\text{H}_2\text{O}$  analyzer, LI-COR, inc., USA) in combination with a dew point mirror (General Eastern, Watertown, MA, USA).



*Data analysis*

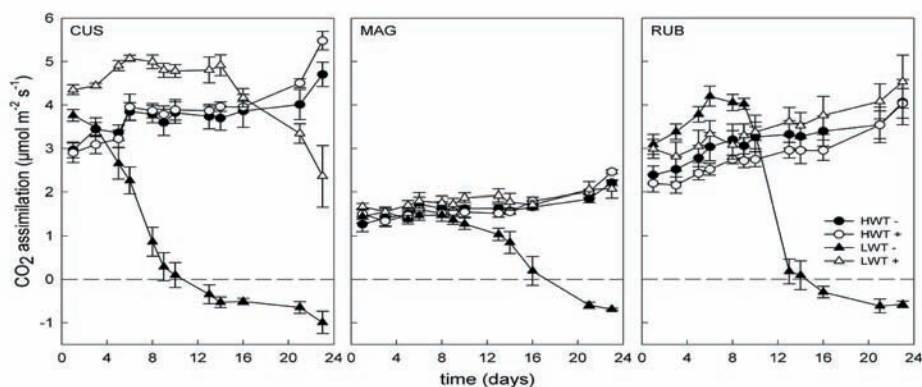
Calculations on net CO<sub>2</sub> assimilation and evaporation follow Von Caemmerer & Farquhar (1981). Per species, data on net CO<sub>2</sub> assimilation over time were analyzed using repeated measures ANOVA (ANOVAR), with water table and presence/absence of precipitation as fixed factors. Since significant ( $P \leq 0.05$ ) interactions between water table and precipitation occurred, the separate impact of precipitation was determined in a similar way, but within water table treatment.

To achieve not only a day to day estimate of assimilation, we also integrated the gas exchange data obtained over the whole experimental period, interpolating for the days between measurements. Because we only measured carbon assimilation during the periods in which the mosses resided in the cuvettes, one has to take into account that we do not present real values of total assimilation. We present these data as cumulative net CO<sub>2</sub> assimilation. Since we found water table  $\times$  species and water table  $\times$  precipitation interactions (ANOVA), we continued the analysis per water table treatment. Next, per water table, interspecific differences on net CO<sub>2</sub> assimilation with and without precipitation were analyzed using ANOVA followed by Tukey post-hoc tests for species.

The dependence of net CO<sub>2</sub> assimilation on the water content, expressed as fw dw<sup>-1</sup>, of the total microcosm was determined by regression analysis. Only the microcosms grown at low water tables without precipitation (LWT-) were used, since these data cover a large range of water contents. Quadratic curves were fitted through the data. Furthermore, regression analyses were performed to analyze the effect of capitulum water content on capitulum layer net CO<sub>2</sub> assimilation. To do so, we used all microcosms except those that were used in the recovery experiment.

Light attenuation by the *Sphagnum* layers was first analyzed using ANCOVA. Species and layer were included as fixed factors, and water table and precipitation as co-variables. Both treatments did not affect the amount of absorbed light. We therefore pooled all data and analyzed the effect of species and layer depth using ANOVA. Since significant interactions occurred ( $P \leq 0.001$ ), the effect of species was analyzed per layer. These data did not always meet the assumptions of equal variances, but ANOVA appears not to be greatly influenced if the assumptions are not met (Heath 1995). Therefore, we decided to perform our analyses without transformations. Per species, CO<sub>2</sub> assimilation of the different layers was analyzed, using ANCOVA with layer as fixed factor and water table and precipitation as co-variables. Assimilation data were sqrt-transformed.

Recovery of the dried-out microcosms over time was analyzed using ANOVAR with species as fixed factor. Tukey's post-hoc tests were used to determine interspecific differences. Not all data met the assumptions of homosphericity. Since Huyn-Feldt conditions were met (Potvin et al. 1990), we were able to base our analysis on corrected degrees of freedom.



**Figure 4.1** CO<sub>2</sub> assimilation ( $\pm$  SEM,  $n = 4$ ) over time ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) for *S. cuspidatum* (CUS), *S. magellanicum* (MAG) and *S. rubellum* (RUB) when grown at high (HWT) or low water tables (LWT) and in the absence (-) or presence (+) of precipitation. Negative values indicate net CO<sub>2</sub> loss of the microcosms.

**Table 4.1** Time period (mean  $\pm$  SEM,  $n = 4$ ) per species in which we found net CO<sub>2</sub> uptake for the LWT- microcosms (see also Fig. 4.1). Data were determined for each individual microcosm (rounded to  $\frac{1}{2}$  days) after which averages were calculated. Different letters indicate significant differences between species ( $P < 0.05$ ; ANOVA followed by Tukey post hoc test).

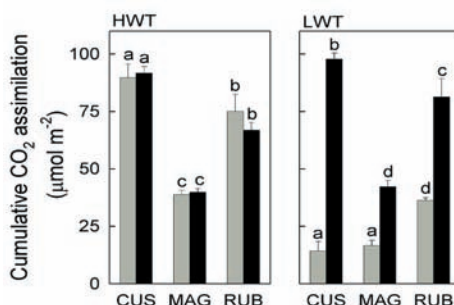
Time period (days) of positive CO <sub>2</sub> assimilation		
	Mean $\pm$ SEM	
<i>S. cuspidatum</i>	10.13 $\pm$ 1.13	a
<i>S. magellanicum</i>	16.75 $\pm$ 0.92	b
<i>S. rubellum</i>	14.13 $\pm$ 0.83	b

## RESULTS

### *Water table, precipitation and species effects on carbon uptake*

For all species, effects of water table and precipitation on net CO<sub>2</sub> assimilation showed significant interactions ( $P \leq 0.01$ ; Fig. 4.1). In the microcosms grown at high water table no effect of precipitation was found. Moreover, net CO<sub>2</sub> assimilation increased during the experiment ( $P \leq 0.001$ ; Fig. 4.1). At low water table with precipitation, the course of net CO<sub>2</sub> assimilation of *S. magellanicum* and *S. rubellum* was similar to these at high water tables. For *S. cuspidatum*, in comparison, it was higher during the first part of the experiment but then decreased (Fig. 4.1). The absence of precipitation gradually depressed CO<sub>2</sub> assimilation ( $P \leq 0.01$ ) for all species: net CO<sub>2</sub> assimilation of *S. cuspidatum* immediately decreased, whereas *S. magellanicum* and *S. rubellum* showed no

decrease in the first days of the experiment. For *S. rubellum*, assimilation even increased during that time (Fig. 4.1). *S. magellanicum* and *S. rubellum* maintained positive net CO<sub>2</sub> assimilation values over a longer period than *S. cuspidatum* (Fig. 4.1, Table 4.1).

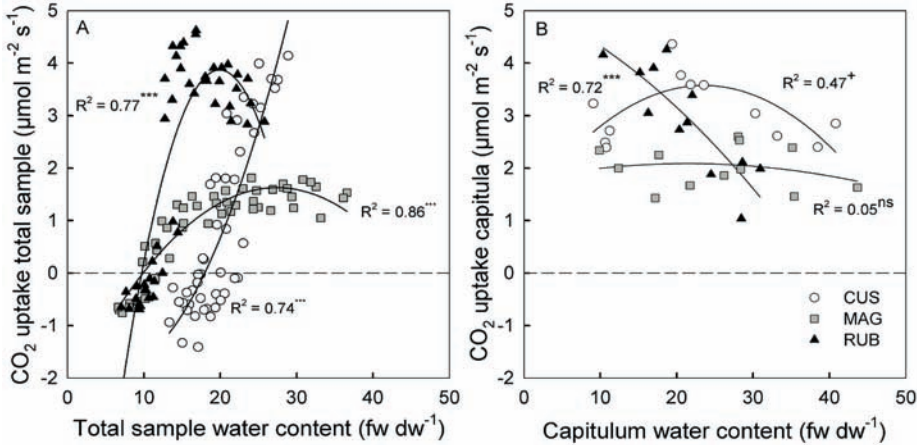


**Figure 4.2** Cumulative CO<sub>2</sub> assimilation ( $\pm$  SEM,  $n = 4$ ) of *S. cuspidatum* (CUS), *S. magellanicum* (MAG) and *S. rubellum* (RUB) at high (HWT) and low (LWT) water tables, and without (grey bars) and with (black bars) precipitation. Since we found significant interactions with water level (ANOVA;  $P < 0.001$ ), data were further analyzed per water level treatment. Different letters indicate significant differences (ANOVA,  $P < 0.05$ ).

Cumulative CO<sub>2</sub> uptake at high water table was highest for *S. cuspidatum* and lowest for *S. magellanicum*, and did not differ between precipitation treatments (Fig. 4.2). At a low water table, *S. magellanicum* assimilation was also lowest (Tukey HSD;  $P < 0.05$ ) but the effects of precipitation differed amongst species ( $F = 24.9$ ,  $P < 0.001$ ). For all species, CO<sub>2</sub> uptake was higher when the mosses receive precipitation; the effect was largest for *S. cuspidatum* whereas it did not differ between *S. magellanicum* and *S. rubellum* (Fig. 4.2). Strikingly, cumulative assimilation at low water table with precipitation was similar to those at high water levels (ANOVA,  $P > 0.05$ ).

#### *Carbon uptake in relation to water content and light penetration*

Over the course of the experiment, the total water content of the microcosms exposed to low water tables without precipitation was shown to change (data not shown), which may affect net CO<sub>2</sub> assimilation. From the microcosms, we were able to examine the relation between total water content and net assimilation. Net CO<sub>2</sub> assimilation of *S. cuspidatum* was high at high water contents but rapidly decreased with decreasing microcosm water content (Fig. 4.3A). *S. magellanicum* and *S. rubellum* showed optimum water contents, that of *S. rubellum* being at a lower total water content than of *S. magellanicum* (Fig. 4.3A). These data are in concert with those of net CO<sub>2</sub> assimilation over the experimental period (Fig. 4.1).



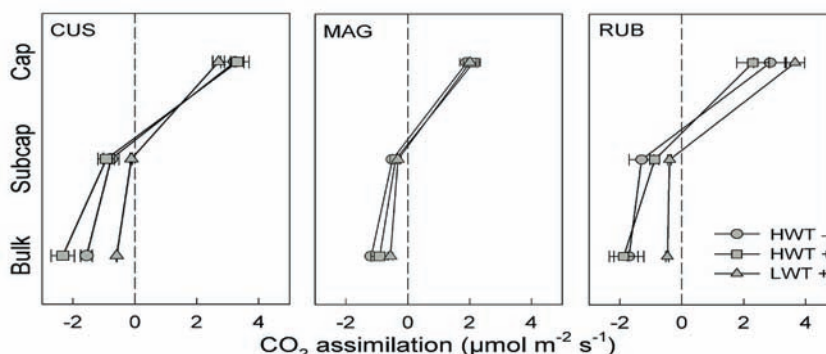
**Figure 4.3** A: Relationship between net CO<sub>2</sub> assimilation and water content of the microcosm for *S. cuspidatum*, *S. magellanicum* and *S. rubellum* grown at low water tables without precipitation (LWT-). B: Relationship between net CO<sub>2</sub> assimilation of the capitulum section and the capitulum water content. Per species, quadratic curves were fitted through the data.

**Table 4.2** Light attenuation of the different *Sphagnum* layers. Numbers represent the percentage of light above each layer that reaches the next layer. Different letters indicate interspecific differences (ANOVA,  $P < 0.05$ ) per layer.

Layer	Species		
	CUS	MAG	RUB
0	100	100	100
0 - 1 cm	2.3 ± 0.17 <sup>a</sup>	0.8 ± 0.14 <sup>b</sup>	0.1 ± 0.07 <sup>c</sup>
1 - 2 cm	0.1 ± 0.01 <sup>a</sup>	0 <sup>b</sup>	0 <sup>b</sup>
2 - 4 cm	0	0	0
4 - 11 cm	0	0	0

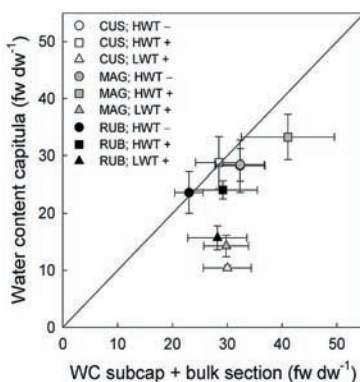
Carbon uptake mainly took place in the capitulum layer (Fig 4.4). Even at the relatively high light intensity used in this experiment, net CO<sub>2</sub> assimilation was negative in the subcapitulum and the bulk layer of all species (Fig. 4.4), indicating that total respiration exceeded potential photosynthesis. Differences between the subcapitulum and bulk layer may not be caused by differences in photosynthetic active material, but rather by the larger volume of respiring peat material in the bulk layer. At low water tables, CO<sub>2</sub> dissimilation decreased in *S. cuspidatum* ( $F = 12.7$ ,  $P \leq 0.001$ ) and *S. rubellum* ( $F = 16.5$ ,  $P \leq 0.001$ ) (Fig. 4.4). For all three *Sphagnum* species, more than 97% of the light was absorbed in the first centimeter of the vegetation (Table 4.2). Minor interspecific differences were found, with absorption in this layer being highest in *S. rubellum* and lowest in the looser growing *S. cuspidatum* (Table 4.2). Some light could reach the layer below the first

centimeter, but deeper than 2 cm basically all light had been absorbed (Table 4.2), highlighting the importance of the capitulum section.

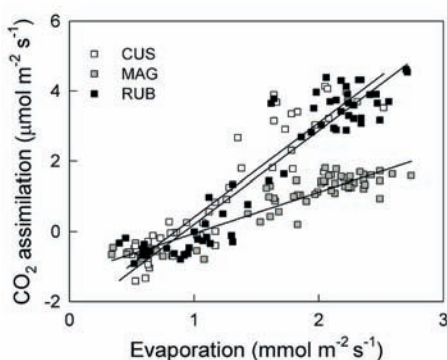


**Figure 4.4** CO<sub>2</sub> assimilation of the different layers (CAP = capitulum (0-2 cm), Subcap = 2-4 cm and Bulk = 4-10/11 cm) per *Sphagnum* species. HWT = high water table, LWT = low water table. +/- = presence/absence of precipitation. Carbon uptake was highest in the capitulum layer for all species (ANOVA,  $P \leq 0.001$ ).

Besides light conditions, also the water conditions in the capitulum layer may determine CO<sub>2</sub> assimilation potential. We found that in most cases water content of the subcapitulum and bulk section is higher than the capitulum water content, especially when grown at low water table (Fig. 4.5). For a better understanding of the effects of water content on the carbon uptake, we assessed the effect of the capitulum water content of all microcosms, except those used in the recovery experiment (LWF-), on the net CO<sub>2</sub> assimilation of the capitulum section. The response of net CO<sub>2</sub> assimilation to capitulum water content differs from that of the response of the total sample, especially at the lower range of water contents (Fig. 4.3 A,B). Furthermore, it is clear that there are interspecific differences in the response of CO<sub>2</sub> uptake to capitulum water content. *S. magellanicum* assimilation was not significantly affected by water content, whereas there seemed to be an optimum water content for *S. cuspidatum*. Net CO<sub>2</sub> assimilation of *S. rubellum* increased with decreasing water content, though the water content may not have been low enough (due to the absence of the LWT- microcosm data) to find the optimum capitulum water content for this species.



**Figure 4.5.** The relationship between capitulum water content and the water content of the underlying layers (subcapitulum and bulk section). Values are means ( $\pm$  SEM,  $n = 4$ ). The solid line indicates a one-to-one relationship.



**Figure 4.6** Relationships between evaporation and  $\text{CO}_2$  assimilation of *Sphagnum cuspidatum* (CUS), *S. magellanicum* (MAG) and *S. rubellum* (RUB) grown at low water table without precipitation (LWT-) for 24 days. All relationships were highly significant: CUS  $R^2 = 0.85$ ,  $F = 336.9$ ,  $P < 0.001$ ; MAG  $R^2 = 0.85$ ,  $F = 331.9$ ,  $P < 0.001$ , RUB  $R^2 = 0.88$ ,  $F = 425.0$ ,  $P < 0.001$ .

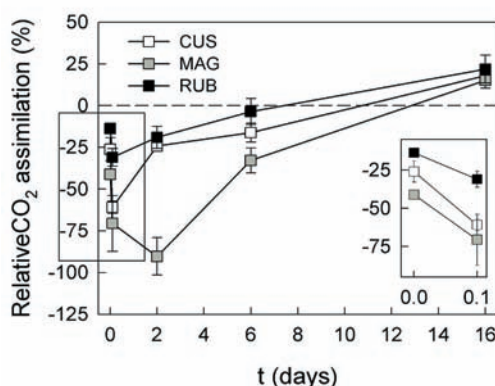
In mosses evaporation cannot be actively regulated, but is a strong indicator of net  $\text{CO}_2$  assimilation (Fig. 4.6). The relationship between evaporation and  $\text{CO}_2$  uptake furthermore indicates the water use efficiency of the species. This was found to be lowest for *S. magellanicum*, which showed lowest assimilation over the course of the experiment. Evaporation takes place in the upper part of the vegetation, and strongly depends on the capitulum water content, again highlighting the importance of the environmental conditions in the capitulum section water content for carbon uptake.

#### *Recovery after drought*

The ability of *Sphagnum* mosses to recover from desiccation may be an important factor that determines the competition between mosses. After rewetting, net  $\text{CO}_2$  assimilation of all the microcosms grown at low water table without precipitation initially further decreased. Nevertheless,



net CO<sub>2</sub> assimilation recovered from inhibition by drought within two weeks. Early recovery of *S. magellanicum* generally was slower than that of the other two species (Fig. 4.7;  $F = 10.7$ ,  $P \leq 0.01$ ). Sixteen days after rewetting, however, assimilation no longer differed between species ( $F = 0.3$ ,  $P = 0.8$ ) and varied from 15% (*S. magellanicum*) to 18% (*S. cuspidatum*) and 22% (*S. rubellum*) of the maximum.



**Figure 4.7** Response of *Sphagnum cuspidatum* (CUS), *S. magellanicum* (MAG) and *S. rubellum* (RUB) to rewetting after a 14-day period of drought, expressed as the percentage of CO<sub>2</sub> assimilation related to the maximum assimilation measured before the drought treatment. The inset figure corresponds to the first 2 ½ hours ( $\approx 0.1$  day) after rewetting.

## DISCUSSION

### *The effect of water table and precipitation on carbon uptake*

Precipitation affected net CO<sub>2</sub> assimilation only when water tables were low. At high water tables, precipitation presumably did not add to the total water content, since the samples were already saturated. During the experiment, assimilation of all mosses that were grown at high water levels increased. Similarly, assimilation of the drought resistant species *S. magellanicum* and *S. rubellum* (Hayward and Clymo 1983; Titus and Wagner 1984) increased at low water table, but only with precipitation. The increase in assimilation may be explained by the rise of the capitula above the water table, due to growth during the experiment, thereby favoring CO<sub>2</sub> exchange (Clymo and Hayward 1982; Silvola and Aaltonen 1984). Alternatively, the mosses may have gradually acclimated physiologically to the experimental conditions (Titus et al. 1983).

Only for *S. cuspidatum* grown at a low water table, the presence of precipitation was not sufficient to maintain net CO<sub>2</sub> assimilation for a prolonged period at a low water table. Net CO<sub>2</sub> assimilation of *S. cuspidatum*, however, was relatively high for a short period (Fig. 4.1). Interestingly, a similar response was observed for *S. rubellum* but then at a different precipitation regimen (Fig. 4.1). Since the green cells of *S. magellanicum* are embedded between large hyaline cells, the

latter species may be less affected by the presence of a water film on its leaves, which impedes  $\text{CO}_2$  diffusion (Rice and Giles 1996). At the beginning of the desiccation process, the water film disappears resulting in a slight increase in assimilation. Progressive desiccation may lead to a decrease in net  $\text{CO}_2$  assimilation. In concert, the absence of precipitation results in large water loss by *S. cuspidatum*, resulting in decreased assimilation. *S. rubellum* is much better in holding water. Concomitantly, without precipitation, the slow drying of this species may have resulted in an initial increase in assimilation because of more optimal conditions (e.g.  $\text{CO}_2$  diffusion rate). The period in which net  $\text{CO}_2$  assimilation is positive is relatively short for *S. cuspidatum*. This period is larger for *S. magellanicum* than for *S. rubellum*, but does not significantly differ between these species. The absolute decline, however, seems much slower for *S. magellanicum* (Fig. 4.1).

Long term carbon sequestering is poorest for *S. magellanicum*. In the case of low water tables and absence of precipitation, cumulative  $\text{CO}_2$  uptake was reduced for all species, yet *S. cuspidatum* suffered more than the other two species (Fig. 4.2). These results stress the importance of hydrological conditions and species composition on raised bogs when assessing changes in carbon budgets as a response to climate change.

#### *Carbon uptake in relation to water content and light penetration*

Net  $\text{CO}_2$  uptake as a response to the water content of the total microcosm is in accordance with that of the low water table treatment curves without precipitation (Figs 4.1 and 4.3A), which suggest that the effects of water content on  $\text{CO}_2$  assimilation over the course of the experiment parallels the response to drying. We show that species differ in their response to total water content (Fig. 4.3A) but also to capitulum water content (Fig. 4.3B). Despite interspecific differences in light absorption by the capitulum layer (Table 4.2), it becomes clear that only a negligible fraction of the light penetrates deeper than two centimeters. Since light is essential for photosynthesis these first centimeters of the vegetation are responsible for the bulk carbon uptake. Moreover, our results parallel the suggestion already made by Rydin and Jeglum (2006), that photosynthesis is most likely restricted to the upper centimeter, since light penetration beyond this first centimeter was very low (Table 4.2). Consequently, when assessing the influence of water content on the net assimilation rate, not water content of the total sample but capitulum water content may be the most important differing factor among different species, since bulk carbon uptake takes place in the upper part of the *Sphagnum* carpet (Fig. 4.4). Capitulum water content and water content of the underlying layers do not relate one-to-one. Generally, capitulum water content is lower than the water content of the underlying layers, especially for the *Sphagnum* grown at low water table (Fig. 4.5). At high water tables, microcosms may have been close to saturated, including the capitula. From our data, however, it becomes evident that water lost by evaporation in the capitula is not totally replaced by capillary transport, resulting in a dryer capitulum section compared to the underlying sections (Fig. 4.5). At low water tables this effect is even stronger. Since mosses cannot regulate water loss by evaporation, evaporation rates more or less indicate capitulum moisture content. Interestingly, net  $\text{CO}_2$  assimilation strongly depends on the amount of evaporation (Fig. 4.6) which indicates that water content of the top layer strongly determines  $\text{CO}_2$  uptake. The efficiency in using water

is lowest for *S. magellanicum*, which is probably the result of its low carbon uptake over the whole range of capitulum water contents.

In literature no consensus exists with respect to the response of photosynthesis to capitulum water content (see for example Rydin 1985; Rydin 1993). From our results we deduce that interspecific differences in assimilation rates in response to capitulum water content can affect the competitive strength between species. Low water contents are clearly beneficial for *S. rubellum*. *S. magellanicum* seems hardly affected by capitulum water content, whereas *S. cuspidatum* shows a decrease in CO<sub>2</sub> assimilation when capitulum water contents become too high or too low.

#### *Recovery after drought*

All *Sphagnum* species recovered from desiccation, but the rewetting period is crucial (Fig. 4.7) and this may explain why earlier studies failed to find recovery after prolonged drought (Silvola 1991; Schipperges and Rydin 1998). Although recovery was similar after sixteen days, *S. magellanicum* showed higher respiration rates directly after rewetting than *S. cuspidatum* and *S. rubellum*. Similar increases in respiration after rewetting have been reported earlier (e.g. Silvola 1991; Schipperges and Rydin 1998; McNeil and Waddington 2003). This 'resaturation respiration' may be the result of increased microbial activity due to leakage of cell contents from damaged cells (Gupta 1977; Gerdol et al. 1996), but may also be due to higher activity of the *Sphagnum* mosses because of recovery of their damaged tissue. *S. magellanicum* appears to be more affected by desiccation than the other two species, yet recovery after two weeks was similar. The initial strong respiration of the *S. magellanicum* microcosms may have large implications when assessing the long term carbon budget of raised bogs.

#### *Implications of hydrological changes*

Palaeobotanical records show that the overall cover of peat mosses on bogs can change in time as a response to changes in climate conditions such as temperature, precipitation, and solar radiation (e.g. Svensson 1988; Mauquoy et al. 2001; Mauquoy et al. 2002). We show that frequent precipitation is important for the long term carbon uptake of *Sphagnum* mosses when water tables drop, which is usually the case in summer. Especially, since rain water directly affects capitulum water content, where most of the CO<sub>2</sub> uptake takes place. We found interspecific differences in the relation between net CO<sub>2</sub> assimilation and capitulum water content. *S. cuspidatum* assimilation can be very high in a narrow range of hydrological conditions. Similarly, *S. rubellum* is restricted to a narrow range of hydrological condition, but dryer. *S. magellanicum* assimilation, on the other hand, is relatively low, but can perform over a broad range of environmental conditions. All mosses were able to recover from desiccation on the long term, but carbon loss during the dry period was largest for *S. magellanicum*. Prolonged drought may alter the competitive balance between species, which concomitantly may change the species composition of the raised bog; favoring hummock species over hollow species. The effect of prolonged drought on long term carbon budgets clearly depends on the peat moss composition; hummock species dominating raised bogs might be less affected than hollow species dominated raised bogs (Strack et al. 2006).

## CONCLUSIONS

In this study we show that the lack of precipitation, rather than low water table, negatively affects CO<sub>2</sub> uptake of *Sphagnum*, with *S. cuspidatum* suffering more than *S. magellanicum* and *S. rubellum*. Capitulum water content is the most important factor determining carbon assimilation, and can be substantially different from the lower layers. Recovery after drought was slow, and two weeks after the precipitation treatment started again, carbon assimilation was still marginal, stressing the potential effect of drought on the carbon budget of raised bogs.

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## PRECIPITATION DETERMINES THE PERSISTENCE OF HOLLOW *SPHAGNUM* SPECIES ON HUMMOCKS

Robroek BJM, Limpens J, Breeuwer A, Van Ruijven J and Schouten MGC (2007)  
*Wetlands* (in press)

On raised bogs, the distribution of *Sphagnum* species is determined by their distance to the water table, but occasionally species are able to survive outside their niche. Hollow species that persist in hummock vegetation are assumed to profit from the higher water content of the surrounding hummock species, although the mechanism responsible is unclear. In this study we elucidated the role of lateral hummock water transport (LHWT) and precipitation on the water content of hollow species occurring in hummocks. This was tested using a full factorial field transplantation experiment with cores of *Sphagnum cuspidatum* in a high and a low hummock. Treatments included direct precipitation (present or absent) and LHWT (present or absent). Fresh weights of the cores were measured at regular time intervals. Our results show a relatively large effect of precipitation on the water content in both the high and low hummock, whereas LHWT only seemed to be an important source of water in the high hummock, which was relatively dry. Furthermore, LHWT played an important role only after large precipitation events, suggesting that lateral water transport is indirectly affected by rain. This study showed that precipitation alone could explain the persistence of hollow species in high hummocks, whereas it was less important for hollow species in low hummocks. Our data suggest that survival and potential expansion of hollow species in higher hummocks is strongly depending on the intensity and frequency of rain events. Changes in precipitation patterns may result in a loss of *Sphagnum* diversity in hummocks.

## INTRODUCTION

Peatland hydrology is mainly driven by the balance between inputs and outputs of water. In raised bogs, precipitation is the most important source of water (Clymo 1983). Climate projections suggest a future increase in global temperature together with changes in precipitation patterns (Sweeney and Fealy 2002; Meehl et al. 2007). How precipitation will be changing is not fully understood, but projections indicate more intense precipitation events, with longer dry periods in between (Meehl et al. 2007). Global increases in temperature and changes in precipitation patterns are expected to alter the species composition and distribution in peatlands (Mauquoy et al. 2002; Bragazza 2006). Shifts in vegetation types and the distribution of different *Sphagnum* species may affect the functioning of peatland ecosystems (Moore 2002), thus understanding the role of hydrological processes to *Sphagnum* vegetation and the influence of precipitation on *Sphagnum* species is increasingly important.

Since precipitation intermittently enters peatlands and *Sphagnum* plants can only store a certain amount of water, movement of water occurs. Water flows can be vertical (seepage) or horizontal (phreatic flow) (Ingram 1983). Both flows are highly dependent on external factors like the magnitude of precipitation, the storage capacity of the peat material, and the water table (Clymo 1983; Van der Schaaf 2002; Price et al. 2005; Rydin and Jeglum 2006). Phreatic flow decreases with decreasing water table (Ingram 1983; Van der Schaaf 2002), and is particularly important for hollows. However, it is less significant for high hummocks, which are generally high above the phreatic water table. Therefore it seems plausible that capillary rise and precipitation primarily determine the water content in hummocks.

In ombrotrophic peatlands, *Sphagnum* mosses are ecosystem engineers (Clymo and Hayward 1982; Andrus 1986). They usually dominate the vegetation and, among others, play a large role in the water balance of these ecosystems. Besides intraspecific competition for light, space, and water, competition can be interspecific and involve different environmental factors such as nutrients, water, and light (Hayward and Clymo 1983; Rydin et al. 1999). The ability to keep their active apical parts (i.e., capitula) moist is considered to be the most important differentiating factor among *Sphagnum* species (Andrus 1986). Since *Sphagnum* species lack stomata and roots, their efficiency in preventing water loss (i.e., water holding capacity) and their ability to transport water to their capitulum is important. Interspecific differences in water holding capacity and capillary water transport largely determine relative occurrences along water table gradients (Andrus et al. 1983). Hummock species are able to grow higher above the water table because of the efficiency of their external capillary system and their ability to hold water (Hayward and Clymo 1982; Ingram 1983; Titus and Wagner 1984; Luken 1985). In contrast, hollow species are usually restricted to habitats closer to the water table because their potential to retain water by capillary rise is inferior. Nevertheless, individuals or small patches of hollow species can be encountered almost at the top of small hummocks. In this particular situation, they are completely surrounded by a matrix of hummock species (Rydin et al. 1999), which may provide advantages to the hollow species. Hollow species that are completely surrounded by hummock species appear to have higher water contents than those in monospecific hollow stands at similar distances from the water table (Titus

and Wagner 1984; Rydin 1985). Luken (1985) indicated that hummock species are very efficient in transferring water via capillary connections.

It has been proposed that water transport from the matrix of hummock species to the hollow species enabled them to maintain higher water contents than single hollow species at the same height (Rydin 1985), and thus to persist above their natural habitat. Indeed, evidence for lateral water transport within a hummock, referred to as lateral hummock water transport (LHWT), was discovered in a laboratory experiment (Rydin and Clymo 1989). Together with a high tolerance to desiccation (Titus and Wagner 1984) and a high potential to recover after desiccation (Clymo 1973; Wagner and Titus 1984; Robroek et al. unpublished), precipitation and water transport from hummock species to hollow species may be essential for the persistence of hollow species in hummocks.

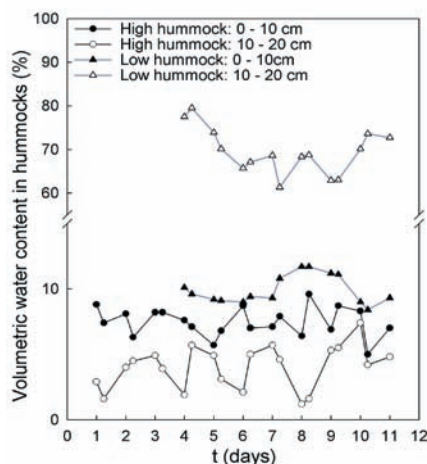
The objective of this study was to determine the role of precipitation and LHWT within a hummock on the persistence of hollow species in these hummocks. In an Estonian raised bog we transplanted cores of hollow species into two hummocks differing in their position from the water table. By eliminating potential LHWT to these transplants and direct precipitation in a factorial design, we were able to assess the role of LHWT and precipitation on the water content of these hollow species. We hypothesized that 1) eliminating LHWT and direct precipitation would be detrimental for the water content of the hollow species and 2) these detrimental effects should be strongest in the hummock that was furthest from the water table.

## METHODS

### *Sampling and experimental design*

Late August 2006, 40 intact cores (diameter: 6.5 cm; depth: 8 cm) of the hollow species *Sphagnum cuspidatum* var. *majus* (Russow) C.E.O. Jensen, hereafter referred to as *S. cuspidatum*, were collected from largely monospecific stands with sparse vascular plant cover (< 5%) in Männikjärve bog (58°52'28.71"N, 26°15'44.40"E) in the Endla Nature Reserve, Estonia. A sharp knife, together with a PVC ring (≈ 7 cm deep) was used to cut the samples. During the cutting the PVC ring was slowly pushed into the peat, after which the PVC ring together with the *S. cuspidatum* sample was removed. Disturbance of the cores was avoided. The transplantation site was selected close (≈ 25 m) to the area of sampling. Prior to transplantation any vascular plants in both the cores and the transplantation sites were clipped flush with the *Sphagnum* because interception of precipitation by vascular plants can be high (Paivinen 1966). Roots were left in the vegetation to enable the *Sphagnum* vegetation to function as naturally as possible.

We initially only intended to work in a high hummock (58 cm above the water table), but soon after the start of the experiment we found a sharp decrease in water content of the hollow samples, which we assumed was caused by the relative low water content of the hummock matrix. Therefore, we decided to expand the experiment to an additional hummock that was lower (20 cm from the water table) and somewhat moister (Fig. 5.1). This low hummock was adjacent to the large hummock. Both hummocks were about 4 m long and 1.5 m wide and dominated by *S. magellanicum*.



**Figure 5.1** Volumetric water content of the hummock matrix (● = high hummock; ▲ = low hummock) surrounding the embedded hollow samples measured at two depth intervals: 0-10 cm (filled symbols) and 10-20 cm (open symbols).

Within both hummocks, we used a full factorial design with two precipitation levels (+ and - precipitation) and two LHWT levels (+ and - LHWT). All treatments were replicated five times per hummock and arranged in blocks. To determine the effect of direct precipitation on the water content of hollow cores, half of the cores (- precipitation) were covered at night and during rainy days by a Petri dish (diameter: 10 cm), suspended on metal pins 2 cm above the cores. To determine the effect of LHWT on the water content of the hollow species that grow in hummocks, this transport was eliminated at half of the cores (-LHWT) by putting them into 200 cm<sup>3</sup> plastic cups. These cups were inserted into the peat in such a way that only a small edge ( $\pm 2$  mm) rose above the vegetation. The cores where LHWT still was possible (+LHWT) were placed into 200 cm<sup>3</sup> plastic cups from which the sides were removed, except for three small strips (0.5 cm) which acted as a frame that enabled us to remove the cores for weight measurements. All cups were bottomless.

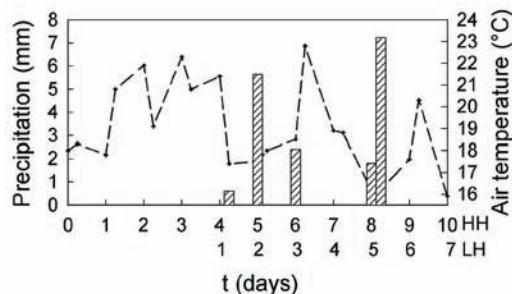
### Measurements

Fresh weight of each sample (*Sphagnum* + cup) was determined before transplantation and repeated thereafter twice per day at fixed times (11H00 and 17H00) over a ten day (high hummock) and a seven day (low hummock) period. This time span was sufficient to detect the effects of precipitation and LHWT. Moreover, anomalies caused by species competition and potential morphological adaptation (Dorrepaal et al. 2003) were omitted due to the short time span of the experiment. The hollow cores were embedded into the low hummock three days later than in the high hummock, but before the end of a dry period (see Fig. 5.2). As a result, the measurement in the low hummock started three days later than the measurements in the low hummock. This may have contributed to

differences in the initial water content of the hollow species in both hummocks, since the adjustment time in the low hummock was smaller. Yet, water content of the hollow samples became stable after only one day, which was before the start of the first rain event.

Water table depth, the amount of precipitation and hummock moisture content were determined just after fresh weight measurements. To assess if precipitation events observed in our study were representative we used data on daily rainfall, collected from 1991 though 1995 by the Estonian Meteorological and Hydrological Institute in Jõgeva, approximately 20 km from the field site, and calculated the relative occurrence of certain amounts of precipitation. Water table depths were measured in two PVC tubes (one for each hummock) that were inserted at the start of the experiment. Precipitation was measured in three plastic cups inserted into the high hummock. This method does not give precise values of precipitation, but it provided a valuable indicator of the magnitude of precipitation. Precipitation data were averaged, and represented the amount of rain over the period between two measurements. Moisture content of the two hummocks was determined using a Profile probe type PR1, combined with a hand-held Moisture Meter type HH2 (Delta-T Devices Ltd, UK), which enabled us to determine the moisture content at two depth intervals: 0-10 cm and 10-20 cm.

At the end of the experiment, the cores were harvested and pre-dried for several hours to prevent weight changes as a result of decomposition or respiration. All cores were transported back to Wageningen, the Netherlands. They were dried at 70°C for at least 48hrs to determine dry weight (DW). Hollow species' water content ( $WC_{\text{hollow}}$ ) was calculated as follows:  $(FW - DW)/DW$ , in which FW was the fresh weight of a sample.



**Figure 5.2** Precipitation (bars represent means;  $n = 3$ ), and air temperature (line) during the experimental period. Note that measurements at the low hummock (LH) started three days later than the high hummock (HH) measurements.

#### Data analyses

Data were tested for normality and equality of variance prior to analysis. Not all data met the assumptions of homogeneity of variances, not even after transformation, but deviations from normality were small. As analysis of variance (ANOVA) is not greatly influenced by this anomaly

(Heath 1995), we decided to use ANOVA on untransformed values.

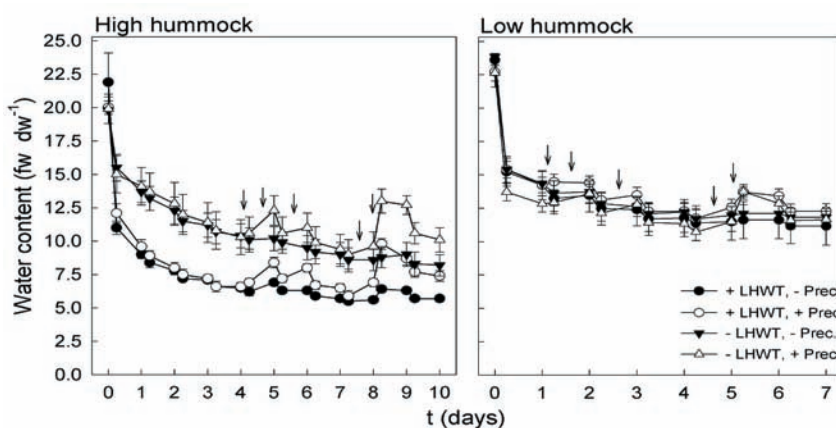
Effects of direct precipitation and LHWT on  $WC_{\text{hollow}}$  were analysed using two-way repeated measurement ANOVA models with precipitation and LHWT as treatment factors. Since the experiment on the low hummock started three days later than on the high hummock, a direct hummock comparison could not be made. Consequently, separate repeated measurement ANOVA's were done for each hummock. As the assumption of homosphericity (Maulchy's test of Sphericity) was not always met by our data, we used the Huyn-Feldt epsilon to adjust the degrees of freedom (Potvin et al. 1990).

Since changes in water content were most pronounced after a rain event, we chose to use those events for further analyses. Since rain events were similar for both hummocks, hummock type was used as an additional factor. The effects of potential lateral hummock water transport and precipitation were analyzed using analysis of co-variance (ANCOVA) with hummock type, precipitation, and LHWT as fixed factors and the amount of precipitation over the preceding period (rain event) as a co-variable. Since rain event had a significant effect on the change in water content of the cores, the effects of hummock type, precipitation and LHWT were analyzed for each rain event.

## RESULTS

### *Environmental conditions*

Air temperature ( $15.8^{\circ}\text{C} - 21.7^{\circ}\text{C}$ ) and the amount of precipitation varied over time (Fig. 5.2). The first days were dry and warm, whereas the last days of the experiment were much more variable. Volumetric water content of the hummocks varied over time, and appeared to be higher at the low hummock at both depth intervals (Fig. 5.1), indicating a stronger influence of the water table.



**Figure 5.3** Treatment effects on the water content of *S. cuspidatum* var. *majus* embedded in a high (left) and a low (right) hummock. Arrows indicate rain events (for precipitation data see Figure 5.2).

LHWT = lateral hummock water transport, Prec. = precipitation.



*Effects of LHWT and precipitation*

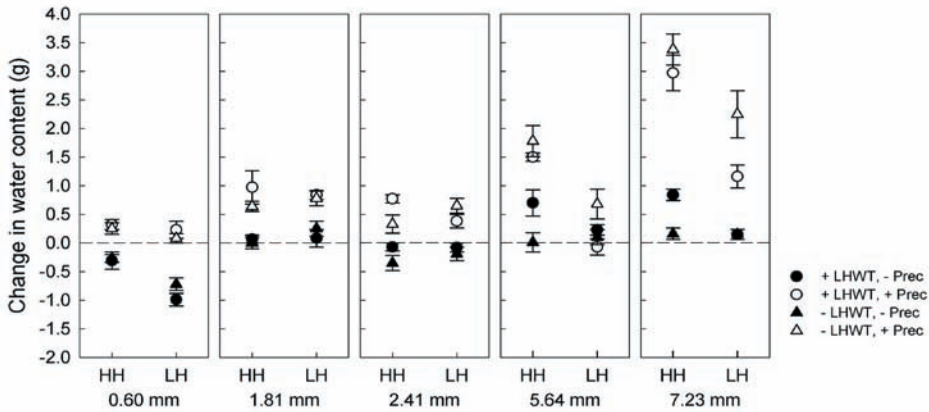
In both hummocks, the wet hollow cores lost water to the surrounding hummock matrix shortly after transplantation (Fig. 5.3), yet water loss seemed to be greater in the relatively drier (Fig. 5.1) high hummock than in the low hummock. In the high hummock, after one day, the cores with LHWT had a lower water content than the cores where LHWT was eliminated ( $F_{1,16} = 23.31$ ,  $P \leq 0.001$ ; Fig. 5.3), which was presumably caused by extra water loss towards the surrounding hummock matrix in the former cores. In the low hummock, which was relatively moist, water loss towards the surrounding matrix was smaller and did not differ between the LHWT treatments ( $F_{1,16} = 0.09$ ,  $P = 0.770$ ; Fig. 5.3). The water content of the hollow species cores that received direct precipitation and those that did not, was similar for both hummocks (high hummock:  $F_{1,16} = 1.80$ ,  $P = 0.198$ ; low hummock:  $F_{1,16} = 0.05$ ,  $P = 0.834$ ). Over the course of the experiment, however, water content of the cores with precipitation rose periodically, whereas this was not the case for those cores that did not receive direct precipitation ( $F_{3,48} = 5.96$ ,  $P = 0.002$  for the high hummock;  $F_{3,42} = 7.46$ ,  $P \leq 0.001$  for the low hummock), indicating the role of precipitation in changing the water content of the cores.

*Changes in water content after rain*

Directly after a precipitation event, all cores that were able to receive precipitation increased in water content ( $F_{1,191} = 152.00$ ,  $P \leq 0.001$ ; Fig. 5.3). This direct effect on water content was higher in the high hummock than in the low hummock ( $F_{1,191} = 6.54$ ,  $P = 0.011$ ), which was probably caused by the relatively high overall water content of the cores in the low hummock.

The change in water content directly after precipitation was highly influenced by the amount of precipitation that preceded measurement ( $F_{1,191} = 135.71$ ,  $P \leq 0.001$ ). After the smallest precipitation event, water content of the cores hardly changed, and those that did not directly receive precipitation even decreased in water content (Fig. 5.4, Table 5.1). Apparently, this precipitation could not compensate for water loss towards the matrix. This decrease was lower in the high hummock than in the low hummock (Fig. 5.4, Table 5.1), and may be from an experimental artefact. The smallest rain event occurred one day after transplantation into the low hummock, at which time the wet hollow transplants were still losing relatively large amounts of water to the hummock matrix. From the second rain event onwards, this effect was no longer noticeable as changes in water content in the absence of rain were equal in the high and low hummocks (Figs. 5.2 and 5.4). After the small rain event, eliminating LHWT also did not affect the water content of the cores. After intermediate amounts of precipitation, direct precipitation increased the water content of the cores (Fig. 5.4; Table 5.1), but again, eliminating the possibility of LHWT had no effect. After the largest precipitation events (Fig. 5.4), precipitation had a strong positive effect on the cores' water content, and this effect was even larger when LHWT was eliminated. With precipitation, the cores without LHWT had a higher positive change in water content than the cores where hummock transport was still possible. Cores where LHWT was possible probably lost water to the surrounding matrix, whereas water loss towards the surrounding matrix was not possible for the cores where LHWT was eliminated. In contrast, when direct precipitation on the cores was

eliminated, LHWT increased the water content (Fig. 5.4, Table 5.1); however, this effect was only significant for the high hummock.



**Figure 5.4** Effects of precipitation, lateral hummock water transport, and hummock type on the water content of hollow species, after a precipitation event. LHWT = lateral hummock water transport, Prec = precipitation. For statistics, see Table 5.1.

**Table 5.1** F-values and *P*-values (ANOVA) for the effects of hummock type, lateral hummock water transport (LHWT), and precipitation (Prec.) on the hollow species' water content at five rain events. Numbers in bold indicate significant *P*-values ( $P < 0.05$ ).

		Amount of preceding rain									
		0.6 mm		1.81 mm		2.41		5.64		7.23	
Source	df	F	<i>P</i>	F	<i>P</i>	F	<i>P</i>	F	<i>P</i>	F	<i>P</i>
Corrected Model	7	18.97	0.000	6.90	0.000	12.78	0.000	14.48	0.000	34.03	0.000
Intercept	1	21.24	0.000	73.42	0.000	19.76	0.000	89.70	0.000	297.19	0.000
Hummock	1	18.94	<b>0.000</b>	0.33	0.570	0.02	0.879	34.49	<b>0.000</b>	32.40	<b>0.000</b>
LHWT * Prec.	1	0.18	0.676	0.54	0.468	2.72	0.109	0.12	0.729	1.69	0.203
Precipitation (Prec.)	1	101.23	<b>0.000</b>	44.22	<b>0.000</b>	75.69	<b>0.000</b>	30.47	<b>0.000</b>	175.80	<b>0.000</b>
Hummock * LHWT	1	0.18	0.676	1.54	0.223	6.98	<b>0.013</b>	4.15	<b>0.050</b>	4.46	<b>0.043</b>
Hummock * Prec.	1	8.37	<b>0.007</b>	0.35	0.558	0.55	0.464	19.83	<b>0.000</b>	12.60	<b>0.001</b>
LHWT * Prec.	1	2.99	0.094	1.32	0.260	0.41	0.524	12.27	<b>0.001</b>	11.26	<b>0.002</b>
Hummock * LHWT * Prec.	1	0.92	0.344	0.01	0.940	3.05	0.090	0.03	0.858	0.00	0.965
Error	32										

## DISCUSSION

Our results show that eliminating lateral hummock water transport (LHWT) affected the water content of the transplanted hollow species. At first glance our results seemed to contradict our hypothesis and the literature (Rydin 1985; Rydin et al. 1999) on the positive effect of LHWT on the water content of hollow species in hummocks. It turned out that where lateral hummock water transport was possible, the cores in the high hummock lost water to the surrounding matrix. Eliminating LHWT reduced the contact surface between the transplanted hollow cores and the surrounding

*Sphagnum* vegetation resulting in reduced water loss from the relatively moist transplanted cores to the relatively dry hummock. In the low hummock such a pattern was not observed. Overall, the moisture content of the low hummock was higher, which may explain why LHWT did not negatively affect the water content of the hollow cores. As argued by Rydin and McDonald (1985a) there is an upper limit along the water table gradient for single hollow species, due to their low capacity to transport water by capillary rise. When surrounded by hummock species the possibilities to survive increased, which was argued to be the result of lateral water transport from the hummock vegetation towards these hollow species. Our results show that precipitation can also be an important source of water for hollow species that grow in high hummocks.

Precipitation provoked a change in water content immediately after a rain event in those samples that could directly receive precipitation, whereas the cores that could not receive precipitation, hardly changed in water content. Interestingly, our results show that LHWT more or less depends on the occurrence of precipitation. Due to the increasing moisture content of the hummock relative to the cores, lateral transport from the surrounding *Sphagnum* vegetation towards the transplanted cores increased after precipitation. Precipitation positively affected the water content of the cores with all amounts of rain, but these effects were largest with the largest amounts of rain. Similarly, LHWT increased with increasing amounts of rain. Our results suggest a direct relationship between precipitation and LHWT. However, the rate of lateral water hummock transport also depends on the storage capacity and the moisture content of both the hummock matrix and the patch of hollow species. This explains why the magnitude of change in water content of the hollow species differed between the two hummocks.

Rydin (1985) concluded that hollow species persist in hummocks by a combination of commensalism and competition. Rydin (1985) and Andrus (1986) further assumed that the expansion of hollow species in hummock vegetation is self-limiting as with increasing patch size the water supply to their capitula is limited due to their inefficient capillary system. In high hummocks, water from capillary rise logically is lower than on low hummocks, making capillary water a less important source of water. Therefore, apart from immediate precipitation, lateral water hummock transport seems to be a crucial factor in survival and expansion of hollow species in hummock habitats. Our results show that LHWT only positively affects the water content of the hollow species with relatively large rain events. We suggest, therefore, that growth potential of hollow species in a hummock depends on the frequency and magnitude of rain events. Since hollow species have a higher relative growth rate (Andrus 1986; Gunnarsson 2005), as long as water is not limiting, water supply by precipitation, be it direct or indirect, may explain the persistence or even expansion of hollow species outside their main habitat. In our study site, large rain events are relatively scarce. Over the 1991-2005 period, 65% of all daily precipitation at site was less or equal to 1 mm day<sup>-1</sup>. In an Atlantic climate, however, large rain events probably occur more regularly. From personal observations, we find that hollow species occur more frequently in hummocks in Irish bogs than in Estonian bogs.

Earlier it was stated that the amount of precipitation cannot be seen as a 'black box' ecosystem driver (Heisler and Weltzin 2006). We suggest that survival and potential expansion of hollow

species outside their main habitat is strongly driven by the frequency, distribution, and intensity of precipitation, but it also depends on the overall water content of the surrounding vegetation, which is affected most by the distance to the water table. Any future changes in precipitation patterns (Meehl et al. 2007) may influence the persistence of these *Sphagnum* species. In order to understand how *Sphagnum* vegetation will respond to changes in precipitation patterns, it is necessary to study the effects of precipitation on the competition between *Sphagnum* species on larger temporal scales.

## CONCLUSIONS

For hollow species to persist in hummock vegetation it is very important that their capitulum water content is high enough to be able to photosynthesize. Hollow species generally are not capable to transport water to their capitula (i.e. capillary rise) when they grow too far from the water table. In literature, lateral water transport from the surrounding hummock vegetation is commonly seen as the most important source of water for these hollow species. Our results indicate that precipitation has a very large effect on the water content of hollow species in low hummocks, as well as in high hummocks. LHWT only seemed to be an important source of water in the high hummock, yet this transport only played an important role after large amounts of precipitation. Precipitation therefore is instrumental for lateral water transport in hummocks. Persistence and perhaps expansion of hollow species in higher hummocks strongly depends on the intensity and frequency of future precipitation patterns.

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## PATCH SIZE, WATER TABLE AND SPECIES IDENTITY AFFECT *SPHAGNUM* PERSISTENCE AFTER FIELD INTRODUCTION

Robroek BJM, Schouten MGC, Limpens J, Crushell PH, Kimmel K, Breeuwer A,  
Van Ruijven J and Berendse F

A lot of peatlands which have been drained and cut-over in the past, are now re-vegetated with a secondary plant cover. After restoration, however, the development of a typical *Sphagnum* vegetation stagnates in a pioneer stage. We simultaneously performed an experiment in Clara bog, Ireland and Männikjärve bog, Estonia, in which we investigated the effects of different water levels and patch size on the competitive strength of different *Sphagnum* mosses after transplantation into *S. magellanicum* vegetation. Over a three year period, changes in cover were monitored for large and small cores of *Sphagnum cuspidatum*, *S. rubellum* and *S. fuscum* after transplantation into a *S. magellanicum* matrix, at a high and a low water table. Water contents and height increment of the surrounding *S. magellanicum* matrix were also measured. We found interspecific differences in cover change over the years. Generally, cover change of the transplanted species was higher in Männikjärve bog compared to Clara bog, presumably as a result of reduced competition from the surrounding *S. magellanicum* vegetation in Estonia. Cover of *S. cuspidatum* decreased with time, and was largest at low water tables. After an initial decrease in cover, *S. rubellum* and *S. fuscum* recovered and showed a net increase, except for the small patches in Clara bog for which the initial decline levelled off. Expansion of both species was promoted by a large patch size and for *S. fuscum* was highest at low water tables, whereas water table did not affect *S. rubellum*. Additionally, an increase in patch size seemed to enhance the ability of species to create their own micro-hydrological environment, which may be more optimal for their growth. Our results indicate that transplantation of species into an existing *Sphagnum* vegetation can be successful, but the success depends on patch size, the hydrological conditions, and the species considered for re-introduction. The patches of the transplanted species should be large enough to allow persistence during the first years. Present hydrological management seems to contradict the conservation aims. It, however, may be important to first restore a vegetation where water tables can be lowered without hampering the functioning of the system. The next step would be the transplantation of large patches of species considered for re-introduction.

## INTRODUCTION

About 3% of the earth's land surface is covered with peatlands. The largest portion of these peatlands is found at high latitudes in the Northern hemisphere. Vast areas of peatlands, however, have been damaged due to agricultural activities, forestry and historic or present day peat extraction (Joosten 1997). Restoring peatlands that have been abandoned after peat extraction is a major issue in nature conservation and a lot of ecological research has been devoted to the restoration of peat bogs. Particularly in Canada and Fenno-Scandinavia huge efforts are put into restoring peatlands after peat extraction (Rocheft 2000; Rocheft 2003; Vasander et al. 2003; Tuittila et al. 2004). These studies mainly focus on the re-establishment of an active *Sphagnum* layer on bare peat soil, since their ecology makes *Sphagnum* mosses important ecosystem engineers and key stone species in peatlands (Van Breemen 1995).

In the Netherlands, almost half of the present day area used to be covered by peatlands, of which approximately two-thirds (c. 1,000,000 ha) were raised bogs (Joosten 1994). Today, less than 0.5% ( $\approx$  4,000 ha) of the Netherlands is covered by bog remnants which were drained and cut-over in the past (Vermeer and Joosten 1992). In contrast to the North American and Fenno-Scandinavian situation, a lot of these remaining peatlands do have an extensive secondary plant cover. However, many characteristic species are absent and the composition of the vegetation may be different from what it used to be (Joosten 1995; Vasander et al. 2003). All *Sphagnum* species are rare without restoration management, which usually occurs by retaining rain water on the surface of the bog remnants. Hydrological restoration in most cases has resulted in the re-establishment of a *Sphagnum* cover, but the peat bog development stagnates in a pioneer phase (Money 1995). After re-introduction, however, *Sphagnum* species that are representative for later developmental stages have been found to persist and even expand in pioneer vegetation (Smolders et al. 2003). Similar results were obtained by Rydin (1993) and Gunnarsson and Söderström (2007) who showed that after introducing small *Sphagnum* patches or fragments into existing *Sphagnum* communities, they were able to persist. These findings suggest that the absence of certain *Sphagnum* species is caused by dispersal and / or establishment limitations, rather than a lack of suitable abiotic conditions. Introduction of *Sphagnum* target species, therefore, may be crucial to restore *Sphagnum* diversity and to accelerate the development of natural vegetation in Dutch bog remnants.

However, it remains unclear which factors are important for successful re-introduction of *Sphagnum* species. Rydin (1993) suggested that establishment of a species into an existing carpet is difficult due to competition, especially for small patches. Competition between *Sphagnum* species can be severe, and the moisture content in the capitula of these mosses and their water use efficiency have been shown to play a key role therein (Titus et al. 1983; Silvola and Aaltonen 1984; Titus and Wagner 1984; Rydin and McDonald 1985b; Silvola et al. 1996). In a peat bog, *Sphagnum* species generally occupy specific positions above the water table, which seems to be related to differences in growth phenology at different water tables (Gunnarsson 2005), the efficiency of the capillary system and the ability to hold water (Hayward and Clymo 1982; Titus and Wagner 1984; Rydin and McDonald 1985a). Hummock species are superior in keeping their capitula moist compared to hollow species. Furthermore, hummock and hollow species differ in

their photosynthetical response to capitulum water content, with hummocks species generally performing better at the lower contents and hollow species performing better at higher contents (Silvola and Aaltonen 1984; Rydin and McDonald 1985b). Therefore the success of transplanting target species may strongly depend on the microhabitat (i.e. the distance to the water table), since it affects the competitive ability of transplanted *Sphagnum* patches. We earlier suggested that the amount of homogeneous peat (i.e. the patch size) may be important for species to create their own micro-hydrological environment in which their growth is optimal (Robroek et al. 2007).

Our main objectives were to investigate the competitive strength of different *Sphagnum* species after introduction into an existing vegetation and to elucidate the role of the water table therein. Additionally, we intended to examine if the size of the transplanted patches is important. Therefore, we performed a three-year experiment in which we transplanted small and large cores of different *Sphagnum* species into an existing vegetation at a high and a low water table. Among Europe there is a huge variation in bog types (Rydin et al. 1999). Differences in temperature, annual precipitation and summer water tables are thought to be responsible for the morphological differences and differences in vegetation between sub-oceanic (i.e. NW European) and continental (i.e. E European) bogs (Schouten et al. 1992). To cover this geographical variation, we simultaneously performed this experiment in Ireland (NW Europe) and Estonia (E Europe). As a matrix species, *S. magellanicum* was chosen, since this species has a wide geographic distribution and a relatively wide range of habitats along the water table (Rydin et al. 1999). We introduced several *Sphagnum* species, each typical for a part of the water level gradient, and monitored their performance for three years. We expected that high water tables would be especially beneficial for the persistence of hollow species. Low water tables, on the other hand, were expected to be most beneficial for the lawn and hummock species. Secondly, larger patch sizes were expected to favour the persistence, because increased patch size is assumed to promote the ability of *Sphagnum* mosses to create their own micro-hydrology.

## METHODS

### *Site description and the regional climate*

Clara bog, Co. Offaly, is one of the last remaining intact raised bogs in Ireland and has long been recognized as being of high ecological importance (Schouten 1981; Crushell et al. 2006). Clara bog (665 ha) is located in the Irish midlands, which are characterized by the high amount of raised bogs, enclosed by Esker ridges. Mean annual temperature is 9.3°C and mean annual precipitation is about 804 mm, as measured during the period 1981-1990 at the Birr weather station. Mean summer precipitation (May – September) is 324 mm, and rainfall is more or less constant over the months (Met Éireann). Männikjärve bog (320 ha) is situated on the southern slope of the Pandivere Upland, Central Estonia. It belongs to the Endla mire system and is of limnogenic origin (Karofeld 1999). The proximity of the Baltic Sea influences the climate slightly. At the most western point the mean annual temperature is 6°C, whereas it is 4.5°C at the country's most eastern points. Mean annual precipitation is 675 mm and mean summer (May – September) is about 329 mm.

Rainfall is heaviest during summer and lightest in spring (Estonian Meteorological and Hydrological Institute).

Plant communities in Estonia and Ireland were similar. *Sphagnum magellanicum* Brid. was the dominant peat moss species at the experimental plots. In both sites, *S. cuspidatum*, *S. rubellum* and *S. fuscum* occurred. *Rhynchospora alba* (L.), *Oxycoccus palustris* Pers. and *Menyanthes trifoliata* L. were the most important vascular plants in the lower parts of the sites, and *Andromeda polifolia* L., *Eriophorum vaginatum* L. and *Erica tetralix* L. occurred frequently in the higher parts.

#### *Experimental set-up*

In June 2003, we transplanted cores of three *Sphagnum* species (*Sphagnum cuspidatum* Ehrh. ex Hoffm., *S. rubellum* Wilson and *S. fuscum* (Schimp.) H. Klinggr.) into an existing vegetation of *Sphagnum magellanicum* at a high and a low water table (intended to be -5 cm and -20 cm, respectively). The natural occurrence along the water table of these species in both bogs is as follows, from wet (hollow) to dry (hummock): *S. cuspidatum* < *S. magellanicum* < *S. rubellum* < *S. fuscum* (Ilomets 1988; Kelly and Schouten 2002). Initially, in Ireland an intermediate water level was included, but because these water levels strongly resembled the high water table, they were omitted from the analysis. At both water tables, the transplants were randomly assigned to one of the replicated blocks (five in Ireland, and six in Estonia). In every block, we randomly transplanted *Sphagnum* species in two patch sizes: one large patch (c. 150 cm<sup>2</sup>) and four small patches (c. 37.5 cm<sup>2</sup>).

Earlier research has shown that vascular plants can have a positive effect on *Sphagnum* growth and reduce water loss of the *Sphagnum* layer (Heijmans et al. 2001). However, they may also cause a shading effect. In order to eliminate the effects of vascular plants, and differences therein between plots, all vascular plants were clipped down to the *Sphagnum* vegetation. Clipping was repeated every May and September. As a control the effects of clipping on the height increment and the water content of the *Sphagnum magellanicum* matrix were examined in separate plots close to the transplantation experiment in Estonia. To do so, we compared clipped plots with control (non-clipped) plots.

#### *Measurements and data-handling*

##### *Sphagnum* performance

Height increment of the *Sphagnum magellanicum* matrix in the transplantation experiment, as well as in the clipping experiment, was measured using a variation on the cranked wire method (Clymo 1970). Plastic rods were inserted to a depth of roughly ten centimetres into the *Sphagnum* vegetation. The rods were anchored in the *Sphagnum* substrate by broom bristles and did not visibly interfere with *Sphagnum* growth. Increment was measured every May and every September, starting May 2004 and ending September 2006. We defined the September– May periods as winter, whereas the May – September periods were defined as summer.

Expansion of the transplanted species was assessed using cover change throughout the experiment. Over the 2003–2006 period, every September a digital photograph of the transplanted

*Sphagnum* mosses was taken. A reference frame was included in the photograph. Cover of each species was analysed using an image processing and analysis program (ImageJ 1.33u; National Institutes of Health, USA). Covers of the four small patches were averaged before analysis, to prevent pseudo-replication.

At harvest, paired samples (2 cm deep, including capitula) were taken from the large transplants and their surrounding *S. magellanicum* matrix. The samples were put in plastic 'zip-lock' bags after which fresh weight was measured. Thereafter, all samples were put in paper bags and pre-dried at room temperature. Finally, they were transported to the Netherlands, after which they were dried at 70° C. for at least 72h. We defined water content as as fresh weight dry weight ratio (fw dw<sup>-1</sup>).

#### Water tables

At the experimental plots in Ireland, water tables were measured in 30 permanent wells every month. It was made sure that these wells covered the experimental site, and where equally divided over the blocks and water tables. Additional measurements were done during visits in May and September. At the experimental plots in Estonia, water table measurements were only done during these visits in the same months, but water tables were also measured monthly in a permanent well which was in the vicinity (< 50 m) of the experimental plot. These data were extrapolated to our measurements. Because Männikjärve bog was frozen during the winter months, we could only calculate mean water tables in the period in which the bog surface was not frozen (May – September). Consequently, water table comparisons between Clara bog and Männikjärve bog only covers these months.

#### Data analysis

All data were tested for normality and equality of variance prior to analysis. Only in the case of *S. fuscum* cover change, data did not meet the assumptions of homogeneity of variances, even after ln-transformation. Nevertheless, we continued our analysis because Analysis of Variance (ANOVA) appears not to be highly influenced if this assumption is violated (Heath 1995).

Total mean summer water tables (2003-2006) at Clara bog and Männikjärve bog were compared using ANOVA with site, year and water table treatment as fixed factors. Because of significant interactions with year, further analyses were performed per year. The effects of site and water table on the total height increment of the *S. magellanicum* matrix were tested using ANOVA. Additionally, ANOVA was used to analyse the interactive effect of season (summer or winter) and water table on the average seasonal height increment of the *S. magellanicum* matrix per experimental plot.

Expansion or reduction of the transplanted patches, expressed as cover change, was tested with repeated measures ANOVA, with site, species, water table and patch size as fixed factors. Initially, block, nested within site, was included as a random factor, but it was omitted from the analysis as block effects were not significant. In case of significant interactions, additional RM-ANOVA's were performed separately for the different levels of the interacting factors. In case

of violation of the assumption of homosphericity (Maulchy's test of Sphericity), we used the Huyn-Feldt epsilon to adjust the degrees of freedom (Potvin et al. 1990).

To elucidate if the patch size of the transplanted species has an effect on the micro-hydrology of the patch, we calculated the difference between the water content of the transplants and the surrounding matrix ( $WC_{\text{patch}} - WC_{\text{matrix}}$ ). Per site, we used the full ANOVA model with species and water table as fixed factors and patch size at harvest as a covariate. As species identity and patch size turned out to be correlated, type III sums of squares (SS) could not be used (Van Ruijven et al. 2003). Instead, we used sequential (type I) SS in the ANOVA, in which species identity and water table were included before patch size. In this way, potential contributions of a species effect to the relationship between patch size and water content were avoided.

**Table 6.1** Mean square values, F-values and P-values for the effects of site, water table and patch size on the cover (area) at harvest for three *Sphagnum* species. Values in bold indicate significant P-values ( $< 0.05$ )

Source	d.f.	<i>S. cuspidatum</i>			d.f.	<i>S. rubellum</i>			d.f.	<i>S. fuscum</i>		
		MS	F	P		MS	F	P		MS	F	P
Intercept	1	207133.2	546.43	<b><math>\leq 0.001</math></b>	1	11561.1	7.18	<b><math>\leq 0.01</math></b>	1	2546.86	2.213	0.15
Site	1	1520.5	4.01	<b><math>\leq 0.05</math></b>	1	9967.5	6.19	<b><math>\leq 0.05</math></b>	1	9047.0	5.64	<b><math>\leq 0.05</math></b>
Water table (WT)	1	9289.4	24.51	<b><math>\leq 0.001</math></b>	1	1243.8	0.77	0.39	1	8167.8	5.10	<b><math>\leq 0.05</math></b>
Patch size (PS)	1	776.6	2.05	0.16	1	11368.5	7.06	<b><math>\leq 0.05</math></b>	1	21781.2	13.59	<b><math>\leq 0.001</math></b>
Site * WT	1	57.9	0.15	0.70	1	196.8	0.12	0.73	1	1900.4	1.19	0.28
Site * PS	1	9.0	0.02	0.88	1	3137.3	1.95	0.17	1	12.9	1.59	0.22
WT * PS	1	73.1	0.19	0.66	1	694.5	0.43	0.52	1	34.0	0.01	0.93
Site * WT * PS	1	7.9	0.02	0.89	1	4047.0	2.52	0.12	1	1603.0	0.02	0.89
Error	36	379.1			36	1609.3			36	2031.5		

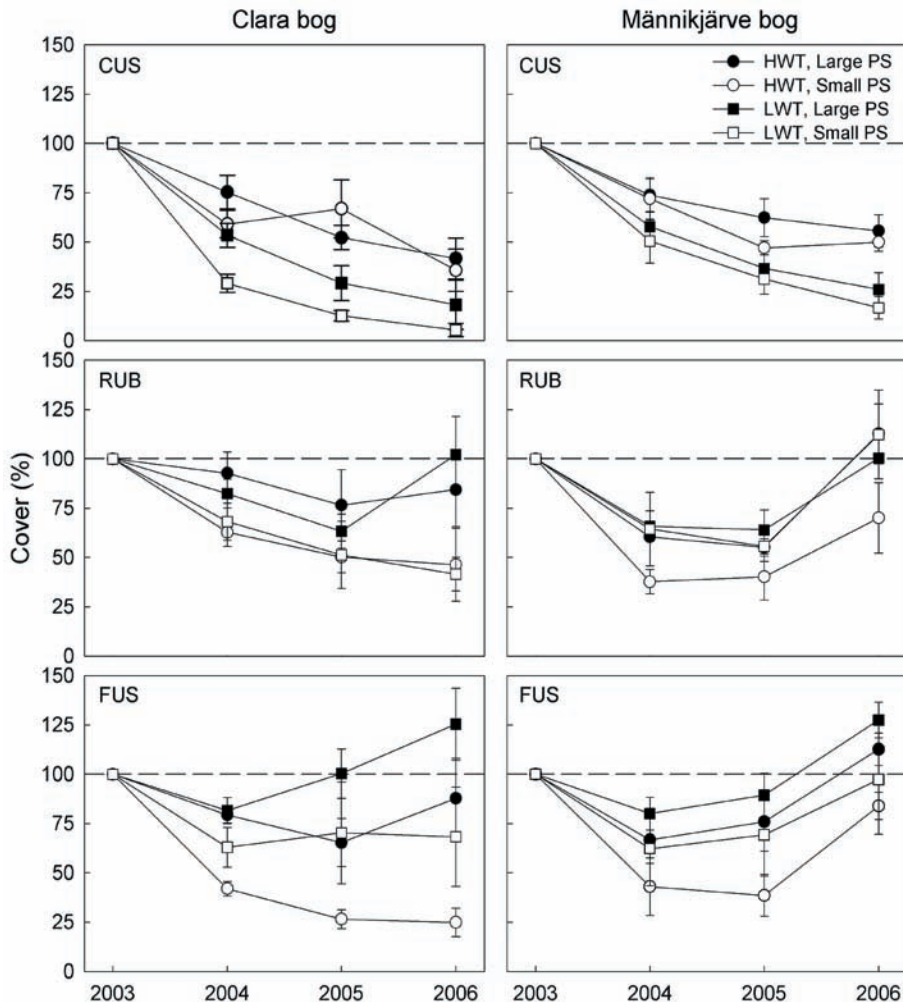
## RESULTS

### Cover change of the transplanted *Sphagnum* species

In general, cover change after transplantation differed between species ( $F_{2,108} = 19.08$ ,  $P \leq 0.001$ ) and larger patches performed better than smaller patches ( $F_{1,108} = 24.98$ ,  $P \leq 0.001$ ), but the latter differed between years ( $F_{6,319} = 11.35$ ,  $P \leq 0.001$ ). The effect of water table on the cover change differed between species ( $F_{2,108} = 12.36$ ,  $P \leq 0.001$ ), hollow species performed better at high water tables, whereas hummock species responded oppositely. Three years after transplantation, cover differed between species (ANOVA,  $F_{2,108} = 38.92$ ,  $P \leq 0.001$ ) and were larger in Männikjärve bog than in Clara bog ( $F_{1,108} = 15.24$ ,  $P \leq 0.001$ ). Cover change also changed over time. Within-subject contrasts show a linear ( $F_{1,108} = 102.92$ ,  $P \leq 0.001$ ) as well as a quadratic ( $F_{1,108} = 241.24$ ,  $P \leq 0.001$ ) component in the direction of the cover change, indicating that after an initial decrease in cover, the cover of the introduced species stabilized or even increased. In addition, we found interspecific differences in cover change over the years ( $F_{6,319} = 23.6$ ,  $P \leq 0.001$ ). *Sphagnum cuspidatum* and *S. rubellum* cover decreased with time, whereas *S. fuscum* cover remained unchanged (Table 1). The cover of *S. cuspidatum* continued to decrease, although the decline appeared to level off (Fig. 6.1). Except for the small patches in Clara bog, the cover of *S. rubellum* and *S. fuscum* increased after an initial decrease (Fig. 6.1). For *S. cuspidatum*, low water tables resulted in a larger decrease compared to high water tables in the first year, after which this difference was maintained, resulting



in a lower cover after three years (Table 6.1 and 6.2, Fig. 6.1). The decrease in cover was similar for both patch sizes (Table 6.2). In contrast, patch size significantly affected cover change of the other two species (Table 6.2). The initial decrease appeared to be less and the subsequent recovery stronger in larger-sized patches (Fig. 6.1). The recovery of *S. rubellum* and *S. fuscum* after the initial decrease was lower in Clara bog, particularly for the small patches (Table 6.1, Fig. 6.1). Expansion of the hummock species *S. fuscum* was promoted by low water tables (Table 6.2, Fig. 6.1).



**Figure 6.1** Change in cover ( $\pm$  SEM) over three subsequent years of *S. cuspidatum* (CUS), *S. rubellum* (RUB) and *S. fuscum* (FUS) grown at different water tables and different patch sizes in Clara bog and Männikjärve bog. For statistics, see Table 6.2

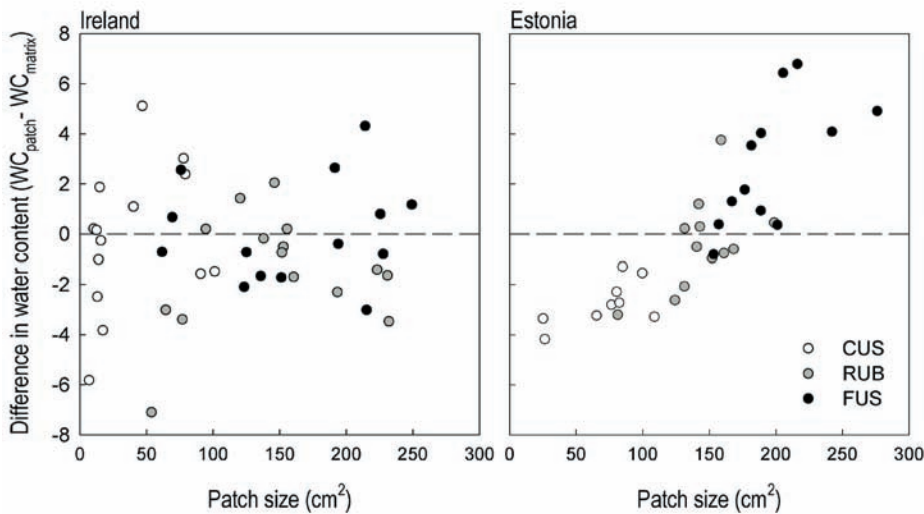
In Clara bog, we did not find any effect of species, water table or patch size on the difference in water content between the transplanted patch and the surrounding *S. magellanicum* vegetation (Fig. 6.2). In Männikjärve bog, however, we found differences between species ( $F_{2,26} = 81.88$ ,  $P \leq 0.001$ ), water table ( $F_{1,26} = 6.92$ ,  $P = 0.14$ ), and patch size ( $F_{2,26} = 16.90$ ,  $P \leq 0.001$ ). As shown in Figure 6.2, *S. cuspidatum* water content generally is lower than its surrounding matrix, whereas that of *S. fuscum* is higher. *S. rubellum* water content was lower in some cases and higher in others. Interestingly, the difference in water content between the transplants and their surrounding matrix was positively related to patch size (Fig. 6.2).

**Table 6.2** Between and within subject effects of RM-ANOVA to test the effects of site, water table, patch size on the cover change over three subsequent years of three *Sphagnum* mosses that were transplanted in a *S. magellanicum* matrix. Values in bold indicate significant  $P$ -values ( $< 0.05$ )

Source	d.f.	<i>S. cuspidatum</i>			d.f.	<i>S. rubellum</i>			d.f.	<i>S. fuscum</i>			
		MS	F	<i>P</i>		MS	F	<i>P</i>		MS	F	<i>P</i>	
Between subjects													
Site	1	1731.1	2.46	0.13	1	49.0	0.04	0.85	1	2136.5	1.05	0.31	
Water table (WT)	1	1985.4	25.60	≤ 0.01	1	1151.6	0.89	0.35	1	14135.9	6.96	≤ 0.05	
Patch size (PS)	1	1920.2	2.73	0.11	1	11454.0	8.87	≤ 0.01	1	27633.5	13.60	≤ 0.001	
Site * WT	1	288.4	0.41	0.53	1	1388.0	1.08	0.31	1	1035.5	0.51	0.48	
Site * PS	1	45.3	0.06	0.80	1	1796.3	1.39	0.25	1	1296.2	0.64	0.43	
WT * PS	1	348.0	0.50	0.49	1	1377.5	1.07	0.31	1	512.8	0.25	0.62	
Site * WT * PS	1	376.8	0.54	0.47	1	962.3	0.75	0.39	1	22.7	0.01	0.92	
Error	36	702.5			36	1290.8			36	2031.5			
Within subjects													
Year	3	39785.5	267.40	≤ 0.001	3	18347.6	30.30	≤ 0.001	3	13465.9	24.90	≤ 0.001	
Year * Site	3	304.4	2.05	0.11	3	5659.1	9.35	≤ 0.001	3	2383.5	4.40	≤ 0.05	
Year * WT	3	2121.5	14.30	≤ 0.001	3	274.0	0.45	0.69	3	2153.6	3.98	≤ 0.01	
Year * PS	3	298.8	2.01	0.12	3	2226.6	3.68	≤ 0.05	3	3859.1	7.13	≤ 0.001	
Year * Site * WT	3	263.1	1.77	0.16	3	249.1	0.41	0.71	3	581.8	1.08	0.36	
Year * Site * PS	3	291.6	1.96	0.12	3	689.0	1.14	0.33	3	497.8	0.92	0.43	
Year * WT * PS	3	52.8	0.34	0.79	3	215.3	0.36	0.75	3	124.2	0.23	0.88	
Year * Site * WT * PS	3	259.7	1.75	0.16	3	1227.3	2.03	0.13	3	58.4	0.11	0.96	
Error	108	148.8			92	605.5			108	541.3			

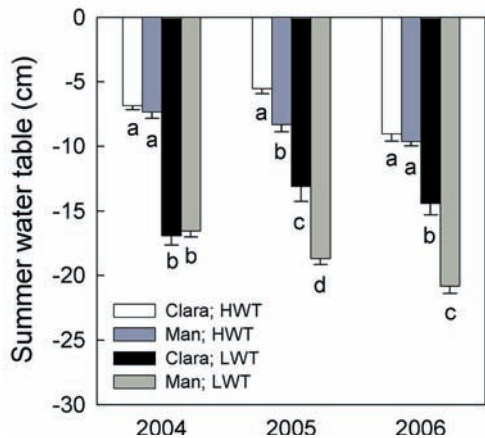
### Water tables and precipitation

Summer water tables differed significantly between the two water-level treatments in both bogs each year (Fig. 6.3). No differences in water table between the two sites were observed in 2004, but in 2005 both water levels in Männikjärve bog were slightly lower than in Clara bog. In 2006, only the low water table was lower in Männikjärve (Fig. 6.3).



**Figure 6.2** The relationship between patch size at harvest of the large transplants and the difference in water content (WC) between the transplanted patch and its surrounding matrix. Data are shown for *S. cuspidatum* (CUS), *S. rubellum* (RUB) and *S. fuscum* in Clara bog, Ireland and Männikjärve bog, Estonia.

Although mean summer precipitation was comparable between the two sites, mean annual precipitation in Estonia was about 200 mm less than in Ireland. Precipitation data for five subsequent days that preceded the sampling for the water content were roughly estimated from data found at the websites of the Irish and Estonian meteorological institutes for Dublin and Tartu respectively (Met Éireann and Estonian Meteorological and Hydrological Institute). Daily precipitation preceding the measurements were 0.8, 12, 0.9, 6.5 and 0 mm (cumulative 20.2 mm for Ireland and 0.8, 0.1, 12.9, 0 and 0 mm (cu



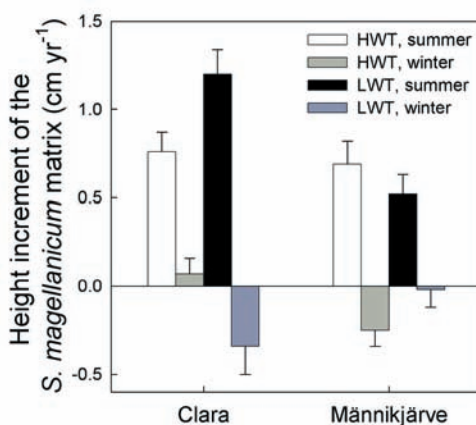
**Figure 6.3** Mean annual summer water table depths (cm  $\pm$  SEM) for every year at Clara bog (Clara), Ireland, and Männikjärve bog (Man), Estonia at high water table (HWT) and low water table (LWT) regimens

### Growth of the *Sphagnum* matrix and effects of clipping

Total height increment of the *Sphagnum magellanicum* matrix at both bogs was not affected by water table ( $F_{1,80} = 0.10$ ,  $P = 0.75$ ), but was generally lower in Männikjärve ( $F_{1,80} = 7.19$ ,  $P \leq 0.01$ ). More harsh winter conditions in Estonia (mean winter temperature is  $-8^{\circ}\text{C}$ ) compared to Ireland (temperatures hardly drop below  $0^{\circ}\text{C}$ ), which may result in a, for Estonia, shorter period in which growth can take place, can be ruled out in explaining this difference. In both experimental plots, the moss height increment was restricted to the summer season (Männikjärve:  $F_{1,212} = 46.77$ ,  $P \leq 0.001$ ; Clara:  $F_{1,278} = 83.17$ ,  $P \leq 0.001$ ; Fig. 6.4). Alternatively, the difference in growth of the matrix vegetation may be explained by differences in the annual amounts of precipitation and in the temporal distribution of this precipitation.

During the winter, we sometimes found negative values for the moss height increment (Fig. 6.4). In Estonia, this may be due to long-term snow cover, which may have compressed the upper *Sphagnum* layer. In Ireland, however, such a snow cover is absent. Perhaps compaction of the upper layers by gravity is larger than the moss growth during winter, which resulted in negative values for height increment.

Clipping the vascular plant vegetation did not affect the *Sphagnum* height increment ( $P > 0.05$ ). Additionally, clipping did not affect the water content of the *Sphagnum* vegetation.



**Figure 6.4** Height increment ( $\text{cm yr}^{-1} \pm \text{SEM}$ ) of the *S. magellanicum* matrix in Clara bog and Männikjärve bog. All data were separated for the summer (May–September) and the winter season (October–April)

## DISCUSSION

### *Interspecific differences in persistence of transplanted Sphagnum mosses and the role of water table and patch size*

In Männikjärve bog the height increment of the existing *S. magellanicum* vegetation was relatively low compared to Clara bog (Fig. 6.3). As a result of reduced competition from the surrounding vegetation, the transplanted species in Männikjärve bog may have declined less and could explain the differences in persistence of the transplants between Männikjärve bog and Clara bog. As expected we found interspecific differences in the response to water table. Water table depth did not affect the cover change of *S. rubellum*, but it affected *S. cuspidatum* and *S. fuscum*. These results concur with earlier experiments where we have found that water table does not play a very important role in the competition between species which were grown together under controlled conditions, except for *S. cuspidatum* (Robroek et al. 2007). This, however, contradicts the results presented by Rydin (1993), who did not find a correlation between mean water table and the change in area of the species he transplanted. In our experiment, *S. cuspidatum* cover declined most at low water tables, whereas low water table was advantageous for *S. fuscum* (Table 6.1 and 6.2). Regarding the natural position of these species along the water table gradient in raised bogs, these effects of water table seem obvious. Especially for species which occur far from the water table, competitive strength increases with decreasing water table.

All transplanted *Sphagnum* species decreased in cover shortly after transplantation, irrespective of the water table (Fig. 6.1). A similar initial decline was observed by Rydin (1993) who transplanted *S. fuscum* into a hollow vegetation. The experimental handling and variation in weather conditions between the years, where ruled out to be causing this decline (Rydin 1993). Our results indicate that different annual water tables are also unlikely since they did not differ too much between years (Fig. 6.3). An alternative explanation is that transplanted patches always decrease initially since the existing vegetation has a strong initial competitive advantage, compared to the transplanted species, which may have been collected from a habitat with a different micro-environment. After the initial decrease, all patches of *S. rubellum* and *S. fuscum*, except for the small ones in Clara bog, recovered after one to two years (Fig. 6.1), resulting in interspecific differences in cover after three years. If a species is able to adapt to, and to persist in the new environment, it gains in competitive ability after which it is able to increase in cover. The mechanism which is instrumental may come from our own data.

As anticipated, patch size of the transplanted species plays an important role in the persistence of species. Interestingly, for *S. cuspidatum* patch size is not important. The competitive strength of this species seems to be relatively poor, presumably due to its inferior water holding capacity and ability to transport water from the phreatic water table to its capitula (Clymo and Hayward 1982; Asada et al. 2003), and as such patch size has no effect. For the other two species patch size does matter. One explanation could be that small patches relatively decrease in cover faster, because their area-perimeter ratio is small compared to that of large patches. This means that the decline of smaller patches is relatively larger than that of larger patches, at similar absolute decline. Alternatively, large patches may be superior in creating their own micro-hydrology.

Consequently, the persistence of large patches of *Sphagnum* mosses may increase because of optimal hydrological circumstances. The water content of *Sphagnum* mosses can be influenced by factors as the water holding capacity, and the ability to transport water from the water table to their capitula by capillary rise (Clymo 1973; Hayward and Clymo 1983). Earlier we suggested that increased patch size may increase the ability of *Sphagnum* mosses to maintain a water content which is optimal for its performance (Robroek et al. 2007). That may also explain why Smolders et al. (2003) did not find an initial decrease after transplantation of several species. The patches they used were relatively large ( $\approx 500 \text{ cm}^2$ ) compared to the transplants used by Rydin ( $\approx 30 \text{ cm}^2$ ) and in our experiment ( $\approx 37.5 \text{ cm}^2$  and  $150 \text{ cm}^2$ ), and as a result may have been able to create their own environment. The data from Estonia unambiguously confirm the proposition that increased patch size enable species to control their own hydrology to a larger extent, since the difference in water content between the transplants and its surrounding vegetation was positively correlated to increased patch size. In Ireland, we, however, did not find such a correlation. Apart from the factors mentioned above, precipitation also plays a role in the water supply of the *Sphagnum* vegetation (Robroek et al. in press). Precipitation patterns in the five days preceding our measurements did differ between the two sites. In Clara bog, precipitation over the five days preceding the measurements was more continuous and cumulative precipitation was slightly higher. The higher precipitation frequency in Clara bog may have diminished differences in water content between the transplants and the matrix. Although our data have to be treated with some caution, they indicate that a large patch size is important for *Sphagnum* species to create their own micro-hydrology which may lead to a more optimal competitive ability especially during dry conditions. More research is needed to draw firm conclusions, however.

#### *Implications for Sphagnum re-introduction*

A lot of research has been carried out into the possibility of re-introducing *Sphagnum* to recently cut-over bogs (e.g. Rochefort 2003). Many bogs, however, have been exploited in the distant past have been re-colonized by secondary vegetation. In recent decades quite a number of such sites have been subjected to restoration measures. Even after hydrological measures, previously occurring *Sphagnum* mosses remain absent (Schouten et al. 1998). This may be due to either unsuitable environmental conditions, dispersal limitations due to the absence of nearby sources, or severe competition which makes it impossible for diaspores to establish in an existing vegetation. Experiments with *Sphagnum* mosses and brown mosses, however, show that it is possible for transplanted species to persist and even expand in an existing vegetation (Kooijman and Bakker 1995; Smolders et al. 2003; Tomassen et al. 2004; Gunnarsson and Söderström 2007; Malson and Rydin 2007), thereby ruling out unsuitable environmental conditions as the sole explanation. Since competition between *Sphagnum* species can be severe, it may be very hard for individual diaspores to establish in existing vegetation (Rydin 1997). Gunnarsson and Söderström (2007) have shown that regionally rare *Sphagnum* species in Sweden were limited by dispersal. Because of the scattered bog remnant in the Netherlands, the absence of hummock species may also be due to dispersal limitation. We show that transplantation of *Sphagnum* species into existing



vegetation can be a tool for nature management, but only if hydrological management results in suitable micro-habitats for those species targeted for re-establishment. Low water tables are shown to be beneficial for the establishment of hummock species, whereas high water tables impede re-establishment. Present management is aimed at retaining water on the surface of peat remnants in order to restore an active and functional *Sphagnum* vegetation. This seems to contradict with restoration aims in which hummock species play a key role. It, however, is important to first restore a self-regulating peat moss vegetation in which water tables can be lowered without affecting its functioning (Van der Schaaf 2002). Transplantation of hummock species would be a next step in restoring peat remnants. The success of these transplantations will increase if the patches that are used are large enough for these species to create their own micro-hydrological environment.

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# HOW OMBROTROPHIC BOG VEGETATION RESPONDS TO WATER TABLE FLUCTUATIONS

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The main goal of this mesocosm experiment was to elucidate how water tables, and fluctuations therein, affect the vegetation of ombrotrophic bogs over a two-and-a-half year period. Furthermore, examined if vascular plant cover influences *Sphagnum* production. Therefore, mesocosms were collected at Saxnäss mosse, Southern Sweden, which subsequently were transported to the experimental field in Wageningen, the Netherlands. *Sphagnum* growth, as well as *Sphagnum* and vascular plant abundance, were assessed at constant (CWL) and fluctuating (FWL) water levels. Changes in production and cover were correlated to modal water table depth during the growing season. Furthermore, the relation between *Sphagnum* production and changes in vascular plant cover was assessed. Our results show that *S. cuspidatum* production and abundance decreased with fluctuating water tables, while *S. magellanicum* responded oppositely. The abundance of graminoid species increased in both treatments during the experiment, but most at the constant water level. The abundance of ericoid species increased when the water table fluctuated. We found no significant relation between vascular plant cover and *Sphagnum* production. From these results we conclude that 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. What the impact of these changes is on future carbon sequestration and hydrological characteristics of raised bogs are import questions for future research.



## 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 considerable biomass production and relatively slow decay rate (Johnson and Damman 1991; Limpens and Berendse 2003a), *Sphagnum* mosses are largely responsible for the formation of peat, and hence the sequestration of carbon. Furthermore, *Sphagnum* regulates the hydrological and hydrochemical conditions at the raised bog surface to a high degree (Van Breemen 1995; Van der Schaaf 2002). To what extent *Sphagnum* mosses affect their environment may depend on the identity of the species. Consequently, the *Sphagnum* species composition and changes therein may affect the functioning of the bog ecosystem.

A major environmental factor controlling the dynamics of *Sphagnum* mosses is depth of the water table, due to its influence on the capitulum water content of these mosses (Rydin 1993; Weltzin et al. 2001; 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. Concomitantly, this determines their occurrence along the water table gradient, from hollows (high water table) to lawns (intermediate water table) and hummocks (low water table). Changes in temperature and precipitation patterns are expected to occur worldwide due to climate change (Sweeney and Fealy 2002; Meehl et al. 2007). Since water table depth, and especially fluctuations therein, are affected by such changes, be it directly by changes in precipitation rate or indirectly by temperature-driven changes in evapotranspiration (Gunnarsson et al. 2004), it is important to know how water table depth influences the composition and production of the *Sphagnum* layer in bogs.

In peatlands, *Sphagnum* mosses grow together with vascular plants. Parallel to the distribution of *Sphagnum* mosses, the vascular plant species assemblage varies over the different microhabitats. In hollows, vascular plants need aerenchyma to be able to withstand prolonged high water tables; examples are graminoid species like *Rhynchospora alba* (L.) Vahl and *Eriophorum vaginatum* L. Further from the water table (i.e. lawns and hummocks), also ericoid species like *Andromeda polifolia* L. and *Calluna vulgaris* (L.) Hull can occur. Changing water tables can have a profound impact on the vascular plant vegetation in bogs. Several studies elucidated that cover and production of vascular plant species increased when water table was lowered (Weltzin et al. 2000; Strack et al. 2006).

In general, *Sphagnum* mosses are suggested to have a competitive advantage over vascular plants in bogs, because most nutrient input comes from atmospheric deposition and *Sphagnum* is much more efficient in the uptake of these nutrients than vascular plants (Heijmans et al. 2002b; Malmer et al. 2003; Bragazza et al. 2004). The latter depend on nutrients from mineralization of subsurface peat (Malmer et al. 1994). Mineralization rates in peat bogs are generally low, due to the waterlogged conditions and the high percentage of decay-resistant *Sphagnum* litter. Consequently, nutrient supply to vascular plants is limited. As stated earlier, future changes in precipitation patterns



are expected which may result in longer dry periods. Prolonged periods in which the water level is low, and concomitant aeration of the deeper peat layers, may increase mineralization rates, resulting in higher nutrient availability for vascular plants. Hence, this positively affects vascular plant growth (Limpens et al. 2006). When vascular plant cover increases, the *Sphagnum* layer becomes more shaded, which can decrease *Sphagnum* growth (Hayward and Clymo 1983; Heijmans et al. 2001; Limpens et al. 2003b; Bubier et al. 2007). Since *Sphagnum* is mainly responsible for the sequestration of carbon in bogs, an increase in vascular plants may thus lead to a decrease in carbon sequestration in this type of ecosystem. Furthermore, changing water levels can have a more direct effect on competition between *Sphagnum* and vascular plants. Low water levels will reduce capillary rise of water to the apical parts (i.e. capitula) of the *Sphagnum* individuals and thus reduce their growth rate because due to reduced capitulum moisture content (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 *Sphagnum*, vascular plant can control their water loss by closing their stomata. Therefore, during periods of low water tables and concomitant low water availability at the surface, reduction of the productivity of mosses may be stronger than that of vascular plants (Malmer et al. 1994).

The objective of this study was to delineate the effects of different water levels, and the fluctuations therein, on the vegetation of intact bog mesocosms. We examined these effects on the *Sphagnum* vegetation as well as on the vascular plants present in these mesocosms. We hypothesised that with increased occurrence of low water tables, hollow *Sphagnum* species lose competitive strength to lawn species. Furthermore, we expect that dwarf shrubs (ericoids) increase in cover and that vascular plants, in general, expand at the cost of *Sphagnum* mosses.

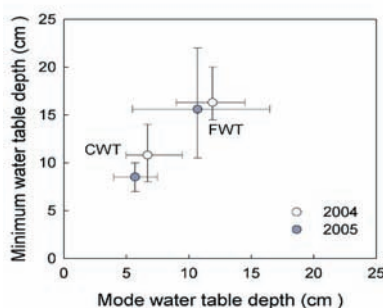
## METHODS

### *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 similar water tables. Vascular plant cover (approximately 25%) was comparable. Mesocosms were chosen in such a way that the *Sphagnum* layer consisted of *S. cuspidatum* Ehrh. Ex Hoffm. and *S. magellanicum* Brid. in more or less equal amounts. Besides these dominant species, mesocosms consisted of a sparse cover of *S. tenellum* (Brid.) Pers. Ex Brid., *S. balticum* (Russow) Russow ex C. Jens. and *S. rubellum* Wils. The most abundant vascular plant species were *A. polifolia*, *C. vulgaris*, *Drosera rotundifolia* L., *Erica tetralix* L., *E. vaginatum*, *Vaccinium oxycoccus* L. and *R. alba*. The mesocosms were put into large PVC containers of similar size, which were perforated at the bottom. Next, the containers were transported to the Netherlands. In Wageningen, the containers were suspended into larger containers (diameter: 80 cm; depth 60 cm), containing an artificial rainwater solution (Garrels and Christ 1965), by hanging them from a lid. This lid covered the water surface between the large and small container, preventing evaporative water loss via the open water surface. All containers were sunk into the soil, in order to prevent large temperature oscillations. All large containers were equipped with an overflow at

5 centimetres below the moss surface, to prevent the water table in the small container to become higher than this level for prolonged periods.

We applied two different water level treatments in this experiment, which differed in water table depth from May to September: one with modal water levels between -5 and -7 cm below moss surface (constant) and one with modal water levels between -8 and -14 cm (fluctuating). The range of water levels was larger in the fluctuating class than in the constant class (Fig. 7.1). Initially, the containers were randomly assigned three different water regimen treatments, which were replicated five times. The treatments were chosen in such a way that they represented three different water level fluctuations: constant around -5 cm, -5 to -15 cm, and -5 to -30 cm. If water tables were about to drop below the appointed maximum water table depth, we raised the water table by adding artificial rainwater into the large container. Since both years of the experiment were relatively wet (Table 7.1), maximum water table depths of -30 cm have not been reached. Furthermore, the water body in the large containers acted as a buffer, which prevented fast fluctuations. Consequently, we decided to categorise the mesocosms into two classes, constant and fluctuating.



**Figure 7.1** Relation between the minimum water level and the modal water level of the constant water level (CWT,  $n = 6$ ) treatment and the fluctuating water level (FWT,  $n = 9$ ) treatment. Data represents water table from May to September.

Error bars indicate minimum and maximum value

**Table 7.1** Weather conditions in Halmstad, Sweden and Wageningen (NL); averages of the 1971-2000 period. The right three columns represent seasonal temperature averages and cumulative precipitation over the experimental period. Autumn = Sep-Nov, Winter = Dec-Feb, Spring = Mar-May, Summer = Jun-Aug.

		Sweden	NL	2003	2003-2004	2004-2005
Temperature (°C)	Autumn	8,2	10,1		10,0	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
Precipitation (mm)	Autumn	358	202		137	202
	Winter	331	177		317	229
	Spring	210	159		128	202
	Summer	302	192	120	248	287

### *Vascular plants*

Vascular plant species composition and their abundance 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 at the start of the experiment in July 2003 and thereafter in October 2003, February 2004, June 2004, July 2004, October 2004, July 2005 and September 2005. Early September 2005, we measured light intensity in each plot at 10 points at the moss surface and above the vegetation with a Skye quantum sensor.

The total above ground vegetation within the point-quadrat frame was harvested in September 2005, one week 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.

### *Sphagnum*

*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). Four of these rods were installed into each mesocosm. 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, defined as the centimetre directly under the capitulum section (Dorrepaal et al. 2003). Subsequently both sections were sorted into *Sphagnum* species, after which dry weight was determined after oven drying for 48 hours at 70°C. For every species, subcapitulum bulk density was expressed as dry weight (g) cm<sup>-3</sup>. Biomass production was calculated by multiplying subcapitulum bulk density with height increment.

Changes in *Sphagnum* cover were measured with the point-quadrat method. The ground cover of most mesocosms consisted completely of *Sphagnum* mosses, so the relative cover per species could be calculated as number of hits per species divided by 150.

### *Nitrogen concentration*

To test whether the water table treatments resulted in differences in distribution of nutrients among the plant species groups, we analysed the nitrogen concentration in *Sphagnum*, ericoids, graminoids and peat. After removal of all aboveground vascular plant parts, a column with a diameter of 10.5 cm and a depth of 30 cm was cut from each mesocosm. These columns were frozen at -20°C, after which they were cut into six slices of 5 cm. The top slice of each column was separated into *Sphagnum* and vascular plant parts. The deeper slices were separated into peat and vascular plant parts. The latter were further sorted into buds of *R. alba*, living stem parts of *E. vaginatum*, roots of ericoid species and roots of graminoid species. All above and below ground vascular plant parts were then pooled in two groups: ericoids, mainly *A. polifolia*, *C. vulgaris*, *E. tetralix* and *O. palustris*, and graminoids, *E. vaginatum* and *R. alba*. This resulted in four fractions per mesocosm: *Sphagnum*, peat, ericoids and graminoids. All fractions were dry milled and analysed for total N concentration with an ICP-mass spectrometer.

### Data analyses

Because water levels were not constant during the experiment and not all mesocosms responded similarly in the two treatments, there was some variation in the water level mean, mode and maximum depth in both treatments. To test which water level variable described best the relation with *Sphagnum* production, we performed a stepwise regression analysis. Water level mode turned out to be the significant variable for *S. cuspidatum* in both years and for *S. magellanicum* over the total period. Maximum depth was the most significant variable for *S. tenellum* and also improved the predicting model for *S. magellanicum* and *S. cuspidatum*. The relation between *Sphagnum* production and water level mode was analysed with a separate regression analysis per species for each year and for the total period. For each species, we used the average production per mesocosm over the 2004 and 2005 growing seasons (May 4<sup>th</sup> through September 15<sup>th</sup>).

To investigate the effect of fluctuating water level on total *Sphagnum* production per mesocosm and changes in *Sphagnum* and vascular plant cover, we used repeated measures (RM-) ANOVA (univariate test) with year as within-subject factor and water level treatment as the between-subject factor. Because the assumption of a spherical variance-covariance matrix could not be met for *S. tenellum* and for most vascular plant species, we used the Huynh-Feldt test for all species.

The effect of water level treatment on vascular plant cover was analysed with a one-way ANOVA for every species. Data were tested for normality and for homogeneity of variances with Levene's test of equality of error variances. To examine the development of the aboveground vascular plant biomass during the experiment, regressions between the final point-quadrat data and the above ground vascular plant biomass at the final harvest for each species were used (Heijmans et al. 2001). These regressions were highly significant ( $P < 0.05$ ;  $0.35 \leq R^2 \leq 0.93$ ;  $9 \leq n \leq 15$ ), except for *D. rotundifolia* ( $P = 0.09$ ,  $R^2 = 0.21$ ,  $n = 13$ ). Species were treated separately because the biomass per hit differed strongly among species. The relation between *Sphagnum* production and vascular plant cover was analysed with a separate regression analysis for each year. The effect of water level treatment on nitrogen concentration and total amount of nitrogen was analysed per fraction, with a one-way ANOVA.

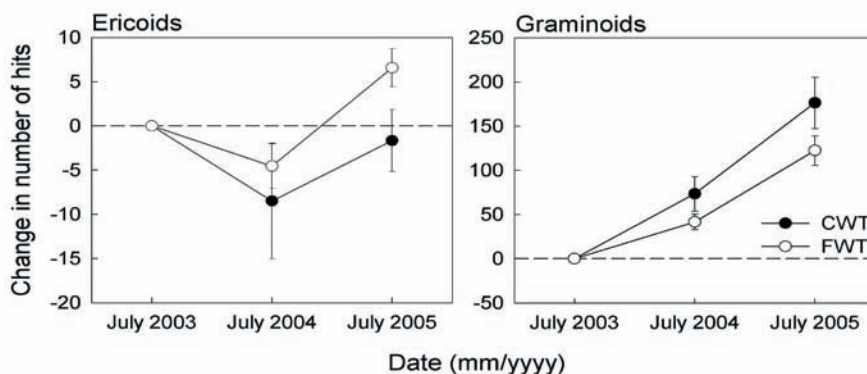
## RESULTS

### Vascular plants

There was no effect of water level treatment on total aboveground vascular plant biomass at the end of the experiment ( $F = 0.2$ ,  $P = 0.66$ ). Mean aboveground biomass ( $221 \pm 16 \text{ g m}^{-2}$ ) corresponded to a light interception of  $37 \pm 3 \%$ . The fluctuating water table treatment positively affected the cover of Ericoid species ( $F = 4.5$ ,  $P = 0.05$ , Table 7.2, Fig. 7.2). All ericoid species except *E. tetralix* contributed to this positive effect of fluctuating water table. The opposite was true for *R. alba* ( $F = 5.4$ ,  $P = 0.04$ ); this graminoid species steadily increased in both treatments, but significantly more in the constant water level treatment.

**Table 7.2** Change vascular plant abundance (based on the number of hits) between July 2003 and July 2005 and effect of two water level treatments thereon; CWT: modal water table between -5 and -7 cm (n=6) and FWT: modal water table between -8 and -14 cm (n=9).

	Water table	Mean $\pm$ SEM	P
Ericoids	CWT	-1.67 $\pm$ 3.50	<b>0.053</b>
	FWT	6.56 $\pm$ 2.15	
<i>A. polifolia</i>	CWT	0.00 $\pm$ 2.21	0.385
	FWT	2.78 $\pm$ 2.05	
<i>C. vulgaris</i>	CWT	-3.17 $\pm$ 3.17	0.165
	FWT	1.00 $\pm$ 1.01	
<i>E. tetralix</i> total	CWT	1.83 $\pm$ 1.22	0.519
	FWT	0.78 $\pm$ 1.01	
<i>O. palustris</i> total	CWT	-0.33 $\pm$ 1.15	0.290
	FWT	2.00 $\pm$ 1.54	
Graminoids	CWT	176.33 $\pm$ 29.01	0.106
	FWT	122.33 $\pm$ 16.69	
<i>E. vaginatum</i>	CWT	-1.00 $\pm$ 8.68	0.573
	FWT	9.33 $\pm$ 0.57	
<i>R. alba</i>	CWT	177.33 $\pm$ 24.20	<b>0.036</b>
	FWT	113.00 $\pm$ 15.82	
<i>D. rotundifolia</i>	CWT	14.33 $\pm$ 5.16	0.926
	FWT	15.00 $\pm$ 4.62	



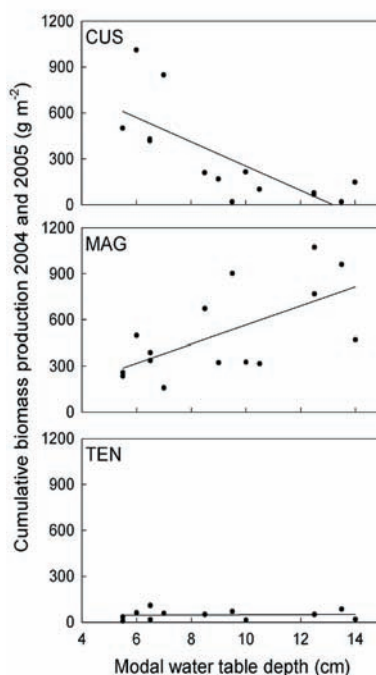
**Figure 7.2** Change in abundance (means  $\pm$  SEM) of Ericoid and Graminoid plants during the experiment at two water table treatments: constant (CWT, n = 6) and fluctuating (FWT, n = 9).

**Table 7.3** F- and P-values (regression analysis) for the effect of the modal water table on the production of *Sphagnum cuspidatum*, *S. tenellum* and *S. magellanicum* in 2004, 2005 and over the total period.

	<i>S. cuspidatum</i>			<i>S. magellanicum</i>			<i>S. tenellum</i>		
	R <sup>2</sup>	F	P	R <sup>2</sup>	F	P	R <sup>2</sup>	F	P
2004	0.55	14.65	<b>0.00</b>	0.18	2.81	0.12	0.02	0.22	0.65
2005	0.42	8.81	<b>0.01</b>	0.11	1.53	0.24	0.03	0.24	0.60
Cumulative	0.54	14.34	<b>0.00</b>	0.26	4.67	<b>0.05</b>	0.00	0.03	0.87

## Sphagnum

Biomass production differed between the three *Sphagnum* species ( $F = 37.3$ ,  $P \leq 0.01$ ), and modal water level differently affected the individual species (interaction effect:  $F = 6.7$ ,  $P \leq 0.01$ ). Biomass production of the hollow species *S. cuspidatum* decreased with increasing modal water level in both growing seasons, while the lawn species *S. magellanicum* increased with increasing modal water level over the whole period (Fig. 7.3, Table 7.3). *S. tenellum* did not show a response to modal water level or lowest water level (data not shown). Total *Sphagnum* production was much higher in 2005 ( $456 \pm 65 \text{ g m}^{-2}$ ) than in 2004 ( $177 \pm 42 \text{ g m}^{-2}$ ) ( $F = 13.6$ ,  $P \leq 0.01$ ). There was no effect of water level treatment ( $F = 0.8$ ,  $P = 0.38$ ) and no interaction between water level treatment and year ( $F = 0.0$ ,  $P = 0.98$ ).



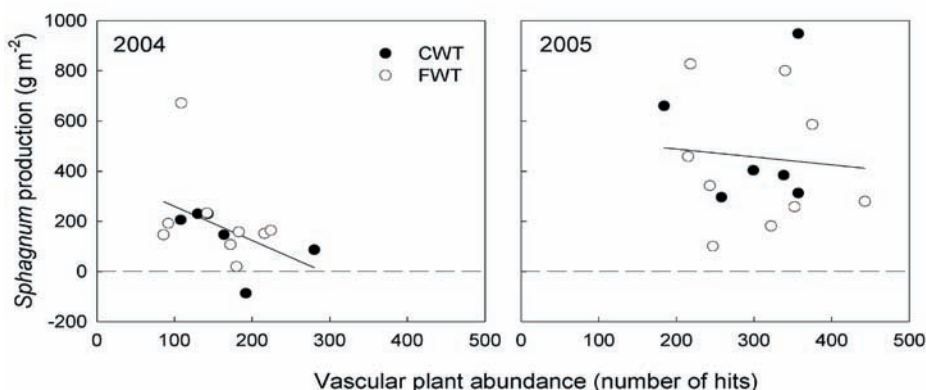
**Figure 7.3** Relation between *Sphagnum* biomass production in the growing season (May to September) and the modal water table over 2004 and 2005. CUS = *Sphagnum cuspidatum*; MAG = *S. magellanicum* and TEN = *S. tenellum*. For statistics see Table 7.3.

**Table 7.4** F- and P-values (RM-ANOVA) for the effect of the water table treatments (constant (n=6) and fluctuating (n=9)) and year on the cover of *Sphagnum cuspidatum*, *S. tenellum* and *S. magellanicum*.

	Water table (WT)			Year			Direction change	WT * Year		
	df	F	P	df	F	P		df	F	P
<i>S. cuspidatum</i>	1	0.04	0.85	2.00	11.88	<b>0.00</b>	-	2.00	1.30	0.29
<i>S. magellanicum</i>	1	0.28	0.61	1.76	10.41	<b>0.00</b>	+	1.76	1.57	0.23
<i>S. tenellum</i>	1	1.55	0.24	1.63	1.18	0.32		1.63	3.34	0.06



Total *Sphagnum* cover did not change during the experiment. However, there was a shift in species cover since *S. cuspidatum* decreased in cover (from 31% to 22%) while *S. magellanicum* increased in cover (from 62% to 71%) (Table 7.4). There was no effect of water level on the cover of the different *Sphagnum* species. 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 abundance had increased even further (Fig. 7.4)



**Figure 7.4** Relation between *Sphagnum* production per monolith ( $\text{g m}^{-2}$ ) and vascular plant cover (number of hits) per water level treatment in A) 2004 and B) 2005. CWT: constant water table ( $n=6$ ), FWT: fluctuating water table ( $n=9$ ). Linear regression: 2004.  $R^2 = 0.204$ ,  $P = 0.091$ ; 2005,  $R^2 = 0.008$ ,  $P = 0.751$ .

#### Nitrogen concentration

For none of the species groups, N concentrations differed between the water level treatments (data not shown). Only [N] in *Sphagnum* tended to be lower with the fluctuating water level than with the constant water level treatment ( $F = 4.3$ ,  $P = 0.059$ ).

## DISCUSSION

The objective of this study was to delineate the effects of differences in water table, and fluctuations therein, on ombrotrophic bog vegetation. We found that *Sphagnum* species responded differently to lower water level. These differences correspond with differences in habitat preference (Andrus et al. 1983; Wallén et al. 1988). Moreover, we found that Ericoids increased with fluctuating water tables. This confirms our hypotheses that increased occurrence of low water tables can cause an expansion of the Ericoid cover in bogs. Other studies show that a correlation exists between Ericoid biomass and water table depth (Weltzin et al. 2003; Strack et al. 2006), but to our knowledge this is the first experiment that shows that also fluctuating water levels can increase the abundance of vascular plants. Interestingly, vascular plant species which are typical for hollow vegetations, like *R. alba*, increased in cover at the fluctuating water treatment (Table 7.2) during the course of the

experiment. The increase in *R. alba*, however, was larger with constant than with fluctuating water level. On the transition between hollows and hummocks we therefore expect to see a shift from Graminoid to Ericoid dominated vegetation when lower water tables occur more often.

The cause for the large increase in cover of *R. alba* in both water level treatments might be found in differences between the Swedish site of origin of the material and the site in the Netherlands where the experiment was conducted. Especially the higher atmospheric nitrogen deposition (South Sweden:  $1 \text{ g N m}^{-2} \text{ yr}^{-1}$ , the Netherlands:  $4 \text{ g N m}^{-2} \text{ yr}^{-1}$  (Tarrasón et al. 2006) and the longer growing season may have enhanced vascular plant growth. Fertilization experiments have shown that when nitrogen deposition increases, the *Sphagnum* layer becomes increasingly enriched with nitrogen and once this layer becomes saturated, the deposited nitrogen becomes progressively available for vascular plants (Limpens et al. 2003b). *R. alba* could have profited from the increased nitrogen in the upper layers of the peat, because of its superficial root system. In earlier greenhouse experiments, *R. alba* also increased strongly in cover (Heijmans et al. 2002c; Limpens et al. 2003b). Nevertheless, it does not seem likely that the increase in nitrogen deposition can explain the observed increase in vascular plants, since nitrogen concentrations in *Sphagnum* were relatively low ( $8.4 \text{ mg g}^{-1} \pm 0.5$ ). The increase in the length of the growing season seems an alternative and more likely explanation for the expansion of *R. alba* during the experiment. Alternatively, the relatively warm and dry summer of 2003 may have had a negative effect on the abundance of *R. alba*. In 2004 and 2005, the amount of precipitation was much higher and *R. alba* may have recovered again. A similar effect was found for *Sphagnum* abundance in bogs in south-western Sweden by Gunnarsson and Flodin (2007). On account of the above, it seems that the increased cover of ericoid species over time was mainly a direct result of lowered water table, but the increased cover of graminoids seems to be a result of prolonged growing season and relatively high amounts of precipitation, while especially *R. alba* profited from the constant high water level.

As hypothesised, *S. cuspidatum* production and cover decreased with decreased water level, while *S. magellanicum* responded oppositely (Fig. 7.3; Table 7.3 and 7.4). The effect of the fluctuating water level treatment on the production and cover of *Sphagnum* seems to be mainly affected by differences in modal water level, indicating that short periods of low water levels can have the same effect on *Sphagnum* growth as permanent lower water levels. The increased production and cover of *S. magellanicum* at fluctuating water level may explain the slightly lower nitrogen concentration in the *Sphagnum* layer in this treatment, since the *Sphagnum* cover in the mesocosms to a large extent consisted of *S. magellanicum*. Nitrogen concentration in the *Sphagnum* layer could have been diluted as a result of increased production of *S. magellanicum* with decreasing water level. Additionally, these interspecific differences in response of production to water level can explain why the total *Sphagnum* production and cover did not change during the experiment and were not affected by water level treatment. These results contradict earlier findings where total bryophyte production was higher in low microtopographical zones (i.e. close to the water table) compared to production in medium and high microtopographical zones (Weltzin et al. 2001; Gunnarsson 2005). In our experiment, water table fluctuated during the growing season in one treatment, which complicates interpretation of the effect of water table depth. Apparently,

the periods of high water level in the fluctuating water level treatment made a higher production possible than would be expected based on mode water level values. Furthermore, our experiment was performed during two relatively wet years, which may explain the relatively high production of *Sphagnum*, especially in the second year with its wet spring and summer. In a greenhouse experiment, we found that competition between *S. magellanicum* and *S. cuspidatum* was not affected by increased temperature with high water tables (Breeuwer et al, unpublished), but that *S. balticum* was ousted by *S. magellanicum* with increased temperature. Our results suggest that predicted climate change resulting in occasional dry periods together with increased temperature (Houghton et al. 2001) in northern peatlands, would lead to an expansion of lawn species at the expense of hollow species.

The expected negative relation between vascular plant cover and *Sphagnum* production was observed in the first growing season, but was absent in the second growing season (Fig. 7.4). This is remarkable since the cover of vascular plants increased with time, from which we expected that the negative effect of vascular plant cover would become stronger during the experiment. The negative effect of higher vascular plant shading in the second year may have been counteracted by the positive effect of higher precipitation and subsequent higher water availability for *Sphagnum* during this year (Table 7.1). Furthermore, the cover of vascular plants was possibly too low to affect *Sphagnum* growth. Heijmans et al. (2002a) suggest that cover of vascular plants has to be at least 60% to have a negative effect on *Sphagnum* production. The value of 221 g m<sup>-2</sup> for total above ground vascular biomass, in our experiment, is not high (Chapin et al. 1995; Press et al. 1998; Heijmans et al. 2002a; Bubier et al. 2003) and light intensity measurements at the moss surface shows that on average only 37 % of the light was intercepted by the vascular plant cover.

How the vegetation changes observed would affect carbon sequestration remains unclear. There are large differences in production between *Sphagnum* species (Gerdol 1995; Gunnarsson 2005), and different species also respond differently to water level (Fenton and Bergeron 2006; Robroek et al. 2007a; Robroek et al. 2007b). In general, hollow species have greater productivity than lawn and hummock species (Strack 2006, Gunnarsson 2005) and all species show lower productivity with decreased water levels. Therefore, a shift in dominant species on bogs as a result of increased water level fluctuations can be expected to affect the total production of *Sphagnum* in bogs. As vascular plant cover will also increase with lowered water table, this can have a negative effect on *Sphagnum* production. Furthermore, also decomposition rates differ between *Sphagnum* species and between *Sphagnum* and vascular plants; rates are generally higher for hollow species than for lawn and hummock species (Johnson and Damman 1993; Belyea 1996) and decomposition rates of vascular plants are higher than for *Sphagnum* (Hobbie 1996; Dorrepaal et al. 2005). Additionally, when water tables decrease or fluctuations increase, this will probably have a positive effect on decomposition rates of all species because of increased aerobic conditions (Belyea 1996). In addition, the percentage of more easily decomposable vascular plant material also increases with lowering of the water table, so the net effect of water level fluctuations on carbon sequestration in peat is still unclear. Belyea (2001) and Strack (2006) already showed a unimodal relationship between the rate of peat formation and water table depth with maximum

rates at intermediate water table depths. Therefore it is very important to take the proportions of different microhabitats in a bog into account, when trying to predict the net effect of water table fluctuations on carbon sequestration in a bog. Predictions on how climate change affects the total carbon accumulation in bogs, becomes even more complicated when we also take into account the expected increase in temperature, especially because increased temperature is expected to affect decomposition more than production.

Summarised, 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 lawn, the species assemblage will shift from vegetation dominated by hollow *Sphagnum* and graminoids, to a vegetation dominated by lawn *Sphagnum* and Ericoids. How these changes will influence carbon sequestration and hydrological characteristics of bogs are important questions for future research.

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# 8

## SYNTHESIS: PERSPECTIVES FOR CLIMATE CHANGE AND PEATLAND MANAGEMENT

Bjorn JM Robroek



## WHAT ARE THE EFFECTS OF A CHANGING ENVIRONMENT ON THE SPECIES COMPOSITION IN RAISED BOGS?

Peatlands, including raised bogs, play an essential role in the sequestering of atmospheric carbon. About 3% of the earth's land surface is covered with peatlands, but about 20% - 30% of the world's soil carbon is stored in them (Clymo et al. 1998; Rydin and Jeglum 2006). Most of that carbon is stored in peat deposits which to a large extent are composed of dead *Sphagnum* remains. The amount of carbon that becomes sequestered strongly depends on the difference between biomass production and decomposition in the *Sphagnum* vegetation. *Sphagnum* species, to a large extent, differ in their biomass production and decomposability (Clymo and Hayward 1982; Lindholm and Vasander 1990; Rochefort et al. 1990; Gunnarsson 2005; Bragazza et al. 2006). As a result, the species composition of the *Sphagnum* vegetation is an important determinant of the carbon uptake rate by raised bogs. Changes in the composition of the *Sphagnum* vegetation may feed back to the global climate (Gorham 1991), and, therefore, it is important to understand which processes in the ecology of raised bogs and in the global climate may alter the *Sphagnum* species composition in these ecosystems.

Projections made by the International Panel on Climate Change, IPCC, suggest worldwide increases in temperature, but these increases are proposed to be largest in the northern hemisphere (Meehl et al. 2007), where most peatlands are situated. Increased temperatures may lead to increased evaporation in raised bogs, which can result in decreased bog water tables (Gunnarsson et al. 2004). Furthermore, precipitation patterns are expected to change, with more precipitation during the winter season and long dry periods in summer.

Since *Sphagnum* species differ in their physiological and morphological properties, changes in environmental conditions at the bog's surface differently affect species. Changes in the climate therefore are believed to impact upon the species composition of the *Sphagnum* vegetation in raised bogs (Moore 2002; Dorrepaal et al. 2003). Several environmental factors may affect the relative performance of *Sphagnum* species:

- 1) Increased temperature may influence the growth of *Sphagnum* mosses. The effects of temperature can either be direct by impacting upon the physiology or indirect by affecting evaporation and as a result the water table, or by increasing the length of the growing season.
- 2) Changes in the water table depth in the raised bog, induced by increased temperature and changed precipitation rates, may impact upon the water content of *Sphagnum* species. Not all mosses have the same ability to transport water from the water table toward their apical parts (i.e. their capitula). Decreased summer water tables, therefore, can alter the performance of species differently.
- 3) Apart from changes in precipitation rates, changes in precipitation patterns may affect the performance of *Sphagnum* mosses. Species which do not possess an efficient capillary transport system may be most affected by changes in precipitation patterns. Additionally, prolonged periods of drought (especially during the summer season) may impact upon species differently.

Divergent responses of *Sphagnum* species to changes in these factors may change the competitive balance between these species, and – as stated above – this may affect the ecosystem functions. This chapter discusses the results found in the different experiments and will elaborate on the implications of these results for the ecosystem functions with climate change. Additionally, the chapter emphasizes on the usefulness and implications of these results for raised bog management.

#### THE EFFECTS OF TEMPERATURE ON *SPHAGNUM* PERFORMANCE

Our results unambiguously show that temperature has a divergent effect on the performance of four *Sphagnum* mosses. Height increment and biomass production of *Sphagnum magellanicum* and *S. rubellum*, two species which naturally have a distribution which extends further southward compared to the other two mosses, *S. fuscum* and *S. austinii* (= *S. imbricatum*), was positively affected by increased temperature (chapter 2). The latter two species remained unaffected by an increase in temperature. Although our results are very clear, in literature the response of *Sphagnum* to temperature seems not so straightforward and may strongly depend on the conditions under which the experiments have been conducted (Sonesson et al. 2002). Some studies report on the absence of an effect by temperature or show that raised temperature can have a negative effect (Gerdol 1995; Gerdol et al. 1998; Weltzin et al. 2001; Sonesson et al. 2002; Gunnarsson et al. 2004), whereas other studies show a positive effect on moss growth and production (Sonesson et al. 2002; Dorrepaal et al. 2003; Dorrepaal et al. 2006). *Sphagnum* species, however, were not always similar to those used in our experiment, indicating an effect of species. Additionally, most of these studies were performed under field circumstances. Temperature rise under field conditions generally goes hand in hand with a decrease in the water table, from which it could be concluded that the effect of temperature as found in those studies may be an indirect effect of a decrease in the water table. Our results indicate that temperature can have a direct effect on the biomass production and hence on the carbon sequestration of *Sphagnum* mosses (chapter 2, Fig. 2.1). The response to increased temperature, however, differs among species, from which it may be concluded that temperature will have a direct effect on the competition between *Sphagnum* species. Prospected rise in the global temperature may result in changes in abundances of *Sphagnum* species within a distinct bog. Additionally, the area of distribution of species may shift. How *Sphagnum* competition is influenced by increasing temperature, direct or indirect by its effect on the hydrology, however, remains uncertain. It seems plausible that temperature impacts on the physiology of these mosses, but temperature also affects the evapotranspiration of the raised bog vegetation which impinges on the raised bog water table (Gunnarsson et al. 2004) and concomitantly on the capitulum water content (Table 2.4). This capitulum water content is shown to be very important for the carbon uptake (and thus for the biomass production) of the *Sphagnum* vegetation, because almost all carbon uptake takes place in this layer (chapter 4).

## THE EFFECTS OF WATER TABLE AND PRECIPITATION

The availability of water for *Sphagnum* mosses strongly depends upon the water table depth and distribution of precipitation (Overbeck and Happach 1957; Buttler et al. 1998). It has been assumed that the water table in raised bogs is the most important determining abiotic factor controlling the distribution of *Sphagnum* species along the raised bog's microtopographical gradient (Clymo and Hayward 1982; Andrus et al. 1983; Andrus 1986). As a result different species occupy different zones along the raised bogs water table. The upper limit along the water table gradient that a *Sphagnum* species can occupy may be related to the ability to keep its capitula wet (Rydin 1993b). As it is known that there are interspecific differences between *Sphagnum* species in their capacity to transport water to their apical parts (i.e. capitula) by capillary water transport and in their capacity to hold water and concomitantly to withstand periods of drought (e.g. Clymo 1983; Rydin and McDonald 1985a), understanding the effects of water availability on the performance of, and the competition between, *Sphagnum* mosses is necessary. The performance of *Sphagnum* mosses and the competition between species can be related to several mechanisms which may be identified as important determinants:

- a. Differences in the ability for capillary water transport: compared to a low *Sphagnum* bulk density, a large bulk density is assumed to increase the ability for capillary water rise, and thus to an increased ability to maintain an optimal capitulum moisture content
- b. Differences in water holding capacity: an increase in bulk density also leads to an increase in the water holding capacity, and thus to cope with periodic drought. Additionally, morphological differences between species in for example the size and storing capacity of the hyaline cells results in interspecific variability in water holding capacity.
- c. Differences in performance at similar water contents: species differ in their water use efficiency, which results to interspecific differences in the response of photosynthesis to water content.

The following section will focus on these mechanisms by synthesising the results which are presented in the different chapters of this thesis.

### *The role of the water table*

*Sphagnum* mosses differ in their bulk density, which is assumed to have an impact on their capability to transport water from the phreatic water table towards the capitula (Hayward and Clymo 1982; Rydin 1985). Our results from chapter 2 (Fig. 2.1) and 3 (Table 3.3) are in accordance with the results from earlier studies where it was shown that hummock species grow in denser matrices (Clymo and Hayward 1982; Titus and Wagner 1984). A higher bulk density is often associated with an efficient capillary water transport system (Clymo and Hayward 1982; Grosvernier et al. 1997; Asada et al. 2003). However, despite interspecific differences in bulk density, we did not find interspecific differences in capitulum water content at a specific water table (Fig. 2.2), from which we conclude that bulk density may not be that good a determinant for capitulum water content.



We hypothesize that patch size and anisotropy of the peat material are better determinant for the capitulum water content. In chapter 6, we found indications that increased patch size is important for *Sphagnum* in maintaining a moisture content that is different from their surrounding *Sphagnum* community. This may be important for species in order to create a habitat that is advantageous to their competitive strength, but the exact mechanisms deserve more attention. We did find, however, that lower water tables resulted in lower capitulum water content, and these reduced water contents hampered those species which naturally occur closest to the water table most (chapter 2). From these results we concluded that changes in the water table will alter the species composition of the *Sphagnum* vegetation. As earlier studies report that hollow and lawn species, at their natural habitats, have a higher productivity than hummock species (for a review, see Gunnarsson 2005), it would be expected that at high water tables hollow species would oust hummock species when they grow together. Yet, when we grew species in mixed cultures, those species that naturally occur furthest from the water table seemed to have more competitive strength, irrespective of the water table (Fig. 3.2). Interestingly, both species in a mix had similar capitulum water contents; again despite of differences in bulk density (Fig 3.3 and Table 3.3). Despite if this convergence in capitulum water content, height increment between competing species differed, from which it may be concluded that capitulum water content itself cannot straightforwardly explain interspecific competition. The competitive outcome between species is more complex and may be determined by interspecific differences in the ability to photosynthesize at distinct moisture contents. Since we only applied precipitation once every two weeks an alternative mechanisms can also explain our results. After application of rain water, the two mosses in the mixture started to lose water at different rates, due to difference in water holding capacity. After two weeks (i.e. when measured), capitulum water contents may have been similar but the integrated moisture content of one of the species (the species that naturally occurs furthest from the water table) may have been higher, resulting in a longer period in which it was able to grow.

These two possible mechanisms could be elucidated by steadily drying three different *Sphagnum* mosses (chapter 4). The latter explanation seemed very plausible, because the period in which CO<sub>2</sub> assimilation was positive was shorter for *S. cuspidatum* than for *S. magellanicum* and *S. rubellum* when grown at low water table and prolonged drought. Yet, the first explanation also may be valid, since parallel to other studies (Titus et al. 1983; Silvola and Aaltonen 1984; Rydin and McDonald 1985b; Silvola 1991), we found interspecific differences in the CO<sub>2</sub> assimilation at similar capitulum water contents. Yet, at the water contents of the mosses in the competition experiment (chapter 3), *S. cuspidatum* had higher assimilation rates than *S. magellanicum*. From this it may be concluded that the higher complete performance of species that naturally occur higher along the water table gradient is due to a combination of factors: its higher water holding capacity and its potentially higher carbon uptake rate at low water content, but further experiments are needed to fully understand these mechanisms.

### *The role of precipitation*

The experiments described in chapter 2 and 3 were performed under prolonged periods without precipitation, as they were primarily aimed at understanding the role of the water table. Yet, apart from the depth of the water table, which may be indirectly influenced by precipitation, the intensity and temporal pattern of precipitation also affect the performance of *Sphagnum* mosses (Gunnarsson and Flodin 2007), presumably because they directly affect the *Sphagnum* capitulum water content. Our results show that precipitation indeed plays an important role in the performance of *Sphagnum* mosses. However, precipitation only seemed to be important when water tables were low, especially for the hollow species *S. cuspidatum* (Fig. 4.1 and 4.2).

Sometimes individuals or small patches of hollow species are observed in hummock vegetation (Rydin 1985; Rydin et al. 1999). It has been suggested that these small patches are able to grow outside their natural habitat by commensalism of water from their surrounding environment. It also has been suggested that expansion of these patches is impossible because their inefficient capillary and water holding systems impair their water supply (Rydin 1985; Andrus 1986). These small patches, however, may - in a certain raised bog - be very important refuges for species for which to date environmental conditions are sub-optimal. Contrary to these earlier suggestions we found that apart from commensalism of water, precipitation is a very important factor for hollow species to grow in habitats which are higher above the water table than their natural habitat (chapter 5). Transport of water from the hummock vegetation towards these hollow species, is indeed an important source of water, yet we show that precipitation is instrumental for this lateral transport of water. This mechanism is especially important in hummocks which are high above the water table. Changes in precipitation patterns may affect the persistence of these small patches. Additionally, CO<sub>2</sub> uptake of hollow species is strongly hampered at low water table without precipitation (chapter 4), from which it can be deduced that prolonged dry periods in summer may be detrimental for these hollow species. Thereby not only *Sphagnum* diversity will be lost, but also a substantial part of ecosystem resilience. It therefore is important to monitor the effects of climatic conditions on the *Sphagnum* vegetation.

Above results indicate a major role for precipitation on the performance of *Sphagnum* species. From our results it is not possible to draw firm conclusions about the role of precipitation on competition between *Sphagnum* mosses. Peatland scientists should execute more research on that role, especially since to date precipitation patterns are very odd. For example, in a lot of European countries, April 2007 was extremely dry and warm. In the Netherlands, some places did not receive any rain during the whole month, and the Dutch average sum was 0.1 mm against a normal sum of 44 mm. May and June, on the other hand, have been relatively wet with 132 mm rain against an normal sum of 62 in May, and 90 mm rain against an normal sum of 72 mm in June (Data: KNMI.nl).

## CAN WE PREDICT CHANGES IN THE VEGETATION AS A RESULT OF ENVIRONMENTAL CHANGES?

Climate projections suggest a future increase in global temperature together with changes in precipitation patterns (Sweeney and Fealy 2002; Meehl et al. 2007). However, it is not fully clear how precipitation patterns will be changing, but projections indicate more intense precipitation events, with longer dry periods in between (Meehl et al. 2007). This may indicate that the vegetation on a raised bog has to adapt to prolonged period of drought. Recently an opposite trend in the change of vegetation was observed in an ombrotrophic Southern Swedish bog, with species that are typical for a more moist habitat becoming more abundant (Gunnarsson and Flodin 2007). Apart from a possible effect of the recent blocking of the drainage systems, increased precipitation in Southern Sweden together with an extended growing season (due to a milder winter) have been proposed to be the reason for the observed vegetation change. Data from our field experiment (chapter 6), however, do not confirm that last suggestion. We found *Sphagnum* only to grow during the summer months (May-September), whereas we hardly found any growth in winter. This holds true for *S. magellanicum* in an Irish as well as in an Estonian bog (Fig. 6.2).

In the different chapters we indicate the role of the temperature, the water table and precipitation on the performance of several *Sphagnum* species and how these factors can influence the competition between *Sphagnum* species. The direct effect of temperature on the competition between *Sphagnum* species is difficult to predict from our results, although it seems that species which naturally are distributed further southward are advantageous and may increase in their area of distribution, as well as in their abundance within a specific peatland. Water table draw down, which can be an indirect effect of increased temperatures, differently affects *Sphagnum* species. All our field studies indicate that reduced water tables caused hollow species to decrease at the expense of hummock species. More importantly, a decrease in water table results in a decrease in the capitulum water content. Capitulum water content plays an important role in the competition between *Sphagnum* species because species differ in their water use efficiency, meaning the response of carbon assimilation is species specific. Additionally, regular precipitation is very important for the uptake of carbon by *Sphagnum* mosses. Changes in the patterns and intensities of precipitation may have strong effects on the vegetation. Especially when water tables are relatively low, predicted summer droughts affect hollow species most. For hollow species, like *Sphagnum cuspidatum*, to persist in hummock vegetation it is very important that their capitulum water content is high enough to be able to photosynthesize. Persistence and perhaps expansion of hollow species in higher hummocks strongly depends on the intensity and frequency of future precipitation patterns. Furthermore, high water tables appeared to promote the increase of graminoids, whereas fluctuating (i.e. periodic low water tables) promoted abundance of ericoid species.

We conclude that, even if we would be able to exactly predict the changes in environmental factors, the direction of potential changes in the composition of the *Sphagnum* vegetation strongly depends on the species that are involved. Competition between *Sphagnum* species is determined by the differences in competitive strength between species, which on its turn is influenced by the photosynthetic capacity at distinct capitulum water content. The capitulum water content

of *Sphagnum* species depends on its capillary system, its water holding capacity and on the surrounding vegetation. Our results, however, show that if the availability of water decreases, either by decreased water tables or by prolonged dry periods, hummock species will benefit at the expense of hollow species. Additionally, vascular plants like Ericoids will increase. Low covers of these vascular plants can be beneficial for *Sphagnum*, but higher covers may be detrimental (Heijmans et al. 2002). It is important that peatland scientists continue to monitor the effects of environmental changes on changes in the composition of peatlands. Especially longer term measurement may provide a lot of information, which will help us to better understand the mechanisms of competition between *Sphagnum* species.

### SPHAGNUM TRANSPLANTATION AS A MANAGEMENT TOOL FOR DUTCH BOGS

Restoration and rehabilitation of living *Sphagnum* vegetation in Dutch bog remnants hitherto stagnates after the re-establishment of *S. fallax* and *S. cuspidatum* (Money 1995). Hummock species are still largely absent or scattered in their occurrence. It has been suggested that the high nutrient status in our bogs is hampering re-establishment of a vegetation in which hummock species are also present (Limpens 2003; Tomassen et al. 2004). A study by Smolders et al. (2003), however, has proven that it is possible to re-introduce *S. magellanicum* and *S. papillosum* into an existing *S. cuspidatum* vegetation. In our transplantation experiment (chapter 6) we show that it is also possible to re-introduce hummock species into an existing vegetation of *S. magellanicum* in Estonia and Ireland. In the Netherlands, nowadays, *S. magellanicum* is observed to increase in abundance, which presumably is due to decreasing levels in Nitrogen deposition (Schouten, pers. comm.). Parallel to Rydin (1993a), all transplanted species initially decreased in cover, but after a while hummock species recovered, whereas hollow species did not. Additionally, this initial decrease was smallest, and subsequent recovery was largest when patch sizes of the transplanted species were largest. Similar effect of size were found recently by Gunnarsson and Söderström (2007). From these results it becomes clear that transplanted patches of *Sphagnum* are able to persist in already existing vegetation, but that the availability of water and the size of the transplants play an important role in the persistence and expansion. Especially this last factor was important. From results presented in chapter 3 and chapter 6 it seems that an increased volume of homogenous peat material (i.e. one species) increases the ability to create a microhydrology that could be optimal for that species.

In that same transplantation experiment, as described above, Rydin (1993a) did not find a clear relation between the average height above the mean water table and the change in area of *S. fuscum* and *S. tenellum* in a *S. balticum* carpet. We, however, found water tables to be important for the persistence and expansion of species, with low water tables being advantageous for hummock species and high water tables being slightly advantageous for hollow species. Present restoration management is aimed at retaining water on the surface in order to restore a self-regulating peat moss vegetation. This seems to contradict with the aim in restoring a vegetation that is characteristic for a natural peatland vegetation which also contains hummock forming species. It.

however, is important that before transplantation of hummock species is used as a conservation tool, a vegetation has developed under which water tables can be lowered without impairing the functioning of the vegetation. Transplantation of hummock species would be a logical next step in peatland restoration. To increase the success of these transplantations *Sphagnum* species, factors like patch size and water table, have to be taken into account.

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# COMPETITION BETWEEN *SPHAGNUM* MOSSES IN EUROPEAN RAISED BOGS THE EFFECTS OF A CHANGING CLIMATE

The importance of European peatlands as carbon sequestering ecosystems has long been recognised. It has been estimated that peatlands, including raised bogs, store about 20% of the world's soil carbon; an amount that is about three times higher than the amount of carbon which is stored in tropical rainforests. In raised bogs, peat mosses (*Sphagnum* spp.) are generally seen as ecosystem engineers, and as such they play an important role in the sequestration of carbon of these systems.

Typically, raised bogs are characterised by a pattern of microtopographical habitats, ranging from wet depressions (hollows) and relatively dry (but regularly inundated) lawns to dry hummocks with a different set of *Sphagnum* species occupying each microhabitat. Hollow species generally occupy habitats close to the water table, whereas hummock species can occupy habitats further from the water table. The tight correlation between *Sphagnum* species and their position along the hydro-topographical gradient is likely the result of a combination of morphological and physiological constraints. Several studies stress interspecific differences among *Sphagnum* mosses in the efficiency of their external capillary system and their ability to hold water: among species there seems to be a trade off between maximum growth rate, the ability to transport water to the capitula and the ability to withstand evaporative water loss. Furthermore, considerable research has been carried out into the habitat preferences of *Sphagnum* species and there is a good knowledge of hydrological and trophic regimes at which the different species usually occur. Since *Sphagnum* mosses lack stomata and roots, their water content in the active apical parts (i.e. capitula) strongly depends on the ability to transport water via an external capillary system and on the capacity to hold water which is supplied by precipitation.

Changes in the global climate are expected to occur in the next 50 – 100 years. Projections made by the International Panel on Climate Change (IPCC) expect temperatures to increase, especially at the Northern hemisphere, where most of the raised bogs can be found. Furthermore,

precipitation patterns are expected to change. How precipitation patterns are evolving is still debatable, but projections expect summers to become drier, whereas winters are expected to become wetter. Combined with increased temperatures, changes in precipitation patterns can directly influence the water table in raised bogs. Changes in the temperature, water table, and precipitation patterns may influence different *Sphagnum* species to a different degree, which can result in changes in the competitive balance between species, and ultimately on the composition of the *Sphagnum* vegetation. This thesis aims to investigate how the main *Sphagnum* species in European raised bog respond to changes in temperature, water table and precipitation, and in particular how water tables and precipitation can alter the competition between species.

The first part of this thesis describes three glasshouse experiments in which we focused on the effect of temperature (chapter 2), water table (chapters 2, 3 and 4) and precipitation (chapter 4) on the performance of several important *Sphagnum* species from European raised bogs. In the first experiment (chapter 2) we elucidated the effects of changes in water level and temperatures on the performance of monospecific stands of four *Sphagnum* mosses, *S. magellanicum*, *S. rubellum*, *S. austinii*, and *S. fuscum*. These mosses were grown at two water levels, -5 cm and -15 cm, and at two temperatures, 15°C and 20°C. The *Sphagnum* species differ in their position along the microtopographical gradient and in their geographical distribution. Height increment, subcapitulum bulk density, biomass production, capitulum water content and cumulative evaporation were measured. Our results showed that height increment and biomass production of *S. magellanicum* was lower at low water table than at high water table, whereas height increment and biomass production of *S. rubellum*, *S. austinii*, and *S. fuscum* were unaffected. Height increment of *S. magellanicum*, *S. rubellum*, and *S. austinii* was higher at high temperature than at low temperature. Biomass production of only *S. magellanicum* and *S. rubellum* was higher at high temperature than at low temperature, corresponding with their more southern distribution. Cumulative evaporation of *S. magellanicum* and *S. rubellum* was lower at low water table and could be explained by hampered water transport towards the capitula. Due to these interspecific responses, we decided to further focus on the effects of water table on the competition between peat mosses (chapter 3). In a glasshouse experiment, we investigated the effect of different water tables on the competition between six *Sphagnum* species, *S. cuspidatum*, *S. magellanicum*, *S. papillosum*, *S. rubellum*, *S. fuscum* and *S. austinii*. Parallel to the previous experiment, the amount of precipitation (234 mm yr<sup>-1</sup>) and the precipitation frequency (every two weeks) was kept low to encourage water table effects. Relevant species combinations and monocultures were grown at different water tables for a 16-month period. We studied changes in cover, height increment and capitulum water content to understand competitive responses. Our result unambiguously showed that species which naturally occur further above the water table (hummock species) generally had higher competitive strength than species which naturally occur closer to the water table (hollow species). Surprisingly, this effect was irrespective of the water table, indicating a minor role for capillary water transport. Cover change seemed to be related to differences in length growth, but not to water table or capitulum water content (WC<sub>cap</sub>). WC<sub>cap</sub> of species within a mixture did not differ, but was lower than the WC<sub>cap</sub> of the individual species growing in monoculture, indicating differences in the ability to supply water to the capitula between mono- and mixed cultures. Subcapitulum bulk density between mono- and mixed cultures did not differ, or were even lower in monocultures, but did differ between species within mixed cultures. Our results indicate that structural heterogeneity of the peat in mixed cultures has a negative effect on the capitulum water content of both species. Furthermore, we show that sustained periods of drought causes species that naturally occur further above the water table to oust species that naturally occur closer to the water table, even if the water table remains high.

That hollow species were ousted while they had similar water contents, be explained by interspecific differences in the response to capitulum water content, but consensus about that could not be found in the literature. Alternatively, although capitulum water contents after two weeks may have been similar, interspecific differences in the water holding capacity may have caused drying curves between species to be different. Consequently, that may have led to interspecific differences in the length of the period in which the water content is optimal for photosynthesis. Our third experiment (chapter 4) was designed to elucidate on the mechanisms that lead to the results as shown in previous chapters. We set out an experiment to assess the interactive effects of water table (low and high) and the presence or absence of precipitation on the CO<sub>2</sub> assimilation and evaporation of three co-occurring peat mosses (*Sphagnum cuspidatum*, *S. magellanicum* and *S. rubellum*) which naturally have a different distribution along the microtopographical gradient along the bogs surface, over a 23 day period. Additionally, we measured which sections of the moss layer were responsible for light absorption and bulk carbon uptake. Thereafter, we investigated the recovery of CO<sub>2</sub> assimilation after prolonged drought. At high water table, CO<sub>2</sub> assimilation of all species gradually increased over time, irrespective of precipitation. At low water table, net CO<sub>2</sub> assimilation of all species declined over time, with the earliest onset and highest rate for *S. cuspidatum*. Precipitation compensated for reduced water tables and positively affected net carbon uptake of all species. Cumulative carbon uptake over the experimental period was lowest for *S. magellanicum*, but stayed positive over the longest period. In addition, CO<sub>2</sub> assimilation of *S. magellanicum* was the slowest to recover after prolonged drought. Almost all light absorption occurred in the first one or two centimeters of the *Sphagnum* vegetation and so did net CO<sub>2</sub> assimilation. CO<sub>2</sub> assimilation rate showed species-specific relationships with capitulum water content. Assimilation for *S. cuspidatum* showed a narrow optimum at relatively high capitulum water content, whereas C assimilation for *S. rubellum* had its optimum at dryer conditions. In contrast, C assimilation of *S. magellanicum* stayed constant at a relatively low rate over a broad range of capitulum water contents.

From the above chapter we concluded that global warming, summer droughts, and concomitant water table draw downs will affect *Sphagnum* mosses differently. These interspecific differences environmental changes will alter the competitive balance between species along the bogs surface, and concomitantly will affect carbon sequestration rates in peatlands. Therefore, it is important that species composition and changes therein are taken into account when evaluating global change effects on raised bog ecosystems.

The last parts of this thesis are focussed on field experiments that were executed in Clara bog, co. Offaly, Ireland and Männikjärve bog, co. Jõgevaa, Estonia. Irish peatlands have declined dramatically and only the last decades the importance of these areas has been acknowledged by the EU. According to the International Mire Conservation Group (IMCG) resolutions, peatland conservation has improved in Ireland the last 20 years, but still deserves more attention since local activities (e.g. turf cutting), agriculture and plans for renewable energy (e.g. wind farms) remain a threat to Irish peatlands. In 1997 the IPCC identified the main factors that affected peatland biodiversity, among which water table draw down and climate change, and proposed several actions that should promote public awareness of the importance of peatland biodiversity. Estonian wetlands (bogs, fens and swamps) cover about 20% of the total land area, but their status has been declining rapidly. Moreover, 70% of all Estonian peatlands have ceased to accumulate carbon, which has been ascribed to drainage, peat extraction, oil shale mining and urban development. On the other hand, Estonia's Nature Conservation laws have led to the conservation of approximately 60% of the countries raised bogs, which are more or less in natural state. The adoption of wise use

principles and implementation of Natura 2000 legislation might be a powerful tool for further raised bog conservation awareness.

On raised bogs, the distribution of *Sphagnum* species is determined by their distance to the water table, but occasionally species are able to survive outside their niche. Hollow species that persist in hummock vegetation are assumed to profit from the higher water content of the surrounding hummock species, although the mechanism responsible is unclear. In chapter 5 we elucidated the role of lateral hummock water transport (LHWT) and precipitation on the water content of hollow species occurring in hummocks. This was tested using a full factorial field transplantation experiment with cores of *Sphagnum cuspidatum* in a high and a low hummock. Treatments included direct precipitation (present or absent) and LHWT (present or absent). Fresh weights of the cores were measured at regular time intervals. Our results showed that precipitation has a relatively large effect on the water content of the transplanted patches in both the high and low hummock, whereas LHWT only seemed to be an important source of water in the high hummock, which was relatively dry. Furthermore, LHWT played an important role only after large precipitation events, suggesting that lateral water transport is indirectly affected by rain. This study showed that precipitation alone could explain the persistence of hollow species in high hummocks, whereas it was less important for hollow species in low hummocks. Our data suggest that survival and potential expansion of hollow species in higher hummocks is strongly depending on the intensity and frequency of rain events. Changes in precipitation patterns may result in a loss of *Sphagnum* diversity in hummocks. Additionally, the persistence of hollow species in hummock vegetation may be important because these patches may act as refugees for species in period in which environmental condition are unfavorable.

A lot of peatlands which have been drained and cut-over in the past, are now re-vegetated with a secondary plant cover. After restoration, however, the development of a typical *Sphagnum* vegetation stagnates in a pioneer stage. We simultaneously performed an experiment in Clara bog, Ireland and Männikjärve bog, Estonia, in which we investigated the effects of different water levels and patch size on the competitive strength of different *Sphagnum* mosses after transplantation into *S. magellanicum* vegetation? Over a three year period, changes in cover were monitored for large and small cores of *Sphagnum cuspidatum*, *S. rubellum* and *S. fuscum* after transplantation into a *S. magellanicum* matrix, at a high and a low water table. Water contents and height increment of the surrounding *S. magellanicum* matrix were also measured. We found interspecific differences in cover change over the years. Generally, cover change of the transplanted species was higher in Männikjärve bog compared to Clara bog, presumably as a result of reduced competition from the surrounding *S. magellanicum* vegetation in Estonia. Cover of *S. cuspidatum* decreased with time, and was largest at low water tables. After an initial decrease in cover, *S. rubellum* and *S. fuscum* recovered and showed a net increase, except for the small patches in Clara bog for which the initial decline levelled off. Expansion of both species was promoted by a large patch size and for *S. fuscum* was highest at low water tables, whereas water table did not affect *S. rubellum*. Additionally, an increase in patch size seemed to enhance the ability of species to create their own micro-hydrological environment, which may be more optimal for their growth. Our results indicate that transplantation of species into an existing *Sphagnum* vegetation can be successful, but the success depends on patch size, the hydrological conditions, and the species considered for re-introduction. The patches of the transplanted species should be large enough to allow persistence during the first years. Present hydrological management seems to contradict the conservation aims. It, however, may be important to first restore a vegetation where water tables can be lowered without hampering the functioning of the system. The next step would be the transplantation of large patches of species considered for re-introduction.



The last experimental chapter (chapter 7) emphasizes on the effects of the water table, and fluctuations therein on the vegetation of intact bog mesocosms. The effects on the composition of the *Sphagnum* vegetation, on the vascular plants, and feed-backs between *Sphagnum* mosses and vascular plants were taken into account.

We collected intact bog mesocosms from Saxnäss mosse, Southern Sweden, which subsequently were transported to the experimental field in Wageningen, the Netherlands. Over a two-and-a-half year period, *Sphagnum* height increment, as well as *Sphagnum* and vascular plant cover in the mesocosms were assessed at constant and fluctuating water levels. The changes in production and in cover, over the experimental period, were correlated to modal water table depth during the growing season. Additionally, the relation between *Sphagnum* production and changes in vascular plant cover was assessed. From this semi-field experiment it became clear that fluctuating water tables hampered production and expansion of *S. cuspidatum*, whereas *S. magellanicum* was stimulated by fluctuating water tables. The abundance of graminoid (e.g. *Rhynchospora alba*) species increased in both treatments during the experiment, but most in the constant water level treatment. The abundance of ericoid species (e.g. *Caluna vulgaris*, *Erica tetralix*) increased when the water table fluctuated. No significant relations between vascular plant cover and *Sphagnum* production could be found. From these results we conclude that periods with low water tables may effectuate a shift in dominant *Sphagnum* species towards hummock species, as well as a shift from graminoid to ericoid vascular plants.

Further implications of changes in the composition of the vegetation on future carbon sequestration and hydrological characteristics of raised bogs are import questions for future research. In the final chapter we conclude that, even if we would be able to exactly predict the changes in environmental factors, the ability of a raised bog to continue being an important carbon sink, strongly depends on the composition of the vegetation. Competition between *Sphagnum* species is determined by the differences in competitive strength between species, which on its turn is influenced by the photosynthetic capacity at distinct capitulum water content. The capitulum water content of *Sphagnum* species depends on its capillary system, its water holding capacity and on the surrounding vegetation. The results presented in this thesis show that if the availability of water decreases, either by decreased water table or prolonged periods of drought, hummock species will benefit at the expense of hollow species. Additionally, vascular plants like ericoids will increase. Low covers of these vascular plants can be beneficial for *Sphagnum*, but higher covers may be detrimental. It is important that peatland scientist continue to monitor the effects of environmental changes on changes in the composition of peatlands. Especially long term measurement may provide a lot of information, which will help us to better understand the mechanisms of competition between *Sphagnum* species.



# CONCURRENTIE TUSSEN VEENMOSSEN IN EUROPESE HOOGVENEN DE EFFECTEN VAN EEN VERANDEREND KLIMAAT



De laatste jaren is er veel aandacht voor de rol van venen in het vastleggen van atmosferisch koolstof. Geschat wordt dat wereldwijd 20 tot 30% van al het bodemgebonden koolstof vastligt in venen; met name in hoogvenen op het noordelijk halfrond. Deze hoeveelheid is ongeveer drie keer hoger dan geschat voor tropische regenwouden. Hoogvenen worden voor een groot deel gedomineerd door veenmossen (*Sphagnum* spp.). Deze mossen worden beschouwd als sleutelsoorten voor het functioneren van het ecosysteem omdat ze de waterbalans en koolstofopslag voor een groot deel bepalen.

Hoogvenen worden veelal gekarakteriseerd door de aanwezigheid van een patroon van micro-topografische elementen, of habitats, die variëren van natte depressies (slenken) en relatief droge, maar regelmatig geïnundeerde gazons tot droge bulten. Elk van deze habitats wordt gekenmerkt door een verschillende set aan veenmossoorten, waarbij slenksoorten voornamelijk gebonden zijn aan de nattere depressies en bultsoorten hoofdzakelijk aangetroffen worden op de hogere bulten. Deze ogenschijnlijke sterke correlatie tussen veenmossen en hun voorkomen langs the hydro-topografische gradiënt wordt verondersteld te worden veroorzaakt door een combinatie van morfologische en fysiologische eigenschappen van de betreffende veenmossoorten. Een aanzienlijke hoeveelheid onderzoek is gedaan naar de habitatvoorkeuren van verschillende veenmossen, en is er veel kennis over de hydrologische condities en nutriënten niveaus waarbij specifieke soorten floreren. Uit verschillende studies blijkt dat er verschillen bestaan tussen veenmossen in hun capaciteit om water vanaf de waterspiegel naar hun capitula (de veenmoshoofdjes; top van het veenmos van waaruit groei plaats vindt) te transporteren door middel van een extern capillair netwerk dat gevormd wordt door de dicht op elkaar groeiende afzonderlijke individuen. Bovendien is gebleken dat veenmossoorten verschillen in hun vermogen om water vast te houden

(watervasthoudend vermogen). Er lijkt een afweging te zijn tussen groeisnelheid enerzijds en het transporteren en vasthouden van water anderzijds.

De komende 50 tot 100 jaar worden er veranderingen verwacht in het klimaat, waaronder een stijging in de temperatuur (IPCC, the International Panel on Climate Change; een Internationaal comité dat zich bezig houdt met deze klimaatsveranderingen.) Deze temperatuurstijging zal voornamelijk plaatsvinden op het Noordelijk halfrond, waar de meeste hoogvenen gelegen zijn. Daarnaast zullen de patronen van regenval en de intensiteit van deze regenval waarschijnlijk veranderen. Hoe deze veranderingen zich zullen uiten is nog steeds onduidelijk, maar het lijkt er op dat de gebieden waar hoogveen ligt, te maken gaan krijgen met drogere zomers en nattere winters. Samen met een verhoging van de temperatuur, kunnen veranderingen in de patronen van regenval een rechtstreekse invloed hebben op de waterstand in hoogvenen. Veranderingen in temperatuur, waterstand en regenval kunnen een verschillend effect hebben op de groei, en daarmee concurrentiekracht, van verschillende veenmossoorten. Op den duur kunnen soortspecifieke verschillen in groei een verandering in de soortensamenstelling van hoogvenen tot gevolg hebben, wat op zijn beurt weer kan doorwerken op het functioneren van deze ecosystemen. Dit proefschrift heeft tot doel te onderzoeken hoe de belangrijkste veenmossen in Europese hoogvenen reageren op veranderingen in temperatuur, waterstand en regenval. De effecten van voornamelijk waterstand en regenval op de concurrentie tussen veenmossen komen daarbij uitgebreid aan bod.

In het eerste deel van dit proefschrift worden drie experimenten beschreven die uitgevoerd zijn onder gecontroleerde omstandigheden in de kas. We hebben daarbij gekeken in hoeverre temperatuur (hoofdstuk 2), waterstand (hoofdstukken 2, 3 en 4) en regenval (hoofdstuk 4) een effect hebben op de groei en concurrentiekracht van verschillende belangrijke veenmossoorten die voorkomen in Europese hoogvenen. Het eerste experiment dat uitgevoerd werd, had tot doel om te onderzoeken of veenmossen die in monocultuur (= slechts één soort veenmos) gehouden werden verschillend reageerden op waterstand en temperatuur (hoofdstuk 2). Daartoe werden er vier soorten veenmos, *Sphagnum magellanicum* (Hoogveenveenmos), *S. rubellum* (Rood veenmos), *S. austinii* (Kamveenmos) en *S. fuscum* (Bruin veenmos), gedurende één jaar blootgesteld aan twee waterstanden (5 cm en 15 cm onder het veenoppervlak) en twee temperaturen (15°C en 20°C). De betreffende mossen verschillen in hun positie langs de micro-topografische gradiënt van het veenoppervlak en hun geografische distributie. Concurrentiekracht werd afgeleid aan factoren als hoogtegroeï, dichtheid van het veenpakket, biomassa productie, watergehaltes van de veenmoshoofdjes en de totale verdamping van water. Uit onze resultaten bleek dat de hoogtegroeï en biomassa productie van *S. magellanicum* lager was bij de lagere waterstand, in vergelijking tot groei en productie bij de hogere waterstand. De andere drie soorten vertoonden een dergelijke respons niet. De hoogtegroeï van *S. magellanicum*, *S. rubellum* en *S. austinii* was groter bij de hoge temperatuur dan bij de lage temperatuur. Biomassa productie daarentegen, werd gestimuleerd door hogere temperatuur voor alleen *S. magellanicum* en *S. rubellum*. Dit resultaat kan waarschijnlijk toegeschreven worden aan de distributie van deze soorten, die een stuk zuidelijker is dan de distributie van *S. austinii* en *S. fuscum*. De totale verdamping van *S. magellanicum* en *S. rubellum* was het laagst bij de lage temperatuur, wat verklaard kan worden doordat bij lage waterstanden de veenmoshoofdjes minder water krijgen, omdat deze soorten een minder goed systeem voor capillair water transport bezitten. Deze verschillen tussen soorten maakten dat het volgende experiment zich toespitste op de effecten van waterstand op de concurrentie tussen veenmossen (hoofdstuk 3). In de kassen hebben we onderzocht hoe combinaties van verschillende soorten reageerden op een hoge (-5 cm) en een lage (-20 cm) waterstand. Voor het experiment

gebruikten we *S. cuspidatum* (Waterveenmos), *S. magellanicum*, *S. papillosum* (Wrattig veenmos), *S. rubellum*, *S. fuscum* en *S. austinii*. Naast monocultures, maakten we combinaties (mixculturen) van die soorten die onder natuurlijke omstandigheden ook naast elkaar kunnen voorkomen. Net als in het vorige experiment gaven we slechts om de twee weken een hoeveelheid regenwater (gelijk aan 234 mm jaar<sup>-1</sup>), waardoor de effecten van de waterstand duidelijker naar voren zouden moeten komen. Van alle mossen werd de hoogtegroeï en het watergehalte van het capitulum gemeten, en van de soorten uit de combinaties werd ook gemeten wat hun verandering in oppervlakte was gedurende het experiment. Onze resultaten lieten zien dat soorten die onder natuurlijke omstandigheden voorkomen op de bulten, in het voordeel waren boven soorten die normaliter dicht bij de waterspiegel voorkomen (slenksoorten). Tot onze verbazing gebeurde dit ongeacht de waterstand, wat erop duidt dat capillair transport van water een minder grote rol speelt dan wordt aangenomen. De verandering in oppervlakte ten gunste van de bultsoorten leek gerelateerd aan de grotere lengtegroeï van deze soorten en bleek vreemd genoeg niet gerelateerd aan een hoger watergehalte in deze bultsoorten; de bult- en slenksoorten die in combinatie groeiden met elkaar hadden een identiek watergehalte. Dit resultaat deed het vermoeden rijzen dat de groeiverschillen in ons experiment wellicht te maken hadden met verschillen in de efficiëntie waarmee soorten met het aanwezige water omgaan. Verder bleek het watergehalte van de hoofdjes in de monoculturen hoger dan het watergehalte van de hoofdjes van dezelfde soorten in de mixculturen, wat deed vermoeden dat er een (fysisch) verschil was in het vermogen van de mix- en monoculturen om water naar de hoofdjes te transporteren. De dichtheden van het veenpakket verschilden niet tussen identieke soorten die in monocultuur of in mixcultuur stonden. De twee soorten die in een mixcultuur goeiden, daarentegen, verschilden wel in hun dichtheid, resulterend in een heterogene samenstelling van het veen in deze cultures. Hieruit concluderen wij dat een heterogeen pakket veen een negatief effect heeft op het watergehalte van de veenmossen. Daarnaast toonden onze resultaten dat onder een regime met veel langdurig droge periodes, soorten die normaal verder van de waterstand voorkomen een competitief voordeel hebben ten opzichte van soorten die dicht bij de waterstand groeien onder natuurlijke omstandigheden, zelfs als de waterstand relatief hoog is.

Het feit dat slenksoorten slechter groeiden dan bultsoorten bij dezelfde watergehaltes in de veenmoshoofdjes, deed ons vermoeden dat er soortverschillen waren in hoe soorten reageren op het watergehalte in de veenmoshoofdjes. Ook in de literatuur werd hierover gespeculeerd, maar de data waren nooit overeenstemmend. Een alternatieve verklaring zou kunnen zijn dat de veenmossen verschilden in hun watervasthoudend vermogen. Elke keer nadat er regenwater gegeven werd, verliezen de verschillende soorten hun water in een verschillend tempo, maar na twee weken (wanneer wij maten) hadden de mossen een identiek laag watergehalte. Het resultaat is echter dat de mossen die hun water minder snel verliezen, langer een watergehalte kunnen handhaven waarbij fotosynthese plaats kan vinden. Hoofdstuk 4 van dit proefschrift beschrijft een experiment waarin wij trachten te onderzoeken of bovengenoemde mechanismen een verklaring zouden kunnen zijn voor de resultaten die we vonden uit het experiment dat beschreven staat in Hoofdstuk 3. Door middel van dit experiment wilden we onderzoeken wat de effecten van de aan- of afwezigheid van regenval bij een hoge of lage watertand waren op de opname van koolstofdioxide (CO<sub>2</sub>) en op de verdamping van drie soorten veenmos (*S. magellanicum*, *S. rubellum* en *S. fuscum*) die elkaar opvolgen langs de micro-topografische gradiënt van een hoogveen. We maten deze variabelen elke dag gedurende een periode van 23 dagen. Daarnaast konden we bepalen tot welke diepte licht doordringt in een veenmosvegetatie en welke lagen van de veenmosvegetatie verantwoordelijk zijn voor de meeste opname van koolstofdioxide. Tot slot, maakte de proefopzet het mogelijk om voor een aantal stalen te bepalen in hoeverre de opname van koolstofdioxide zich herstelt na langdurige (zestien dagen) verdroging. We vonden dat, ongeacht de aan- of afwezigheid



van regenwater, de opname van koolstofdioxide gedurende het experiment het hoogst was bij de hoge waterstand. Bij de lage waterstand nam bij afwezigheid van regenwater de opname van koolstofdioxide gedurende het experiment af. Deze afname begon het eerst bij de slenksoort *S. cuspidatum*. Toevoeging van regenwater compenseerde voor de lage waterstand en beïnvloedde de opname van koolstofdioxide op een positieve manier. De totale opname van koolstofdioxide gedurende het experiment was het laagst voor *S. magellanicum*, hoewel voor deze soort de opname het langst duurde. Daarnaast was het herstel na een zestien dagen durende verdroging het langzaamst.

Alle licht werd opgenomen in de eerste (twee) centimeter van de veenmosvegetatie. Als gevolg daarvan vond ook hier de meeste opname van koolstofdioxide plaats. De veenmossen verschillend wat betreft de opname van koolstofdioxide in hun respons op het watergehalte van de veenmoshoofdjies. De opname van *S. cuspidatum* (slenksoort) bereikte een optimum onder een klein bereik van relatief hoge watergehaltes, terwijl *S. rubellum* (bultsoort) een optimum bereikte over een veel breder bereik van watergehaltes, die meer in het lage bereik vielen. De koolstofopname van *S. magellanicum*, daarentegen, bleef vrijwel constant over een breed bereik aan watergehaltes, maar was relatief laag over dit hele bereik.

De resultaten uit bovenstaande hoofdstukken leidden tot de conclusies dat een verhoging van de temperatuur, langdurige droge periodes in de zomer en daarmee gepaard gaande lagere waterstanden veenmossoorten verschillend beïnvloeden. Deze resultaten laten zien dat het belangrijk is om de soortensamenstelling en eventuele veranderingen daarin in kaart te brengen en mee te nemen bij evaluaties naar de effecten van klimaatsveranderingen op veensystemen.

Het tweede deel van dit proefschrift beschrijft een tweetal experimenten die uitgevoerd zijn in 'Clara bog', een veen in het centrale deel van Ierland, en in 'Männikjärve bog' een veen dat deel uitmaakt van een veencomplex in het natuurreservaat Endla, gelegen in het oostelijk deel van Estland. Ierse veensystemen zijn sterk in aantal en in achteruitgegaan en de meesten verkeren nog nauwelijks in een natuurlijke staat. De laatste jaren wordt door een EU echter het nut van deze gebieden ingezien. Volgens de 'International Mire Conservation Group (IMCG)' is de bescherming van Ierse venen de laatste jaren enorm verbeterd, maar verdient deze bescherming nog steeds aandacht, aangezien lokale afgraving, landbouw, en plannen voor innovatieve energiewinning (bv. De aanleg van windmolen parken) nog steeds een bedreiging vormen voor Ierse venen. In 1997 heeft de IPCC Ierse vereniging voor de bescherming van veengebieden (IPCC, Irish Peatland Conservation Council) een aantal factoren geïdentificeerd die een negatief effect hebben op de biodiversiteit in venen, waaronder de daling van waterstanden en klimaatsverandering. De IPCC heeft daarnaast een campagne gestart om het brede publiek het nut van hoogvenen te laten. Estse venen nemen ongeveer 20% van het areaal in, maar hun status gaat snel achteruit. Reeds 70% van de Estse venen leggen geen koolstof meer vast. Dit wordt toegeschreven aan drainage, afgravingactiviteiten, de winning van olieschalie (ofwel olie kleisteen), en urbanisatie. Daartegenover staat dat de Estse natuurbeschermingswetten ertoe geleid hebben dat ongeveer 60% van de een beschermde status hebben. Deze hoogvenen verkeren dan ook in een min of meer natuurlijke staat. De navolging van een aantal grondbeginzelen die wijzen op een 'verstandig gebruik' van deze gebieden en de toewijzing van deze gebieden tot de Natura 2000 wetgeving zullen er verder toe leiden dat men de noodzaak ziet dat deze gebieden beschermd blijven.

Hoewel de verspreiding van veenmossen langs het veenoppervlak grotendeels wordt bepaald door de afstand tot de waterstand, worden soms soorten aangetroffen buiten hun natuurlijke standplaats. Slenksoorten worden bijvoorbeeld regelmatig aangetroffen op bulten, maar dan slechts enkele individuen. Deze individuen worden verondersteld te profiteren van de hogere

watergehaltes van de omringende bultsoorten, maar de exacte mechanismen die daarbij een rol spelen zijn onduidelijk. In hoofdstuk 5 onderzochten wij de rol van lateraal water transport vanuit de bultvegetatie en de rol van regenval op het watergehalte van slenksoorten die in een bultvegetatie groeien. Hiervoor transplanteerden wij kleine kernen van de slenksoort *Sphagnum cuspidatum* in een hoge en een lage bult in Männikjärve bog, Estland. Bij de helft van de transplantaten werden de directe watertoevoer door regen en door lateraal water vanuit de bultvegetatie afgesneden. Op regelmatige tijden werd het versgewicht van de getransplanteerde slenksoorten bepaald. Wij vonden een duidelijk effect van regen op het watergehalte van de slenksoorten in beide bulten, terwijl lateraal water vanuit deze bulten slechts een effect had op het watergehalte van de slenksoorten in de hoge, drogere bult. Daarnaast leek lateraal water transport alleen plaats te vinden na hevige regenval. Dit wijst erop dat het transport van water vanuit de bultvegetatie naar slenksoorten die daarin groeien, indirect gevoed wordt door regenwater. De resultaten van dit experiment wijzen erop dat slenksoorten zich alleen dan kunnen handhaven en eventueel uitbreiden als de intensiteit en frequentie van regenval hoog genoeg is. Veranderingen in de patronen van regenval, en in het bijzonder langdurige droogte in de zomerperiodes, zouden kunnen leiden tot een afname van de diversiteit aan veenmossen in bulten. Slenksoorten die in bulten voorkomen hebben wellicht een functie in de veerkracht van het veenecosysteem. Zo zouden deze individuen kunnen dienen als potentiële uitbreidingskernen bij natter klimaat.

De meeste venen die in het verleden zijn gedraineerd en afgegraven hebben tegenwoordig een secundaire vegetatie, maar daarin ontbreken vaak de typische soorten voor intacte veen ecosystemen. Er wordt momenteel veel energie gestoken in het restaureren van deze aangetaste gebieden. Hoewel na restauratie vaak een veenmosvegetatie ontstaat, ontbreken er vaak de bultvormende veenmossen. Dit kan twee oorzaken hebben: ten eerste zouden de juiste omgevingfactoren kunnen ontbreken; ten tweede is het mogelijk dat er geen 'donor populatie' of diaspore aanwezig zijn waardoor deze soorten zich niet kunnen herstellen. In hoofdstuk 6 wordt een experiment beschreven waarin werd onderzocht of verschillende soorten zich konden handhaven en eventueel uitbreiden nadat ze getransplanteerd werden in een reeds bestaande veenmosvegetatie. Daarbij werden ook de rol van de waterstand en het effect van de grootte van de transplantaten meegenomen. Zowel in Clara (Ierland) als in Männikjärve (Estland) werden grote en kleine kernen van *S. cuspidatum*, *S. rubellum* en *S. fuscum* getransplanteerd in een bestaande vegetatie van *S. magellanicum*, bij een hoge en een lage waterstand. Gedurende een periode van drie jaar werden, naast de veranderingen in het oppervlak van de transplantaten, de waterstanden in het veen en de hoogtegroeï van de bestaande veenmosvegetatie gemeten. De verandering in het oppervlak van de transplantaten varieerde per jaar. Het oppervlak van *S. cuspidatum* nam alle jaren af. Deze afname was het grootst bij de lage waterstand. De andere twee soorten namen aanvankelijk ook in oppervlak af, maar herstelden zich gedurende het tweede en derde jaar. Bij *S. fuscum* was het herstel groter bij een lage waterstand. *S. rubellum* reageerde niet op de waterstand. *S. rubellum* en *S. fuscum* hadden voordeel van een grote oppervlak van het transplantaat. Dit gold niet voor *S. cuspidatum*. Door een groter oppervlak leken de getransplanteerde veenmossen beter in staat om hun eigen hydrologie te creëren, waardoor ze wonnen in concurrentiekracht. Een interessant gegeven was dat de transplantaten in Männikjärve beter in staat waren zich te handhaven dan in Clara. Dat zou verklaard kunnen worden door het feit dat in Clara de groei van de omringende veenmosvegetatie hoger was dan in Männikjärve. Onze resultaten deden ons concluderen dat het mogelijk is om veenmossen te transplanteren, maar het succes daarvan hangt af van een aantal factoren. Het hydrologisch beheer van een veengebied moet overeenkomen met de eisen die een te transplanteren soort stelt aan zijn omgeving. Het huidige Nederlandse beheer waarin het verhogen van de waterstanden centraal staat lijkt haaks te staan op het terug krijgen van

een systeem waarin ook bultsoorten een plek hebben. Het is echter eerst zakak een veenvegetatie te herstellen waarbij de waterstanden verlaagd kunnen worden zonder dat de zelfregulerende functie van deze vegetatie gelijk verloren gaat. De volgende stap zou het transplanteren van de gewenste bultsoorten kunnen zijn, waarbij in ogenschouw wordt gehouden dat de monsters die getransplanteerd worden groot genoeg zijn.

Het laatste experiment (hoofdstuk 7) wijdt uit over de effecten van waterstanden, en fluctuaties daarin, op de vegetatie van intacte veenkernen. Deze kernen (50 cm in doorsnede) werden gehaald uit Saxnäss mosse, een klein veentje in het zuiden van Zweden. Vervolgens werden de kernen in grote bakken gehangen, die ingegraven waren in Wageningen en gevuld waren met schoon regenwater. Deze proef had het doel om inzicht te geven in de effecten van waterstanden en waterstandsfluctuaties op de compositie van zowel de veenmossen als de vaatplanten. Gedurende twee-en-een-half jaar werden daartoe hoogtegroeï van de veenmosvegetatie, en abundanties van soorten veenmos en vaatplanten gevolgd onder een constant hoge en een fluctuerende (en dus periodiek lage) waterstand. Veranderingen in productie en abundanties werden gerelateerd aan de modus van de waterstand zoals die gemeten werden gedurende het groeiseizoen. Daarnaast relateerden we de veenmos productie aan de abundantie van vaatplanten. Dit experiment liet zien dat de productie van de slenksoort *S. cuspidatum* geremd werd wanneer de waterstanden fluctueerden. *S. magellanicum*, een soort die onder natuurlijke omstandigheden verder van de waterstand af kan groeien, werd juist gestimuleerd door fluctuaties in de waterstand. Grasachtigen zoals Witte Snavelbies (*Rhynchospora alba*) namen toe onder beide hydrologische regimes, maar de toename was het grootst bij de constante waterstand. Ericoiden zoals Kraaiheide (*Caluna vulgaris*) en Dopheide (*Erica tetralix*) profiteerden juist van de fluctuerende waterstand. Ondanks de toename van vaatplanten konden we geen effect daarvan vinden op de productie van de veenmossen. De resultaten van dit experiment laten zien dat periodes met lage waterstanden een verschuiving teweeg kunnen brengen in de veenmosvegetatie ten gunste van bultvormende soorten. Daarnaast zullen droge periodes leiden tot een toename van heidesoorten. Implicaties van verschuivingen in de soortensamenstelling op de koolstofopname en hydrologie van hoogvenen blijft een interessant en noodzakelijk onderwerp voor verder onderzoek.

In het laatste hoofdstuk (hoofdstuk 8) concluderen we het moeilijk is om een voorspelling te doen over hoe hoogvenen zich zullen gaan gedragen met betrekking tot hun rol als koolstof vastleggende ecosystemen. De richting van veranderingen in het klimaat en de samenstelling van de veenmosgemeenschap speelt daarbij een uiterst belangrijke rol. Concurrentie tussen veenmossen wordt in hoge mate bepaald door verschillen in concurrentiekracht. Deze concurrentiekracht wordt vervolgens weer bepaald door de efficiëntie waarmee soorten met het watergehaltes in hun hoofdjes kunnen omgaan. Op zijn beurt wordt dit watergehalte bepaald door door de efficiëntie van het capillair water transport, het vermogen om water vast te houden en door de omringende vegetatie. Dit proefschrift laat duidelijk zien dat een afname in de hoeveelheid water die beschikbaar is voor veenmossen, hetzij door een afname in de waterstand hetzij langdurige periodes zonder regen, zal leiden tot een toename van bultvormende soorten ten koste van slenksoorten. Daarnaast zullen heidesoorten toenemen in abundantie. Op den duur kan een toename in vaatplanten ongunstig zijn voor de veenmosvegetatie. Het blijft belangrijk voor wetenschappers om de effecten van klimaatsveranderingen op de samenstelling van de plantengemeenschappen in hoogvenen te onderzoeken. Voornamelijk langlopende experimenten in combinatie met modellering kunnen de huidige kennis, opgedaan uit kortlopende studies, toetsen.

# TURBASAMMALDEVAHELINE KONKURENTS EUROOPARABADES MUUTUVA KLIIMA EFEKTID



translated by Kai and Andres Kimmel

Euroopa turbaalade tähtsust süsinikku siduvate ökosüsteemidena on juba kaua tõdetud. On hinnatud, et turbaalad, seejuures rabad, säilitavad ligikaudu 20% maailma mulla süsinikust; kogus, mis on umbes kolm korda suurem troopilistes vihmametsades talletunud süsiniku kogusest. Rabades kasvavaid turbasamblaid (*Sphagnum* spp.) on üldlevinult nähtud kui ökosüsteemi insenere ja sellistena mängivad nad tähtsat rolli nende süsteemide süsiniku sidumises.

Tüüpiliselt on rabadele iseloomulik mikrotopograafiliste elupaikade muster, mis ulatub märgadest lohkudest (älved) ja suhteliselt kuivadest (kuid regulaarselt üle ujutatud) murudest kuni kuivade mätasteni koos igas mikroelupaigas esinevate erinevate *Sphagnum*´i liikide kogumitega. Älve liigid haaravad enda alla tavaliselt veetaseme lähedal asuvad elupaigad, samas kui mäta liigid suudavad asustada elupaikasid, mis on veetasemest kaugemal. *Sphagnum*´i liikide ja nende hüdro-topograafilisel gradiendil asuva positsiooni tugev korrelatsioon on tõenäoliselt morfoloogiliste ja füsioloogiliste piirangute kombinatsiooni tulemus. Mitmed uurimused on rõhutanud liikidevahelisi erinevusi *Sphagnum* sammalde seas nende välimise kapillaarse süsteemi efektiivsuses ja nende võimes hoida vett: liikide seas näib toimivat kompromiss maksimaalse kasvu kiiruse, kapiitulisel vee transportimise võime ja evaporatiivse veekao talumise võime vahel. Enamgi veel, märkimisväärsed teaduslikke uuringuid on tehtud *Sphagnum* sammalde elupaikade eelistuste alal ja on olemas hea arusaamine hüdroloogilistest ja troofilistest režiimidest, mille korral erinevad liigid harilikult esinevad. Kuna *Sphagnum* sammaldel ei ole stomatat ja juuri, siis nende veesisaldus aktiivsetes tipmistes osades (nt. kapiitul) sõltub tugevalt võimest transportida vett läbi välimise kapillaarse süsteemi ja suutlikusest hoida sademetega lisanduvat vett.

Oodatakse, et globaalse kliima muutused ilmnevad järgmise 50-100 aasta jooksul. Rahvusvahelise Kliima Muutuste Paneeli (IPCC) poolt tehtud kavandites eeldatakse temperatuuri tõusu, seda eriti põhjapoolkeral, kus võib leida ka enamuse rabadest. Veelgi enam, oodatakse ka sademete jaotuse muutust. Kuidas sademete jaotused muutuvad on seni vaidlusaluseks küsimuseks, kuid

eeldatakse suvede muutumist kuivemaks, samas kui talved muutuvad niiskemaks. Kombineerituna kõrgemate temperatuuridega, võivad muutused sademete jaotuses mõjutada otseselt veetasemeid rabades. Temperatuuri, veetasemete ja sademete jaotuse muutused võivad mõjutada erinevaid turbasambla liike erineval määral, mis võib kaasa tuua muutused liikidevahelise konkurentsi tasakaalus ja lõpptulemusena *Sphagnum* taimestiku koosseisus. Käesolevad teesid seavad eesmärgiks uurida, kuidas Euroopa rabade peamised turbasambla liigid reageerivad temperatuuri, veetasemete ja sademete muutustele; ja eriti seda, kuidas veetasemed ja sademed võivad muuta liikidevahelist konkurentsi.

Käesolevate teeside esimeses osas kirjeldan kolme kasvuhoone-eksperimenti, milles keskendusin temperatuuri (peatükk 2), veetaseme (peatükk 2, 3 ja 4) ja sademete (peatükk 4) toimele /efektidele mitmete Euroopa rabadele omaste tähtsate *Sphagnum*'i liikide talituses. Esimeses eksperimendis (peatükk 2) selgitame veetasemete ja temperatuuride muutuste toimet nelja *Spagnum* sambla - *S. magellanicum*, *S. rubellum*, *S. austinii*, ja *S. fuscum* - üheliigilistele kogumikele. Need samblad olid kasvatatud kahel veetasemel, -5 cm ja -15 cm, ja kahel temperatuuril, 15°C ja 20°C. *Sphagnum*'i liigid erinevad oma positsioonis piki mikrotopograafilist gradienti ja geograafilises levikus. Mõõdeti pikkuse juurdekasvu, kapiitulumise erikaalu, biomassi produktsiooni, kapiituli veesisaldust ja kumulatiivset evaporatsiooni. Tulemused näitasid, et *S. magellanicum*'i pikkuse juurdekasv ja biomassi produktsioon oli madalate veetasemete korral madalam kui kõrgete veetasemete korral, samas kui *S. rubellum*'i, *S. austinii* ja *S. fuscum*'i pikkuse juurdekasvu ja biomassi produktsiooni veetasemete muutumine ei mõjutanud. *S. magellanicum*'i, *S. rubellum*'i ja *S. austinii* pikkuse juurdekasv oli kõrgemal temperatuuril suurem kui madalamal temperatuuril. Ainult *S. magellanicum*'i ja *S. rubellum*'i biomassi produktsioon on kõrgemal temperatuuril kõrgem kui madalamal temperatuuril, vastates nende lõunapoolsemale levikule. *S. magellanicum*'i ja *S. rubellum*'i kumulatiivne evaporatsioon oli madalatel veetasemetel madalam ja võib olla seletatud kapiituli-suunalise veetranspordi tõkestatusega. Nende tulemuste tõttu otsustasime edasises keskenduda veetaseme toimele turbasamalde vahelises konkurentsis (peatükk 3).

Kasvuhoone-eksperimentis uurisime erinevate veetasemete toimet/mõju kuue *Sphagnum*i liigi - *S. cuspidatum*, *S. magellanicum*, *S. papillosum*, *S. rubellum*, *S. fuscum*, *S. austinii* - vahelisele konkurentstile. Sarnaselt eelmisele eksperimendile olid sademetehulk (234 mm/aastas) ja sademete sagedus (kahe nädala järel) hoitud madalal tasemel, et soodustada veetasemete efekti. Vastavaid liikide kombinatsioone ja monokultuure kasvatati erinevatel veetasemetel 16 kuu jooksul. Uurisime muutusi kattuvuses, pikkuse juurdekasvus ja kapiituli veesisalduses, et aru saada konkurentsis toimuvatest reageeringutest. Tulemus näitas ühetähenduslikult, et liigid, mis loomulikult esinevad kõrgemal veepinna kohal (mätta liigid) omavad üldiselt kõrgemat konkurentsijõudu kui liigid, mis loomulikult esinevad veepinna läheduses (älve liigid). Üllatavalt oli see efekt/mõju sõltumatu veetasemest, viidates kapillaarse veetranspordi väiksemale osale. Kattuvuse muutused näisid olevat seotud erinevustega lineaarses juurdekasvus, kuid mitte veetasemetega või kapiituli veesisaldusega ( $WC_{kap}$ ). Segunenud liikide  $WC_{kap}$  ei erinenud, kuid oli madalam kui monokultuuris kasvavate individuaalsete liikide  $WC_{kap}$ , viidates erinevustele segunenud ja monokultuuride võimes varustada veega kapiitulit. Kapiitulumise erikaal segunenud ja monokultuurides ei erinenenud, või oli isegi madalam monokultuurides, kuid erines segunenud kultuurides erinevates liikides. Tulemused näitavad, et turba struktuurne heterogeensus segunenud kultuurides omas negatiivset efekti mõlema liigi kapiituli veesisaldusele. Veelgi enam, näitame, et kestvad põuaaperioodid põhjustavad loomulikult veetaseme läheduses esinevate liikide välja tõrjumise loomulikult kõrgemal veetaseme kohal esinevate liikide poolt, isegi kui veetase jääb kõrgele tasemele.

Et älve liigid tõrjuti välja kui nende veesisaldused olid sarnased, seda võib seletada liikidevaheliste erinevustega reageeringutes kapiituli veesisaldusele, kuid konsensus



teaduskirjanduses selle kohta ei ole leitud. Alternatiivselt, kuigi kapiituli veesisaldused kaks nädalat hiljem võisid olla sarnased, võisid liikidevahelised erinevused veehoiu suutlikuses olla põhjuseks, et kuivamiskõverad on sõltuvalt liikidest erinevad. Järelikult võib see viia liikidevaheliste erinevusteni ajavahemiku kestvuses, mil veesisaldus on optimaalne fotosünteesiks. Kolmas eksperiment (peatükk 4) oli kujundatud eelmistes peatükkides näidatud tulemusteni viivate mehhanismide selgitamiseks. Planeerisime eksperimendi, et hinnata veetasemete (madal ja kõrge) interaktiivseid mõjusid ja sademete olemasolu või puudumise mõju CO<sub>2</sub> assimilatsioonile ja aurumisele kolmel koos esineval turbasamblal (*Sphagnum cuspidatum*, *S. magellanicum* ja *S. rubellum*), mis loomulikult levivad soopinnal piki mikrotopograafilist gradienti erinevalt, 23 päeva jooksul. Lisaks mõõtsime, millised samblakihi sektsioonid olid vastutavad valguse absorptsiooni ja süsiniku mahu loovutamise eest. Pärast seda uurisime CO<sub>2</sub> assimilatsiooni taastumist pärast pikaajalist põuaperioodi. Kõrgete veetasemete puhul suurenes kõigi liikide CO<sub>2</sub> assimilatsioon sõltumata sademetest järkjärgult aja jooksul. Madalate veetasemete puhul kahanes kõigi liikide neto CO<sub>2</sub> assimilatsioon, sealjuures kõige varasema alguse ja suurima kiirusega *S. cuspidatum* jaoks. Sademed kompenseerisid taanduvad veetasemed ja mõjutasid positiivselt kõigi liikide süsiniku neto loovutamist. Kumulatiivne süsiniku loovutamine eksperimendi perioodi jooksul oli madalaim *S. magellanicum* jaoks, kuid püsis positiivsena pikima ajavahemiku jooksul. Lisaks oli *S. magellanicum* CO<sub>2</sub> assimilatsioon aeglaseima taastumisega pärast pikaajalist põuaperioodi. Peaaegu kogu valguse absorptsioon ilmnes *Sphagnum* taimestiku esimestes ühes või kahes sentimeetris ja samuti toimis CO<sub>2</sub> assimilatsioon. CO<sub>2</sub> assimilatsioon kiirus näitas liigiliselt spetsiifilist relatsiooni kapiituli veesisaldusega. Assimilatsioon näitas *S. cuspidatum* jaoks kitsast optimumi suhteliselt kapiituli veesisalduse puhul, samas kui C assimilatsioon *S. rubellum* jaoks omas optimumi kuivemate seisundite juures. Kontrastina püsis C assimilatsioon *S. magellanicum* jaoks konstantne suhteliselt madala kiiruse juures üle kapiituli veesisalduste suure ulatuse.

Eelnevas peatükis jõudsime järelduseni, et globaalne soojenemine, suvised põuaperioodid ja kaasnevad veetasemete langused hakkavad turbasamblaid mõjutama erinevalt. Need liikidevahelised erinevused keskkonnamuutustes hakkavad muutma liikidevahelise konkurentsi tasakaalu rabade pinnal ja kaasnevalt mõjutama süsiniku sidumise määra turbaaladel. Seetõttu on tähtis, et liigiline koosseis ja muutused selles on võetud arvesse, kui anname hinnanguid globaalsete muutuste toimele rabade ökosüsteemides.

Viimased osad teesidest on keskendunud väli-eksperimentidele, mis viidi ellu Clara rabas Irimaal (Offaly maakond) ja Männikjärve rabas Eestis (Jõgeva maakond). Irimaa turbaalad on dramaatiliselt kahanenud ja ainult viimastel kümnenditel on nende tähtsust tunnustanud EU poolt. Rahvusvahelise Soode Kaitse Grupi (IMCG) resolutsioonide järgi on turbaalade kaitse Irimaal viimase 20 aasta jooksul paranenud, kuid väärub siiski rohkem tähelepanu, sest kohalikud tegevused (nt. turbaalõikamine), põllumajandus ja plaanid taastuva energia tootmiseks (nt. tuulepargid) ohustavad jätkuvalt Irimaa turbaalasid. IPCC töi 1997. aastal välja peamised faktorid, mis mõjutavad turbaalade loodusliku mitmekesisust, nende seas veetasemete langemine ja kliimamuutus; ja tegi ettepaneku mitmeteks tegevusteks, mis peaks edendama turbaalade loodusliku mitmekesisuse tähtsuse teadvustamist ühiskonnas. Eesti märgalad (rabad, madalsood ja soometsad) katavad umbes 20% kogu maismaast, kuid nende olukord on kiiresti halvenenud. Pealegi on 70% kõigist Eesti märgaladest lõpetanud süsiniku sidumise/akumulatsiooni, mille võib kirjutada kuivendustööde, turba kaevandamise, põlevkivi kaevandamise ja linnastumise arvele. Teisalt, Eesti Vabariigi looduskaitseadused on viinud ligikaudu 60% peaaegu looduslikus seisundis rabade kaitse alla võtmisele. Säästliku majandamise printsiipide rakendamine ja Natura 2000 seadusandluse täitmine võivad olla võimsad instrumendid rabade kaitse vajaduse edasiseks teadvustamiseks.

Rabades on *Sphagnum*'i liikide levik määratud kaugusega veetasemest, kuid mõnikord on liigid võimelised ellu jääma väljaspool nišši. Eeldatakse, et älve liigid, mis püsivad mätta taimestik, saavad kasu ümbritsevate mättaliikide kõrgemast veesisaldusest, kuigi vastav mehhanism on ebaselge. Peatükis 5 selgitasime mätta lateraalse veekande (MLVK) ja sademete osa mätastel esinevate älve liikide veesisalduses. Seda testi kasutades täielikku faktoriaal väli-transplantatsiooni eksperimenti *Sphagnum cuspidatum*'i tuumikutega kõrgetel ja madalatel mätastel. Töötlemise hulka kuulusid: otsesed sademed (esineb või puudub) ja MLKV (esineb või puudub). Tuumikute kaalu mõõdeti regulaarsete ajavahemike järel. Tulemused näitasid, et sademetel on suhteliselt suur mõju/efekt ümberistutatud lappide veesisaldusele mõlemal, nii kõrge kui madalal mätal, samas kui MLKV oli ainult näiliselt tähtsaks vee allikaks kõrgele mätal, mis oli suhteliselt kuiv. Enamgi veel, MLKV mängis tähtsat osa ainult pärast suuri sademete hulka; viidates, et lateraalne veekanne on kaudselt mõjutatud vihmast. See uurimus näitas, et sademed üksi võivad seletada älve liikide püsivust kõrgetes mätastes, samas kui see on vähem tähtis älve liikidele madalates mätastes. Meie andmed tähendavad, et älve liikide püsijäämine ja potentsiaalne ekspansioon kõrgemates mätastes on tugevalt sõltuv vihmasadude intensiivsusest ja sagedusest. Muutused sademete jaotuses võivad põhjustada *Sphagnum*'i mitmekesisuse kadumise mätastel. Lisaks, älveliikide püsimine mätta taimestik võib olla tähtis, sest need laigud võivad olla liikidele pelgupaikadeks ajavahemikel, mil keskkonnatingimused on ebasoodsad.

Enamus Euroopa turbaaladest on degradeerunud turba kaevandamise tõttu. Nende degradeerunud turbaalade taastamiseks on tehtud palju jõupingutusi. Kuigi *Sphagnum* taimestik areneb pärast taastamist, puuduvad selles üldiselt liigid, mis loomulikult ilmnevad kaugemal piki veetaseme gradienti (mätta liigid). See võib olla põhjustatud sobimatutest keskkonnatingimustest või ebaefektiivsest "kandumisest" läheduses asuvast "doonor" populatsioonist. Peatükis 6 esitame eksperimenti tulemused, mille peamiseks eesmärgiks oli selgitada, millised on erinevate veetasemete ja algse laigu mõõtmete efektid *Sphagnum* sammalde püsivusele pärast ümberistutamist olemasolevasse *S. magellanicum*'i taimkattesse. Clara rabas Iirimaa ja Männikjärve rabas Eestis seirati kolmeaastase ajavahemiku kestel muutusi suurte ja väikeste *Sphagnum cuspidatum*'i, *S. rubellum*'i ja *S. fuscum*'i laikude, mis olid ümber istutatud olemasolevasse *S. magellanicum*'i taimkattesse, kattuvuses. Ümberistutamine oli teostatud madalatel ja kõrgetel veetasemetel. Samuti mõõdeti ümbritseva *S. magellanicum*'i maatriksi veetasemed ja pikkuse juurdekasv. Tulemused näitavad, et on olemas liikidevahelised erinevused kattuvuse muutumises aastate jooksul. *S. cuspidatum*'i kattuvus vähenes kõigil aastatel ja vähenemine oli suurim madalatel veetasemetel. Pärast algset vähenemist kattuvuses taastusid *S. rubellum* ja *S. fuscum* siiski viimastel aastatel. *S. fuscum*'i jaoks oli taastumine kõrgeim madalate veetasemet puhul, samas kui veetase ei mõjutanud *S. rubellum*'it. Laigu suured mõõtmised olid kasulikud kõigi liikide jaoks, peale *S. cuspidatum*'i. Üldiselt oli ümberistutatud liikide püsivus Männikjärve rabas kõrgem võrreldes Clara rabaga, kus ümbritseva taimestiku pikkuse juurdekasv oli suurim. Sellest järeldame, et liikide ümberistutamine juba eksisteerivasse taimkattesse võib olla edukas, kuid edu sõltub mitmetest teguritest. Hüdroloogiline kaitsekorraldus peab olema kooskõlas liikide kaitsekorralduse eesmärgiga. Lisaks peavad ümberistutatud liikide laigud olema küllalt suured, et jääda püsima esimestel aastatel. Lõpuks mõjutavad taas-rajamise edu lokaalsed keskkonnatingimused, mis mõjutavad juba eksisteeriva taimkatte konkurentsi jõudlust, ja seetõttu tuleb korraldada nende seire enne kui ümberistutamine algab.

Viimane eksperimentaalne peatükk (peatükk 7) rõhutab veetasemete toimet ja fluktuatsioone looduslike rabade proovialade taimkattes. Arvesse võeti mõjud *Sphagnum* taimestiku koosseisule, soontaimedele ja tagasihoidlikele *Sphagnum* sammalde ja soontaimede vahel.

Kogusime loodusliku raba proovid Saxnässe soost Lõuna-Rootsis, ja transportisime eksperimentaal-alale Wageningenis, Hollandis. Kahe ja poole aasta jooksul hindasime *Sphagnum*'i pikkuse juurdekasvu, samuti ka *Sphagnum*'i ja soontaimede kattuvust proovialadel konstantse ja kõikuvate veetasemete juures. Muutusi produktsoonis ja kattuvuses eksperimendi ajavahemikus korreleeriti modaalse veetaseme sügavusega kasvuperioodi jooksul. Lisaks hinnati *Sphagnum*'i produktsooni ja soontaimede kattuvuse vahelist suhet. Sellest pool-välieksperimendist ilmnas, et kõikuvad veetasemed tõkestasid *S. cuspidatum*'i produktsooni ja ekspansiooni, samas kui need stimuleerisid *S. magellanicum* 'i produktsooni ja levikut. Kõrreliste (nt. *Rhynchospora alba*) rohkus suurenes eksperimendi jooksul mõlemas töötlemises, kuid enam konstantse veetaseme puhul. Kanarbikuliste (nt. *Calluna vulgaris*, *Erica tetralix*) rohkus suurenes, kui veetase kõikus. Soontaimede kattuvuse ja produktsooni vahel ei olnud võimalik leida tähenduslikku relatsiooni. Nendest tulemustest järeldame, et madalate veetasemetega perioodid võivad esile kutsuda dominantsetes *Sphagnum*'i liikides muutuse mätталиikide suunas, samuti ka soontaimede puhul muutuse kõrrelistest kanarbikuliste suunas.

Taimestiku muutuste seostamine süsiniku sidumisega tulevikus ja rabade hüdroloogiliste karakteristikutega on tähtis teema tulevasteks uuringuteks. Viimase peatükis järeldame, et väga raske on öelda, kuidas rabade taimkate hakkab muutuma, isegi juhul kui me oleme võimelised täpselt prognoosima muutusi keskkonnategurites. Rabade võime olla jätkuvalt tähtis süsiniku siduja/koguja sõltub tugevalt taimkatte koostisest. Konkurents *Sphagnum*'i liikide vahel on määratud konkurentsijõu erinevustest liikide vahel, mis omakorda on mõjutatud fotosünteesilisest suutlikusest erinevate kapiituli veesisalduste korral. *Sphagnum*'i liikide kapiituli veesisaldus sõltub nende kapillaarsest süsteemist, nende veehoiu suutlikusest ja ümbritsevast taimkattest. Tulemused, mis on esitatud nendes teesides, näitavad, et kui vee kättesaadavus väheneb, ükskõik kas vähenenud veetaseme või pikaajalise põuaperioodi tõttu, saavad älve liikide kulul eelistuse mätta liigid. Lisaks suurenevad soontaimed, nagu kanarbikulised. Nende soontaimede madal kattuvus võib olla *Sphagnum*'i jaoks kasulik, kuid suurem kattuvus võib olla kahjulik. Väga tähtis on, et teadlased jätkaksid turbaaladel taimkatte koostise muutusi põhjustavate keskkonnamuutuste toimete seiret. Eriti just pikaajalised mõõtmised võivad varustada meid suure hulga informatsiooniga, mis aitab meil paremini mõista *Sphagnum*'i liikide konkurentsimehhanismi.









## Bedankt - Thanks - Aitäh

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Ik weet nog goed dat tijdens het sollicitatie gesprek voor dit promotieonderzoek gevraagd werd of ik vroeger ook al bezig was met de natuur. Ik snapte destijds de functie van die vraag niet, ik solliciteerde toch op een



functie waarvoor je experimenteel werk moest doen! Blijkbaar was het antwoord dat ik gaf bevredigend en toen ik eenmaal begonnen was begon de functie van de vraag langzaam duidelijk te worden. Ik voelde me, zeker in het begin, een beetje een vreemde eend in de bijt, met allemaal collega's om mij heen die naar mijn mening meer iets weg hadden van lopende flora's, vogel-, libellen-, kever-, of vlinder gidsen dan van ecologen die bezig waren te onderzoeken hoe systemen nu eigenlijk functioneren. Het is allemaal goed gekomen en ik ben me op mijn gemak gaan voelen. Gelukkig maar, want hoewel een promotie onderzoek voor de buitenwereld vaak een solo project lijkt, ligt een deel van het succes bij je (oud-) collegas. Bij deze wil ik al mijn mede-AIO's, post-docs en vaste staf van NCP en REG bedanken; dank voor alle discussies, kritiek en steun. Maar ook voor de spelletjes-avonden, BBQ's en filmavonden. Een speciaal woord van dank wil ik uit spreken richting de ondersteunende dames en Tony, die elke keer weer zorgden dat alle papierwerk in orde was.

De afgelopen vier jaar waren de hoogveenonderzoekers aan de leerstoelgroep Natuurbeheer en Plantenecologie ruim vertegenwoordigd. Naast Matthijs en Juul, hebben Monique en Angela veel bijgedragen aan de tot stand koming van dit proefschrift. Monique, dank dat ik altijd bij je kon binnenlopen. Angela wil ik in het bijzonder bedanken voor de samenwerking. We hebben veel gediscussieerd en meegemaakt samen... bijvoorbeeld ons oponthoud bij de Estse douane, het samen koukleumend vegetatie opnamen maken in de winter, of de hevige, maar toch ook wel gezellige regens tijdens het veldwerk in Zweden. Op mijn nieuwe werk heb ik een kamer voor me alleen. Dat was wel even wennen. Niet meer even een praatje tussendoor om eens goed mijn hart te luchten (dank daarvoor). Een klein voordeel...ik hoef die domme koptelefoon niet meer op. Ik wens je heel veel succes bij DLG en bij alles wat je gaat doen in de toekomst.

Van mijn collega's wil ik in het bijzonder stil staan bij Jasper, Jinze, Jort en Roy. Jullie aanwezigheid heeft er mede toe bijgedragen dat ik me op mijn plek ben gaan voelen bij NCP. Ik zal jullie zeker gaan missen. Jasper, de aanschaf van een aantal oranje balletjes kon niet verkomen dat ik tot op de dag van vandaag nog geen enkele potje tafeltennis van je heb gewonnen...ja misschien ééntje. Zonder het voetballen, de concerten, het delen van muziek, de Belgische bieren, en nog veel meer was het maar saai geweest. Maar nog belangrijker, jouw inbreng was enorm belangrijk voor mijn onderzoek. Ik heb veel van je geleerd, dank daarvoor! Voorlopig blijf ik in Utrecht, dus af en toe een avondje bij de Belg met jou en onze 'bier-liefhebber' Jort zie ik wel zitten. Jort, jouw humor zal mij lang bijblijven...je hebt, om je eigen quote te gebruiken "heel hard je best gedaan". Wij zaten de laatste tijd in precies hetzelfde schuitje...dat proefschrift moest af en de tijd begon te dringen. Dat geldt helemaal voor jou, want naast het schrijven van je proefschrift was je ook nog eens een drukke papa. Desondanks heb je toch alles netjes op tijd af. Ik heb daar bewondering voor! Bedankt ook voor alle gezellige ritten naar Wageningen, samen met Jasper. Ik zal je humor en relativeringsvermogen gaan missen. Roy en Jinze, bedankt voor de gezellige avonden in Wageningen, Utrecht en Amersfoort (en Amsterdam...Dylan). Ik hoop dat we dit soort avonden zullen blijven ondernemen. Jullie zijn het voorbeeld van hoe je naast hard werken ook nog een hoop lol kunt hebben. Elke leerstoelgroep zou mensen als jullie in dienst moeten hebben.

Jan, Maurits, Frans en Henk. Ik heb het al een keer gezegd in 'De Koperen Kop'...er zou geen onderzoek van de grond komen als jullie er niet waren. Stiekem zijn jullie de stille kracht achter het succes van NCP. " Wij [jullie] slepen de AIO's er wel doorheen", het was geen woord teveel gezegd. Ik heb een fantastische tijd met jullie gehad in het lab en in Ierland, Estland en Zweden.

Hendrik, bedankt dat je me in de gelegenheid hebt gesteld om fotosynthese aan mossen te meten. Ik ben zeer onder de indruk van je bevologenheid en je drang om alles zo scherp mogelijk te formuleren. Ik vond het leerzaam en leuk om met je samen te werken. Nu de hamvraag: "wie van ons is eigenlijk het koppigst?".

Naast mijn eigen onderzoek heb ik ook een aantal studenten mogen begeleiden bij hun scriptie of afstudeeronderzoek. Thijs, Jerina, Maurits en Sylvia, ik vond het leuk om jullie begeleider te zijn.

Jef, Els, Karen (dit moet in het Belgisch), u maakt zelfs een AiO cursus in het nietige Wemeldinge tot een plezierig avontuur. Hopelijk tot snel. Ge zijt altijd welkom in Utrecht.

I was in the lucky position to travel a lot during my PhD research, mainly because my field experiments were executed in Estonia and Ireland. Words can hardly express my appreciation of all those people I met during my visits, but I will try in their own language. Edgar Karofeld was kind enough to translate my text in Estonian...thank you for that. Ma hindasin väga Endla Looduskaitseala inimeste külalislahkust Eestis. Tänu teile tundsin ma end iga kord oodatu ja teretulnuna kui ma külastasin teie kaunist keskust. Katrin, ma loodan, et Sa jätkad retkede juhtimist ja eriti soode looduse ilu õpetamist veel pikka aega. Sind oli väga inspireeriv kuulata ja õppida tundma eesti teed suhtumises loodusesse. Suur tänu! Erilised tänusõnad kuuluvad Kaile. Ma jään Sind ikka meenutama kui enesesse vaatavat meeldivat inimest, tänu kellele sain ma teha oma uuringuid looduskaitsealal. Tänan Sind mind aitamast, informatsiooni jagamast, diskuteerimast ja mind esmatuvustamast eesti keelega (mis Sa arvad, kas ma võiksin kunagi sõnu korrektselt hääldama hakata?). Tänan Sind! Kindlasti tulen ma veel tagasi ja loodan, et kaitseala on ka siis just selline nagu minu viimasel sealolekul. Ma loodan, et Eesti poliitiliste otsuste tegijad mõistavad teie kaitseala tähtsust ja teie, kõigi kaitseala töötajate ja eesti sooteadlaste pingutused tasuvad ennast ära. Soovin teile kõike head!

Ireland will always have a special place in my heart. Although I find conserving peatlands very important, I have to admit that the smell of a turf fire always made me feel comfortable. Clara is a peculiar place, with a lot of nice people though. Cathy and Michael and the rest of the Quinn family, thanks for the warm welcome every time I came to the Estate. I hope that I can visit you in the near future again...Michelle and Clare, good luck with the Holistic centre. Joe, next time I would love to participate in the Gaelic football! Anthony, how was Liège? Thanks also to everyone working for the Irish Peatland Conservation Council (Martin, how are you?) , An Taisce and to the National Parks and Wildlife Service of the Environment, Heritage and Local Government for the hospitality and the possibilities to work in their reserves. Special thanks to Jim Ryan and Colm Malone. Your help was much appreciated. Patrick and Aideen, thanks for the good times in the bog and the pubs in Clara, Cork and Kenmare (please send my regards to your uncle Dennis). You will always be welcome when you are visiting the Netherlands again. Good luck with your boys. Patrick, you are such a fine person to work with, especially in a canoe, although counterbalancing is not your strongest point (or was it me who was not counterbalancing?). Thanks for introducing me to the Irish way of life...I liked it! And of course thanks that you wanted to be my side-kick.

Het laatste half jaar van mijn promotie onderzoek heb ik gecombineerd met het geven van Biologie lessen aan een middelbare school in Breukelen (RSG Brokdele). Ik heb een ontzettend leuke, vermoeiende en leerzame tijd gehad, en ik wil bij deze alle leerlingen van de klassen 2a, 2b, 2g, 3ha, 3hb en 3hd bedanken. Ik vond jullie (meestal) geweldig en moest vaak lachen om jullie fratsen. Ik wens jullie het allerbeste. Eveline, Francien, Babette, Arjen, Hans, Esther en Clary, jullie waren leuke collega's. Bedankt dat jullie me steunden.

Gelukkig was er naast werk volop gelegenheid om ander dingen te doen. Ik noem maar wat...concerten, festivals en films bezoeken, stappen, sporten, etc. Jean, Floor, Rob, Steven, Nisha (thanks for the good time in the US), Gerold, Joze, AJ, Ayco, Sanna (Nakemin!), Bianca, Chris, Annemarie, Joost, Bart, Maaïke, Rudy, Chantal, Birgit, Sipke, Dirk, Volkert, Cristina, Maurits, Ramona, Ralf, Sander, Boudewijn, Lutera, Annelieke, Maaïke, Rianne, Merijn, Ilona, Alette, Josephine, Judith, Eveline, Maïte, Karel, Marjan, Tim, Sai-Hong, Barbara en Toeno (in willekeurige volgorde), bedankt voor alles.

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Tot slot, Mieke. Ik ben ongelofelijk blij met wat wij samen hebben. Je bent onzettend belangrijk geweest afgelopen jaren. Niet alleen heb je me een paar keer geholpen met het veldwerk, je hebt me ook continu gesteund en ervoor gezorgd dat er voldoende afleiding was. Je gaat straks aan je eigen promotieonderzoek beginnen, en ik hoop dat ik dan net zoveel voor jou kan betekenen. Doe bis de betste!

# CV

## Curriculum vitae

De auteur van dit proefschrift werd op 18 september 1978 in Heerlen geboren. In 1990 werd begonnen aan de HAVO aan het St. Antonius Doctor College te Kerkrade. In 1995 werd deze opleiding succesvol afgerond en vervolgde met een VWO opleiding aan het College Rolduc te Kerkrade. In 1997 werd ook deze opleiding succesvol afgerond en in datzelfde jaar werd begonnen aan de studie Biologie aan de Universiteit Utrecht. Tijdens deze studie werden twee stages gelopen. De eerste stage betrof onderzoek naar de effecten van ammonium op de mossen *Sphagnum squarrosum* en *Polytrichum commune* en werd verricht bij de leerstoelgroep Landschapsecologie. De tweede stage werd gedaan bij de leerstoelgroep Gedragsbiologie. In het kader van een herbebossingproject werd in het Centraal Amerikaanse El Salvador gekeken naar het gedrag en de ontwikkeling van de phoride vlieg *Pseudohypocera kerteszi*, een voedsel parasiet in het nest van angelloze bijen (de natuurlijke bestuivers van inheemse planten). Tussen beide stages werd de studie één jaar onderbroken om aan de slag te gaan als secretaris van de Utrechtse Biologen Vereniging, de studievereniging van de faculteit Biologie van de Universiteit Utrecht. De studie Biologie werd afgesloten bij de leerstoelgroep Plantensystematiek met een doctoraalscriptie over de 'ecologische theorie van speciatie'. Na het behalen van het doctoraaldiploma in 2003, werd begonnen als promovendus aan de leerstoelgroep Natuurbeheer en Plantenecologie van Wageningen UR, resulterend in dit proefschrift.

Sinds 1 september 2007 werd Bjorn, na een kort uistapje naar het middelbaar onderwijs, aangesteld als post-doc en junior docent bij het Copernicus Onderzoeksinstituut, Departement Innovatie- en Milieuwetenschappen, Leerstoelgroep Omgevingswetenschappen aan de Universiteit Utrecht.







## List of publications

### *Peer reviewed papers (published or accepted)*

- Robroek BJM, Limpens J, Breeuwer A. and Schouten MGC (2007). Effects of Water level and Temperature on performance of four *Sphagnum* mosses. *Plant Ecology* 190:97-107.
- Robroek BJM, Limpens J, Breeuwer A, Crushell PH and Schouten MGC (2007). Interspecific competition between *Sphagnum* mosses at different water tables. *Functional Ecology* 21:805-812.
- Robroek BJM, Limpens J, Breeuwer A, Van Ruijven J and Schouten MGC (in press). Precipitation determines the persistence of hollow *Sphagnum* species on hummocks. *Wetlands* xx:xx-xx

### *Other publications*

- Robroek BJM, De Jong H and Sommeijer MJ (2003). The behaviour of the kleptoparasite, *Pseudohypocera kerteszi* (Diptera, Phoridae) in hives of stingless bees (Hymenoptera, Apidae) in Central America. *Proceedings of the Section Experimental and Applied Entomology, NEV* 12:65-70.
- Robroek BJM, De Jong H, Arce HG and Sommeijer MJ (2003). The development of *Pseudohypocera kerteszi* (Diptera, Phoridae), a kleptoparasite in nests of stingless bees (Hymenoptera, Apidae) in Central America. *Proceedings of the Section Experimental and Applied Entomology, NEV* 12:71-74.
- Robroek BJM, Schaepman-Strub G, Limpens J, Berendse F and Breeuwer A. (eds.) (2007). *Proceedings of the First International Symposium on Carbon in Peatlands*. Wageningen, the Netherlands.

### *Submitted manuscripts*

- Robroek BJM, Schouten MGC, Limpens J, Berendse F and Poorter H. Interactive effects of water table and precipitation on net CO<sub>2</sub> assimilation of three co-occurring *Sphagnum* mosses differing in distribution above the water table.
- Robroek BJM, Schouten MGC, Limpens J, Crushell PH, Kimmel K, Breeuwer A, Van Ruijven J and Berendse F. Patch size, water table and species identity affect *Sphagnum* persistence after field introduction
- Breeuwer A, Robroek BJM, Limpens J, Heijmans MMPD, Schouten MGC and Berendse F. How ombrotrophic bog vegetation responds to fluctuating water table.
- Breeuwer A, Heijmans MMPD, Robroek BJM and Berendse F. The effect of temperature on growth and competition between *Sphagnum* species.
- Limpens J, Robroek BJM, Heijmans MMPD and Tomassen HBM. Can substrate-derived CO<sub>2</sub> affect *Sphagnum* succession?

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The SENSE Research School declares that Mr. Bjorn Jozef Maria Robroek has successfully fulfilled all requirements of the Educational PhD Programme of SENSE with a work load of 38 ECTS, including the following activities:

**SENSE PhD courses:**

- Environmental Research in Context
- Research Context Activity: Organizing The First International Symposium on Carbon in Peatlands, 15 – 18 April 2007, Wageningen the Netherlands
- Basic and Advanced Statistics
- Interactions Between Element Cycles and Ecosystems
- Summer School Understanding Global Environmental Change: pressure, state and impact

**Other PhD courses and activities:**

- Estuarine Ecology, NIOO
- Project and Time Management
- Debating Course, Utrecht University
- Techniques for Writing and Presenting a Scientific Paper
- NWO – Talent Classes, Politics – Impact – Survival - Success
- Excursion Estonia, Stichting Bargerveen
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**Oral Presentations:**

- SENSE Summer Symposium, 23 June 2005, Ede, The Netherlands
- IX International Congress of Ecology, 7- 12 August 2005, Montreal, Quebec, Canada
- Restoration Ecology Meeting, 4 April 2006, Utrecht, The Netherlands
- 12<sup>th</sup> International Mire Conservation Group, Biennial Symposium, 24 – 26 July 2006, Tammela, Finland

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