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Research article

Patterns in moss element concentrations in fens across species, habitats, and regions

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ABSTRACT

The ionome and stoichiometry of fen mosses have not yet been studied in extensive data sets despite their potential to explain ecological behaviour of the species and to indicate nutrient limitation or oversupply. We analysed element concentrations (N, P, K, Ca, Mg, and Fe) in apical parts of dominant peat and brown mosses along the complete pH/calcium gradient in fens of three Central European regions (the Western Carpathians, the Bohemian Massif and, marginally, the West-Bohemian mineral springs). We obtained data from 143 localities for 56 species, with the most replicates for calcium-tolerant *Sphagnum warnstorfii*. Tissue element concentrations were to a great extent determined by species identity, except for magnesium, iron, and potassium (in the potassium-poor region). Water chemistry determined substantially species' magnesium, potassium (in the potassium-poor region), and partially also calcium concentrations. Calcium and potassium concentrations were generally most predictable by water chemistry, water table depth (WTD), and species identity, while concentrations of nitrogen, phosphorus, and especially iron were least predictable. Principal component analysis across the species showed the same two principal gradients in all regions. One reflected the ratios between iron and the other ions and the other the ratios between calcium + magnesium and other ions, sorting the species from calcicole (*Scorpidium cossonii*) to acidicole (*Sphagnum fallax*). Particular species differed strongly with respect to calcium concentration in both the biomass and the water, and median calcium concentration in a species coincided greatly with median concentration in the water. Tissue phosphorus, nitrogen, and potassium also differed significantly among the species, but analogous coincidences with the concentrations in water were not found. The results for iron and magnesium were inconsistent between the regions. Within particular species, correlations between biomass and water element concentrations were either positive or negative, but largely nonsignificant. The rare moss *Hamatocaulis vernicosus* had higher element concentrations (except for nitrogen) than would be predicted from water chemistry, resembling the pattern of R-strategy plants. In the Western Carpathians, calcium concentrations in *S. warnstorfii* decreased significantly with WTD, becoming stabilised at around 5 mg/g at WTD >15 cm. The inter-regional differences in species element concentrations were usually explainable by different iron, magnesium, and potassium concentrations in water, with signs of phosphorus immobilisation by iron such as generally higher N:P ratios in the iron- and simultaneously phosphorus-richer region (Bohemian Massif). Because moss chemical composition combines the effects of species identity and various effects of the environment, caution is needed in any meta-analysis.

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Introduction

Fens are fascinating but threatened ecosystems with unique and diverse species composition and history (Hájek et al., 2006; Grootjans et al., 2012; Horsák et al., 2012). This is why they became a model system for developing and testing ecological theories. In particular, studying the relationships between water chemistry (notably pH, base saturation, and nutrient availability) and species composition and diversity have a long tradition (du Rietz, 1949; Sjörs and Gunnarsson, 2002; Tahvanainen, 2004; Pawlikowski et al., 2013). Besides water chemistry, element concentrations in moss (Brehm, 1971; Gignac, 1990; Malmer et al., 1992) and vascular plant tissues (Waughman, 1980) have been analysed since the 1970s, giving information about plant nutrient uptake and changes in nutrient availability along the dominant pH gradient, as well as about the relationship between water level, evapotranspiration, and water calcium and biomass calcium concentrations (Brehm, 1971; Aulio, 1982; Gignac, 1990). Nevertheless, most data on moss element concentrations in wetlands came from ombrotrophic bogs (e.g., Pakarinen and Tolonen, 1977; Gerdol, 1990; Wojtuń, 1994; Bragazza et al., 2004), whilst fens have been represented only marginally, either by a low number of species, a low number of replicates, or both (Pakarinen and Tolonen, 1977; Aulio, 1982; Gignac, 1990; Malmer et al., 1992; Bombonato et al., 2010).

Two decades ago, an increasing amount of data on plant-biomass nutrient concentrations has resulted in the development of a powerful method how to indicate the nature of nutrient limitation by using nutrient ratios in aboveground biomass (Koerselman and Meuleman, 1996; Güsewell, 2004). Ecological stoichiometry (especially the N:P ratio) became popular across habitats (Güsewell, 2004; Sardans et al., 2012; Fujita et al., 2013; Wang and Moore, 2014). As a consequence, recent studies on moss element concentrations in bogs focus almost exclusively on either large-scale patterns in the nutrient ratios along the nitrogen deposition gradients (e.g., Bragazza et al., 2004; Jiroušek et al., 2011; Wang and Moore, 2014) or experimental testing of the impact of nitrogen or phosphorus addition on tissue chemistry and stoichiometry (Limpens et al., 2003; Fritz et al., 2012; Millett et al., 2012). Recent mainstream peatland science thus pushed the research on ions other than nitrogen and phosphorus in fen bryophytes to the margin of interest, although the present knowledge is very limited. This study ultimately aimed to gather a comprehensive data set across a suite of species, habitats, and regions in order to address the question of generality and predictability of patterns in moss element concentrations. Why is this important? There are still a couple of unresolved questions in bryophyte and peatland ecology that could be at least partially addressed by a rigorous, sample-rich study of bryophyte biomass concentrations of major elements.

First, it is still not entirely clear what underlies the ecological behaviour of bryophytes along the environmental gradients. Is their calcicole behaviour a result of tolerance to, or avoidance of, excess calcium in tissues, or a mirror of changes in nutrient availability (Paulissen et al., 2004; Kooijman and Hedenäs, 2009)? Does the pattern in biomass element concentrations reflect the well-known vegetation gradients within mires that correspond to water pH/calcium level and nutrient availability (Wheeler and Proctor, 2000; Hájek et al., 2006)? More generally, is element biomass concentration a species-specific trait that corresponds to the species' tolerance to environmental conditions? The hypothesis about the tolerance of calcicole mosses to high biomass calcium concentrations as well as the more general ionome concept (Salt et al., 2008) predict genes and gene networks that control directly the mineral nutrient composition of an organism. If this is true, then nutrient concentrations could be a useful indicator of general ecological demands of the species (or an ecotype) and an excellent species trait, which would be applicable in functional ecological analyses. On the other hand, bryophytes are widely used as biondicators of either background pollution by toxic metals (Samecka-Cymerman et al., 2005; Harmens et al., 2010, 2012; Díaz et al., 2013; Vuković et al., 2013) or atmospherically deposited nutrients (Bragazza et al., 2004; Harmens et al., 2011; Jiroušek et al., 2011), or the nature of nutrient limitation (Bragazza et al., 2004; Pawlikowski et al., 2013) – this last approach is based on a fundamentally different premise. If it is valid, then biomass nutrient concentration is an excellent proxy of mineral-nutrient availability, which could be used in the cases when the concentration in water strongly fluctuates seasonally (Hájek and Hekera, 2004; Jiroušek et al., 2013). Unfortunately, studies aimed at disentangling species-specific and environmental effects on biomass chemistry are rare, and they involved bryophytes only marginally (Bombonato et al., 2010).

Second, there are major structural types of fens (dominated by non-sphagnaceous 'brown' mosses, calcium-tolerant sphagna, or calcifuge sphagna) that differ in species composition and diversity of many taxonomic groups (Hájek et al., 2006). However, these major types are successionally interlinked; brown mosses can be replaced by calcium-tolerant sphagna, followed by calcifuge sphagna. Chemical limits of these developmental stages differ by region and may even be changing recently because of ongoing environmental changes (Kooijman, 2012). For the former successional shift, an interaction between water table depth (WTD) and calcium concentration might be crucial. Peat mosses do not tolerate overflooding by calcium-rich water (Granath et al., 2010), which is mirrored in the prevalence of brown mosses over peat mosses in rather calcium-poor fens of precipitation-rich areas (Sekulová et al., 2013; Jiménez-Alfaro et al., 2014). For the latter successional shift, enhanced availability of either nitrogen and phosphorus (Kooijman, 2012) or iron (Hájek et al., 2002) may cause acidicole peat mosses to spread in rather calcium-rich conditions and outcompete calcium-tolerant species, but the underlying physiological mechanisms are unknown.

The analysis of biomass element concentrations across species, habitats, and regions would provide the critical data to solve these questions. Specifically, this study examined these patterns, compared particular species belonging to different ecological groups, and tested the following hypotheses:

(i) The overall patterns in biomass chemistry across the species and fen habitats reflect the major vegetation gradients within fens and do not differ among the regions.
(ii) If there is a difference between the regions in the ecological behaviour of a species with respect to water chemistry, the biomass element concentration will be similar and different ecological behaviours can be explained by an interaction between particular water chemistry variables (e.g., iron and calcium).
(iii) The concentration of elements in moss biomass is species-specific, reflecting the species' ecological behaviour in nature, but it can be partially affected by the depth to calcium-rich water table.

Materials and methods

Field research

Three contrasting Central European regions were selected for the research (Fig. 1). They differ in the representation of calcareous and non-calcareous bedrock and general water chemistry pattern. In the Inner Western Carpathians (Slovakia, hereafter referred to as the *Western Carpathians*), the study fens are developed in the montane belt where calcareous substrate is abundant