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Functional Traits in *Sphagnum*

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Abstract

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Peat mosses (*Sphagnum*) are ecosystem engineers that largely govern carbon sequestration in northern hemisphere peatlands. I investigated functional traits in *Sphagnum* species and addressed the questions: (I) Are growth, photosynthesis and decomposition and the trade-offs between these traits related to habitat or phylogeny?, (II) Which are the determinants of decomposition and are there trade-offs between metabolites that affect decomposition?, (III) How do macro-climate and local environment determine growth in *Sphagnum* across the Holarctic?, (IV) How does N₂ fixation vary among different species and habitats?, (V) How do species from different microtopographic niches avoid or tolerate desiccation, and are leaf and structural traits adaptations to growth high above the water table?

Photosynthetic rate and decomposition in laboratory conditions (innate growth and decay resistance) were related to growth and decomposition in their natural habitats. We found support for a trade-off between growth and decay resistance, but innate qualities translated differently to field responses in different species. There were no trade-offs between production of different decay-affecting metabolites. Their production is phylogenetically controlled, but their effects on decay are modified by nutrient availability in the habitat. Modelling growth of two species across the Holarctic realm showed that precipitation, temperature and vascular plant cover are the best predictors of performance, but responses were stronger for the wetter growing species. N₂ fixation rates were positively related to moss decomposability, field decomposition and tissue phosphorus concentration. Hence, higher decomposition can lead to more nutrients available to N₂-fixing microorganisms, while higher concentrations of decomposition-hampering metabolites may impede N₂ fixation. A mesocosm experiment, testing effects of water level drawdown on water content and chlorophyll fluorescence, showed that either slow water loss or high maximum water holding capacity can lead to desiccation avoidance. Furthermore, leaf anatomical traits rather than structural traits affected the water economy.

This thesis has advanced the emerging field of trait ecology in *Sphagnum* by comparing many species and revealing novel mechanisms and an ever more complex picture of *Sphagnum* ecology. In addition, the species-specific trait measurements of this work offers opportunities for improvements of peatland ecosystem models.

Keywords: peat mosses, functional traits, NPP, decay resistance, N₂ fixation, desiccation resistance, climate

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*"Dude, suckin' at something is the first
step to being sorta good at something."*
Jake the Dog

Till Idunn och Finn

List of Papers

This thesis is based on the following papers, which are referred to in the text by their Roman numerals.

- I Bengtsson, F., Granath, G. and Rydin, H. (2016) Photosynthesis, growth, and decay traits in *Sphagnum* – a multispecies comparison. *Ecology and Evolution*, 6: 3325–3341. doi:10.1002/ece3.2119
- II Bengtsson, F., Rydin, H. and Hájek, T. (2018) Biochemical determinants of litter quality in 15 species of *Sphagnum*. *Plant and Soil*, 425: 161–176. doi:10.1007/s11104-018-3579-8
- III Bengtsson, F., Rydin, H., Baltzer, J.L., Bragazza, L., Bu, Z.-J., Caporn S.J.M., Dorrepaal, E., Flatberg K.-I., Galanina, O., Gałka, M., Ganeva, A., Goia, I., Goncharova, N., Hájek, M., Haraguchi, A., Harris, L.I., Humphreys, E., Jiroušek, M., Kajukalo, K., Karofeld, E., Koronátova, N.G., Kosykh, N.P., Laine, A.M., Lamentowicz, M., Lapshina, E., Limpens, J., Linkosalmi, M., Ma, J.-Z., Mauritz, M., Mitchell, E.A.D., Munir, T.M., Natali, S.M., Natcheva, R., Noskova, M., Philippov, D.A., Rice, S.K., Payne, R.J., Robinson, S., Robroek, B.J.M., Rochefort, L., Singer, D., Stenøien, H.K., Tuittila, E.-S., Vellak, K., Waddington, J.M. and Granath, G. Environmental drivers of *Sphagnum* growth in mires across the Holarctic region. (Manuscript)
- IV van den Elzen, E., Bengtsson, F., Fritz, C., Rydin, H. and Lamers, L.P.M. Variation in symbiotic N₂ fixation among *Sphagnum* and feather mosses. (Manuscript)
- V Bengtsson, F., Granath, G., Cronberg, C. and Rydin, H. Mechanisms behind species-specific water economy responses to water level drawdown in peat mosses. (Manuscript)

The published papers are open access.

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Introduction

In northern peatlands, peat mosses (the bryophyte genus *Sphagnum*) are important ecosystem engineers building up thick layers of peat, i.e. poorly decomposed organic matter. *Sphagna* are able to do so as they effectively engineer a wet and acidic environment that inhibits decomposition, and produce peat that is in itself decay resistant (Rydin and Jeglum 2013). Therefore, they represent a substantial component of carbon storage and maintenance of carbon sequestration in peatlands. While *Sphagnum* species are hugely important to ecosystems and potential climate change feedbacks, species-specific ecophysiological functional trait data are lacking, and responses to environmental factors are uncertain.

Production, peat and carbon storage in mires

In non-tropical systems, plant annual carbon (C) uptake varies from 500–700 g m⁻² yr⁻¹ in temperate regions, to below 200 g m⁻² yr⁻¹ in arctic regions (Cramer et al. 2001), while carbon uptake in northern peatlands averages 192 g m⁻² yr⁻¹ for bogs and 208 g m⁻² yr⁻¹ for poor fens (based on data in Moore et al. 2002). Despite net primary production (NPP) being relatively low, peatland ecosystems have remained important carbon sinks throughout the Holocene as production has exceeded decomposition (Yu 2012). As a result, northern peatlands store *ca.* 500 Gt C (Yu et al. 2010; Loisel et al. 2014), which equals more than 50% of the carbon in the atmosphere today (829 Gt; IPCC 2013).

Peatlands are long-term carbon sinks, and are predicted to continue to act as sinks in a warmer climate up to a certain point, when they instead become sources of carbon (Gallego-Sala et al. 2018). For example, a changing climate with more frequent droughts and water level drawdowns could promote vascular plant growth in peatlands due to aerated peat (Rydin and Jeglum 2013). Also nitrogen deposition promotes vascular plants and reduces *Sphagnum* growth (Berendse et al. 2001; Limpens et al. 2011), and may increase the chances of vegetation shifts. Vascular plants in *Sphagnum*-dominated peatlands can account for 50% of gross primary productivity of the ecosystem (Gavazov et al. 2018). However, vascular plant litter decays faster than *Sphagnum* litter (Dorrepaal 2005) and can increase soil respiration through priming (Gavazov et al. 2018). A changing climate could thus

convert peatlands from sinks to sources of carbon through vegetation shifts. However, this topic is complex and subject to ongoing debate (Bacon et al. 2017).

As *Sphagnum* species are the dominant vegetation formers in many northern peatlands, responses of sphagnum to changes in climate and environment will govern vegetation shifts in peatlands. Globally, NPP is largely determined by precipitation and water availability, and in northern regions (above 50°N) temperature and solar radiation become increasingly important (Schloss et al. 2001; Gallego-Sala et al. 2018). Studies that have tried to determine which environmental and climatic drivers are the most strongly linked to variation in *Sphagnum* NPP have come to different conclusions. Gunnarsson (2005) found in a meta-study that temperature, precipitation, altitude and latitude explained 40% of the variation in productivity. Also Moore (1989) identified annual mean temperature as a key driver of *Sphagnum* production, while a meta-analysis by Krebs et al. (2016) found that growth in *Sphagnum papillosum* was primarily influenced by precipitation frequency and the quotient of precipitation:temperature. Others have found solar radiation to be a major influence on *Sphagnum* length growth. A meta-study (Loisel et al. 2012) found that cumulative photosynthetically active radiation (PAR) for days over 0°C was the most important driver of growth. This is an indication of PAR conditions over the entire growing season being influential.

While peatlands seem resistant and resilient to environmental change (Waddington et al. 2015; Robroek et al. 2017), predictions for future development are hampered by the lack of empirical data of large-scale performance variation in *Sphagnum* mosses. And, although the species of *Sphagnum* may seem similar at first, they occupy different niches, and will have species-specific growth responses to climatic and environmental factors, such as water level changes. These responses will be governed by functional traits of the mosses.

Functional traits in the genus *Sphagnum*

The origin of *Sphagnum* dates back about 200 Myr, but the diversification of species in boreal ecosystems is as recent as 15 Myr (Shaw et al. 2010). Some species are notoriously hard to identify, while the genus as a whole is unmistakable. Although the species share a lot of characteristics, there are clearly different strategies within the genus. Species' niches along environmental gradients are due to differences in traits and often different trait combinations are linked to different subgenera (Johnson et al. 2015).

Sphagnum species have different niches primarily along two environmental gradients: a hydrological and an electrochemical (Rydin and Jeglum 2013). The hydrological gradient is a change in microtopography where

different species grow at different Heights above the Water Table (HWT) (Fig. 1). Typically, the dry-growing hummock species are from the subgenus *Acutifolia*, while the wet-growing hollow species are from the subgenus *Cuspidata*. In the subgenus *Sphagnum*, there is more habitat variation between and within species. The hummock species require adaptations to avoid and/or tolerate desiccation, while hollow species need to rely on favourable weather to avoid drying out (Schipperges and Rydin 1998).

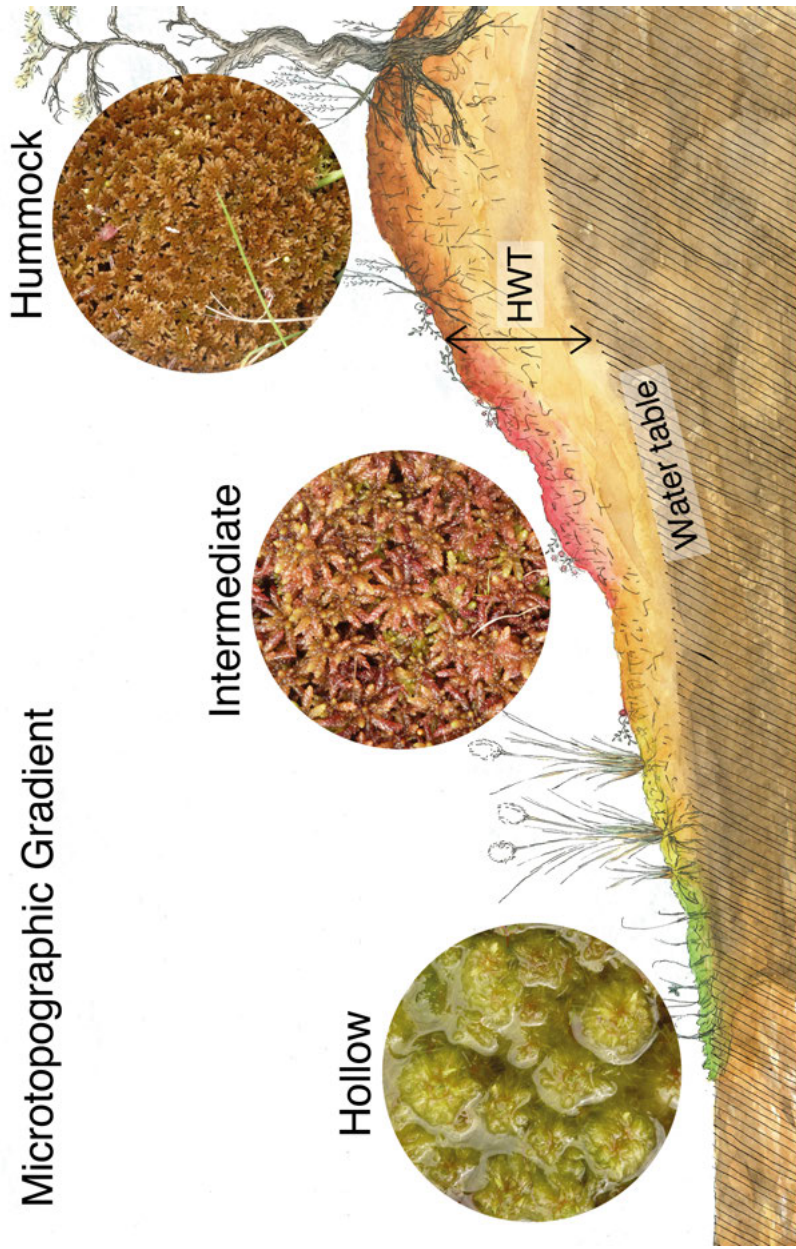


Figure 1. *Sphagnum* species have different microtopographical niches, i.e. they grow at different Heights above the Water Table (HWT). For example, *S. cuspidatum* grows in hollows, *S. magellanicum* on the open bog at intermediate water levels, and *S. fuscum* typically forms hummocks

The electrochemical gradient depends on inflow of mineral rich water, which produces a gradient from rich fens with pH 6 or higher to bogs with pH around 4. In bogs, the peat layer is thick enough that the living vegetation has no access to ground water and is thereby purely rain-fed. In addition to being responsible for forming the thick peat layer, *Sphagnum* mosses help promote *Sphagnum* performance by actively acidifying their environment using cation exchange sites on their cell-walls (Clymo 1963).

Colony structure, shoot morphology and leaf anatomy

The *Sphagnum* shoots build up colonies with more or less tightly packed shoots with their tops growing at equal heights, creating a more or less even surface of photosynthetic tissue. How tightly the shoots are packed affects the surface roughness of the colony. A smoother surface created by smaller shoots evaporates less and provides the moss colony with higher water retention (Elumeeva et al. 2011). Hence, the shoot numerical density is considered a key functional trait for *Sphagnum* water balance (Elumeeva et al. 2011; Laing et al. 2014). How tightly shoots are packed affects the extracellular pore spaces, which comprise 90% of the *Sphagnum* colony's water holding capacity (Hayward and Clymo 1982). A larger volume of smaller spaces, which is a character typical of hummock species, results in stronger capillary forces, and is reflected in a higher bulk density (BD; weight per volume). Consequently, BD is a key trait of *Sphagnum* water economy and the maintenance of a high water table (Hayward and Clymo 1982; Thompson and Waddington 2008; Waddington et al. 2015).

Growth in a *Sphagnum* shoot occurs mainly in the capitulum, which is a collection of tightly packed branches surrounding the apical meristem (Fig. 2). In the event of drought, *Sphagnum* mosses must keep their capitula moist enough to photosynthesise and sustain growth. The water content in the capitulum must stay above 50% of the water content for photosynthesis optimum in order for the moss to maintain photosynthesis and growth (Schipperges and Rydin 1998; Rydin 1993). Relative to other bryophytes, sphagna are desiccation avoiders rather than desiccation tolerant plants (Hájek 2014; Marschall and Proctor 2004). However, there is evidence of tolerance, and of that some species can develop tolerance during slow desiccation processes (Li et al. 1992; Hájek and Vicherová 2013).

The branches are formed in the capitulum in fascicles which will spread out along the stem as it elongates. The branches within a fascicle are clearly differentiated in some species into spreading and pendant branches, where the pendant branches are thought to “wick” water from lower down the water table (Clymo and Hayward 1982). Along the branches, leaves are spirally arranged. The leaves of some species, in particular from the subgenus

Sphagnum, are curved (i.e. convex), which increases water-holding capacity (Såstad and Flatberg 1993; Malcolm 1996).

The branch leaves are one cell-layer thick and constitute two different types of cells: hyaline and chlorophyllous cells. Each of the narrow chlorophyllous cells borders a hyaline cell, which is a large, and when mature, dead cell (Clymo and Hayward 1982). These hollow cells have structurally rigid cell walls and capacity to store water. This is where the last water resources are kept. The hyaline cells are responsible for 10% of the water holding capacity (Hayward and Clymo 1982).

The hyaline cells have pores that passively allow flow of water in and out of the cell (Malcolm 1996). Total area of pores affect water economy, as well as the radius of a single pore. A smaller pore helps the cell hold on to water (Lewis 1988). On which side of the leaf, ventrally (towards the stem)

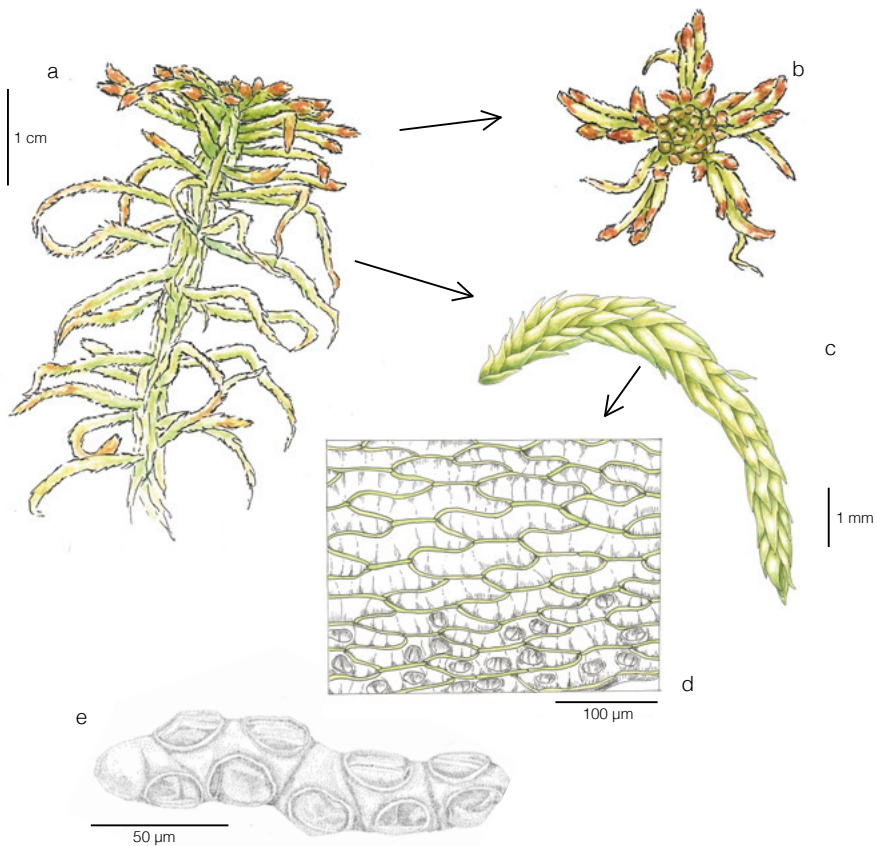


Figure 2. a) A *Sphagnum* shoot with a capitulum at the top, side view, b) Capitulum with apical meristem and tightly packed branches, view from above, c) Branch with overlapping leaves (a–c, *S. fallax*), d) Leaf, one cell layer thick constituting hyaline and chlorophyllous cells (*S. fuscum*, ventral side) and e) Hyaline cell with pores (*S. girgensohnii*)

or dorsally, the pores are placed changes their level of exposure to the outside environment. A similar duality occurs in chlorophyllous cells which in relation to the surrounding hyaline cells are dorsally or ventrally exposed, or sometimes even completely enclosed. While the chlorophyllous cells are better protected against desiccation and solar radiation when exposed on the ventral side, this also aggravates CO₂-diffusion. Wet growing species more often have their chlorophyllous cells exposed on the dorsal side of the leaves, while dry growing species more often expose the cells on the ventral side (Rice and Schuepp 1995).

In addition to shoot morphology and leaf anatomy, colony structure also affects the water economy, i.e. water holding, water retention, and desiccation avoidance, of *Sphagnum*.

Sphagnum mosses produce peat

Sphagnum litter, together with other bryophytes, has been estimated to constitute up to 45% of boreal peat (Turetsky 2003) in both *Sphagnum* and sedge dominated peatlands. Many *Sphagnum* species decompose at a relatively slow rate, allowing them to accumulate peat.

Species differ in decay rates, and research show a trade-off between decay and growth (Turetsky et al. 2008; Laing et al. 2014). Generally, drier growing – hummock species – degrade at a slower rate, and wetter growing – hollow species – at a faster rate (Clymo 1965; Johnson and Damman 1991; Belyea 1996; Limpens and Berendse 2003). Differences are caused both by intrinsic decay resistance of individual species, and by the environment which is created by the moss itself and can be seen as a functional trait: a type of extended phenotype (Dawkins 1982). The height above the water table (HWT) and biochemical properties affect this. However, which biochemical properties that contribute the most to the litter quality of the *Sphagnum* mosses is not clear (e.g. Verhoeven and Liefveld 1997; Freeman et al. 2001; Hájek et al. 2011).

There are several biochemical compounds that *Sphagnum* species produce that putatively improve intrinsic decay resistance. Sphagnan is a cell-wall polysaccharide that has been found to block nitrogen mineralisation of plant litters. This carbohydrate appears to actively inhibit microbial decomposers and is closely tied to the cation exchange capacity (CEC) of the mosses (Hájek et al. 2011). CEC is therefore used as a proxy of sphagnan, but also determines acidifying capacity of the species, which increases the competitiveness and may contribute to decay resistance (Clymo 1963).

The soluble phenolics have often been stated to have a role in hampering decomposition (Verhoeven and Liefveld 1997), while others argue that the soluble phenolics are present in too low concentrations to affect decay (Painter 1991; Mellegård et al. 2009). However, the soluble phenolics may

have an indirect effect on decomposition through impairing activity of phenol oxidase in anoxic peat (Freeman et al. 2001). The more abundant lignin-like phenolics are thought to contribute to structural integrity of the cell walls by shielding them (Tsuneda et al. 2001). Overall, these have been the least studied compounds so far, and results have been varying; while removing lignin-like polymeric phenolics from litter *in vitro* did not increase *Sphagnum* decomposition (Hájek et al. 2011), there are reports of effects *in situ* (Turetsky et al. 2008; Hájek et al. 2011).

Symbiotic N₂ fixation

Although NPP in *Sphagnum* dominated peatlands is low compared to other ecosystems, it is not as low as one would expect given the extremely nutrient poor conditions. *Sphagnum* mosses are homes to diverse microbial communities, some of which have recently been shown to contribute to the carbon uptake potential of peatlands (Jassey et al. 2015). Symbiotic N₂-fixing microorganisms (diazotrophs) contribute to the N pools of peatlands; in *Sphagnum* peatlands, the contribution of diazotrophic N₂ fixation is estimated to be around 35% of the N input (Berg et al. 2013; Larmola et al. 2014). N₂ fixation in *Sphagnum* has been found to explain the discrepancy between the low N inputs through atmospheric deposition and the N assimilation of *Sphagnum* species (Vile et al. 2014). The drivers of the varying rates of N₂ fixation are not well known, and this type of data is needed to understand the relative contribution of N₂ fixation to the total ecosystem N input (Galloway et al. 2004; Vitousek et al. 2013).

Functional trait studies

Functional trait data are necessary for predictions in environmental research such as terrestrial ecosystem modeling (Wullschleger et al. 2014) and species distribution modeling (Moor et al. 2015). In peatlands, species composition may change overall growth, decay, and thereby affect carbon sequestration. Previous studies collecting trait data for *Sphagnum* have been limited in scope and investigate 46 species. Studies across wide geographical scales are also largely missing and mainly constituting meta-studies. Peatland models have recently incorporated *Sphagnum* specific growth (Turetsky et al. 2012) although these functions are still lacking in Earth system models (e.g. ORCHIDEE, Qui et al. 2018).

Aims of the thesis

The overarching aims of this thesis work are to evaluate the importance of traits driving biomass accumulation and decomposition in *Sphagnum*, and to gather trait information for sphagna as a basis for ecological and environmental research.

Specifically, I address the following questions:

- Are growth, photosynthesis and decomposition and the trade-offs between these traits related to habitat or phylogeny of *Sphagnum*? In Paper I we investigated functional traits related to growth and decomposition in *Sphagnum* species, and compared innate growth and intrinsic decay resistance, with realized growth and decomposition.
- Which are the determinants of decomposition and are there trade-offs between metabolites that affect decomposition? In Paper II we quantified the biochemical compounds of *Sphagnum* litter quality, and analysed which compounds determine intrinsic decay resistance and whether there are phylogenetic constraints on metabolite production.
- How do macro-climate and local environment determine growth in *Sphagnum* across the Holarctic realm? In Paper III we investigated which climatic and environmental factors affect *Sphagnum* growth on global and local scales in two species with circumpolar distributions.
- How does N₂ fixation vary among different species and habitats? In Paper IV we investigated the relationships between symbiotic N₂ fixation, and growth and decay in *Sphagnum*.
- How do species from different microtopographic niches avoid or tolerate desiccation, and are leaf and structural traits adaptations to growth high above the water table? In Paper V we investigated species responses to a simulated water table drawdown and identified different strategies related to water economy in *Sphagnum*.

Methods

Sampling sites and species

The mire complex Kulflyten (59°54'N, 15°50'E), Västmanland province, in central-southern Sweden, was central to this thesis and chosen because of the access to many *Sphagnum* species from different HWT niches (Fig. 3). This mire complex comprises a raised ombrotrophic bog with pools and fen soaks (areas which are richer in solutes), pine bog areas (the pine clad outer areas of the bog), and a lagg fen of varying width surrounding the bog. Young spruce forest surrounds the mire with a bottom layer primarily consisting of *Sphagnum girgensohnii* and common feather mosses. In addition, a small rich fen was included, Glon (60°31'N, 17°55'E), in the province of Uppland, where the lime-rich moraines make rich fens relatively abundant. The mean July and December temperatures, respectively, are 16.6°C and –2.6°C at Kulflyten, and 16.8°C and –1.0°C at Glon. Annual precipitation averages



Figure 3. Photo from the bog expanse on the mire Kulflyten.

733 mm at Kulflyten and 649 mm at Glon (1982–2013) (SMHI 2014). Nitrogen deposition is about $0.4 \text{ g m}^{-2} \text{ yr}^{-1}$ at Glon and $0.6 \text{ g m}^{-2} \text{ yr}^{-1}$ at Kulflyten (Lamarque et al. 2013). These two sites are included in all chapters of this thesis. In Paper III we sampled across the Holarctic region including mainly ombrotrophic mires, but also fens in a few cases (Fig. 4).

The *Sphagnum* species were chosen to represent different habitats along the bog–fen gradient, the HWT gradient and a canopy openness gradient, with focus on ecologically important species (Table 1). In general terms, I refer to higher HWT levels as hummocks and lower levels (lawn, carpet, pool) as hollows.

In all studies we selected sampling patches to be uniform, species-specific and to have low vascular plant cover. Overall, we sampled species in their main habitats to define strategies for different species. However, to widen the perspective, two species were sampled in different habitats: *Sphagnum fuscum* in open bog and rich fen, and *S. magellanicum* in open bog, pine bog and spruce forest (Papers I, II, IV, V). Recently, *S. magellanicum* was split

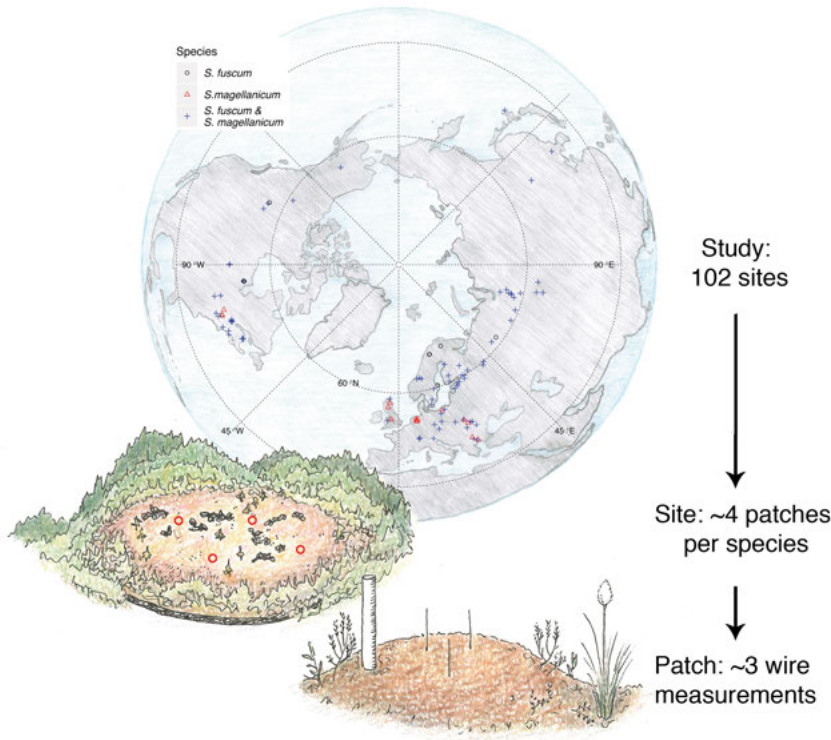


Figure 4. The sampling design in Paper III included 102 sites distributed across the Holarctic region. At each site we sampled *Sphagnum magellanicum* and *S. fuscum* at around four patches each, if they were both present at the site, and at each site we took around three measurements of length increment, and one measurement of bulk density to calculate NPP.

into three species (Hassel et al. 2018). *Sphagnum magellanicum* is only found in South America, while in the northern hemisphere, *S. medium* Limpr. is more common in open bogs, and *S. divinum* Flatberg & Hassel in mire margins and poor fens (Hassel et al. 2018). This division was not known at the time of our sampling and the results therefore refer to *S. magellanicum* s.l.

Sampling designs

In Paper I, we measured growth, photosynthetic capacity, decomposition in lab and field, colony structure, and HWT for 15 species (Table 1). We sampled each species with 10 replicates, however with the exception that we measured CO₂-exchange only for half of the samples (2013). Growth was measured during two vegetation seasons (2012 and 2013).

In Paper II, we measured biochemical composition of litter from the same species but from half of the patches in Paper I. This was done to allow us to relate decay of moss litter from Paper I to litter quality. The moss litter used to determine litter quality was sampled in October 2013.

In Paper III, we sampled across the Holarctic at 102 sites with the aim of covering as wide geographic and climatic gradients as possible (Fig. 4). Three of the sites were excluded due to inconsistencies in sampling. During two growing seasons (2013 and 2014), we measured growth, HWT and vascular plant cover for two species at *ca.* four patches per site. We preferred sites where the species co-occurred, but also used sites where they did not.

We used climatic data from NASA GESDISC (Global Modeling and Assimilation Office (GMAO) 2015) land surface and flux diagnostic products (M2T1NXLND, M2TMNXFLX). We extracted meteorological variables for the specific measurement periods at each site and year, and calculated the average temperature (°C), total precipitation (kg m⁻² yr⁻¹), evaporation (kg m⁻² yr⁻¹) and PAR (PARDF + PARDR, W m⁻²) and the average number of consecutive days without rain (d). Data on nitrogen deposition were extracted from the model synthesis of Lamarque et al. (2013).

In Paper IV we measured N₂ fixation in four *Sphagnum* species and two feather mosses, each with five replicates in September 2014. The *Sphagnum* samples came from the same patches used in Paper I, again to be able to compare to performance and trait data from Paper I.

Paper V included 13 species with five replicates each. We primarily used patches from Paper I. To set up a mesocosm experiment, we sampled *Sphagnum* cores (21 cm deep, 16 cm diameter) in PVC pipes in August 2015. In the lab, we exposed the cores to water level drawdown, while measuring capitulum water content and chlorophyll fluorescence (F_v/F_m).

Table 1. Study species of the thesis, from which habitats and which sites they were sampled, and in which papers of the thesis they were included. Nomenclature follows Flatberg (2013).

<i>Sphagnum</i> species	Subgenus	Microtopographic habitat	Vegetation type	Site	Paper
<i>S. capillifolium</i>	<i>Acutifolia</i>	Hummock	Pine bog	Kulflyten	I, II,
<i>S. fuscum</i>	<i>Acutifolia</i>	Hummock	1) Open bog 2) Rich fen	Kulflyten, Glon**	I, II, III, IV, V
<i>S. girgensohnii</i>	<i>Acutifolia</i>	Hummock	Spruce forest	Kulflyten	I, II, V
<i>S. rubellum</i>	<i>Acutifolia</i>	Hummock–Intermediate	Open bog	Kulflyten	I, II, IV, V
<i>S. warnstorffii</i>	<i>Acutifolia</i>	Hummock–Intermediate	Rich fen	Glon	I, II, V
<i>S. angustifolium</i>	<i>Cuspidata</i>	Hummock	Mire edge	Kulflyten	I, II, V
<i>S. balticum</i>	<i>Cuspidata</i>	Intermediate	Open bog	Kulflyten	I, II, V
<i>S. cuspidatum</i>	<i>Cuspidata</i>	Hollow	Open bog	Kulflyten	I, II, V
<i>S. fallax</i>	<i>Cuspidata</i>	Intermediate	Lagg fen	Kulflyten	I, II, IV, V
<i>S. lindbergii</i>	<i>Cuspidata</i>	Intermediate	Open bog	Kulflyten	I, II, V
<i>S. majus</i>	<i>Cuspidata</i>	Hollow	Open bog	Kulflyten	I, II, V
<i>S. tenellum</i>	<i>Cuspidata</i>	Intermediate	Open bog	Kulflyten	I, II, V
<i>S. magellanicum</i> s.l.*	<i>Sphagnum</i>	1) Intermediate 2&3) Hummock	1) Open bog 2) Pine bog 3) Spruce forest	Kulflyten**	I, II, III, IV, V
<i>S. papillosum</i>	<i>Sphagnum</i>	Intermediate	Open bog	Kulflyten	I, II, V
<i>S. contortum</i>	<i>Subsecunda</i>	Intermediate	Rich fen	Glon	I, II

* Hassel et al. (2018) split *Sphagnum magellanicum* into three species, two of which grow in the northern hemisphere. Papers III–V bring this up, while papers I–II were published before the split.

** In Paper III these species were sampled at 85 (*S. fuscum*) and 91 (*S. magellanicum* s.l.) sites.

Ecophysiological traits

The traits measured and analysed in each paper can be seen in Table 2.

Colony structure

We measured numerical density (ND) by counting the individual shoots in a specified area, and bulk density (BD). In Paper V we split the cores from the mesocosm experiment into three BD sections: BD1 = first 5 cm under the capitula, BD2 = 5–10 cm under the capitula, and BD3 = the remaining moss core, 10–max 20 cm under capitula.

Growth and photosynthesis

We measured two aspects of growth, length increment (LI) and biomass accumulation (NPP). LI was measured using brush wires (Fig. 5). At least three brushes per patch were inserted into the vegetation. NPP was acquired from multiplying LI with BD of the section just below the capitulum.

Photosynthetic capacity was defined as the maximum photosynthetic rate (i.e. at optimum water and light conditions). It was measured in the lab using an infrared gas analyser in ambient air, following Granath et al. (2009). Ca-



Figure 5. Brush wires were used to measure length increment of *Sphagnum* mosses. In the start of the season the brushes were inserted into the *Sphagnum* carpet by first pressing the bristles into a narrow tube that was then inserted down between shoots without disturbing the shoots or peat. When the tube was pulled out and the wire held in place the bristles spread and attached to the vegetation. The length of the wire was then measured (season start height), and measured again at the end of the season (season end height), and the difference between these measurements is the length increment (LI). In the autumn a moss core was collected to obtain bulk density (BD). LI and BD are the two parameters needed to calculate NPP ($LI \times BD = NPP$).

pitula were moistened and placed in an airtight chamber in which gas exchange was monitored as capitula were drying. The maximum CO₂ exchange rate was recorded and the capitulum water content was measured at this point.

F_v/F_m (Maximum potential quantum yield of photosystem II) is a proxy of stress on the photosynthetic apparatus. A value below *ca.* 0.8 indicates a damaged or down-regulated photosystem II (Murchie and Lawson 2013). During the water level experiment (described below), after equilibration with the water level, F_v/F_m was assessed with a pulse-modulated fluorometer after 30 minutes of dark acclimatisation.

Decay

The decomposition of the moss litter was measured using litterbags in the field and in the lab. Moss material was collected in the beginning of summer 2013. The capitula were removed, and the following 3 cm of the shoots were collected and defined as litter. Roughly 100 mg of dry litter was placed into nylon mesh bags. One set of bags was placed in the field at the original patch for each litter, around 5 cm underneath the moss surface, and another set incubated in the lab with water from the bog. The inoculum was supplemented with nutrients to avoid nutrient limitation for the microorganisms. We assessed field decomposition as mass loss (%) after 14 months in the field and lab decomposition as mass loss after 7 and 14 months lab incubation.

Chemical composition and tissue nutrient concentrations

We extracted holocellulose (HC) by bleaching coarsely homogenized litter, following Ballance et al. (2007), and weighed the dry material. From the holocellulose, we extracted the cell-wall polysaccharide sphagnum by acid hydrolysis, and expressed it based on litter mass (mg g⁻¹). We determined cation exchange capacity (CEC) as the amount of exchangeable NH₄⁺ at pH 7 in homogenized litter saturated with NH₄⁺. For extraction of acetone soluble phenolics we followed Bärlocher and Graça (2005), samples were analysed spectrophotometrically. Lignin-like phenolics were assessed gravimetrically from ball-milled litter as sulphuric acid-insoluble residuum (Klason lignin; KL) using a modified procedure, due to these polymeric phenolics in *Sphagnum* being prone to dissolving by acid hydrolysis (Farmer and Morrison 1964; Straková et al. 2010). From the first supernatant during this extraction, we measured dissolved phenolics (soluble KL) spectrophotometrically (Ehrman 1996). We also measured two aspects of chemical stability. As a proxy of carbohydrate concentration, we measured the absorbance ratio between 205 nm:280 nm absorbances, in the supernatant after hot-acid digestion (sphagnum extraction).

Carbon and nitrogen concentrations were analysed in ball-milled litters with an elemental analyser (Papers I, III, IV). P was analysed as phosphate using FIA after digestion of milled litter with perchloric acid (Paper I). P and K were measured using inductively coupled plasma emission spectrometry (Paper IV).

N₂ fixation

Subsamples of moss were ¹⁵N-enriched during 48 hours incubation. Isotopic ratios (¹⁵N/¹⁴N) and atom percent were determined for ground enriched and background subsamples using an elemental analyser. The increase in atom percent in the enriched samples compared to background samples represents ¹⁵N accumulation during the incubation time. The increase was converted to rate based on moss dry weight and expressed as nmol N₂ g⁻¹ d⁻¹.

Water economy

We set up a mesocosm experiment in a growth room, where the water table was gradually lowered from 20 mm under the moss capitula to 50, 100, 150 and finally 200 mm. After each lowering of the water table, the water content of the mosses was given time to equilibrate with the water level, and we then measured capitulum water content (g g⁻¹) and chlorophyll fluorescence yield (F_v/F_m). We extracted the water content at HWT 20 mm (WC₂₀) and 200 mm (WC₂₀₀) and the slopes of water loss (WC_{slope}) to use as responses in models. The water content at the maximum F_v/F_m was extracted from fitted models to be used in analyses.

Leaf traits

The leaf traits were measured in ImageJ from scanning electron microscopy (SEM) micrographs. The micrographs were acquired from one sample per species, and in this sample, leaves were picked from one mature branch. The leaves were mounted on aluminum stubs and imaged in the SEM under 5000V. We quantified eight traits (Table 2) on one leaf of each species showing the dorsal side and one leaf showing the ventral side.

Statistical analyses

We used standard statistical procedures, such as multiple regressions and ANOVA, to analyse relationships between traits (Papers I, II, IV), and PCA to evaluate how traits cluster species according to habitats and phylogeny (Papers I & II). PC axes were extracted to be used as predictors in models (Papers II & V). Linear mixed effects models were used to evaluate climatic

and environmental variables as predictors of growth (Paper III), and to analyse structural, morphological and anatomical traits as predictors of water content responses. Statistical analyses were performed in R (R Core Team 2017).

Table 2. The traits that were measured in each chapter of the thesis and whether the data was also analysed in another paper, and abbreviations and units for each trait.

Trait	Measured in Paper	Used also in Paper	Abbreviations used	Units used
Numerical density	I, III, V		ND	cm ⁻²
Bulk density	I, III, IV, V		BD	mg cm ⁻³ , kg m ⁻³
Length increment	I, III	IV (from PI)	LI	mm
Biomass accumulation	I, III	IV (from PI)	G _i , G _a , NPP	g, g m ⁻²
Photosynthetic capacity	I	IV (from PI)	NP _i , NP _g , NP _a	mg h ⁻¹ , mg g ⁻¹ h ⁻¹ , mg cm ⁻² h ⁻¹
Height above the water table	I, III, V		HWT	mm, cm
Vascular plant cover	III			%
Field decay	I	II, IV		%
Lab decay	I	II, IV		%
Holocellulose, sphagnum, soluble phenolics, lignin-like phenolics, total KL	II	IV	Holocellulose = HC, lignin-like phen. = KL	mg g ⁻¹
CEC	II			µeq g ⁻¹
Soluble KL	II			mg g ⁻¹ , % of total KL
C, N	I, III, IV	II (from PI)		%, mg g ⁻¹
P	II, III, IV			mg g ⁻¹
K	III, IV			mg g ⁻¹
N ₂ fixation	IV			nmol g ⁻¹ d ⁻¹
Leaf length and width	V			µm
Dorsal and ventral pore area	V			µm ² , %
Dorsal and ventral pore diameter	V			µm
Dorsal and ventral chlorophyll cell exposure	V			proportion
Water content responses	V		WC ₂₀ , WC ₂₀₀ , WC _{slope}	g g ⁻¹
Max WC at max F _v /F _m	V			g g ⁻¹
F _v /F _m at HWT 20, 50, 100, 150, 200 mm	V			

Results and Discussion

Growth and decay traits (I)

Innate qualities, i.e. the traits we measured in lab conditions (photosynthetic capacity, lab mass loss) showed different patterns than field responses (LI, NPP, field mass loss). We tested the often stated hypothesis of hummock species having a higher decay resistance than hollow species. While we found support for this, and for the trade-off between measures of growth and decomposition (Turetsky et al. 2008; Laing et al. 2014), these relationships were not strong (Figs 6, 7). Mass loss in lab as a response of growth was better explained (including subgenus as a factor in the regression; $R^2_{\text{adj}} = 0.51$) than field mass loss was ($R^2_{\text{adj}} = 0.06$). Photosynthetic rate as a predictor of lab decay yielded a similar relationship as NPP ($R^2_{\text{adj}} = 0.53$).

We happened to measure growth in one wet and one dry year. In the wet year species from the subgenera *Cuspidata* and *Sphagnum* grew the most, while in the dry year differences among species, sections and habitats evened out. Reciprocal litter bag experiments have indicated that species is a more important factor to decomposition than mire-habitat (Turetsky et al. 2008). We found that there is a higher intrinsic resistance to decay in most *Acutifolia* species. In contrast there are greater habitat constraints by wetness in *Cuspidata* species, as well as in *S. rubellum* (the wettest-growing *Acutifo-*

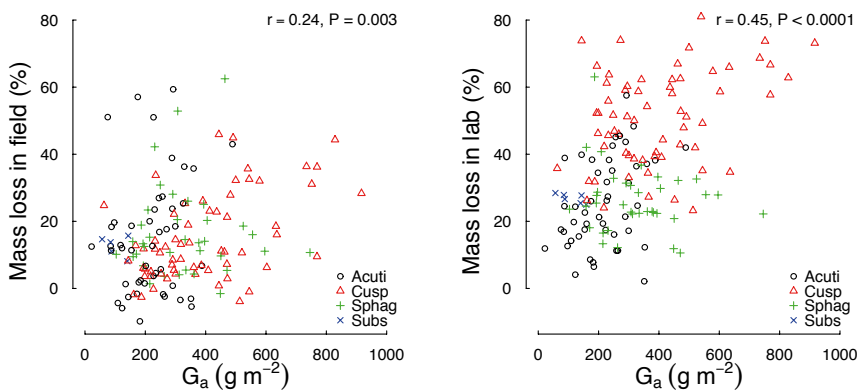


Figure 6. Relationships between decay rate in the field (left; $n = 150$) or in the lab (right; $n = 148$) and the growth in biomass on an area basis G_a (total g m^{-2} for 2012 and 2013).

lia species) and *S. magellanicum* (in its wet bog habitat). We interpreted this as species from *Cuspidata* producing overall more easily decomposable litter, but that their field decay was hampered because of anoxia also at shallow peat depths in their wet habitats. In conclusion, fast growing species could only realise their potential in a wet year and while they also decompose fast in lab, their field decomposition was more retarded than other species.

We also tested the importance of environment and phylogeny in driving functional traits and found that both affected the traits and the trade-offs. In a PCA analysis we saw that species were not perfectly clustered according to either vegetation type or phylogeny (Fig. 7). Some species clustered with others in the same subgenus, whereas others clustered more with others from similar vegetation types.

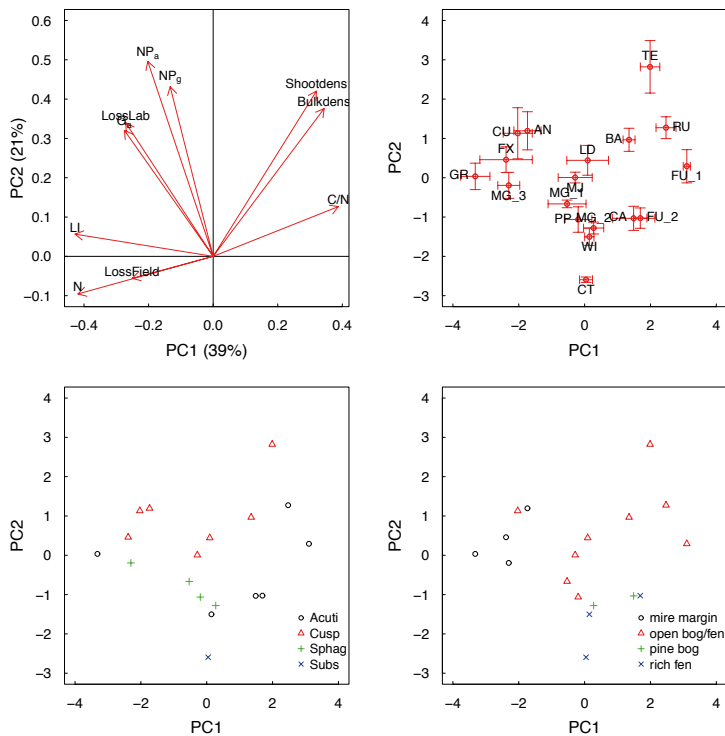


Figure 7. PCA Top left: Trait space showing the factor loadings of the variables: Shootdens = average shoot density between 2012 and 2013; Bulkdens = average bulk density between 2012 and 2013; C/N ratio of litter; N = nitrogen content of litter; LossField = mass loss during 2 seasons (%); LI = pooled length increment in 2012 and 2013 (mm), G_a = pooled biomass growth (g m^{-2}) 2012 and 2013; LossLab = mass loss of litter under standard conditions expressed per unit dry mass (NP_i ; $\text{mg g}^{-1} \text{h}^{-1}$); and per unit area (NP_a ; $\text{mg cm}^{-2} \text{h}^{-1}$). Top right: shows the species distribution along the PC axes (mean \pm SE). Bottom left: species grouped by *Sphagnum* subgenus, and bottom right shows species grouped by vegetation type.

Determinants of decay resistance (II)

We found that the quantity of several metabolites produced by sphagnum vary among species and habitat. ANOVAs ($P < 0.0001$) showed that the subgenera differed in concentrations of the carbohydrate sphagnum, soluble and lignin-like phenolics, and in CEC. Subgenus *Acutifolia* had higher concentrations than *Cuspidata*. A PCA including all the measured metabolites clustered species clearly into their subgenera, indicating a phylogenetic constraint on metabolite production (Fig. 8). Using the PC axes 1 and 2 as predictors of lab mass loss, we only found support for PC1 ($R^2 = 0.56$). PC1 was controlled primarily by lignin-like phenolics (total KL), soluble phenolics and sphagnum (also expressed as CEC), supporting the effects of these compounds in increased intrinsic decay resistance.

We could not detect any trade-offs between compounds affecting litter decay, but rather we found that “more is more”. We found negative correlations between lab mass loss and sphagnum ($r = -0.61$) and soluble phenolics ($r = -0.57$), similar to previous reports for sphagnum (Painter 1991; Børshheim et al. 2001; Painter 2003; Hájek et al. 2011) and soluble phenolics (Freeman et al. 2001; Bragazza et al. 2006). Additionally, we found a negative correlation between lab mass loss and the previously understudied lignin-like phenolics ($r = -0.59$). We used the sum of the three main compounds (after cen-

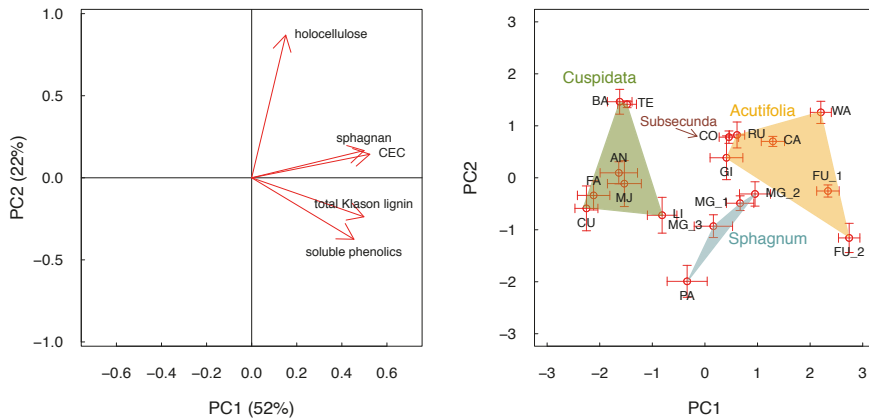


Figure 8. PCA including only the measured metabolites. Left: The metabolites include holocellulose, sphagnum, soluble phenolics, total Klason lignin and CEC = cation exchange capacity. Right: The distribution of the species in the trait space (with x and y standard error bars), and envelopes around species from the same section. *Sphagnum* species codes: AN = *S. angustifolium*, BA = *S. balticum*, CA = *S. capillifolium*, CO = *S. contortum*, CU = *S. cuspidatum*, FA = *S. fallax*, FU_1 = *S. fuscum* (open bog), FU_2 = *S. fuscum* (rich fen), GI = *S. girgensohnii*, LI = *S. lindbergii*, MG_1 = *S. magellanicum* (open bog), MG_2 = *S. magellanicum* (pine bog), MG_3 = *S. magellanicum* (spruce forest), MJ = *S. majus*, PA = *S. papillosum*, RU = *S. rubellum*, TE = *S. tenellum*, WA = *S. warnstorffii*.

tering and scaling the concentrations) as a predictor of lab mass loss (Fig. 9) and found that not only sphagnum and soluble phenolics, but also the lignin-like compounds are all important determinants of decay resistance.

Adding the tissue nutrients (C, N, P) to the PCA changed the species clustering and the regression, indicating that effects of the metabolites on decay are modified by nutrient concentrations in the litter, which is under habitat control.

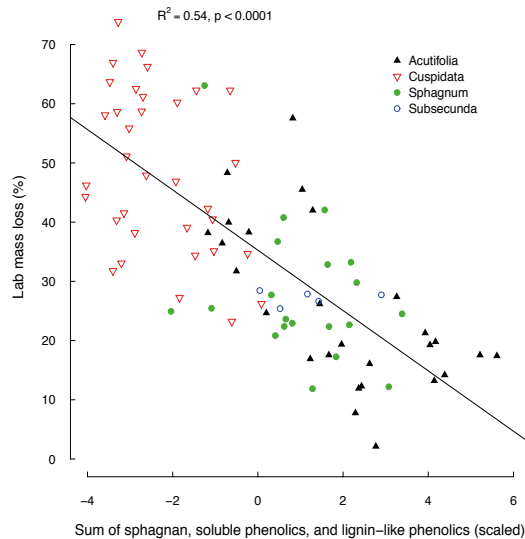


Figure 9. The lab mass loss (%) as a function of the summed metabolite concentrations of sphagnum, soluble phenolics and lignin-like phenolics (centered and scaled variables; $df = 84$).

Determinants of growth (III)

Our coordinated effort of measuring selected species' growth during the same vegetation seasons and with the same methods produced a unique global dataset. We found that variation in *Sphagnum* growth can be as large within as between peatlands, which means that both local environmental variables and global factors can influence growth. Our models with length increment as growth response had better fit than models with NPP.

In support of meta-studies (Gunnarsson 2005; Moore 1989) we found that the best climatic predictors of growth were *precipitation* and *temperature* (Table 3). These had stronger positive effects on *S. magellanicum* than on *S. fuscum*. The local factor *vascular plant cover* had a consistent negative effect on *Sphagnum* performance across our models, but no differential effects on species. In contrast to other studies, our data did not suggest that distance

to the water table controls *Sphagnum* growth within a species, or that current N deposition affected *Sphagnum* growth. Photosynthetically active radiation also had little impact when controlled for climatic variables, in contrast to (Loisel et al. 2012).

The difference in length growth between species was apparent, but *Sphagnum* NPP was relatively stable over space, time and species. *Sphagnum fuscum* – typical hummock forming species that is smaller, denser, and drier growing – had weaker responses to climate predictors than the larger, looser and wetter growing *S. magellanicum*. The two species represent different strategies within *Sphagnum*. Consequently, it seems probable that *S. fuscum* will retain its function better in a changing climate, while *S. magellanicum* will increase its competitive ability in a wetter and warmer climate, but will fail if the warmer climate coincides with lower precipitation.

Table 3. Significant effects ($p < 0.1$) of the models. In addition to main effects the models included interactions between species and the other predictors. +/- after variable name shows directions of main effects. Colors signify: The categorical factors Year and Species are shown in white boxes when significant. For other predictors, blue = positive effect, red = negative effect, purple = different responses in the two species (f, *S. fuscum*; m, *S. magellanicum*) and the directions of species effects are then given. R^2 -values represent variances explained in the models including only main effects.

Species		m>f
<div>LI</div> <div>(mm yr⁻¹)</div> <div>R² = 0.47</div>	precipitation	+ m(+)>f(+)
	temperature	+ m(+)>f(+)
	evaporation	m(+)<f(+)
	vascular	–
	plant cover	–
	N tissue	+

Species		m<f
<div>NPP</div> <div>(g m⁻² yr⁻¹)</div> <div>R² = 0.05</div>	Year	2014<2013
	precipitation	+ m(+)>f(+)
	temperature	+ m(+)>f(+)
	evaporation	m(–)<f(+)
	vascular	–
	plant cover	–

Variation in N₂ fixation (IV)

We found appreciable variation in rates of N₂ fixation, both among species and among habitats. Habitat was a relatively important factor determining N₂ fixation rates in our data, as shown by lower rates of N₂ fixation in open bog samples compared to mire margin and spruce forest samples. N₂ fixation rates in mires have been found to be higher in wetter areas (Granhall and Selander 1973; Larmola et al. 2014). In our data, *S. fallax* growing in the wet lagg fen had consistently among the highest N₂ fixation rates. The different habitats sampled for *Sphagnum magellanicum* differed in N₂ fixation rates between the open bog and the treed habitats. The treed habitats are richer in P (Aerts et al. 1999), which is reflected in the higher P concentrations in *Sphagnum* tissue there (Fig. 10b). Availability of P is limiting to N₂ fixation

(Vitousek et al. 2013; van den Elzen et al. 2017), consequently, a tree-covered habitat with higher P input may lead to increased N_2 fixation rates.

Analysing relationships between *Sphagnum* traits and N_2 fixation, we found that decomposability, i.e. lower intrinsic decay resistance, was positively related to N_2 fixation ($R^2 = 0.50$; Fig. 10a). We also found positive relationships with field decomposition ($R^2 = 0.16$) and tissue P concentration ($R^2 = 0.19$; Fig. 10b). We interpreted these results as an effect of decomposability on N_2 fixation where higher concentrations of the biochemical compounds that hamper decomposition (Paper II) may also limit diazotrophic activity. We specifically found a negative relationship between lignin-like phenolic compounds and N_2 fixation ($R^2 = 0.21$). The realised decomposition makes nutrients from the *Sphagnum* tissue available, and thereby increases the activity of the N-fixers. More nutrients available in the habitat may increase N_2 fixation, while it may also be a result of N_2 fixation increasing the nutrient concentration of the *Sphagnum* tissue, which in turn, promotes decomposition. To conclude, if a higher input of P to the ecosystem stimulates N_2 fixation, long term *Sphagnum* growth increases through increased N availability. Higher availability of both N and P may result in increased turnover rates, resulting in a positive feedback loop.

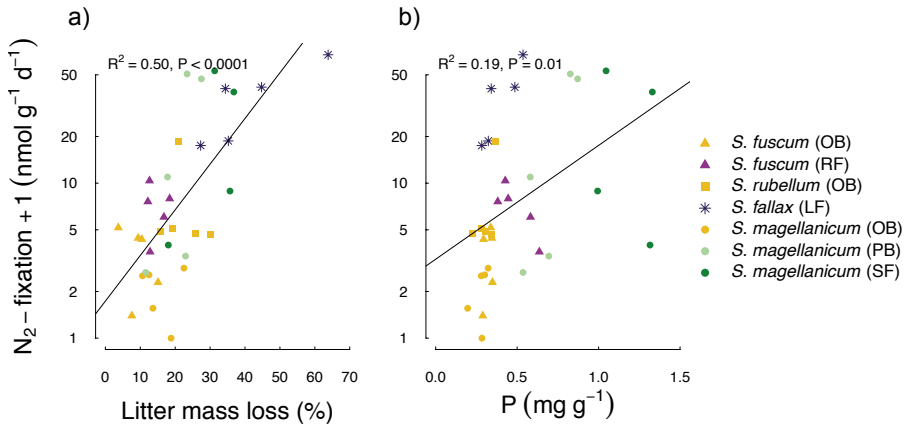


Figure 10. N_2 fixation rate +1 on a logarithmic scale, plotted against a) decomposability (litter mass loss (%) after 7 months incubation in the lab) and b) P concentration ($mg\ g^{-1}$) of *Sphagnum* dry weight.

Water economy (V)

Most species that were sampled at high HWT lost water slowly during the water level drawdown experiment, indicated by shallow slopes of water loss (WC_{slope}) (Fig. 11). However, *Sphagnum magellanicum* that was sampled at high HWT in the pine bog had a steep slope (more negative WC_{slope}), but this was accompanied with a high maximum water holding capacity (i.e. high capitulum water content at the 20 mm water level). Our interpretation is that a high capitulum water content during drought can be achieved either by slow water loss or high maximum water holding capacity.

We found that the stress response F_v/F_m is linked to water content in a similar way as photosynthesis, which in *Sphagnum* is impeded by drought or in very wet conditions due to lower CO_2 diffusion. In our models this relationship was only strong for hollow species, indicating that the drought conditions of the experiment were not severe enough for photosystem II to be damaged in hummock species. The estimated water content at maximum F_v/F_m for each species and plotted this against the field HWT (Fig. 12). Drier growing species had in general lower water content at their maximum F_v/F_m , but, again, *S. magellanicum* sampled in the pine bog was aberrant. It grew among the driest and had a very high WC at maximum F_v/F_m .

Growth and decomposition is tied to where along the microtopographical (HWT) gradient a species grows (Paper I). This in turn is determined by

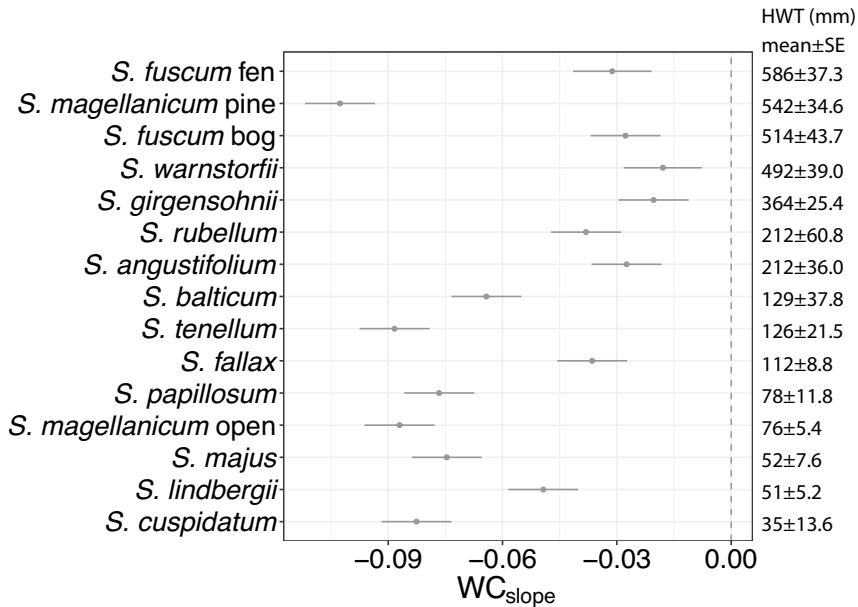


Figure 11. The slopes of the regression lines between capitulum water content and water level (WC_{slope}) in the water level drawdown experiment plotted for each species with 95% confidence intervals. The species are ranked according to their mean HWT.

structural, morphological and anatomical traits. We found some support of leaf anatomical traits influencing the water economy. When the water availability was high (WL 20 mm), larger leaves (PC2) was the most influential predictor of increasing water content. This may be due to that the leaves in the species with larger leaves are also more curved, leading to a higher extracellular water holding capacity (Såstad and Flatberg 1993). At low water level (WL 200 mm) the capitulum water content was higher in species growing at a high microtopographic position in the field. In these conditions larger hyaline cell pore sizes, total pore areas, and more exposed chlorophyllous cells (PC1) were associated with higher water content. Surprisingly, there was weak support of higher bulk density leading to higher capitulum water content, and no support of numerical density increasing water content.

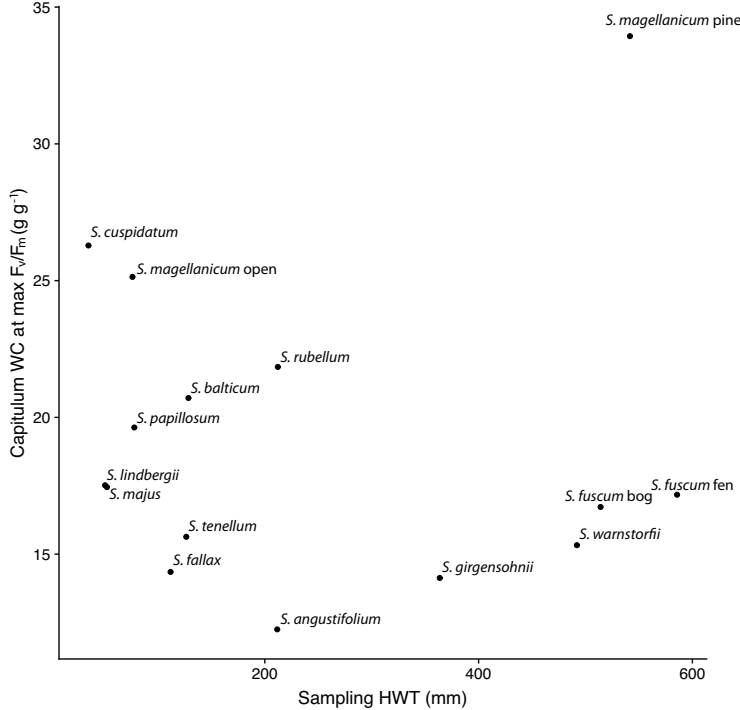


Figure 12. The water content at the predicted maximum F_v/F_m is plotted in relationship to mean sampling height above the water table (HWT) for each species

Conclusions

Inclusion of a relatively wide range of species and habitats has produced a more complex picture of the ecology of the genus *Sphagnum*. We showed that while the previously described growth-decay trade-off exists, the picture is more complicated. While species did not align perfectly within subgenus according to growth and decay traits, they did cluster within subgenera in a PCA using the metabolites. We concluded that some metabolites are under phylogenetic control, but that their effects on decay are modified by nutrient concentrations in the litter, which is under habitat control. Consequently, if a species has high intrinsic decay resistance, the habitat is of less importance.

The high intrinsic decay resistance of hummock sphagna, which is interlocked with their anatomical and morphological stress-avoiding adaptations, can be seen as a trade-off for fast competitive growth. Higher concentration of the metabolites that determine litter quality is necessary for success in drier habitats, while fast growth is facilitated by water availability in wetter habitats. We saw that the hummock growing *S. fuscum* engineers a stable environment with high intrinsic decay resistance allowing it to grow at similar pace in drier and wetter weather conditions. The wetter growing *S. magellanicum*, on the other hand, produced lower amounts of decay resistant biochemical compounds and was more sensitive to weather conditions. Holarctic species realize their potential only in a wet year, while growth in a dry year is hampered for such species, and in line with this, we found that *S. magellanicum* responds with more growth in wetter and warmer conditions, which means its growth would be impeded by a drier climate. This may be true for other wet growing species as well, but needs empirical evidence.

We found that while our hypothesis about water economy traits being related to HWT niches was true for most species, there seems to be two different strategies for hummock species to maintain moisture during water level drawdown. Our interpretation was that while most hummock species avoid desiccation by capillary forces and water retention, *S. magellanicum* from the pine bog instead is capable of a large water holding capacity. The water holding capacity makes this species able to benefit more strongly from rain events. It seems to be able to do so only in treed habitats, since this is where it forms hummocks.

As well as being able to form hummocks, *Sphagnum magellanicum* had higher N_2 fixation rates in treed habitats. This suggests that a drier climate leading to water level drawdowns and thereby promotion of higher tree cover in mires, may result in a competitive advantage for this species. Although the Holarctic data showed that *S. magellanicum* had lower growth under low precipitation, this result was based on including only open mires. The negative effects of vascular plants on growth in the Holarctic data is most likely due to the small vascular plants bestowing competition, while trees rather provide a protective canopy. Better possibility for *S. magellanicum* to main-

tain moisture level under a canopy, increased growth with the help of N₂-fixers and higher growth under higher temperatures, may all provide advantages in a changed climate. These differences aside, *S. magellanicum* from treed and open bog habitats were similar in metabolite signals, and the lower intrinsic decay resistance may lead to degradation of more of its peat in such aerated conditions.

S. magellanicum in the northern hemisphere is now described as *S. medium*, mainly growing on open bogs, and *S. divinum*, with a main distribution in mire margin habitats. However, after publishing our results a morphological assessment indicates that the samples from each habitat, contain both species (det. Kjell Ivar Flatberg). The genetic differences between the species are small, and it is possible that both species are sufficiently plastic to succeed in either habitat.

In addition to advancing the emerging field of trait ecology in *Sphagnum* by comparing many species and revealing novel mechanisms in the ever more complex picture of *Sphagnum* ecology, the species-specific trait measurements of this work offers opportunities for improvements of peatland ecosystem models. The trait data from Paper I & II have already come in use in modeling relating traits to ecosystem processes through mechanistic pathways (Mazziotta et al. 2018), and there is a wide international interest in building a trait data-base for *Sphagnum*. Functional trait relationships are necessary for understanding the long-term dynamics of peatland communities; in a changing world such relationships will have implications for carbon sequestration and management of carbon stocks.

Funktionella egenskaper hos vitmossor

Torv och kollagring

Föreställ dig tiden då landväxterna tog sig upp på land för cirka 500 miljoner år sedan. Då var landskapet kargt och alldeles kalt. Vi skulle inte ha kunnat andas luften för att koldioxidhalten var för hög. Mossor tillhör de första organismgrupper som koloniserat land. Landväxterna sänkte koldioxidhalten i atmosfären genom fotosyntes – under vilken växter tar upp koldioxid och släpper ut syre. Då skapades förutsättningar för andra organismers evolution. Föreställ dig nu landskapet efter en istid. Marken har skrapats bar från biologiskt material. De första kolonisatorerna, de arter som klarar sig, är mossor och lavar. De gör det möjligt för de flesta andra organismer att kolonisera.

Landväxterna tar upp mycket kol som de lagrar i vävnaderna, och här är vitmossor (*Sphagnum*; Figur 2) en av de starkast lysande stjärnorna. De bildar stora myrmarker där de dominerar växtligheten och lagrar kol i form av torv. Torv är döda växtdelar som inte brutits ner fullständigt. Trots att dessa marker inte täcker mer än 3 % av landytan är mer kol bundet i vitmossornas torv än i något annat växtsläkte, dött eller levande. Om vi jämför den mängd kol som uppskattas vara bundet i *Sphagnum* (600Gt) med så mycket kol som det finns i atmosfären (810Gt) kan vi förstå att dessa torvmarkers öde kan påverka vårt.

Vitmossor är intressanta eftersom de är “ekosystemingenjörer”, vilket betyder att de skapar sina egna miljöer. De är de vanligaste växterna i sina habitat, och eftersom de kan hålla otroliga mängder vatten ser de till att marken blir så pass blöt att den blir syrefattig. De producerar också biokemiska ämnen, och skapar en näringsfattig och sur miljö. Detta leder till att de flesta nedbrytande organismerna inte trivs, och att de flesta kärlväxter inte kan växa tillsammans med dem. Som doktorand i växtekologi har jag jobbat med att mäta olika egenskaper hos olika arter av vitmossor och hitta skillnader i ekologin hos olika arter. Jag har studerat de egenskaper som är till nytta för vitmossorna, dessa kallas för funktionella egenskaper. Olika arter kommer att påverkas olika vid ett förändrat klimat, och den data mitt doktorandprojekt genererat kan användas för att i sin tur studera climateffekter.

Snabb tillväxt eller långsam nedbrytning – olika strategier

Kapitel I handlar om tillväxt och nedbrytning hos 15 olika vitmossor. Vi mätte hur mycket de växte per säsong i längd och vikt i fält med hjälp av små flaskborstar. Borstarna sattes ned i vegetationen på våren, vi mätte hur mycket de stack upp, och sedan mätte vi hur mycket som fortfarande stack upp på hösten (Figur 5). Skillnaden i mätningarna från hösten och våren är tillväxten i längd. Sedan mätte vi även den maximala fotosynteshastigheten i labb, vilket kan ses som mossans potentiella tillväxt. Nedbrytning mättes både i fält och i labb, genom att packa in mossmaterial i nätpåsar och placera dem i fält eller labb. Efter en tid mättes hur mycket vikt de förlorat. Labb-nedbrytningsförsöken skedde under samma förhållanden för alla arter och visar arternas inneboende motstånd mot nedbrytning. Fältstudien visar snarare den faktiska nedbrytningen.

Med denna typ av data kunde vi diskutera de avvägningar, ”trade offs”, som arterna gör för att vara framgångsrika i olika miljöer. Det har länge funnits en idé om att arter som växer blötare kan växa snabbare, men att de då producerar mer lättnedbrutet material, och därför bryts också ner fortare. Vi kunde visa detta i viss utsträckning, men också påpeka undantag eftersom vi jämförde så många arter. Eftersom vi mätt både ”inneboende” och ”verkliga” egenskaper, kunde vi dra slutsatsen att de snabbväxande arterna endast kan hindra nedbrytning och växa fort när förhållandena är gynnsamma. De långsamväxande arterna skapar mer stabila förhållanden, som gör dem motståndskraftiga mot nedbrytning och kan växa även när det är torrare.

Vitmossornas motståndskraft mot nedbrytning

Kapitel II handlar om vitmossornas biokemi. Vi analyserade samma arter, från samma platser, som i kapitel I och kunde därför jämföra biokemiska ämnen direkt med nedbrytningshastighet på labb. Här var målet att ta reda på vilka ämnen som är viktigast för nedbrytningsresistensen, och hur mycket av dem det finns i mossorna. Vi kom fram till att de arter som bryts ner långsamt, har mer av alla de metaboliter som andra forskare tidigare föreslagit hindrar nedbrytning. Däremot påverkas nedbrytningen av den miljö mossan växer i. De arter som växer blött bryts ner långsamt så länge deras habitat håller sig blött, men de har dålig motståndskraft mot nedbrytning så fort det blir torrt. Arter med hög inneboende motståndskraft bryts ner förhållandevis långsamt oavsett miljö. Vi kunde också dra slutsatsen att de biokemiska egenskapernas mängd är väldigt lika inom olika grupper av vitmossorna. Det verkar som om vissa grupper kanske inte har möjlighet att utveckla större produktion av ämnena.

Mer regn och värme gynnar vitmossornas tillväxt

Kapitel III handlar om tillväxt på en global skala och om vilka omvärldsfaktorer som påverkar tillväxten hos två vitmossor: rostvitmossa och praktvitmossa. De är båda vanliga och kan växa vid relativt olika förhållanden. De förekommer på olika sorters myrar, vid varierande vattenstånd och är viktiga ur ett ekologiskt perspektiv som de främsta torvbildarna. Här mättes deras tillväxt på cirka 100 myrar kring den nordliga hemisfären, och sedan analyserades vilka faktorer som påverkade tillväxten. Ökad nederbörd och högre temperatur var de faktorer som mest ökade tillväxten. Praktvitmossan – den art som främst växer i blötare förhållanden – påverkades mest. Detta skulle kunna betyda att om ett varmare klimat också är blötare, skulle vitmossorna kunna växa mer, och kunna lagra mer kol.

Kvävefixerande bakterier kan hjälpa vitmossor att växa

Kapitel IV handlar om de symbiotiska kvävefixerande mikrober som bor i vitmossorna. Myrar är naturligt kvävefattiga, och därför borde tillsatser av kväve vara viktiga här. Kvävefixering står för cirka 35 % av kvävetillgången i myrar. Vi mätte kvävefixering i fem olika vitmossor och två vanliga skogslevande mossor. Vi upptäckte att vitmossor som bryts ner långsamt också har lägre kvävefixering. Troligen hämmar de ämnen som gör dem motståndskraftiga mot nedbrytning inte bara nedbrytande mikroorganismer, utan även kvävefixerarna. Vi upptäckte också att praktvitmossan, som vi samlat i både öppna och trädklädda miljöer, hade högre kvävefixeringen i de trädklädda habitaterna. Praktvitmossan innehöll mer fosfor i de här habitaterna. Vi tror att mer fosfor i mossorna kan leda till mer tillgänglig näring för kvävefixerarna, vilket ökar kvävefixeringen. Detta skulle kunna öka mossornas tillväxt.

Vattenhushållning: hur vitmossor undviker uttorkning

Kapitel V handlar om hur vitmossor undviker uttorkning genom att hålla mycket vatten både mellan skott, grenar och blad, och inuti sina celler. Vitmossor har nämligen stora, döda celler som kan fyllas med vatten (Figur 2). I ett experiment placerade vi mossvegetation i rör och utsatte dem för en gradvis sänkning av vattennivån. Sedan mättes vatteninnehåll i mosskottens toppar efterhand. När vi jämförde hur snabbt de förlorade vatten såg vi att de flesta arter som kan växa torrare förlorade vatten långsamt. Det fanns dock ett undantag: praktvitmossan som vuxit där det fanns träd växte väldigt torrt, men förlorade ändå vatten snabbt. När vi tittade på vatteninnehållet vid vår blötaste experimentnivå såg vi att praktmossan har förmåga att hålla mer

vatten än andra arter. Därför kan den förlora mycket vatten, men ändå behålla tillräckligt mycket för att klara sig. Den verkar ha en alternativ strategi för att klara av att växa torrt, men den kan bara göra det när det finns träd.

För att ta reda på vilka egenskaper vitmossor behöver för att kunna hålla vatten mätte vi egenskaper som hur tätt vitmosskott växer och hur mycket de väger. Vi mätte arternas blad och andra bladegenskaper. Sedan testade vi om dessa egenskaper påverkar vatteninnehållet vid olika vattentillgång. Vi kom fram till att bladegenskaperna var de viktigaste egenskaperna för vattenushållning jämfört med exempelvis hur tätt de växer.

Vid varje vattennivå mätte vi även stressnivån hos mossorna. Detta kan göras genom att mäta klorofyllfluorescensen, som visar om deras fotosyntesapparat skadats. Mossornas fotosyntes går ner när det är för torrt, men även när det är för blött. Då hindras koldioxid från att nå fram till klorofyllcellerna. Vi visade att det fungerar så även när det gäller klorofyllfluorescensen. Detta stämde bäst för de arter som växer blött. Experimentets förhållanden var nog inte tillräckligt hårda för att de torktåliga vitmossorna som är anpassade för att växa högt över vattennivån, skulle få försämrade klorofyllfluorescens på grund av uttorkning. Vi lyckades helt enkelt inte stressa dem nog.

Myrens mossor i ett förändrat klimat

Eftersom vi inkluderade så många arter blev bilden av vitmossornas ekologi mer komplicerad än vad som tidigare antagits. Framförallt kunde vi visa att för de arter som bryts ner långsamt spelar miljön en stor roll för både nedbrytning och tillväxt. De arter som producerar mindre av de ämnen som står för motståndskraften mot nedbrytning är nämligen mer känsliga för torka. När vi jämförde två arters tillväxt i förhållande till klimat och miljö drog vi slutsatsen att båda kan växa mer när det är blötare och varmare, men den blötare växande arten, praktvitmossa, gynnas mer. I den studien mätte vi praktvitmossans tillväxt på öppna myrar. Praktvitmossan visade sig också ha högre kvävefixering i skogen, där den klarar av att växa torrare. Ett torrare klimat kommer troligen leda till mer träd på myrar. Jag tror att dessa fördelar för praktvitmossan i trädklädda habitat kan leda till att den kommer att bli vanligare i framtiden.

Data som beskriver enskilda arters egenskaper och hur arter svarar på olika miljöfaktorer behövs för att kunna förutspå förändringar i vegetation, det vill säga vilka arter som växer var. Dessa vegetationsförändringar kommer att påverka hur våra myrar fortsätter att lagra kol, eller om de istället kommer att börja släppa ut mer kol. Min förhoppning är att de data mitt avhandlingsarbete genererat kommer att visa sig mycket användbara för sådana förutsägelser.

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