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Factors shaping submerged bryophyte communities: A conceptual model for small mountain streams in Germany

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ABSTRACT

Several models explaining species composition of aquatic bryophytes are available for specific regions. However, a more general, conceptual model applicable to a broader range of regions is lacking.

We present a conceptual model ranking environmental factors determining submerged bryophyte communities in small mountain streams. It was tested on a dataset of 54 stream sections after removing the effect of stream size and altitude. Species responses were modeled with pH as predictor variable based on 97 stream sites covering six mountain regions all over Germany. Multiple regressions revealed the importance of primary growth factors (light, Ep(CO_2)) and substrate for the total submerged bryophyte coverage.

The known distinction of hard- and softwater bryoflora was clearly supported. The floristic composition of headwaters was predominantly determined by the bicarbonate/ionic strength complex. Species response to pH values supported this result and thus our conceptual model. The primary growth resources light, Ep(CO_2) and availability of coarse streambed material explained one third ($R_{adjusted}{}^2 = 0.34$) of total submerged bryophyte cover. Disturbances, predominantly spates, reduce biomass but do not affect the basic floristic structure.

In conclusion, conceptual models and monitoring methods focusing on aquatic bryophytes need to clearly distinguish "aquatic" from "submersed by chance". All "aquatic bryophytes" found in Germany can also occur at least temporarily at non-submerged sites. Therefore, a distinction between primary growth factors and additional resources is recommended to disentangle factors determining aquatic bryophyte communities.

Introduction

Ecological information for the small group of submerged bryophytes and their role in stream ecosystems is sparse. Reasons may be their low dominance and spatially heterogeneous arrangement in many stream types (Stream Bryophyte Group, 1999) or their reputation as an exclusive group studied only by specialists. In zoological investigations submerged bryophytes are commonly regarded as a substrate (phytal) because they provide a unique habitat for macroinvertebrates (Butcher, 1933; Suren, 1993; Riis and Biggs, 2003). They also offer macroinvertebrates shelter against physically and chemically related impacts (e.g. Glime, 1994; Parker et al., 2007). Aquatic bryophytes have rarely been used for classification purposes (e.g. stream typology) or as bioindicator (Zechmeister et al., 2003), as there are much fewer experts for bryophytes than for macroinvertebrates, amphibians or algae (Fritz et al., 2009). In contrast to vascular plants, the high potential for vegetative and generative (spores) propagation of submerged bryophytes leads to a high similarity of its flora in the holarctic, thus Central Europe and Scandinavia share many species with Northern America and Canada (Frahm and Vitt, 1993; Dierßen, 2001).

Terms like water mosses, stream bryophytes or aquatic bryophytes are difficult to define in a rigorous way biologically. All three terms assume that the aquatic medium is either the only or the most favored site where these species show maximum growth and complete their life cycle including spore-germination, protonema formation, gametophyte- and sporophyte induction and growth as well as spore dispersal (Tremp, 1999). Following this definition all aquatic bryophytes in Germany might be regarded as facultative aquatics as discussed already decades ago by Elßmann (1923). Some of them prefer – but not mandatory – a permanent submerged stage, but even with the genus *Fontinalis* sporophyte development does not occur in a long-term fully denudated situation. From early desiccation experiments (Irmscher, 1912) it is

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known that leaves of *Fontinalis antipyretica* die after 14 days but the stems will regenerate after four weeks of drought. Several species of the genus *Fontinalis* can survive up to one year in humid places (Glime, 1971) or even falling dry over several weeks, as is commonly found in ephemeral and periodical karstic streams or in mountain streams over wintertime. In such conditions aquatic bryophytes survive on the dry land, under cold-dry conditions or even covered with snow.

Compared to submerged vascular plants "water mosses" seem to be ecologically unspecialized, considering that the vegetative stages of most mosses, even such of dry habitats as *Grimmia pulvinata* or *Bryum argenteum*, are able to survive completely submerged conditions over one year (Elßmann, 1923). Growth experiments by Zastrow (1934) showed that aquatic and amphibic forms of aquatic bryophytes could be transferred into each other and vice versa. Goebel (1889; cited in Gessner, 1955) called bryophytes "halbe Wasserpflanzen" (semi waterplants) as submerged forms of amphibic or terrestrial bryophytes are often not only falsely identified but also treated as new species.

Summing up Gessner's (1955, p. 270) remark about the amphibic mode of life of some bryopytes "... viable in both air and water, but nowhere completely at home" seems justified. The search for specific adaptive species traits to cope with the selective forces of their habitat is therefore questionable. The only but most important trait shared by all aquatic bryophytes is their high regenerative capacity, e.g. sprouting from small pieces of stems tightly attached with rhizoids and leaves which are able to develop rhizoids.

It is stated that their non-adaptive strategy makes them so successful in dealing with the harsh environment of the land–water ecotone in headwater streams, where aquatic vascular plants, adapted well to the aquatic environment, cannot cope with such selective forces. Aquatic bryophytes try to occupy highly disturbed sites of severe stress. Grime (1977) assigned no viable plant strategy to such habitat characteristics. But Kautsky's (1988) stunted strategy type, complementing the CSR strategy, matches the comparatively small, slow-growing, long living species with many various types of vegetative diaspores well.

At the small scale in streams, a vertical bryophyte zonation on boulders and walls can be found (Watson, 1919; Glime, 1970; Craw, 1976; Glime and Vitt, 1987). It shows an increasing species richness within the gradient from submerged to the semi-aquatic, hygropetric or splash zone (Vitt et al., 1986; Glime and Vitt, 1987; Muotka and Virtanen, 1995). Muotka and Virtanen (1995) described the shift from truly aquatic species to facultative aquatics and semi aquatics along the vertical gradient as being gradual. This zone can also be regarded as shelter zone for aquatic species from where recovery after spates might occur (Tremp and Kohler, 1993). Besides vertical zonation in structurally rich streams, longitudinal changes, classified and termed upper, middle and lower zone (Holmes and Whitton, 1977), on vegetation occur. Often the upper zone is dominated by bryophytes. The upper zone in silicate streams can be divided floristically further when alkalinity and pH rise with distance from the source (Demars and Thiébaut, 2008) and can be distinct when a stable acidity gradient of physiological relevance – i.e. pH 4–7 – is developed (Tremp and Kohler, 1993; Tremp, 1999).

Numerous publications in relation with the European Water Framework Directive (EU, 2000; Hering et al., 2006; Szoszkiewicz et al., 2006) stimulated scientific research in this field and gave proposals for monitoring. However the application (Staniszewski et al., 2006) and applicability (Demars and Edwards, 2009) of macrophytes, and even more bryophytes in freshwater monitoring is still limited and sometimes questionable due to lack of sound data. Hence, the present paper has the following three objectives:

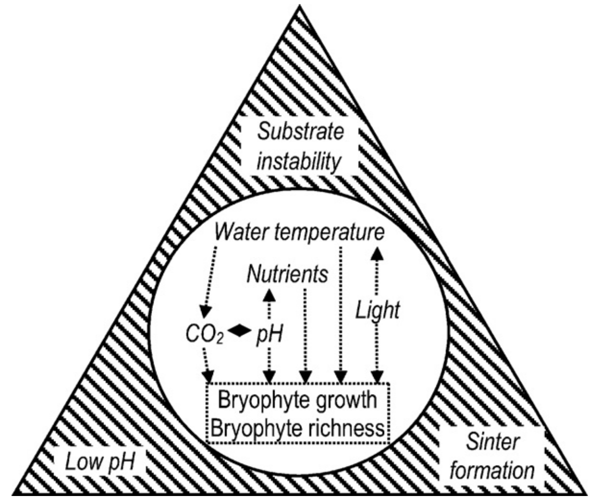

Fig. 1. Conceptual model of the abiotic environment and strictly submerged bryophytes in streams. The bryophyte community firstly differs between hardwater and softwater type. The three corners of the triangle indicate site factors which reduce submerged bryophytes directly: mechanical stress due to substrate instability/current velocity and the subsequent grinding of plant material. Carbonate-incrustation and high acidity reduces aquatic species occurrence dramatically. Apart from these extremes the primary growth factors (inner circle) shape the bryophyte community.

(i) we propose an integrative conceptual model for submersed bryophyte composition and structure;
(ii) we then test some of its predictions using data collected across Germany;
(iii) finally we compare our findings with existing conceptual models from Northern America, New Zealand and Finland.

A conceptual model of aquatic bryophyte occurrence

Several conceptual models in aquatic bryophyte ecology can be found, for regions of different relief energy, i.e. for alpine streams (Suren, 1996; Suren and Ormerod, 1998; Suren and Duncan, 1999) or lower mountainous streams of the boreal zone (Muotka and Virtanen, 1995), and a general model for aquatic macrophytes (Riis and Biggs, 2001). A conceptual model, applicable to a broader range of regions, however, is lacking (Fig. 1). The ranking of the impact of environmental variables on species composition depends primarily on the specific range of the values of variables considered, secondly on the regions investigated, and thirdly on the bryophyte mapping method. Many investigations, however, cover only a restricted range of environmental parameters (many sampling points in the same stream). For example, the effect on the floristic composition only becomes evident when a wide range of substrates is covered. Moreover, all complexes of environmental variables can be overridden by the influence of the relief energy (see Table 1).

Fig. 1 shows the factors and factor complexes which are postulated as primary for structuring aquatic bryophyte communities in headwater streams. The model highlights first the softwater–hardwater gradient, which differentiates the community structure. Secondly, it depicts the productivity factors (=primary growth factors), which enable growth of permanent submerged bryophytes, and thirdly the disturbance regime due to transported solids (bed instability, grinding effect), which modifies the aquatic bryophyte communities and in its extremes prevents the development of true aquatic macrophyte vegetation. This view is obtained from streams where movement of bed material is common, destroying vegetation almost completely. Nevertheless, some bryophytes can be found at sheltered sites as in the lee of large boulders above the middle water layer. The conceptual model (Fig. 1;