



Research article

Calcium intolerance of fen mosses: Physiological evidence, effects of nutrient availability and successional drivers



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ABSTRACT

Species composition of peatlands is determined by the dominance of either *Sphagnum* or non-sphagnaceous (brown) mosses. *Sphagnum* species are more or less intolerant to alkaline waters rich in calcium bicarbonate, but the physiological background of this intolerance is poorly understood. Recently, sphagna have been widening their realized niches, expanding to alkaline brown-moss fens and altering their functioning. One possible reason is increased nutrient availability, but existing evidence is equivocal. We approached this problem by a series of laboratory experiments with 15 fen moss species cultivated submerged in solutions corresponding to natural poor- to rich-fen waters. We tested basic ecophysiological mechanisms of calcium tolerance (ion compartmentalization, cell-wall cation-binding properties, phosphorus and iron uptake), the breadth of fundamental pH/calcium niches for protonemata and adult plants, interspecific competition, and relationships between nutrient availability and pH/calcium tolerance. Our results suggest that calcium toxicity in calcifugous bryophytes is caused by insufficient control over the balance of intracellular Ca^{2+} uptake/efflux. Cell-wall cation-exchange sites of living mosses remain unsaturated with Ca^{2+} even in calcareous solutions, contradicting the proposed inhibitory effect of Ca^{2+} -oversaturation on cell-wall expansion and monovalent cation uptake. Growth and biomass accumulation of brown mosses was highest in alkaline fen waters, but they could also survive and germinate in poor-fen waters. Calcium-tolerant sphagna survived along the entire poor–rich gradient, but their growth was inhibited by calcium bicarbonate. The three most obviously expanding sphagna produced protonemata even under calcareous conditions. Flowing but not stagnant alkaline fen waters were toxic for calcifugous sphagna, the strongest competitors in poor-fen waters. Increased potassium availability facilitated the survival of calcifugous sphagna in alkaline fens, corroborating field observations that potassium facilitates sphagnum expansion. Surprisingly, the rare and declining moss *Hamatocaulis vernicosus* was supported by nitrogen and phosphorus more than its competitors. Our comparison of fundamental and realized niches suggests that the dominance of particular moss functional groups in fens is governed by a competitive hierarchy altered by different calcium levels. The expansion of calcium-tolerant sphagna into brown-moss fens therefore requires perturbation that weakens competition. Additionally, expansion of calcifugous sphagna to alkaline environments may be stimulated by potassium availability.

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1. Introduction

Two contrasting ecosystems occur within peatlands. One is dominated by *Sphagnum* species and one by so-called brown

mosses, i.e. non-sphagnaceous, usually weft-forming calcium-tolerant bryophytes (Vitt, 2000). Brown-moss fens (calcareous and extremely rich fens, referred to as alkaline fens in the present study) are usually an earlier successional stage and may turn into *Sphagnum* fens rather rapidly. Because this successional transition is connected with great changes in species composition, species richness, conservation value, nutrient cycling and carbon dynamics, it turned out to be an attractive topic of current peatland ecology (Granath et al., 2010; Soudzilovskaia et al., 2010; Tahvanainen, 2011; Laine et al., 2015). However, little is still known about the mechanisms triggering this important ecosystem

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change, and its physiological background has not yet been studied.

The ecosystem shift between brown-moss fens and *Sphagnum* fens is generally linked with altered hydrology and expansion of *Sphagnum* mosses. The genus *Sphagnum* represents mostly calcifugous species that are well adapted to acidic, ion-poor conditions (bogs and poor fens), which they help to create through acidification, water retention, and production and accumulation of poorly decomposable peat (Rydin and Jeglum, 2006). If environmental conditions in fens allow the establishment and spreading of *Sphagnum* at the expense of dominant brown mosses, their ecosystem engineering features could isolate fen vegetation from the influence of calcareous ground water and consequently speed up the succession from alkaline fens to acidic poor fens, i.e. from species-rich to species-poor habitats (Kooijman, 2012). In addition, *Sphagnum* expansion is associated with the disappearance of rare, EU-protected species (Štechová et al., 2012) and short-lived fen specialists (Peterka et al., 2014).

The range of conditions under which fen mosses can establish and expand their fundamental niches with respect to water alkalinity (i.e. calcium bicarbonate concentration) is still unknown. Consequently, we lack a fundamental comparison of realized niches that would allow us to separate the effects of competition and environmental toxicity on species distribution—information valuable for the conservation of the rich fen biota. As bryophytes generally show great dispersal ability, limitation by water chemistry has a crucial effect on their distribution (Hájek et al., 2011); spore germination and protonema development thus may be the critical phase of initial species recruitment (Forman, 1964).

The alkaline to acidic fen transition had occurred frequently during the entire Holocene (Kuhry et al., 1993; Wehrli et al., 2010); it is, however, more frequent and more rapid in modern agricultural landscapes. The reasons are not entirely clear. Experimental and correlative studies provide somewhat equivocal results, stressing the role of different factors alleviating the influence of alkaline water on late-successional species. These are either water table decline, or increasing availability of phosphorus, ammonium, potassium or iron (van Diggelen et al., 1996, 2015; Hájek et al., 2002, 2014; Kooijman and Paulissen, 2006; Navrátilová et al., 2006; Kooijman, 2012; Peterka et al., 2014). The lack of a thorough understanding of successional drivers in fens is, among others, caused by our poor understanding of basic physiological mechanisms that may be involved in calcium (in)tolerance of fen mosses (i.e. their calcifuge–calcicole behaviour). In this study, we therefore aimed to elucidate the ecophysiological mechanisms behind calcifuge–calcicole behaviour of fen bryophytes, to test their possible modifications by altered nutrient availability and finally to understand the observed successional patterns.

Although the mechanisms behind calcium toxicity in bryophytes are unknown, it is well understood that calcifugous species (i.e. *Sphagnum* mosses) are intolerant to high concentrations of the calcium cation ($[Ca^{2+}]$) when combined with high pH, while the separate effects of the two factors seems to be negligible (Clymo, 1973). In alkaline fen waters, high pH is maintained by buffering properties of bicarbonate anions, associated with Ca^{2+} . Flooding by alkaline water should thus have a strong negative effect on *Sphagnum* species. Yet, it had a strongly negative effect on the competition ability and survival of the transplanted bog species *Sphagnum fuscum*, but not on rich-fen sphagna (Granath et al., 2010). Studies of calcifuge–calcicole behaviour of vascular plants and other eukaryotes have revealed that nutrient deficiency, processes at the cell-wall level and/or intracellular metabolism may be involved in calcium toxicity. As concerns the intracellular compartment, the intolerance seems to be linked with regulation of calcium homeostasis. The calcium cation is a key component of signalling pathways in the plant cell (White and Broadley, 2003).

Hence, its cytosolic concentration (the influx–efflux balance) must be strictly regulated. Because Ca^{2+} cannot be accumulated in the cytosol, high external $[Ca^{2+}]$ enhances Ca^{2+} accumulation in vacuoles (Conn et al., 2011) and stimulates the expression of transporters responsible for extracellular Ca^{2+} efflux (Ca^{2+} -ATPases and Ca^{2+}/H^+ exchangers; Garcíadeblas et al., 2001; Kamiya et al., 2006). Consequently, calcicoles may differ from calcifuges in their tolerance of intracellular Ca^{2+} accumulation (Zohlen and Tyler, 2004) and linked expression of calcium transporters in the vacuolar or plasma membrane. Moreover, since the function of Ca^{2+}/H^+ antiporters is regulated by pH (Pittman et al., 2005), the increased toxicity of Ca^{2+} under high pH, enhanced by flooding, might be explained by increased intracellular Ca^{2+} accumulation.

The involvement of the apoplast (cell wall) compartment in calcium toxicity has been studied mainly with respect to inhibition of plant growth. The plant cell wall is interwoven by unesterified pectin chains bearing negatively charged carboxyl groups. Cross-linking of pectic carboxyls by Ca^{2+} is fundamental for maintaining the dimensional structure and firmness of the cell wall (Hepler and Winship, 2010). However, full saturation of pectic residues by Ca^{2+} under high pH makes the cell wall more rigid (Fraeye et al., 2009), inhibiting its loosening necessary for cell growth (Proseus and Boyer, 2006; Hepler and Winship, 2010). Aside from growth, cation exchange sites might interfere with nutrients uptake. In Ca^{2+} -rich solution of high pH, Ca^{2+} may condense (in terms of Manning's counterion condensation theory) on carboxyl cation-exchange sites of the cell wall and create an apoplastic barrier that prevents intracellular uptake of univalent cations, such as K^+ and NH_4^+ (Dainty and Richter, 1993).

Nutrient deficiency due to low iron and phosphorus availability has been suggested as the crucial reason why calcareous environments are unfavourable for vascular plants (Zohlen and Tyler, 2004) or lichens (Paul et al., 2009), as these elements become insoluble (Boyer and Wheeler, 1989; Zak et al., 2010). Phosphates precipitate with calcium whereas iron precipitates mainly as carbonate or (hydr)oxides, but also as phosphate. Calcicoles are able to make these nutrients available by exuding low-molecular-weight acids and phenolics (Tyler and Ström, 1995; Paul et al., 2009; Ishimaru et al., 2011), but this mechanism has not been described in bryophytes even though they exude the same organic acids as tracheophytes (Lenton et al., 2012). Recent nutrient analyses of fen mosses revealed that potassium availability may facilitate the expansion of poor-fen sphagna into alkaline fens (Hájek et al., 2014; Hájek et al., unpublished results); a physiological explanation based on experimental evidence is missing, however.

In our study, we conducted a series of greenhouse cultivation experiments in order to assess fundamental niches of dominant fen mosses (in the protonema and the gametophore developmental stage) with respect to water chemistry. We tested whether nutrient deficiency and/or processes on levels of the cell wall and intracellular metabolism may be involved in calcium (in)tolerance of fen bryophytes, and discuss the results in the context of *Sphagnum* establishment in alkaline fens.

Specifically, we tested the following hypotheses concerning calcium intolerance of fen mosses exposed to alkaline fen water:

- Tolerance of fen mosses to calcium bicarbonate in artificial rich fen waters reflects the calcifuge–calcicole pattern observed in the field. Cells are unable to maintain a calcium balance, which results in Ca^{2+} accumulation.
- Saturation of cell-wall pectic residues by Ca^{2+} inhibits plant growth and/or uptake of other nutrients.
- As in vascular plants, low availability of iron and/or phosphates limits moss growth (production).

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