

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

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**Abstract:** 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 shows that precipitation alone can explain the persistence of hollow species in high hummocks, whereas it was less important for hollow species in low hummocks. Our data suggest that the survival and potential expansion of hollow species in higher hummocks strongly depends on the intensity and frequency of rain events. Changes in precipitation patterns may result in a loss of *Sphagnum* diversity in hummocks.

**Key Words:** diversity, Estonia, lateral water transport, peatlands, rain water, raised bogs, *Sphagnum cuspidatum*, water content

### 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 under-

stood, 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, such as 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

In 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 ( $\approx$  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 ( $\approx$  25 m) to the area of sampling. Prior to transplantation, any vascular plants in both

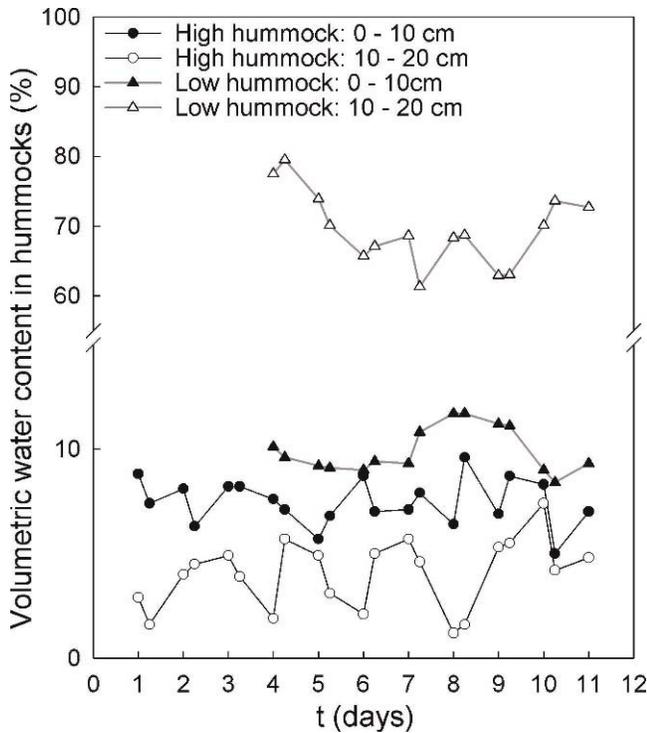


Figure 1. Volumetric water content of the hummock matrix (● = high hummock; ▲ = low hummock) surrounding the embedded hollow samples measured at two depth intervals: 0–10 cm (filled symbols) and 10–20 cm (open symbols).

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 (Figure 1). This low hummock was adjacent to the large hummock. Both hummocks were about 4 m long, 1.5 m wide, and dominated by *S. magellanicum*.

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

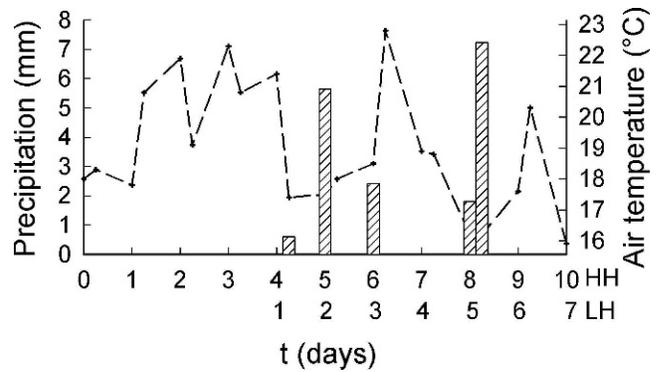


Figure 2. Precipitation (bars represent means; n = 3), and air temperature (line) during the experimental period. Note that measurements at the low hummock (LH) started three days later than the high hummock (HH) measurements.

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) that acted as a frame, which 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 (11:00 and 17:00) over a 10-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 Figure 2). As a result, the measurement in the low hummock started three days later than the measurements in the high 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. However, 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, 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 1991–1995 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, Cambridge, 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 48 hrs 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.

#### Data Analyses

Data were tested for normality and equality of variance prior to analysis. Not all data met the assumptions of homogeneity of variances, even after transformation; however, 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 analyzed 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 (15.8–21.7°C) and the amount of precipitation varied over time (Figure 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 (Figure 1), indicating a stronger influence of the water table.

### Effects of LHWT and Precipitation

In both hummocks, the wet hollow cores lost water to the surrounding hummock matrix shortly after transplantation (Figure 3), yet water loss seemed to be greater in the relatively drier (Figure 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 ( $F_{1,16} = 23.31$ ,  $p \leq 0.001$ ; Figure 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 ( $F_{1,16} = 0.09$ ,  $p = 0.770$ ; Figure 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

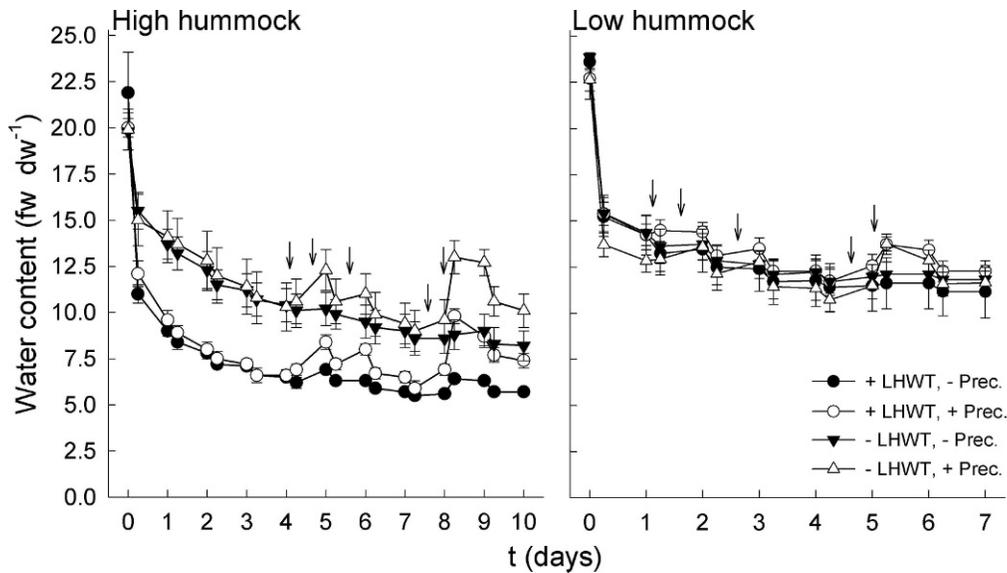


Figure 3. Treatment effects on the water content of *S. cuspidatum* var. *majus* embedded in a high (left) and a low (right) hummock. Arrows indicate rain events (for precipitation data see Figure 2). LHWT = lateral hummock water transport, Prec. = precipitation.

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 ( $F_{1,191} = 152.00, p \leq 0.001$ ; Figure 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 (Figure 4, Table 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 (Figure 4, Table 1), and may be from an experimental artefact. The smallest rain event

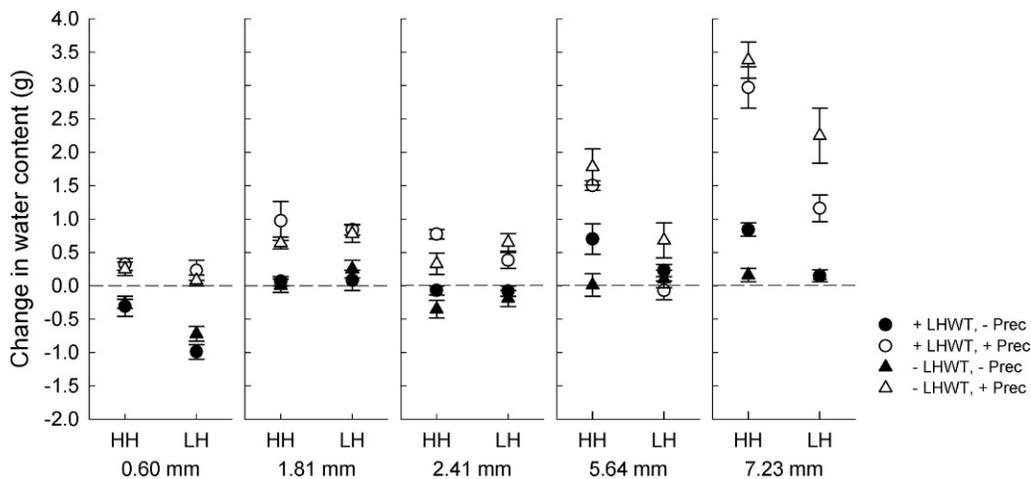


Figure 4. Effects of precipitation, lateral hummock water transport (LHWT), and hummock type on the water content of hollow species, after a precipitation (Prec.) event. For statistics, see Table 1.

Table 1. F-values and p-values (ANOVA) for the effects of hummock type, lateral hummock water transport (LHWT), and precipitation (Prec.) on the water content of the hollow species at five rain events. Numbers in bold indicate significant p-values ( $p < 0.05$ ).

Source	df	Amount of Preceding Rain									
		0.6 mm		1.81 mm		2.41 mm		5.64 mm		7.23 mm	
		F	p	F	p	F	p	F	p	F	p
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										

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 (Figures 3 and 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 (Figure 4, Table 1), but again, eliminating the possibility of LHWT had no effect. After the largest precipitation events (Figure 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 (Figure 4, Table 1); however, this effect was only significant for the high hummock.

## 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 that LHWT has 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 (1985), 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 this site was  $\leq$  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.

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