

Diversity and distribution of stream bryophytes: does pH matter?

Authors: Tessler, Michael, Truhn, Kam M., Bliss-Moreau, Meghan, and Wehr, John D.

Source: Freshwater Science, 33(3): 778-787

Published By: Society for Freshwater Science

URL: https://doi.org/10.1086/676996

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at <u>www.bioone.org/terms-of-use</u>.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Diversity and distribution of stream bryophytes: does pH matter?

Michael Tessler^{1,2}, Kam M. Truhn^{1,3}, Meghan Bliss-Moreau^{1,4}, and John D. Wehr^{1,5}

¹Louis Calder Center—Biological Field Station and Department of Biological Sciences, Fordham University, Armonk, New York 10504 USA

Abstract: Bryophytes can strongly influence biodiversity and ecosystem function in low-order streams. Mosses and liverworts have substantial biodiversity and biomass in streams, yet few investigators have examined which factors influence bryophyte species distributions, and fewer have examined assemblages across a wide pH gradient. We examined bryophyte assemblages across a pH gradient in 26 southeastern New York (USA) streams. We recorded bryophyte species richness, diversity, and abundance, in conjunction with pH, width, depth, canopy cover, substratum size, temperature, dissolved O₂, turbidity, conductivity, current velocity, dissolved organic C, dissolved Ca, Mg, Fe, NH_4^+ , NO_3^- , soluble reactive P (SRP), and abundance of other autotrophs. pH ranged from \sim 4 to 7 and corresponded to the type of underlying bedrock. Nearly all streams had low or undetectable concentrations of SRP. Several species, e.g., Hygrohypnum eugyrium and Codriophorus aduncoides, were apparent pH generalists, whereas others were pH specialists. For example, Hygrohypnum ochraceum occurred only in neutral pH, whereas Andreaea rothii was restricted to low-pH sites. Vector fitting on a nonmetric multidimensional scaling ordination identified stream pH and amount of bedrock as key factors affecting species distributions. Latitude, longitude, altitude, canopy cover, and aqueous Ca, Mg, SRP, and turbidity also were correlated with species distributions, but many factors were colinear. Nearly all sites had low SRP, and species distributions were strongly related to pH, so we assayed several species and populations for phosphomonoesterase (PMEase) activity under different pH conditions. Species and populations from low-pH streams tended to have stronger PMEase activity at lower pH than those from higher pH streams, suggesting that species and populations may be adapted to specific pH conditions. Differential PMEase activity may be one mechanism by which aquatic bryophytes persist in low-pH environments.

Key words: aquatic bryophytes, pH, headwaters, streams, phosphatase activity, diversity

Bryophytes (mosses, liverworts, and hornworts) are a vital component of many headwater streams, where they often form the dominant plant communities (Vitt et al. 1986). Few other habitats are dominated by bryophytes. Even mire communities, where bryophytes form most of the ground layer, include many vascular plant species that make up a significant portion of the community biomass (Slack and Glime 1985). In headwater streams, bryophytes are often the most productive group of autotrophs and account for a significant portion of in-stream primary production (Stream Bryophyte Group 1999). Aquatic bryophytes can have substantial effects on ecosystem function, including hydraulic, nutrient, and trophic dynamics (Stream Bryophyte Group 1999). Thus, understanding of variables driving their abundance and composition is vital to the conservation of these systems (Cattaneo and Fortin 2000).

Stream bryophytes also form part of the base of stream food webs, directly as a food source for macroinverte-

brates and indirectly by providing habitat for periphyton and other organisms (Glime and Clemons 1972, Suren 1991, Torres-Ruiz et al. 2007). They increase habitat heterogeneity and habitability, and serve as shelter and oviposition sites for stream-dwelling organisms. Large generalist consumers, such as Canada Geese and crayfish, avoid consuming bryophytes that contain acetylenic fatty acids and other compounds. Thus, stream bryophytes provide enemyfree space for macroinvertebrates and algae (Parker et al. 2007). Other long-chain fatty acids produced by bryophytes have been measured in several different types of macroinvertebrate larvae (Torres-Ruiz et al 2007). Bryophytes alter or reduce microhabitat water velocity, thereby allowing accumulation of periphyton and detritus, which, in turn, are often colonized or consumed by macroinvertebrates (Suren 1991, Georgian and Thorp 1992). Invertebrates living on stream bryophytes usually have similar or higher species richness and density than on bare substrata (Suren

E-mail addresses: ²mtessler@amnh.org; ³kamtruhn@gmail.com; ⁴blissmoreau@gmail.com; ⁵wehr@fordham.edu

DOI: 10.1086/676996. Received 21 June 2013; Accepted 1 January 2014; Published online 3 June 20014. Freshwater Science. 2014. 33(3):778–787. © 2014 by The Society for Freshwater Science.

1991), and certain invertebrate species are more common on bryophytes than in other habitats (Egglishaw 1969). For these reasons, bryophytes may provide a more diverse and stable ecological habitat than other substrata within headwater environments (Glime and Clemons 1972, Suren 1991, 1992).

The importance of bryophytes in streams and the paucity of studies on them led a group of aquatic ecologists (Stream Bryophyte Group 1999) to review the state of this research and to propose several focal areas for future study. One suggested area was a review of the factors influencing the distributions of stream bryophyte communities over a broad geographic range. Surprisingly few studies have been conducted in this area, and even fewer have addressed multiple factors affecting the distributions of stream bryophytes (e.g., Slack and Glime 1985, Glime and Vitt 1987). This knowledge gap is important because stream bryophytes are undoubtedly influenced by several factors (Stream Bryophyte Group 1999). One likely factor of importance is pH because its effect on some other bryophytes is well established. For example, in mire communities, certain Sphagnum species occur within narrow pH ranges (Slack 1990).

The influence of pH on stream bryophytes has been examined sporadically, and several investigators described preliminary evidence that pH may be an important determinant of stream bryophyte species abundance (Cattaneo and Fortin 2000), richness (Heino et al. 2005), diversity (Glime and Vitt 1987), and spatial distribution (Slack and Glime 1985, Virtanen et al. 2009). Unfortunately, most studies have been conducted across narrow pH gradients. We are aware of very few studies, all of which were conducted in Europe, in which species distribution was examined across strong pH gradients. In those studies, pH was a strong influence on species' distributions (Paavola et al. 2006, Virtanen et al. 2009). In a study of a small, lownutrient upland stream in Wales (UK), Ormerod et al. (1987) observed that strong pH gradients could profoundly affect the bryophyte flora and, in turn, macroinvertebrate assemblages.

Few data are available on nutrient uptake or availability in bryophytes, a situation that prompted the Stream Bryophyte Group (1999) to suggest this area as an important focus for future research. In headwaters where bryophytes often thrive (Crum and Anderson 1981), stream water is often poor in available P, particularly soluble inorganic P (Christmas and Whitton 1998a). In low-pH headwater streams, soluble P tends to be sorbed onto sediments by Al and Fe complexes (Tate et al. 1995, Gross 2000). Meyer (1979) demonstrated that sorption of added P by stream sediments in a headwater stream (Bear Brook, New Hampshire, USA) peaked at about pH 4.8 and declined between pH 5 and 6 (not tested at greater pH). Bryophyte abundance, and possibly species richness, appears to be strongly influenced by low concentrations of inorganic P. Bryophyte cover increased 10^{\times} , the dominant species changed (*Schistidium agassizii* to *Hygrohypnum* sp.), and a new species (*Fontinalis neomexicana*) was recruited during a long-term (16-y) study of the effects of inorganic P fertilization on the Kuparuk River in Alaska (Bowden et al. 1994, Slavik et al. 2004).

One mechanism by which aquatic bryophytes may obtain sufficient P for growth and reproduction across a pH gradient is via phosphatase activity. In particular, production of phosphomonoesterase (PMEase) allows stream bryophytes to use organic P when inorganic P supplies are in quantities that limit bryophyte growth and reproduction (= physiologically limiting; Christmas and Whitton 1998a), as often appears to be the case (e.g., Bowden et al. 1994). Along stream gradients in the UK from headwaters to lowland sites, aquatic mosses had significantly greater PMEase activity in upland reaches than in sites further downstream (Christmas and Whitton 1998a, b). These researchers also reported that higher-altitude sites had significantly lower pH, lower P, and lower tissue-P content (Christmas and Whitton 1998a, b). The mechanism or links between altitude, pH, and P availability were not clear, but the patterns were significant. These data indicated that low-pH streams were more physiologically limiting for bryophytes in terms of inorganic P near the headwaters than downstream. Stream reaches also can vary in the species of bryophytes present, and PMEase activity has rarely been compared among species or populations in streams with different pH levels (Turner et al. 2001).

The northeastern USA is especially rich in aquatic bryophytes and is an excellent area in which to examine the influence of pH on their distributions. Waters draining the Shawangunk Mountains of New York State and nearby forested areas have a wide range of pH because of the unique mix of bedrock (Chowdhury and Giles 2007). Some of these geologies also may be sensitive to humancaused changes in pH, a trend that the bryophyte flora may help to identify (Thiebaut et al. 1998). In addition, the Shawangunk waterways drain into the Catskill Aqueduct, which is part of the delivery system for New York City drinking water. In-depth knowledge of the waterways in this area is critical for maintaining high-quality drinking water for New York City.

The broad objective of our study was to examine the influence of pH on bryophyte distributions and how these conditions may affect nutrient acquisition. We also compared other ecological variables to bryophyte species distributions, species richness, diversity, and abundance. We tested 2 hypotheses: 1) some species will exhibit narrow pH optima, whereas others will occur across broad pH ranges, and 2) bryophyte species and populations from lower-pH streams will have lower pH optima for PMEase than species and populations from more neutral streams.

METHODS

Study sites

We sampled 26 streams in southeastern New York State: 15 from Minnewaska State Park, Mohonk Preserve, and adjacent areas, and 11 from Harriman State Park and adjacent areas. Minnewaska State Park (~8500 ha) and Mohonk Preserve (~2800 ha) are in Ulster County and contain a large portion of the Shawangunk Mountain Ridge, which is composed of highly resistant Shawangunk conglomerates, surrounded by Martinsburg shale (Fisher et al. 1970, Chowdhury and Giles 2007). Surficial geology of Harriman State Park (~18,600 ha; Rockland and Orange Counties) is predominantly metamorphic (mainly gneiss), with some granite (Fisher et al. 1970). We selected streams to represent a wide pH range within a small geographic area. Streams sampled had \geq 1 aquatic bryophyte species present and measurable flow.

Species distributions

In each stream, we sampled a 20-m reach in spring and summer. We recorded the abundance of all submerged bryophytes in spring on a semiquantitative scale (Holmes and Whitton 1977). We collected voucher specimens (Tessler #1-221) in March 2012 and deposited them at the Louis Calder Center (Fordham University). Nomenclature followed Flora of North America Editorial Committee (2004-2007+) for mosses and Ley and Crowe (1999) for liverworts. All bryophytes sampled were predominantly aquatic in habit, sensu Vitt and Glime (1984), and we sampled under stable baseflow conditions. We also recorded abundances of broad categories of autotrophs (vascular plant, macroalgae, and aquatic lichen) when present. We calculated species richness, diversity (Simpson and Shannon), and total abundance for species recorded in ≥ 3 streams (Begon et al. 1990). We used a species accumulation curve to assess sampling sufficiency (accumresult [exact method] and accumplot functions; BiodiversityR package; Kindt and Coe 2005) in R (version 2.15.1; R Project for Statistical Computing, Vienna, Austria). The curves suggested that 15 streams represented adequate sampling intensity, and we sampled 26.

We collected water samples and measured ecological variables concurrently during 1 wk in March 2012 and 1 wk in June 2012. At every reach, we recorded stream width (\pm 0.1 m) and depth (\pm 1 cm), estimated % forest canopy cover with a canopy densiometer (Forest Densiometers, Bartlesville, Oklahoma; Strickler 1959), and visually estimated the size of rock substrata with a modified Wentworth scale (Cummins 1962).

We measured temperature, pH, dissolved O_2 (DO), turbidity, and specific conductivity of the water in situ with a Hydrolab Quanta (Hach Industries, Loveland, Colorado) and current velocity with a Flo-Mate flow meter (Marsh-McBirney, Frederick, Maryland). We collected water samples in acid-washed 8-mL sampling tubes, syringe-filtered them (0.2-µm pore size), preserved them with H_2SO_4 or HCl to a pH < 2.0, stored them cold (\leq 4.0°C), and analyzed them for dissolved NO_3^- , NH_4^+ , soluble reactive P (SRP; Astoria 2 analyzer; Astoria, Clackamas, Oregon), dissolved organic C (DOC; TOC-L TOC analyzer; Shimadzu, Columbia, Maryland), and Fe, Ca, and Mg (1100B atomic absorption spectrophotometer; Perkin–Elmer, Waltham, Massachusetts). We analyzed NH_4^+ with the phenol-hypochlorite method. We analyzed NO_3^- as NO_2^- with the sulfanilamide-NNED method, after reduction to NO_2^- with a Cd–Cu column (APHA 1985). We removed inorganic C and measured the remaining C as DOC (Potter and Wimsatt 2009).

To elucidate patterns in species distributions in our 26 streams, we used nonmetric multidimensional scaling (NMDS) of species (metaMDS function in the vegan community ecology package (version 2.0-4; Oksanen et al. 2012) in R. We tested all 30 ecological vectors (including species richness, diversity, and abundance) individually for significant correlations with the NMDS ordination for both March and June samplings with the envfit function of vegan with 1000 permutations, and fitted significant variables to the NMDS ordination. Linearity of these species composition-environmental variable relationships was reviewed using the ordisurf function of vegan with a maximum likelihood (ML) model. We also tested the relationships among all significant variables with Spearman correlation analysis. We used an a priori p = 0.01 as a cutoff for statistical significance to minimize α inflation and potential problems with Bonferroni corrections (after Cisneros et al. 2011).

Phosphomonoesterase activity and pH

We used a subsample of 10 sites from the Shawangunk region to examine the general relationship between aqueous pH and P, bryophyte-P content, and PMEase activity. We measured streamwater pH and inorganic P at each site (as above) and bryophyte P tissue concentration (n =31) (Solorzano and Sharp 1980). We assayed PMEase activities in specific bryophyte species and populations to test whether habitat pH could influence PMEase activity under a range of pH conditions. We sampled bryophytes and water from low-pH Peters Kill (pH 4.35) and nearneutral Palmaghatt Kill (pH 6.50). Fontinalis cf. dalecarlica was sampled from both sites, Hygrohypnum ochraceum from Palmaghatt Kill, and Scapania undulata from Peters Kill. We washed all specimens 10× in deionized water to remove loosely attached algae (microscopic observations were used to exclude any with substantial algal growth) and used apical 2-cm tips to ensure that PMEase activity was measured in areas of active growth (Turner et al. 2001). We placed ½ of the tips in water from Peters Kill (low pH) and ¹/₂ in water from Palmaghatt Kill (neutral) for 24 h to equilibrate any recent PMEase activity. We conducted assays with para-nitrophenyl phosphate (pNPP) as a substrate following the methods of Turner et al. (2001). We used 4 experimental pH levels (4.0, 5.0, 6.0, and 7.0; the range tested by Turner et al. 2001), in a 2 (sites) \times 4 (pH) factorial design, with 5 replicates/species.

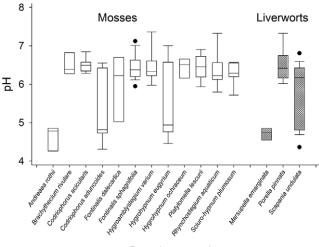
We used Spearman correlations to test correlations between pH and stream inorganic P or bryophyte tissue P. We used 2-way analysis of variance to test for effects of species/population, pH, or their interaction on PMEase activity (separate experiments run in Peters Kill and Palmaghatt Kill water). We set an a priori p = 0.05 as a cutoff for statistical significance, and we $\sqrt{(x)}$ -transformed data prior to these analyses to improve normality.

RESULTS

Species distributions

In total, 33 species (25 mosses and 8 liverworts) were collected. Of these, 15 were recorded from \geq 3 streams. Some species occurred in broad or restricted pH ranges (Fig. 1). For instance, *Andreaea rothii* was restricted to low-pH sites, *H. ochraceum* was restricted to more neutral sites, and *Codriophorus aduncoides* occurred in low and neutral pH streams.

To test the importance of pH to bryophyte species distributions, we constructed and analyzed an NMDS ordination that was constrained to 2 dimensions (stress = 11.470; Fig. 2A, B). The *envfit* analyses indicated that pH was the strongest or 2^{nd} strongest variable driving species distributions, depending on season. pH was the most significant variable in spring ($r^2 = 0.605$, p < 0.001; Table 1, Fig. 2A) and was 2^{nd} strongest in summer ($r^2 = 0.485$, p < 0.001) when bedrock was the most significant variable ($r^2 = 0.001$) when bedrock was the most significant variable ($r^2 = 0.001$) when bedrock was the most significant variable ($r^2 = 0.001$) when bedrock was the most significant variable ($r^2 = 0.001$) when bedrock was the most significant variable ($r^2 = 0.001$) when bedrock was the most significant variable ($r^2 = 0.001$) when bedrock was the most significant variable ($r^2 = 0.001$) when bedrock was the most significant variable ($r^2 = 0.001$) when bedrock was the most significant variable ($r^2 = 0.001$) when bedrock was the most significant variable ($r^2 = 0.001$) when bedrock was the most significant variable ($r^2 = 0.001$) when bedrock was the most significant variable ($r^2 = 0.001$) when bedrock was the most significant variable ($r^2 = 0.001$) when bedrock was the most significant variable ($r^2 = 0.001$) when bedrock was the most significant variable ($r^2 = 0.001$) when bedrock was the most significant variable ($r^2 = 0.001$) when bedrock was the most significant variable ($r^2 = 0.001$) when bedrock was the most significant variable ($r^2 = 0.001$) when bedrock was the most significant variable ($r^2 = 0.001$) when bedrock was the most significant variable ($r^2 = 0.001$) when bedrock was the most significant variable ($r^2 = 0.001$) when bedrock was the most significant variable ($r^2 = 0.001$) when bedrock was the most was the



Bryophyte species

Figure 1. Box-and-whisker plots showing pH of streams (26 streams sampled during 2 seasons) in which each bryophyte species was found (spring samples). Lines in boxes are medians, box ends are the upper and lower quartiles, whiskers are 5th and 95th percentiles, and the outer points are extreme values.

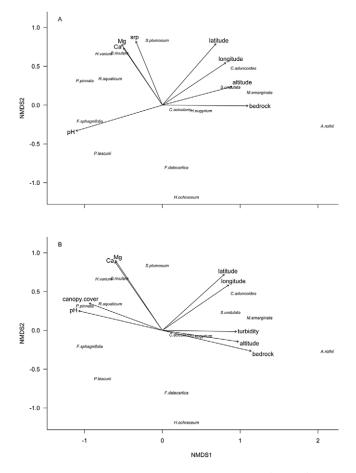


Figure 2. Nonmetric multidimensional scaling (NMDS) ordinations of bryophyte species from 26 streams, with significant ($p \le 0.01$) spring (A) and summer (B) environmental vectors fitted using *envfit*. Arrows indicate the direction of the (increasing) environmental gradient, and their lengths are proportional to their correlations with the ordination. Full species names are listed in Fig. 1. SRP = soluble reactive P.

0.545, p < 0.001; Table 1, Fig. 2B). However, these variables were significantly correlated in summer ($r_s = -0.575$, p = 0.002; Table 2).

Aside from pH and bedrock, these analyses identified latitude, longitude, altitude, and dissolved Ca and Mg as important factors in both seasons. Species distributions were significantly correlated with SRP concentration in spring, and % canopy cover and turbidity in summer (Table 1, Fig. 2A, B). Latitude, longitude, and SRP in the spring, and turbidity in the summer all had linear relationships with the NMDS axes, whereas the other significant variables showed nonlinear relationships.

Ten environmental variables were identified as affecting species distributions, but several were significantly correlated with each other (Table 2). For instance, pH was significantly correlated with latitude ($r_{\rm s} = -0.736$, p < 0.001) and altitude ($r_{\rm s} = -0.680$, p < 0.001) in spring, and

782 | Distribution of stream bryophytes M. Tessler et al.

Table 1. The range of environmental variables and the findings from correlations between the environmental variables and the nonmetric multidimensional scaling ordination for spring and summer using *envfit* analysis. Significant findings ($p \le 0.01$) are displayed in bold.

			Envfit:	spring	Envfit: s	ummer
Environmental variables	Range: spring	Range: summer	p	r^2	p	r^2
рН	4.24-7.14	4.77-7.51	<0.001	0.605	<0.001	0.485
Bedrock (%)	0-75	1-75	<0.001	0.548	<0.001	0.545
Latitude	41.148-41.767	41.148-41.768	<0.001	0.497	0.002	0.458
Longitude	74.066-74.329	74.066-74.330	0.004	0.436	0.003	0.423
Mg (mg/L)	0.06-2.80	0.04 - 3.27	0.005	0.399	0.002	0.465
Altitude (m)	149-541	150-541	0.006	0.386	0.003	0.389
Ca (mg/L)	0.1-6.5	0.1-7.7	0.003	0.357	0.002	0.457
Soluble reactive P (µg/L)	5.5 - 10.4	0.5-20.7	0.008	0.357	0.959	0.004
Dissolved organic C (mg/L)	1.7-6.8	1.8-8.5	0.017	0.315	0.164	0.168
Flow (cm/s)	0.03-0.91	0.05-1.51	0.018	0.304	0.033	0.258
Canopy cover (%)	16-100	4-100	0.026	0.291	0.008	0.398
Conductivity (µS/cm)	21-96	0-41	0.043	0.240	0.196	0.148
Macroalgae abundance	0-5	1-5	0.063	0.224	0.077	0.216
Turbidity (NTU)	12.6-54.0	6.0-58.0	0.085	0.203	0.010	0.360
Temperature (°C)	4.0-13.2	12.8-20.4	0.086	0.196	0.187	0.152
Boulders (%)	0-90	1-90	0.203	0.132	0.198	0.145
Shannon diversity	0.562-2.221	0.562-2.222	0.301	0.108	0.440	0.080
Species richness	2-11	3-11	0.317	0.104	0.503	0.064
Lichen abundance	0-3	0-3	0.325	0.101	0.251	0.127
Simpson diversity	0.375-0.875	0.375-0.876	0.345	0.097	0.463	0.078
Dissolved O_2 (mg/L)	9.10-12.91	5.72-10.15	0.345	0.094	0.030	0.288
Fe (mg/L)	0.06-0.20	0.01-0.53	0.372	0.083	0.710	0.039
Dissolved O_2 (%)	76-100	60-98	0.453	0.075	0.097	0.208
Abundance	4-16	5-16	0.573	0.052	0.313	0.113
NO_3^- (µg/L)	0.003-0.156	0.003-0.203	0.646	0.040	0.086	0.212
NH_4^+ (µg/L)	22.0-65.2	1.2-97.4	0.681	0.037	0.320	0.111
Depth (cm)	7-40	7-56	0.775	0.024	0.041	0.262
Riffles and runs (% area)	50-98	70-98	0.813	0.023	0.602	0.050
Vascular plant abundance	0-3	0-3	0.840	0.016	0.692	0.035
Width (cm)	1.1-5.6	1.0-6.7	0.894	0.011	0.498	0.067

bedrock ($r_{\rm s} = 0.575$, p = 0.002) and % canopy cover ($r_{\rm s} = 0.536$, p = 0.005) in summer. Species richness, diversity, and abundance were correlated, but only abundance was correlated with any other variable (longitude, $r_{\rm s} = -0.547$, p = 0.004).

PMEase activity and pH

Concentrations of inorganic P in stream water were positively correlated with pH during the summer sampling period ($r_s = 0.915$, p < 0.001; Fig. 3A). Bryophyte tissue P concentrations were significantly, but weakly, correlated with streamwater pH ($r_s = 0.374$, p = 0.038; Fig. 3B).

PMEase activity experiments using source water from 2 streams adjusted to 4 pH levels, indicated 2 broad pat-

terns in bryophyte responses to pH, depending on population and species. Several bryophytes showed decreased activity with greater pH, whereas others had peaks in activity with moderate acidity (Fig. 4A, B). The pH effect was most pronounced in *Fontinalis* cf. *dalecarlica* collected from the lower pH site (Peters Kill), whereas PMEase activity in *F*. cf. *dalecarlica* from neutral Palmaghatt Kill was largely indifferent to pH over the experimental range of 4 to 7 or peaked at moderate pH. Activity levels of *F*. cf. *dalecarlica* also differed by population, with greater PMEase in Peters Kill plants than in those from Palmaghatt Kill.

PMEase activity in *Scapania undulata* (from Peters Kill) also varied inversely with pH in Peters Kill source

(top right) and summer (bottom left, and in italics). Signifi	oottom left,	, and in ital	ics). Signif.	icant findin	cant findings $(p \le 0.01)$		are displayed in bold	ld.						
Variable	Lat	Long	Alt	Ca	Mg	SRP	Bedr	Can	Ηd	Turb	S	D	H′	Abun
Latitude (Lat)		0.481	0.327	-0.139	-0.145	0.189	0.228	0.019	-0.736	-0.119	0.045	0.002	-0.002	-0.370
Longitude (Long)	0.481		0.123	-0.396	-0.398	-0.204	0.319	-0.082	-0.394	-0.218	0.002	-0.050	-0.073	-0.547
Altitude (Alt)	0.327	0.123		-0.501	-0.397	0.019	0.438	0.005	-0.680	-0.302	0.217	0.178	0.180	0.180
Ca	-0.254	-0.579	-0.442		0.899	0.506	-0.666	0.070	0.450	0.108	-0.129	-0.110	-0.120	-0.038
Mg	-0.191	-0.552	-0.369	0.960		0.585	-0.605	0.005	0.419	0.195	-0.049	-0.048	-0.061	0.040
Soluble reactive P (SRP)	-0.222	-0.455	-0.104	0.573	0.593		-0.320	0.243	-0.025	0.195	0.021	0.012	-0.013	0.075
Bedrock (Bedr)	0.228	0.319	0.438	-0.661	-0.643	-0.496		-0.056	-0.447	-0.283	0.154	0.147	0.132	0.007
Canopy cover (Can)	0.250	-0.090	-0.035	0.337	0.311	0.022	-0.087		0.200	0.234	-0.106	-0.109	-0.126	0.077
рН	0.023	-0.266	-0.421	0.488	0.440	0.414	-0.575	0.536		0.441	-0.159	-0.138	-0.132	0.131
Turbidity (Turb)	0.215	0.568	0.397	-0.395	-0.326	-0.170	0.233	-0.085	-0.410		-0.011	-0.004	0.022	0.229
Species richness (S)	0.045	0.002	0.217	-0.076	-0.040	-0.160	0.154	0.088	-0.139	0.158		0.970	0.973	0.588
Simpson diversity (D)	0.002	-0.050	0.178	-0.054	-0.022	-0.182	0.147	0.092	-0.101	0.082	0.970		0.997	0.630
Shannon diversity (H')	-0.002	-0.073	0.180	-0.067	-0.033	-0.182	0.132	0.071	-0.100	0.053	0.973	0.997		0.639
Abundance (Abun)	-0.370	-0.547	0.180	0.147	0.154	0.056	0.007	0.095	-0.143	-0.090	0.588	0.630	0.639	

Table 2. Spearman correlations between environmental variables identified as significant in *envitt* and measures of species richness, diversity, and abundance for spring

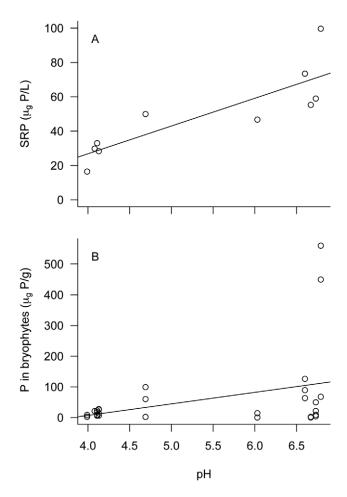


Figure 3. The relationship between aqueous pH and soluble reactive P (SRP) in stream water (A) and P content in bryophyte tissues (B) in 10 streams.

water, whereas PMEase activity peaked at an intermediate pH in Palmaghatt Kill source water. In contrast, *H. ochraceum* from Palmaghatt Kill had maximum PMEase activity at an experimental pH of 5, regardless of the source stream water (Fig. 4A, B). Two-way ANOVA for the experiment using Palmaghatt Kill water revealed significant populations/species (F = 84.655, p < 0.001) and pH (F = 34.379, p < 0.001) effects on PMEase activity, and a significant interaction of these factors (F = 6.839, p < 0.001). A similar test for experiments using Peters Kill water also yielded significant populations/species (F = 46.690, p < 0.001) and pH (F = 38.309, p < 0.001) effects on PMEase activity, but a nonsignificant interaction of these factors (F = 4.6690, p < 0.001) and pH (F = 3.8.309, p < 0.001) effects on PMEase activity, but a nonsignificant interaction of these factors (F = 2.523, p = 0.064).

DISCUSSION

Few investigators have evaluated aquatic bryophyte distributions in relation to a wide pH range. We are aware of only 3 such studies, all conducted in Europe (Ormerod et al. 1987, Paavola et al. 2006, Virtanen et al. 2009), and none examined the influence of pH on distributions and its potential link to nutrient acquisition. Our study suggests that pH strongly influenced species distributions. These results are corroborated by the European studies, in which pH was one of the strongest influences on bryophyte species distributions. Several species in our study streams had relatively narrow pH optima, occurring in low (e.g., *A. rothii, M. emarginata*) or neutral (e.g., *H. ochraceum, Codriophorus acicularis*) pH waters. Others, such as *H. eugyrium*, had comparatively broad pH tolerances. *Andreaea rothii*, although usually reported as growing in seepy acidic environments, is not generally reported as being truly aquatic (e.g., Allen 2005). The populations we

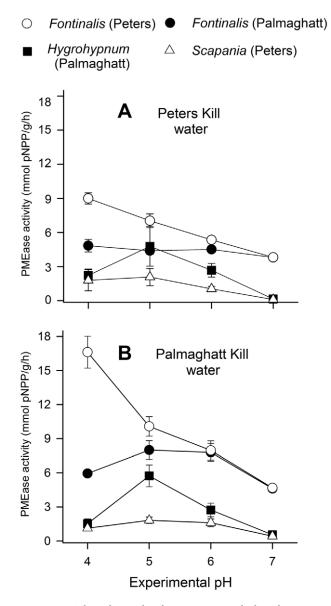


Figure 4. The relationship between pH and phosphomonoesterase (PMEase) activity for several bryophyte species and populations collected from a low-pH stream (Peters Kill) (A) and a neutral stream (Palmaghatt Kill) (B).

examined were always submersed. The influence of pH could not be assessed directly in the field portion of our study because pH was correlated with several other significant variables (e.g., altitude, bedrock, and % canopy cover).

The distribution of individual species did vary with pH, but we did not observe a general trend with species richness, diversity, or abundance, in contrast to some past studies. Some investigators have observed greater species richness and diversity at sites with low pH (Suren and Ormerod 1998, Heino et al. 2005), whereas in a study in the Canadian Rockies, alkaline sites had greater diversity (Glime and Vitt 1987). Bryophyte abundance also was negatively correlated with pH in some locations (Cattaneo and Fortin 2000). However, Paavola (2003) suggested that pH was less important than habitat heterogeneity and size of substrata for bryophyte species abundance and richness.

Canopy cover and turbidity, factors that have not been studied extensively for stream bryophyte distributions, also were significantly related to species distributions in our streams. Canopy cover was suggested as a significant predictor of variation in cover of terrestrial pleurocarpous mosses (Pharo and Vitt 2000) and of species richness for epiphytic bryophytes (Steffan-Dewenter et al. 2007). Aquatic bryophytes also can be more susceptible to burial by sediment than other aquatic macrophytes (Jones et al. 2012), and experimental increases of fine sediments in New Zealand decreased bryophyte abundance (Matthaei et al. 2006).

The Shawangunk ridge is largely composed of conglomerate bedrock that causes streams to have low pH, but the shale that the ridge sits on buffers water (Chowdhury and Giles 2007). Percent bedrock in the stream bed was the most significant factor in summer, but it was significantly correlated with pH, a finding that seems logical given our knowledge of this bedrock's influence on water pH. We also demonstrated that Mg and Ca were positively correlated, and Mg, Ca, and bedrock were significant factors in the vector-fitting analyses. Tahvanainen (2004) found a strong unimodal growth response to Ca in Scorpidium revolvens, which matches the Ca concentrations of fens in this species' natural distribution in Sweden. However, in the same study, Tahvanainen (2004) found no correlation between Mg and plant growth, despite the absence of S. revolvens from high-Mg fens.

SRP, but not NH₄⁺ or NO₃⁻, was identified as a significant factor influencing species distributions. Bryophytes have an important role in P cycling in headwater streams (Meyer 1979), and many species have the ability to acquire organic P when SRP is present in physiologically limiting concentrations (Christmas and Whitton 1998a, Turner et al. 2001).

In our study, pH and SRP were strongly linked with stream bryophyte distributions, so we assayed PMEase activity in selected species and populations. Studies conducted in Europe have shown that phosphatases, particularly PMEase, allow stream bryophytes to use organic P where inorganic P is largely unavailable, such as in low-pH streams, and that PMEase activity peaks at a pH < 7 (Tate et al. 1995, Christmas and Whitton 1998b, Gross 2000, Turner et al. 2001). Collectively, the results of these studies suggest that organic P may be an important resource for aquatic bryophytes in streams with below-neutral pH and physiologically limiting concentrations of inorganic P. Our findings corroborate those of these earlier works, in that we observed a significant positive correlation between inorganic P and pH in headwater streams (i.e., low levels of P at low pH), and bryophyte PMEase activity peaked at pH levels below neutral. Bryophytes also had greater P concentrations in their tissues in streams with higher pH. This correlation was significant but weaker than for stream inorganic P and was strongly influenced by 2 data points, a result that suggests that PMEase may compensate for physiologically limiting supplies of inorganic P. This idea is further supported by data from Ellwood et al. (2008), who found that phosphatase activity increased as tissue P decreased in Fontinalis squamosa.

PMEase activity in all species and populations measured appeared to peak at pH < 7, a result suggesting that organic P may become a necessary source of P at lower pH. However, different species and populations appear to be differentially adapted to dealing with inorganic P shortages because PMEase activity differed between species and populations. Those found in lower-pH streams tended to have peak PMEase activity at the lowest pH conditions tested, whereas those found in more neutral water tended to have peak PMEase activity at intermediate levels of pH. Within a single river system, Christmas and Whitton (1998a) observed that individuals of 2 bryophyte species had PMEase activity that increased with upstream distance, where inorganic P became increasingly scarce while pH decreased. Thus, phosphatase enzyme differences between species and populations may provide an explanation for why species' and populations' distributions in streams appear to be strongly linked to pH. In addition, pH may alter the availability of other required nutrients (Brady and Weil 2008), and species may have correspondingly different nutrient requirements.

Our data suggest that pH is an important factor affecting stream bryophyte distributions, and that its influence may be coupled with the ability of plants to acquire scarce supplies of P. Given that some species appear to have narrow or broad tolerances, further studies, such as reciprocal transplants coupled with laboratory experiments, are needed to identify the ways in which pH may more directly affect aquatic bryophyte activity, growth, and distribution.

ACKNOWLEDGEMENTS

We thank Jim Lewis for advice on the field study design and for commenting on an earlier draft of this manuscript. Saman-

786 | Distribution of stream bryophytes M. Tessler et al.

tha Nguyen also offered advice on the manuscript. Thanks to John Thompson for help finding sites and Mohonk Preserve, Harriman State Park, and Minnewaska State Park for research permits. The Louis Calder Center provided grant support to MT, and MB-M was supported by NSF grant #0139767, awarded to JDW. We thank Catharina Grubaugh and Joe Rozek for field assistance.

LITERATURE CITED

- Allen, B. 2005. Maine mosses: Sphagnaceae-Timmiaceae. New York Botanical Garden Press, New York.
- APHA (American Public Health Association). 1985. Standard methods for the analysis of water and wastewater. 16th edition. American Public Health Association, American Water Works Association, Water Environment Federation, Washington, DC.
- Begon, M., J. L. Harper, and C. R. Townsend. 1990. Ecology: individuals, populations, and communities. 2nd edition. Blackwell Scientific Publications, Boston, Massachusetts.
- Bowden, W. B., J. C. Finlay, and P. E. Maloney. 1994. Long-term effects of PO_4 fertilization on the distribution of bryophytes in an arctic river. Freshwater Biology 32:445–454.
- Brady, N. C., and R. R. Weil. 2008. The nature and properties of soils. Pearson Education, Inc., Upper Saddle River, New Jersey.
- Cattaneo, A., and L. Fortin. 2000. Moss distribution in streams of the Quebec Laurentian Mountains. Canadian Journal of Botany 78:748–752.
- Chowdhury, S., and C. Giles. 2007. Water quality analysis of the Mohonk Preserve and adjacent properties, July–November 2006. State University of New York New Paltz, New Paltz, New York.
- Christmas, M., and B. A. Whitton. 1998a. Phosphorus and aquatic bryophytes in the Swale–Ouse river system, northeast England. 1. Relationship between ambient phosphate, internal N:P ratio and surface phosphatase activity. Science of the Total Environment 210/211:389–399.
- Christmas, M., and B. A. Whitton. 1998b. Phosphorus and aquatic bryophytes in the Swale–Ouse river system, northeast England. 2. Phosphomonoesterase and phosphodiesterase activities of *Fontinalis antipyretica*. Science of the Total Environment 210/211:401–409.
- Cisneros, K. O., A. J. Smit, J. Laudien, and D. S. Schoeman. 2011. Complex, dynamic combination of physical, chemical and nutritional variables controls spatio-temporal variation of sandy beach community structure. PLoS ONE 6(8):e23724.
- Crum, H. A., and L. E. Anderson. 1981. Mosses of eastern North America. Columbia University Press, New York.
- Cummins, K. W. 1962. An evaluation of some techniques for the collection and analysis of benthic samples with special emphasis on lotic waters. American Midland Naturalist 67: 477–504.
- Egglishaw, H. J. 1969. The distribution of benthic invertebrates on substrata in fast-flowing streams. Journal of Animal Ecology 38:19–33.
- Ellwood, N. T. W., S. M. Haile, and B. A. Whitton. 2008. Aquatic plant nutrients, moss phosphatase activities and tissue composition in four upland streams in northern England. Journal of Hydrology 350:246–260.
- Fisher, D. W., Y. W. Isachsen, and L. V. Rickard. 1970. Geologic map of New York: lower Hudson sheet. Geologic Survey, New

York. (Available from: http://www.nysm.nysed.gov/pubsforsale /detail.cfm?pubID=5235)

- Flora of North America Editorial Committee. 2004–2007+. Flora of North America. Oxford University Press, New York.
- Georgian, T., and J. H. Thorp. 1992. Effects of microhabitat selection on feeding and rates of net-spinning caddisfly larvae. Ecology 73:229–240.
- Glime, J. M., and R. M. Clemons. 1972. Species diversity of stream insects of *Fontinalis* spp. Compared to diversity on artificial substrates. Ecology 53:458–464.
- Glime, J. M., and D. H. Vitt. 1987. A comparison of bryophyte species diversity and niche structure of montane streams and stream banks. Canadian Journal of Botany 65:1824– 1837.
- Gross, W. 2000. Ecophysiology of algae living in highly acidic environments. Hydrobiologia 433:31–37.
- Heino, J., J. Soininen, J. Lappalainen, and R. Virtanen. 2005. The relationship between species richness and taxonomic distinctness in freshwater organisms. Limnology and Oceanography 50:978–986.
- Holmes, N. T. H., and B. A. Whitton. 1977. The macrophytic vegetation of the River Tees in 1975: observed and predicted changes. Freshwater Biology 7:43–60.
- Jones, J. I., A. L. Collins, P. S. Naden, and D. A. Sear. 2012. The relationship between fine sediment and macrophytes in rivers. River Research and Applications 28:1006–1018.
- Kindt, R., and R. Coe. 2005. Tree diversity analysis: a manual and software for common statistical methods for ecological and biodiversity studies. World Agroforestry Centre (ICRAF), Nairobi, Kenya. (Available from: http://www.worldagroforestry.org /resources/databases/tree-diversity-analysis)
- Ley, L. M., and J. M. Crowe. 1999. An enthusiast's guide to the liverworts and hornworts of Ontario. Lakehead University Print Shop, Thunder Bay, Ontario.
- Matthaei, C. D., F. Weller, D. W. Kelly, and C. R. Townsend. 2006. Impacts of fine sediment addition to tussock, pasture, dairy, and deer farming streams in New Zealand. Freshwater Biology 51:2154–2172.
- Meyer, J. L. 1979. The role of sediments and bryophytes in phosphorus dynamics in a headwater stream ecosystem. Limnology and Oceanography 24:365–375.
- Oksanen, J., F. G. Blanchet, R. Kindt, P. Legendre, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, and H. Wagner. 2012. vegan: community ecology package. R package version 2.0-4. R Project for Statistical Computing, Vienna, Austria. (Available from: http://CRAN .R-project.org/package=vegan)
- Ormerod, S. J., K. R. Wade, and A. S. Gee. 1987. Macro-floral assemblages in upland Welsh streams in relation to acidity, and their importance to invertebrates. Freshwater Biology 18:545–557.
- Paavola, R. 2003. Community structure of macroinvertebrates, bryophytes, and fish in boreal streams: patterns from local to regional scales, with conservation implications. PhD Dissertation, University of Jyväskylä, Jyväskylä, Finland. Studies in Biological and Environmental Science 121:1–42.
- Paavola, R., T. Muotka, R. Virtanen, J. Heino, D. Jackson, and A. Mäki-Petäys. 2006. Spatial scale affects community concordance among fishes, benthic macroinvertebrates, and bryophytes in streams. Ecological Applications 16:368–379.

Volume 33 September 2014 | 787

- Parker, J. D., D. E. Burkepile, D. O. Collins, J. Kubanek, and M. E. Hay. 2007. Stream mosses as chemically-defended refugia for freshwater macroinvertebrates. Oikos 116:302–312.
- Pharo, E. J., and D. H. Vitt. 2000. Local variation in bryophyte and macro-lichen cover and diversity in montane forests of western Canada. Bryologist 103:455–466.
- Potter, B. B., and J. C. Wimsatt. 2009. Determination of total organic carbon and specific UV absorbance at 254 nm in source water and drinking water. EPA/600/R-09/122. US Environmental Protection Agency, Washington, DC.
- Slack, N. G. 1990. Bryophytes and ecological niche theory. Botanical Journal of the Linnean Society 104:187–213.
- Slack, N. G., and J. M. Glime. 1985. Niche relationships of mountain stream bryophytes. Bryologist 88:7–18.
- Slavik, K., B. J. Peterson, L. A. Deegan, W. B. Bowden, A. E. Hershey, and J. E. Hobbie. 2004. Long-term responses of the Kuparuk River ecosystem to phosphorus fertilization. Ecology 85:939–954.
- Solorzano, L., and J. H. Sharp. 1980. Determination of total dissolved phosphorus and particulate phosphorus in natural waters. Limnology and Oceanography 25:754–758.
- Steffan-Dewenter, I., M. Kessler, J. Barkmann, M. M. Bos, D. Buchori, S. Erasmi, H. Faust, G. Gerold, K. Glenk, S. R. Gradstein, E. Guhardja, M. Harteveld, D. Hertel, P. Höhn, M. Kappas, S. Köhler, C. Leuschner, M. Maertens, R. Marggraf, S. Migge-Kleian, J. Mogea, R. Pitopang, M. Schaefer, S. Schwarze, S. G. Sporn, A. Steingrebe, S. S. Tjitrosoedirdjo, S. Tjitrosoemito, A. Twele, R. Weber, L. Woltmann, M. Zeller, and T. Tscharntke. 2007. Tradeoffs between income, biodiversity, and ecosystem functioning during tropical rainforest conversion and agroforestry intensification. Proceedings of the National Academy of Sciences of the United States of America 104:4973–4978.
- Stream Bryophyte Group. 1999. Roles of bryophytes in stream ecosystems. Journal of the North American Benthological Society 18:151–184.
- Strickler, G. S. 1959. Use of the densiometer to estimate density of forest canopy on permanent sample plots. Pacific Northwest Old Series Research Notes 180:1–5.

- Suren, A. M. 1991. Bryophytes as invertebrate habitat in two New Zealand alpine streams. Freshwater Biology 26:399–418.
- Suren, A. M. 1992. Enhancement of invertebrate food resources by bryophytes in New Zealand alpine headwater streams. New Zealand Journal of Marine and Freshwater Research 26: 229–239.
- Suren, A. M., and S. J. Ormerod. 1998. Aquatic bryophytes in Himalayan streams: testing a distribution model in a highly heterogeneous environment. Freshwater Biology 40:697–716.
- Tahvanainen, T. 2004. The growth of *Scorpidium revolvens* in relation to calcium and magnesium. Lindbergia 29:123–128.
- Tate, C. M., R. E. Broshears, and D. M. McKnight. 1995. Phosphate dynamics in an acidic stream: interactions involving algal uptake, sorption by iron, and photoreduction. Limnology and Oceanography 40:938–946.
- Thiebaut, G., A. Vanderpoorten, F. Guerold, J.-P. Boudot, and S. Muler. 1998. Bryological patterns and streamwater acidification in the Vosges Mountains (N.E. France) an analysis tool for the survey of acidification processes. Chemosphere 36:1275–1289.
- Torres-Ruiz, M., J. D. Wehr, and A. A. Perrone. 2007. Trophic relationships in a stream food web: importance of fatty acids for macroinvertebrate consumers. Journal of the North American Benthological Society 26:509–522.
- Turner, B. L., R. Baxter, N. T. W. Ellwood, and B. A. Whitton. 2001. Characterization of the phosphatase activities of mosses in relation to their environment. Plant, Cell and Environment 24:1165–1176.
- Virtanen, R., J. Ilmonen, L. Paasivirta, and R. Muotka. 2009. Community concordance between bryophyte and insect assemblages in boreal springs: a broad-scale study in isolated habitats. Freshwater Biology 54:1651–1662.
- Vitt, D. H., and J. M. Glime. 1984. The structural adaptation of aquatic Musci. Lindbergia 10:95–110.
- Vitt, D. H., J. M. Glime, and C. LaFarge-England. 1986. Bryophyte vegetation and habitat gradients of montane streams in western Canada. Hikobia 9:367–385.