Plant and Environment Interactions

Effects of Acidification on Bryophyte Communities in West Virginia Mountain Streams

Steven L. Stephenson,* Susan Moyle Studlar, Carolyn J. McQuattie, and Pamela J. Edwards

ABSTRACT

Bryophytes (mosses and liverworts) are often more responsive to water chemistry changes than are vascular plants. In this study, the relationships of bryophyte communities to stream pH and water chemistry were studied, using six streams on or near the Fernow Experimental Forest in Tucker County, West Virginia. Streams were surveyed with line transects using stratified random sampling. Bryophyte communities, based on species composition and structure, fell into three groups, corresponding to basic, moderately acidic, and very acidic stream water. For streams with sandstone beds, species diversity declined with decreasing pH, and no bryophytes were present at pH 3.15. The dominant species in moderately acidic to highly acidic streams is *Scapania undulata*, a species found to have exceptional tolerance to high acidity and toxic metal levels in Europe and Japan. *Scapania undulata* was transplanted from a stream with a pH of 5.97 to one with a pH of 3.15. In 3 mo, ultrastructural damage was observed. Acidity (pH) probably was not the only factor involved in controlling species composition and cell ultrastructure, since the two most acidic streams are subject to acid mine drainage and have very high concentrations of dissolved solids, particularly SO_4 and Al. Other trace metals commonly associated with acidic surface waters also may have contributed to the differences in species composition.

BRYOPHYTES (mosses and liverworts) are the major producers in many mountain streams, providing food and shelter for some aquatic invertebrates, including insect larvae (Brusven et al., 1990; Gerson, 1982; Naiman, 1983; Ormerod et al., 1984; Slack and Glime, 1985; Suren and Winterbourn, 1992). Moss productivity was consistently three to five times higher than that of periphytic algae in three Quebec streams (Naiman, 1983). Lakes may display bryophyte-dominated zones, where low levels of light and nutrients lead to reduced competition from phytoplankton and vascular macrophytes (Spence, 1975).

Bryophytes are composed of thin sheets of tissue in intimate contact with the environment. They may respond more quickly to environmental change than vascular plants, which are structurally more complex and have well-developed cuticles (Rao, 1982; Proctor, 1984; Bates, 1992). Changes in bryophyte communities can provide a relatively inexpensive means of monitoring temporal and spatial changes in air and water pollution (Burton, 1986). Studies in Europe and North America have shown that the composition of aquatic bryophyte communities is strongly related to water chemistry. Important interacting factors include acidity (pH), cation concentrations (e.g., Ca and K), and heavy metal (e.g., Pb and Zn) concentrations (McLean and Jones, 1975; Wehr et al., 1987; Glime and Vitt, 1987: Vitt et al., 1986). In North American wetlands, extensive studies have shown that a bog-to-fen vegetation gradient is linked closely to an acidity–alkalinity gradient; this vegetation gradient is delimited more precisely by bryophytes than by higher plants (Vitt and Chee, 1990). Detailed studies of stream bryophyte communities in North America have been limited to the Appalachians (Glime, 1968; Slack and Glime, 1985) and the Rockies (Glime and Vitt, 1987; Vitt et al., 1986).

The purpose of this study was to relate bryophyte community composition and structure to pH and water chemistry in six streams located on or near the Fernow Experimental Forest in the Allegheny Mountains, Tucker County, West Virginia. Two of these streams are polluted by acid mine drainage. The effect of acidic stream water (pH 3.2) on the cellular ultrastructure of *S. undulata*, a leafy liverwort common in montane streams in the northern hemisphere, also was evaluated.

S.L. Stephenson, Dep. of Biology, Fairmont State College, Fairmont, WV 26554; S.M. Studlar, Dep. of Biology, West Virginia Univ., Morgantown, WV 26506; C.J. McQuattie, USDA Forest Service, 359 Main Road, Delaware, OH 43015; and P.J. Edwards, USDA Forest Service, Timber and Watershed Lab., Parsons, WV 26287. Received 7 June 1993. *Corresponding author (sls@fscvax.wvnet.edu).

Published in J. Environ. Qual. 24:116–125 (1995).

MATERIALS AND METHODS

The Study Areas

Three of the streams studied are located on the Fernow Experimental Forest near Parsons in Tucker County, West Virginia. Two of them, the Watershed 3 (WS3) and Watershed 4 (WS4) streams, are on adjacent catchments, located at ≈39°03′00″ N and 79°41′00″ W. Soils of these two watersheds are derived from underlying acidic shales and sandstones (Helvey and Kunkle, 1986). Elevations at the stream sampling points in WS3 and WS4 are 740 and 755 m, respectively. Dominant tree species on both catchments include sugar maple (*Acer saccharum* Marshall), American beech (*Fagus grandifolia* Ehrh.), northern red oak (*Quercus rubra* L.), sweet birch (*Betula lenta* L.), and black cherry (*Prunus serotina* Ehrh.).

Other than salvage logging of dead American chestnut [*Castanea dentata* (Marshall) Borkh.] during the 1940s, the WS4 catchment has not been disturbed since ≈1905, when it was heavily cut (Edwards and Helvey, 1991). On WS3, all stems >2.54 cm in diam. at breast height outside of a 20-m wide stream-protecting bufferstrip were cut in 1969 to 1970. The bufferstrip was harvested in 1972 (Patric, 1980). Ammonium sulfate fertilizer has been applied aerially every March, July, and November since 1989 to the WS3 catchment at an annual rate of 167 kg ha^{-1} (Edwards and Kochenderfer, 1993).

The third stream on the Fernow Experimental Forest is the south branch of Hickman Slide, located at ≈39°03′40″ N and 79°39′40″ W. The elevation of the sampling point is ≈700 m. The soils are relatively basic and fertile, due to the underlying Greenbrier limestone geologic formation (Losche and Bever-

Abbreviations: WS3, Watershed 3; WS4, Watershed 4; IV, importance value; DOC, dissolved organic carbon; CC, coefficient of community; PS, percentage similarity; TEM, transmission electron microscopy.

age, 1967). Dominant overstory vegetation is composed of northern red oak, yellow poplar (*Liriodendron tulipifera* L.), American beech, and American basswood (*Tilia americana* L.). The area has been subjected principally to a series of patch cuttings on 15-yr intervals.

Sampling also was carried out in three streams located ≈ 10 km east of Parsons, along Forest Service Road 18. All three streams are located between 39°07′30″ to 39°05′30″ N and 79°35′00″ to 79°30′00″ W. Elevations of the sampling points for the streams are 957 m for Big Run, 933 m for Tub Run, and 920 m for Finley Run. All three streams are acidic, although the sources of acidity differ. Acidity in Big Run is derived from natural bogs, in Tub Run from bogs and mine drainage from abandoned strip mines and associated spoil piles, and in Finley Run from abandoned mines and spoil piles. These three streams are underlain by acidic sandstones, siltstones, and shales (Cardwell et al., 1968). Major species of trees in this area include red maple (*A. rubrum* L.), black cherry, sweet birch, yellow birch (*B. alleghaniensis* Britton), and hemlock [*Tsuga canadensis* (L.) Carriere]. Rosebay rhododendron (*Rhododendron maximum* L.) occurs on portions of all three streambanks. This area also was cut heavily near the turn of the century; however, since that time, other cutting has been limited to a few firewood removals. Accidental fires were common in the area until the 1950s, when the use of coal-fired steam engines by the railroads was terminated.

Field Sampling

Each of the six streams was sampled with a series of line transects (Mueller-Dombois and Ellenberg, 1974). Twenty-five transects were used for WS3 and WS4 (sampled in June 1989), 20 were used for Hickman Slide (sampled July 1991), and 10 for the three other streams (August 1990). Line transects were placed at random locations within contiguous 10-m stream segments along a representative portion of each stream. Each transect comprised a one-dimensional plot from which data on number (i.e., frequency) of occurrences and cover for each bryophyte species present were collected. Each transect was delimited with a flexible plastic measuring tape placed across the stream. A cover value (length of tape intercepted) was recorded for each occurrence of a bryophyte in the transect and a specimen of the bryophyte was collected for laboratory identification. Ecologists use importance value indices (sum of one or more measures of relative abundance) to summarize the relative contribution of a species to a community (Barbour et al., 1987). As used in this study, the importance value (IV) for a given species in a particular stream equals one half the total of relative cover (i.e., accumulated length occupied by any one species/total for all species) plus relative frequency; IVs were calculated using the values in Table 1. Bryophyte nomenclature follows Anderson et al. (1990) and Stotler and Crandall-Stotler (1977). Voucher specimens are deposited in the herbaria of Oklahoma State University and West Virginia University.

Five to fifteen rock samples from each stream were taken to the laboratory for qualitative observations on bryophyte establishment. In addition, quantitative data on bryophyte biomass and relative abundance of the different types of stream bed substrates available to bryophytes were collected from WS3 and WS4 on 3 to 5 June 1992. Estimates of coverage of bare rock, soil, organic debris, and water were made using a flexible plastic netting (grid), which was placed across the entire stream bed. The netting consisted of contiguous rows of five 4.5 by 4.5-cm square meshes; each square represented a potential quadrant. One square in each row was randomly sampled, providing 34 to 70 (mean = 52) samples per transect. The proportion of the quadrant occupied by each substrate type was estimated by the coverage class method described by Daubenmire (1968). After coverage values were recorded, all of the bryophytes present within the quadrant were removed and placed in a small paper bag. In the laboratory, bryophyte samples were washed to remove soil and organic debris, oven dried to a constant weight, and weighed.

Stream parameters measured or determined at the site of each transect were the direction (or aspect) of streamflow, maximum water depth, and distance across the bottom of the stream bed. Big Run, Tub Run, and Finley Run were wider and deeper than Hickman Slide, WS3, and WS4. Average stream bed width (with ranges) for Hickman Slide, WS3, WS4, Big Run, Tub Run, and Finley Run based on transect measurements were 2.20 (0.71–5.39), 2.23 (1.86–4.43), 1.91 (1.47–4.03), 5.69 (3.46–7.95), 4.13 (2.60–5.10), and 2.15 (1.00–3.34) m, respectively. Average water depths (with ranges), in the same order, were 1.0 (0.0–7.6), 2.8 (1.3–4.4), 1.8 (0–3.8), 21.4 (12.7–30.5), 17.0 (8.3–22.9), and 17.0 (5.7–31.1) cm. All six streams had east- and west-facing banks. Hickman Slide flowed north (aspect 345) and the remaining streams flowed south (aspect ≈ 190° for Finley Run and WS3, and ≈ 160° for WS4, Big Run, and Tub Run).

Laboratory Analysis

Water samples from each stream were collected in 1-L polyethylene bottles. Grab samples were collected weekly from WS3 and WS4 from January 1989 to June 1990. Hickman Slide was sampled monthly in April and May 1991 and weekly from February to March 1992. Big, Tub, and Finley Runs were sampled monthly from April to October 1991 and once more in May 1992. Winter samples were not collected for Big, Tub, and Finley Runs because they are not accessible during that time. Although the sampling periods for the streams were not identical, the concentrations measured are thought to be representative of the seasons sampled.

Samples were brought from the field to the laboratory in coolers and then stored at 4°C until analysis at the U.S. Forest Service's Timber and Watershed Laboratory in Parsons, WV. The USEPA-approved protocols and methods were used for all phases of sample handling and analyses (Edwards and Wood, 1993). Electrical conductivity and pH were determined by a Wheatstone bridge and potentiometrically, respectively, on nonfiltered, nonpreserved aliquots. Acidity and alkalinity were determined by titrating nonfiltered, nonpreserved aliquots to a single endpoint and double endpoint, respectively (American Public Health Association et al., 1985). All other aliquots were vacuum filtered through 0.45-µm filters. Anion concentrations were determined by ion chromatography. Ammonia nitrogen and dissolved organic carbon (DOC) were preserved to $pH < 2$ with sulfuric acid, and analyses were done using an NH_3 analyzer and C analyzer. Base cation concentrations were measured by atomic absorption spectrophotometry and total Al concentrations by direct current plasma spectrophotometry on aliquots preserved with nitric acid to $pH < 2$.

Five rock fragments with the leafy liverwort *S. undulata* present were collected from WS4 on 15 May 1991, transplanted to Finley Run, and left undisturbed until 28 Aug. 1991, when they were removed and returned to the laboratory. The rock fragments used in these experiments were selected on the basis of having an abundant (>50% total cover) and relatively uniform growth of *S. undulata*. All of the fragments were at least 12-cm wide and 3-cm thick. Except for episodes of unusually high water, fragments of this size or larger do not

Table 1. Cover and frequency (cover, frequency) for bryophytes present in the six streams. Cover for any one species is the percentage of the total transect length occupied by that species, whereas frequency is the number of transects in which it occurred.

	Stream					
Species	Hickman Slide	WS3	WS4	Big Run	Tub Run	Finley Run
No. of transects	20	25	25	10	10	10
Hygroamblystegium tenax	12.2,19	–	–	–	–	–
Brachythecium rivulare	11.5,17	–	–	–	–	–
Plagiomnium ciliare	1.0,9	0.3,4	1.3,8	–	–	–
Lophocolea cuspidata†	0.8,8	–	–	–	–	–
Conocephalum conicum†	0.2,5	–	–	–	–	–
Thuidium delicatulum	0.2,4	1.0,7	2.5,10	–	–	–
Br. plumosum	0.5,3	0.5,5	0.2,4	–	–	–
Fissidens bryoides	<0.1,4	1.8,15	<0.1,1	–	–	–
Rhizomnium punctatum	<0.1,2	0.2,2	0.4,4	–	–	–
Hypnum curvifolium	1.2,2	<0.1,1	–	–	–	–
Eurhynchium hians	<0.1,1	–	–	–	–	–
Scapania undulata†	–	2.4,19	7.9,22	29.2,9	0.9,4	–
Platylomella lescurii	–	2.5,14	2.7,5	–	–	–
Hygrohypnum eugyrium	–	2.8,7	1.3,2	–	–	–
Hy. micans	–	0.2,2	2.1,6	–	–	–
Jubula pennsylvanica†	–	0.2,1	3.9,6	–	–	–
Sematophyllum marylandicum/ demissum	–	<0.1,1	1.2,5	–	–	–
Pseudotaxiphyllum elegans	–	0.4,5	<0.1,1	–	–	–
Atrichum undulatum	–	<0.1,2	–	–	–	–
Bryhnia novae-angliae	–	0.3,4	–	–	–	–
Chiloscyphus polyanthos†	–	0.2,2	–	–	–	–
Mnium sp.	–	<0.1,1	–	–	–	–
Pellia sp.†	–	0.1,1	–	–	–	–
Plagiothecium denticulatum	–	<0.1,3	–	–	–	–
Mn. longirostrum	–	–	0.1,1	–	–	–
Hyp. imponens	–	–	<0.1,1	–	–	–
Calypogeia sp.†	–	–	<0.1,2	–	–	–
Marsupella emarginata†	–	–	–	11.9,6	–	–
Mn. ambiguum	–	–	–	<0.1,1	<0.1,1	–
Pellia epiphylla†	–	–	–	<0.1,1	–	–
Pohlia sp.	–	–	–	<0.1,1	–	–
Dicranella heteromalla	–	–	–	<0.1,1	–	–
Species richness	11	19	15	6	2	0
Mean number of species per transect	3.7	3.8	3.1	1.9	0.5	0.0
Total bryophyte cover, %	27	11	16	37	<1	0
Bryophyte biomass, g m^{-2}	NS‡	31	80	NS	NS	0

† Liverwort.
‡ NS = not sampled.

tend to move about in these stream beds, and there was no evidence that any of those used in the present study changed position after being placed in the stream. Rock fragments transplanted from WS4 to Finley Run were maintained under cool, moist conditions, while transported between the two streams; transport time was ≈30 min. These fragments were placed in sections of the streambed of Finley Run fairly comparable (i.e., with respect to water depth, flow rate, and canopy cover) to sections of the streambed of WS4 from which they had been collected. The transport time for the controls (undisturbed *S. undulata* in WS4) to the laboratory was about 2 h less than that for transplanted *S. undulata*. It seems unlikely that this difference is important; aquatic bryophytes removed from a stream and left exposed on the bank showed cellular damage only after 1 to 4 wk (Peñuelas, 1984). Typically, in bryophyte transplant experiments (e.g., Martinez-Abaigar et al., 1993), bryophytes are removed from the field to the laboratory (or vice versa) rapidly (in 24 h or less) and under cool conditions (5°C). Prolonged exposure to heat is particularly damaging to aquatic bryophytes (Glime, 1987). After the transplanted rock fragments were returned to the laboratory, shoots of *S. undulata* were removed, washed several times in distilled water, and prepared for transmission electron microscopy (TEM). Control *S. undulata* (colonies undisturbed in WS4 until 28 August) were similarly washed and prepared for TEM.

Transmission Electron Microscope Studies

Shoots of *S. undulata* occurring on rock fragments transplanted from the WS4 stream to Finley Run for ≈3 mo were compared with *S. undulata* shoots occurring naturally in WS4 and Tub Run and collected on the same date (28 August). After being photographed under a stereomicroscope to document morphological differences, several leaves were removed from each shoot. In preparation for electron microscopy, these leaves were cut into 1 mm^2 pieces and immersed in 3% (v/v) phosphate-buffered glutaraldehyde for 16 h at 4°C. Leaf pieces were then post-fixed in 2% (v/v) osmium tetroxide (2h, 4°C), dehydrated in a graded ethanol series (30 to 100%, v/v), and infiltrated with Epon-Araldite epoxy resin. Ultrathin (≈90 nm) cross sections of leaves were cut using a LKB Ultratome III (LKB, Sweden) and post-stained with uranyl acetate and lead citrate. All cross sections were examined and photographed using a Hitachi HU 11E transmission electron microscope.

RESULTS AND DISCUSSION

Bryophyte Communities and Stream Chemistry

Twenty-nine species of bryophytes (22 mosses and 7 liverworts) were found along the transects in the six

Table 2. Mean values for chemical characteristics determined for the six streams sampled in the present study. Standard deviations given in parentheses. Aluminum was analyzed for only one set of May 1991 samples.

	Stream					
Characteristic	Hickman Slide	WS3	WS4	Big Run	Tub Run	Finley Run
pH	7.91	6.06	5.95	4.17	3.89	3.15
Conductivity, $\mu s\ cm^{-1}$	195 (22)	20 (2)	22 (2)	60 (7)	127 (41)	490 (65)
NO_3-N, mg L^{-1}	1.44 (0.14)	0.75 (0.21)	0.76 (0.17)	0.12 (0.05)	0.06 (0.03)	0.04 (0.04)
SO_4, mg L^{-1}	11.04 (0.51)	3.64 (0.33)	4.60 (0.45)	7.58 (0.59)	35.00 (13.44)	124.51 (54.39)
Cl, mg L^{-1}	0.61 (0.08)	0.49 (0.05)	0.56 (0.06)	5.54 (2.65)	0.50 (0.12)	0.79 (0.19)
Ca, mg L^{-1}	30.63 (2.89)	1.35 (0.16)	1.64 (0.15)	0.86 (0.22)	2.50 (1.27)	6.51 (3.50)
Na, mg L^{-1}	0.64 (0.08)	0.39 (0.04)	0.39 (0.03)	2.89 (0.98)	0.27 (0.05)	0.29 (0.05)
Mg, mg L^{-1}	2.25 (0.91)	0.68 (0.07)	0.76 (0.05)	0.29 (0.04)	1.97 (0.88)	4.84 (1.49)
K, mg L^{-1}	0.69 (0.09)	0.79 (0.12)	0.68 (0.06)	0.34 (0.13)	0.76 (0.23)	0.88 (0.24)
Al, mg L^{-1}	0.07	0.01	0.01	0.55	2.37	12.22
NH_4-N, mg L^{-1}	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.01 (0.01)	0.03 (0.03)	0.06 (0.04)
Dissolved organic C, mg C L^{-1}	4.90 (1.23)	0.91 (0.32)	0.92 (0.47)	5.11 (1.15)	3.56 (0.88)	2.79 (0.69)
Alkalinity, mg $CaCO_3$ L^{-1}	76.68 (10.12)	0.85 (0.34)	0.67 (0.32)	–	–	–
Acidity, mg $CaCO_3$ L^{-1}	–	–	–	10.61 (0.68)	25.65 (9.20)	105.35 (18.93)

streams (Table 1). Four taxa identified only to genus also are treated as species for comparing species richness among streams. For the five streams on sandstone (i.e., all but Hickman Slide), total species richness and number of species per transect decreased with decreasing pH, dropping off sharply below pH 5.97 (Tables 1 and 2; Fig. 1). If pH were the only controlling factor, one would expect the highest species richness on Hickman Slide (pH 7.9, with a limestone stream bed); however, species richness there was only moderate (Table 1), suggesting other factors were involved. Total bryophyte cover was highest at or near the ends of the pH gradient (Hickman Slide, pH 7.9 and Big Run, pH 4.2), whereas in the streams with the two highest acidities (Finley Run and Tub Run) (Table 2) bryophyte cover was zero or very low (Table 1; Fig. 1).

Quantitative data on relative abundance of stream bed substrates and bryophyte biomass obtained from WS3 and WS4 indicate that the major portion of these stream beds is represented by bare rock. Coverage values recorded for rock (79%) and soil (10%) in the more-recently disturbed watershed (WS3) were slightly higher than the corresponding values (72 and 7%, respectively) for the less-disturbed watershed (WS4). WS4 had a higher value for organic debris (21%) than did WS3 (11%). Most bryophyte productivity studies have been conducted in circumpolar regions (Russell, 1988), but

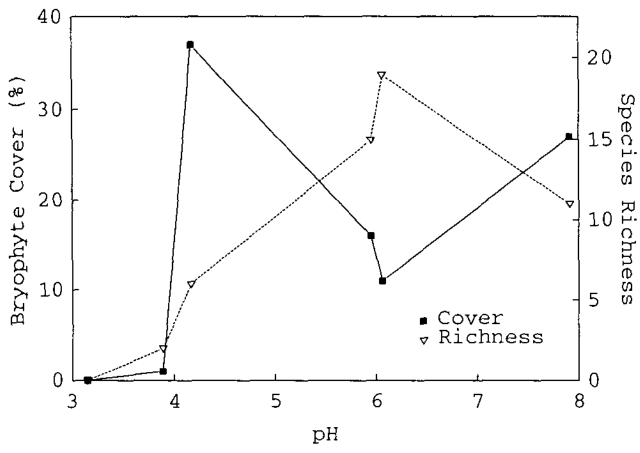

Fig. 1. Bryophyte cover and species richness in relation to pH.

several studies have used streams in temperate regions. Naiman (1983) reported gross productivity of 2.0 g m^{-2} d^{-1} for mosses in three Quebec rivers. Duffer and Dorris (1966) found that the most productive section of the Blue River in Oklahoma was dominated by the moss *Leptodictyum*. The values for biomass obtained in the present study (31 g m^{-2} for WS3 and 80 g m^{-2} for WS4) suggest considerable variability between these streams. Greater biomass in WS4 was associated with a smaller proportion of the stream bed covered by water (14% compared with 25% in WS3). Dawson (1973) also found high variability within and between streams in the high Pyrenees (France); overall standing crops were 92 g m^{-2} and 325 g m^{-2} for two streams, with a standard error of 90 g m^{-2}. The standing crop of bryophytes in a montane Japanese stream was $\approx$ 124 g m^{-2} at the stream's edge and $\approx$48 g m^{-2} in the stream's center, with *Scapania* present; lower mid-stream biomass was attributed to abrasion (Horikawa and Kotake, 1960). The low bryophyte cover of Tub and Big Runs implies low biomass values in these very acid (pH ~4) streams, although biomass was not measured. Stokes (1986) concluded, however, that acidification of aquatic communities usually does not result in reduced biomass for producers, although marked changes in species composition often occur. The reduced bryophyte cover observed in this study may be a response to other chemical factors related to pH.

Water chemistry for WS3 and WS4 was very similar for all analyses (Table 2). Thus, for chemistry comparison purposes these two streams can be grouped together within a mid-range class. When this class is arranged with the other four streams in order of decreasing pH, two overall chemistry patterns are evident (Table 2). Nitrate levels decreased with decreasing pH, while most other chemical constituents generally had higher concentrations at the extreme ends of the pH gradient. Electrical conductivity, a measure of total dissolved solids, was high for Hickman Slide due to the fairly high Ca and SO_4 concentrations. For the remaining streams, conductivity increased sharply with decreasing pH. Much of this response probably was attributable to the increased SO_4 and Al concentrations associated with the streams of

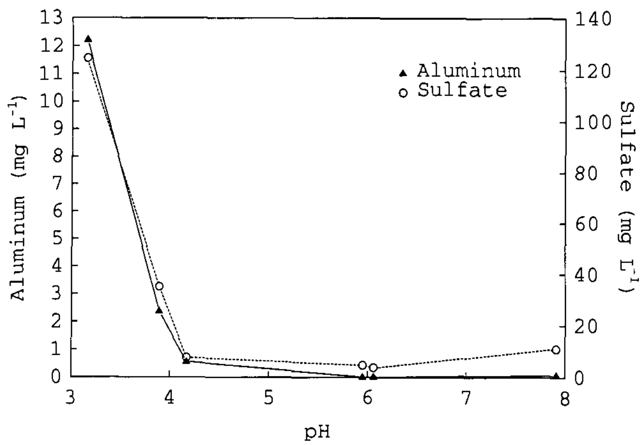

Fig. 2. Relationship between pH and Al and SO_4 concentrations.

lower pH (Fig. 2). High Al and SO_4 concentrations were present in Tub Run, which had impoverished bryophyte communities, and extremely high concentrations were present in Finley Run, which was devoid of bryophytes (Tables 1 and 2). Sulfate level in Finley Run (127 mg L^{-1}) exceeded the tolerance level (100 mg L^{-1}) of SO_4 for four aquatic mosses (Frahm, 1976). It is possible that aquatic bryophytes sequester little sulfate, as do several terrestrial species (Raeymaekers and Glime, 1990). Sulfate concentrations in acidic systems, however, commonly are associated with high concentrations of Al and heavy metals via ion pairing (Reuss and Johnson, 1986). High concentrations of other trace metals have been found in Tub and Finley Runs during previous sampling periods (P. Edwards, 1988, unpublished data). Thus, bryophyte occurrence or absence may have been controlled by SO_4 and pH or by other factors, including levels of Al or other trace metals associated with acidic conditions, or some combination of these factors.

Based on coefficient of community (CC) and percentage similarity (PS) indices (Gauch, 1982) computed using importance values, bryophyte communities fell into three groups corresponding to basic (Hickman Slide), moderately acidic (WS3 and WS4), and highly acidic (Big Run and Tub Run) streams (Table 1). Each group of streams had two to five species not found in the other streams and distinctive patterns of dominance. For example, WS3 and WS4 had a CC value of 0.545 (maximum possible = 1.0) and a PS value of 52.5 (maximum possible = 100.0), but the average values for all possible pairwise combinations of either of these two streams with the others were only 0.087 (CC) and 16.3 (PS). *Hygroamblystegium tenax*, (IV = 35.5), and *Brachythecium rivulare* (IV = 35.5) were the dominant species in Hickman Slide. In the more acidic streams, the importance value of *S. undulata* increased from 0 to 88.6 with decreasing pH, but it was absent at the lowest pH of 3.2 (Tables 1 and 2). *Platylomella lescurii*, *Hy. eugyrium*, and *Hy. micans*, important in WS3 and/or WS4 (IV ≥ 12 in one or both streams), are characteristic emergents in montane streams (Crum and Anderson, 1981; Slack and Glime, 1985); their absence from Hickman Slide may indicate inadequate streamflow, whereas their absence from Big Run, Tub Run, and Finley Run may indicate unfavorable chemical conditions. Although no bryophytes were found in Finley Run, *S. undulata*, *Leucobryum glaucum*, and *Pseudotaxiphyllum distichaceum* were conspicuous on the streambank just above water level.

Glime and Vitt (1987) reported that aquatic bryophyte community composition on limestone stream beds was distinctively different from that on sandstone or granite. In terrestrial habitats, the differences between bryophyte communities on limestone and on siliceous rocks can be even more striking, with little species overlap (Bates, 1978). The physiological bases for the differences between calcicoles and calcifuges are poorly understood. Levels of H, Ca, Al, or other toxic elements may be interacting factors, to which individual species respond differently (Bates, 1992; Buescher et al., 1990; Andersson, 1988), and a simple relationship between species diversity and pH may not exist. Bryophyte community richness on limestone compared with nonlimestone areas varies with the region surveyed (Downing, 1992). Streams of the Rockies with limestone stream beds showed higher bryophyte diversity than more acidic streams of the Adirondacks with sandstone and granite stream beds (Glime and Vitt, 1987).

Species distributions by habitat in this study generally matched expectations based on descriptions in standard taxonomic treatments, including Crum and Anderson (1981), Smith (1978, 1990), and Schuster (1966, 1969, 1974, 1980, 1992a, 1992b). The calcicoles that dominate Hickman Slide, however, are not restricted to calcareous substrates, whereas some taxa in the other streams are known calcifuges that are rarely associated with limestone. Such calcifuges include the liverworts *S. undulata*, *Marsupella emarginata*, and *Jubula pennsylvanica*, as well as the mosses *Ps. elegans*, *Sematophyllum marylandicum*, and *Se. demissum*. Our data are consistent with those of Wehr and Whitton (1983) and McKnight and Feder (1984) who found that liverworts become more important with decreasing stream pH. Extensive surveys in Europe have shown that bryophyte communities exposed to acid mine drainage are relatively simple. Species tolerant of low pH and high levels of toxic metals in Europe include two species (*M. emarginata* and *S. undulata*) found in the most acidic streams sampled in the present study. In the most polluted streams draining European mines, *S. undulata* may be the only bryophyte species present (Ormerod et al., 1984; Whitton et al., 1982; McLean and Jones, 1975; Burton, 1986). A high level of dominance by this species, therefore, is potentially useful as an indicator of high levels of heavy metal pollution, although it is confined to oligotrophic (low phosphate) streams with a pH above 3 (Whitton et al., 1982). Although *S. undulata* is occasionally found on limestone in North America, the species shows a strong preference for acidic habitats in North America (Schuster, 1974) and Europe (Ormerod et al., 1984). In Japan, *S. undulata* was one of only three bryophytes found in a stream with a pH between 3.9 and 4.6 (Satake et al., 1989a). Thus, our data for West Virginia support findings for Europe and Japan, i.e., sharply reduced species richness below pH 5.9, with a marked increase in the importance of acidophytic metal-tolerant liverworts, notably *S. undulata*.

Only controlled experiments can determine whether bryophyte community impoverishment in acidic streams is due to high acidity, trace metal concentrations, or other aspects of stream chemistry. The terrestrial moss *Pleurozium schreberi*, when treated with simulated acid rain (pH 3) for 2 yr showed decreased growth, chlorosis, and accelerated leaching of Ca and Mg (Raeymaekers and Glime, 1990), though Farmer et al. (1992) concluded from the extreme conditions and long exposure times that *Pl. schreberi* is relatively acid-tolerant. Comparable field experiments have not been done for aquatic species; however, Glime and Keen (1984) demonstrated membrane damage and chlorosis in several species of aquatic mosses subjected to 0.01 mg L^{-1} Cu. They recommended that aquatic bryophytes be used for both early warning and cleanup of heavy metals in aquatic ecosystems.

The chemical and vegetation gradient described here for six Appalachian streams shows some similarities to the fen-to-bog gradient in Canadian wetlands (Slack et al., 1980; Vitt and Chee, 1990). Hickman Slide has pH, Ca, and electrical conductivity levels comparable to those of rich fens, and this stream's leading dominant is a member of the Amblystegiaceae, the dominant family of rich fens. Big Run and Tub Run have pH values comparable to those of bogs, but bogs are dominated by *Sphagnum*. These very acidic streams are dominated by *S. undulata*, which evidently tolerates Ca and Mg concentrations higher than those found in bogs.

Species Richness and Water Depth

Water level plays an important role in determining zonation and species richness in stream bryophyte communities (Glime, 1970; Glime and Vitt, 1987). Most stream bryophytes are facultatively aquatic; few can survive prolonged submersion and abrasion by current (Vitt and Glime, 1984). In this study the three streams with either no bryophytes or low species richness (Finley, Tub, and Big Runs) also had the greatest average depths (17–21 cm vs. 1–3 cm). Bryophyte colonies in these three streams generally were submerged, whereas those in the other three streams were generally emergent (Studlar, 1990, unpublished data). Although stream chemistry is probably the primary factor accounting for no or low bryophyte cover and richness in the three highly acidic streams, in deeper streams water level could play a secondary role. Year-round streamflow data and controlled experiments would be necessary to evaluate the role of water level in bryophyte distribution patterns.

Role of Establishment

Microscopic observations of rocks collected from WS3 and WS4 stream beds revealed that apparently bare rock surfaces were encrusted with organic matter that included moss protonemata and minute shoots ($\leq$1–2 mm high) of mosses and liverworts; species present were *Fissidens bryoides*, *P. lescurii*, *Rhizomnium punctatum*, *Hy. micans*, *S. undulata*, and *J. pennsylvanica*. In contrast, on rocks from the Big Run stream bed, the only conspicuous new growth consisted of green shoots of *S. undulata* arising from a firmly anchored network of black stems. Rocks from Tub Run were coated with a reddish-brown crust that may have interfered with establishment of other bryophyte species.

Several workers have demonstrated that difficulty in establishment (from spores or propagules) can limit the distributions of bryophytes (Herben et al., 1991; Alpert, 1988; Duncan and Dalton, 1982). The persistent protonemata of *Rh. punctatum* help explain its abundance in British streams (Smith, 1978). In several small streams in the Adirondacks, *S. undulata* was the only species that colonized small unstable rocks (Slack and Glime, 1985). Fragments of two mosses in stream drift required at least 9 wk of contact with the substrate before rhizoids were initiated (Glime et al., 1979). Two stream moss species on overturned stones began to recolonize the upper surface (by extension growth) after 2 mo (Englund, 1991). The ability of a species to colonize substrates newly exposed by erosive forces is as important a factor to species success as tolerance of established individuals.

Bryophytes tend to decrease in a downstream direction as sedimentation increases (Sheath et al., 1986). McKnight and Feder (1984) found that Fe oxide precipitates severely restricted periphyton establishment in Rocky Mountain streams affected by acid mine drainage whereas *S. undulata*, the only bryophyte species in the stream, apparently grew in Fe oxide precipitates between rocks. Thus, the decreases in species richness in the more-acidic streams quite possibly reflected establishment problems as well as a greater tolerance by mature individuals to stream conditions. In Hickman Slide, protonemata were not observed on rocks, but invasion of bare rock surfaces by extension growth was observed for *Br. rivulare*, *H. tenax*, and *Lophocolea cuspidata*. Since streamflow was lower in this stream, disturbance may have been less frequent than in the moderately acidic streams, and higher cover values more readily attained by simple extension growth, especially when the colonies were above water.

The slightly higher species density (i.e., number of species per transect) in WS3 compared with WS4 also may reflect differences in establishment. Perhaps greater disturbance (timber removal and debris clearing in the stream channel) in past decades in WS3 generated more bare surfaces and more opportunities for invasion by various species. Experimental studies involving transplants are needed to clarify further the roles of substrate size, stability, disturbance regimes, water chemistry, and competition on bryophyte establishment.

Cell Ultrastructure and Acidity

The visual appearance of *S. undulata* differed in streams of different pH levels. Shoots from WS4 (Fig. 3, top shoots) were green and generally flattened, whereas shoots from WS4 transplanted for $\approx$3 mo into highly acidic Finley Run had become greenish-brown and curled (Fig. 3, bottom shoot). Many shoots of *S. undulata* growing naturally in Tub Run (Fig. 4) were dark brown, curled, and smaller than those from WS4 or the trans-

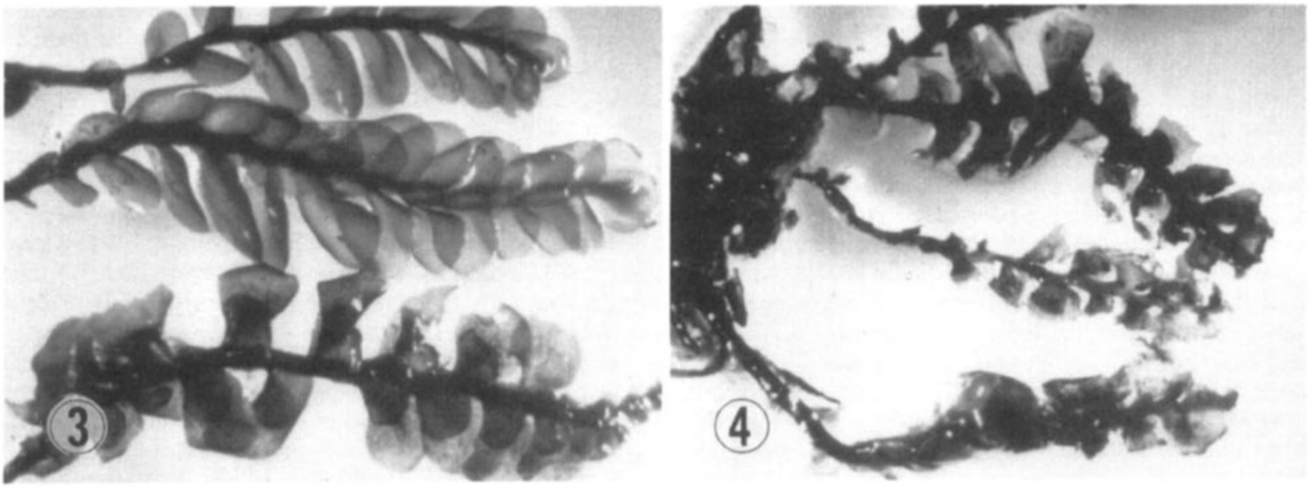

Fig. 3 and 4. Shoots of *Scapania undulata* photographed under a stereomicroscope. Fig. 3. *S. undulata* occurring naturally in WS4 (pH 5.97) (top two shoots) and transplanted from WS4 to Finley Run (pH 3.15) for ≈3 mo (bottom shoot). Leaves from transplanted shoot were curled and darker in color (greenish-brown) than those from WS4. ×70. Fig. 4. Shoots of *S. undulata* occurring naturally in Tub Run (pH 3.91). Leaves of shoots were smaller than leaves shown in Fig. 3 and were dark brown in color. ×70.

planted shoots. In addition, individual leaves of *S. undulata* from Tub Run were much thinner than leaves from WS4 (10 vs. 30 μm).

Viewed by transmission electron microscopy, leaves of *S. undulata* from WS4, Tub Run, and Finley Run (transplants) had significantly different cellular structure. Cell walls of leaves from WS4 were moderately dense (Fig. 5). Microorganisms frequently were attached to cell walls (Fig. 5) but no wall disruption was seen. In contrast, cell walls from shoots transplanted from WS4 to Finley Run (Fig. 6) had a dense inner wall layer and a moderately-dense outer layer that appeared to be degraded in discrete areas (Fig. 6 and 7). Numerous microorganisms were observed near many sites of wall deterioration (Fig. 7). These microorganisms in Finley Run may have contributed directly to cell wall breakdown, or they simply may have been benefiting from nutrients released. No channels through the cell wall, characteristic of enzymatic action by bacteria (Satake and Miyasaka, 1984), were observed. Cell walls from leaves of *S. undulata* growing naturally in Tub Run (Fig. 8) were extremely dense and much thinner than those from *S. undulata* growing naturally in WS4 or transplanted to Finley Run. These thin, dense, mottled walls may be characteristic of growth under extremely acidic conditions, or they may be the consequence of other stream chemistry factors, including high Al or sulfate (Table 2). Cellular organelles, such as chloroplasts and nuclei, were similar in structure in both WS4 and Finley Run-transplanted leaves (Fig. 5 and 6); however, chloroplasts in leaves from Tub Run (Fig. 8) were small and relatively dense. Few microorganisms were observed in association with cell walls of *S. undulata* in Tub Run.

Cell wall breakdown of *S. undulata* transplanted to Finley Run may be the result of acidity or other chemical factors, such as a high Al concentrations (Table 2) in this stream. Aquatic bryophytes and some aquatic plants are known to be capable of accumulating toxic metals, including Pb, Zn, and Al, to extraordinary levels (sometimes by factors of 10 000 or more) without showing macroscopic signs of damage (Caines et al., 1985; Farmer, 1990). Satake et al. (1989b) reported that *S. undulata* accumulated Pb, Zn, and Hg to levels that accounted for 1.6, 0.8, and 0.3%, respectively, of its dry weight, whereas Satake and Nishikawa (1990) found that this species accumulated 8530 times higher Al levels than the surrounding water at pH 4.2. Although sequestering toxic ions in cell walls apparently represents an effective protective mechanism in some bryophytes, eventually some ions move into the cytoplasm and may interfere with normal cell function (Tyler, 1990). Understanding the consequences of metal toxicity of the biology of *S. undulata* is of general interest, particularly in West Virginia, since high levels of Al, Fe, Mn, and sometimes Ni, Cu, and Zn, are found in coal spoils (Carvey et al., 1977) and can be leached to surface waters.

Scapania undulata tolerates high levels of Al in its environment. It was the only bryophyte in a Japanese river containing high levels of Al precipitates (Satake et al., 1989a). Current data on Al dynamics, however, are somewhat contradictory. Caines et al. (1985) reported that this liverwort sequesters Al at pH 5.5 and releases it at a lower pH, potentially exacerbating fish kills. Yet Satake and Nishikawa (1990) report maximum uptake of Al at pH 4.7. Effects of Al and other toxic metal ions are complicated by other factors, including organic matter chelation and antagonistic effects of cations, such as Ca (Farmer, 1990; Whitton et al., 1982).

CONCLUSIONS

The structure and composition of bryophyte communities in West Virginia montane streams vary with stream pH and chemistry. There are distinctive assemblages of species in very acidic (pH 3.9–4.2), moderately acidic (pH 6.0) and basic (pH 7.9) streams. Species richness was strongly reduced in very acidic streams, and no bryophytes were found in a stream with a pH of 3.15. The most acidic streams (pH < 4.0) drained abandoned mines and displayed high conductivities, Al and SO_4 concentrations; interacting chemical factors probably contributed to species impoverishment. The liverwort *S.*

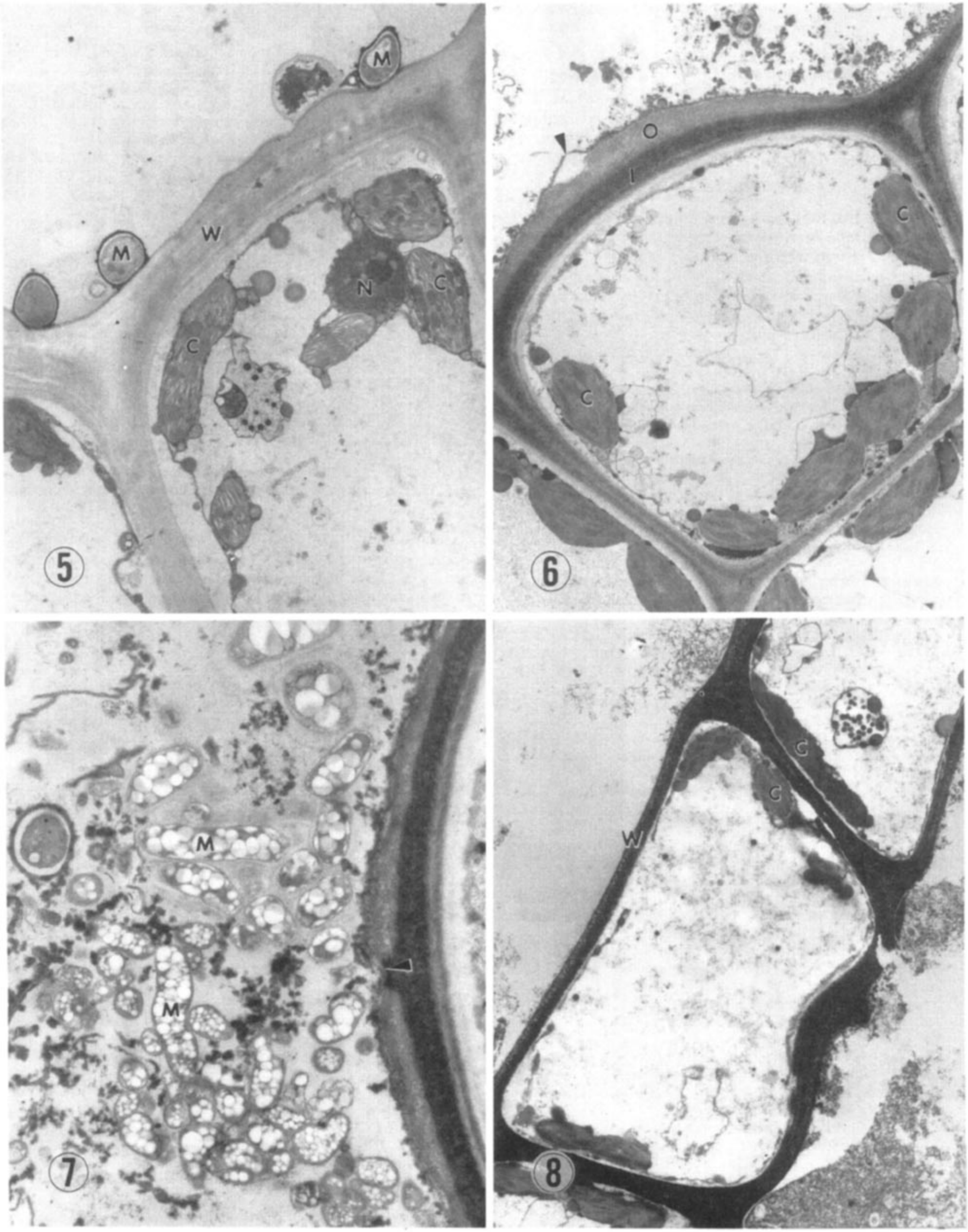

Fig. 5–8. Cross sections of *S. undulata* leaves viewed by transmission electron microscopy. Fig. 5. Upper portion of leaf cell of shoot from WS4. W, cell wall; C, chloroplast; N, nucleus; M, microorganisms attached to cell wall. ×5200. Fig. 6. Leaf cell from shoot transplanted to Finley Run for ×3 mo. Cells had developed a dense inner cell wall (I). The outer cell wall (O) showed deterioration in a discrete area (arrow). Chloroplasts (C) were similar to those from leaf cell in WS4. ×5200. Fig. 7. Microorganisms (M) associated with outer cell wall of shoot transplanted from WS4 to Finley Run. Arrow, area of wall deterioration. ×9500. Fig. 8. Leaf cell from shoot occurring naturally in Tub Run. Cell walls (W) were thin and very dense. Many chloroplasts (C) were small and flattened. ×5200.

undulata is dominant in very acidic streams, but shows serious damage when transplanted to a stream with pH 3.15. Our data suggest that in North America, as in Europe and Japan, *S. undulata* is a potential indicator of acidic, metal-contaminated streams.

ACKNOWLEDGMENTS

We would like to thank Laura Fridley, Kimberly Ruggles, Emmett Fox, John Pearce, Marc Layne Godwin, and Frederica Wood for assisting with the field and laboratory work. We also offer our thanks to Linda Loughry for assisting with the typing. This research was supported in part by funds provided by the USDA Forest Service under Cooperative Agreements 23-337, 23-509, and 23-598.

REFERENCES

Alpert, P.R. 1988. Survival of a desiccation-tolerant moss, *Grimmia laevigata* beyond its observed microdistributional limits. J. Bryol. 15:219-228.

American Public Health Association, American Water Works Association, and Water Pollution Control Federation. 1985. Standard methods for the examination of water and wastewater. 16th ed. APHA, Washington, DC.

Anderson, L.E., H.A. Crum, and W.R. Buck. 1990. List of the mosses of North America north of Mexico. Bryologist 93:448-499.

Andersson, M. 1988. Toxicity and tolerance of aluminum in vascular plants. A literature review. Water Air Soil Pollut. 39:439-462.

Barbour, M.G., J.H. Burk, and W.D. Pitts. 1987. Terrestrial plant ecology. 2nd ed. Benjamin/Cummings, Menlo Park, CA.

Bates, J.W. 1978. The influence of metal availability on the bryophyte and macrolichen vegetation of four rock types of Skye and Rhum. J. Ecol. 66:457-482.

Bates, J.W. 1992. Mineral nutrient acquisition and retention by bryophytes. J. Bryol. 17:223-240.

Brusven, M.A., W.R. Meehan, and R.C. Biggam. 1990. The role of aquatic moss on the community composition and drift of fish-food organisms. Hydrobiologia 196:39-50.

Buescher, P., N. Koedam, and D. van Speybroek. 1990. Cation-exchange properties and adaptation to soil acidity in bryophytes. New Phytol. 115:177-186.

Burton, M.A.S. 1986. Biological monitoring of environmental contaminants (plants). Monitoring and Assessment Research Centre, King's College London, Univ. of London, London.

Caines, L.A., A.W. Watt, and D.E. Wells. 1985. The uptake and release of some trace metals by aquatic bryophytes in acidified waters in Scotland. Environ. Pollut. Ser. B 10:1-18.

Cardwell, D.H., R.B. Erwin, and H.P. Woodward (ed.). 1968. Geologic map of West Virginia. West Virginia Geol. and Econ. Surv., Morgantown, WV.

Carvey, K., D.R. Farrar, and D.C. Glenn-Lewin. 1977. Bryophytes and revegetation of coal spoils in southern Iowa. Bryologist 80: 630-637.

Crum, H.A., and L.E. Anderson. 1981. Mosses of eastern North America. Vol. I and II. Columbia Univ. Press, New York.

Daubenmire, R. 1968. Plant communities: A textbook of plant synecology. Harper & Row Publ., New York.

Dawson, F.H. 1973. Notes on the production of stream bryophytes in the high Pyreenes (France). Ann. Limnol 9:231-240.

Downing, A.J. 1992. Distribution of bryophytes on limestone in eastern Australia. Bryologist 95:5-14.

Duffer, W.R., and T.C. Dorris. 1966. Primary productivity in a southern Great Plains stream. Limnol. Oceanogr. 11:143-151.

Duncan, D., and P.J. Dalton. 1982. Recolonization on bryophytes following fire. J. Bryol. 12:53-63.

Edwards, P.J., and J.D. Helvey. 1991. Long-term ionic increases from a central Appalachian forested watershed. J. Environ. Qual. 20:250-255.

Edwards, P.J., and J.N. Kochenderfer. 1993. Artificial watershed acidification on the Fernow Experimental Forest. p. 70-79. *In* Proc. of the 1991 West Virginia Academy of Science, Montgomery, WV. 6 Apr. 1991. McClain Publ., Parsons, WV.

Edwards, P.J., and F. Wood. 1993. Field and laboratory quality assurance/quality control protocols and accomplishments for the Fernow Experimental Forest watershed acidification study. General Tech. Rep. NE-177. USDA For. Serv., Radnor, PA.

Englund, G. 1991. Effects of disturbance on stream moss and invertebrate community structure. J. N. Am. Benthol. Soc. 10:143-153.

Farmer, A.M. 1990. The effects of lake acidification on aquatic macrophytes: A review. Environ. Pollut. 65:219-240.

Farmer, A.M., J.W. Bates, and N.B. Bell. 1992. Ecophysiological effects of acid rain on bryophytes and lichens. p. 284-306. *In* J.W. Bates and A.M. Farmer (ed.) Bryophytes and lichens in a changing environment. Clarendon, Oxford.

Frahm, J.P. 1976. Weitere toxitoleranzversuche an wassermoosen. Gewässer Abwässer 60/61:113-123.

Gauch, H.G., Jr. 1982. Multivariate analysis in community ecology. Cambridge Univ. Press, New York.

Gerson, U. 1982. Bryophytes and invertebrates. p. 291-332. *In* A.J.E. Smith (ed.) Bryophyte ecology. Chapman & Hall, London.

Glime, J.M. 1968. Ecological observations on some bryophytes in Appalachian Mountain streams. Castanea 33:300-325.

Glime, J.M. 1970. Zonation of bryophytes in the headwaters of a New Hampshire stream. Rhodora 72:276-279.

Glime, J.M. 1987. Phytogeographic implications of a *Fontinalis* (Fontinalaceae) growth model based on temperature and flow conditions for six species. Mem. New York Bot. Garden 45:154-170.

Glime, J.M., and R.E. Keen. 1984. The importance of bryophytes in a man-centered world. J. Hattori Bot. Lab. 55:133-146.

Glime, J.M., P.C. Nissila, S.E. Trynoski, and M.D. Fornwall. 1979. A model for attachment of aquatic mosses. J. Bryol. 10:313-320.

Glime, J.M., and D.H. Vitt. 1987. A comparison of bryophyte species diversity and niche structure of montane streams and stream banks. Can. J. Bot. 65:1824-1837.

Helvey, J.D., and S.H. Kunkle. 1986. Input-output budgets of selected nutrients on an experimental watershed near Parsons, West Virginia. Res. Pap. NE-584. USDA Forest Service, Broomall, PA.

Herben, T., H. Rydin, and L. Söderström. 1991. Spore establishment probability and the persistence of the fugitive invading moss, *Orthodontium lineare*: A spatial simulation model. Oikos 60:215-221.

Horikawa, Y., and A. Kotake. 1960. The bryophyte communities on stream-sides of the Sandankya Gorge, Hiroshima Prefecture. Hikobia 2:32-44.

Losche, C.K., and W.W. Beverage. 1967. Soil survey of Tucker County and part of northern Randolph County, West Virginia. USDA-SCS, USDA-For. Serv., and West Virginia Agric. Stn. U.S. Gov. Print. Office, Washington, DC.

McKnight, D.M., and G.L. Feder. 1984. The ecological effect of acid conditions and precipitation of hydrous metal oxides in a Rocky Mountain stream. Hydrobiologia 119:129-138.

McLean, R.O., and A.K. Jones. 1975. Studies of tolerance to heavy metals in the flora of the rivers Ystwyth and Clarach, Wales. Freshwater Biol. 5:431-444.

Martinez-Abaigar, J., E. Nuñez-Olivera, and M. Sañchez-Diaz. 1993. Effects of organic pollution on transplanted aquatic bryophytes. J. Bryol. 17:553-566.

Mueller-Dombois, D., and H. Ellenberg. 1974. Aims and methods of vegetation ecology. John Wiley & Sons, New York.

Naiman, R.J. 1983. The annual patterns and spatial distribution of aquatic oxygen metabolism in boreal forest watersheds. Ecol. Monogr. 53:73-94.

Ormerod, S.J., K.R. Wade, and A.S. Gee. 1984. Macro-floral assemblages in upland Welsh streams in relation to acidity, and their importance to invertebrates. Hydrobiologia 119:129-138.

Patric, J.H. 1980. Effects of wood products harvest on forest soil and water relations. J. Environ. Qual. 9:73-80.

Peuelas, J. 1984. Pigment and morphological response to emersion and immersion of some aquatic and terrestrial mosses in N. E. Spain. J. Bryol. 13:115-128.

Proctor, M.C.F. 1984. Structure and ecological adaptation. *In* A.J.E. Smith (ed.) Bryophyte ecology. Chapman & Hall, London.

Raeymaekers, G., and J.M. Glime. 1990. Effect of simulated canopy throughfall on the composition of percolate and the chlorophyll content from *Pleurozium schreberi* (Brid.) Mitt. Mem. Soc. Roy. Bot. Belg. 12:67–76.

Rao, D.N. 1982. Responses of bryophytes to air pollution. p. 445–471. *In* A.J.E. Smith (ed.) Bryophyte ecology. Chapman & Hall, London.

Reuss, J.O., and D.W. Johnson. 1986. Acid deposition and the acidification of soils and waters. Springer-Verlag, New York.

Russell, S. 1988. Measurement of bryophyte growth: 1. Biomass (harvest) techniques. p. 249–257. *In* J.M. Glime (ed.) Methods in bryology. Hattori Botanical Lab., Miyazaki, Japan.

Satake, K., and K. Miyasaka. 1984. Evidence of high mercury accumulation in the cell wall of the liverwort *Jungermannia ulcanicola* Steph. to form particles of a mercury-sulfur compound. J. Bryol. 13:101–105.

Satake, K., and M. Nishikawa. 1990. Accumulation of scandium in the shoots of aquatic bryophytes in acid water. Hydrobiologia 199: 173–177.

Satake, K., M. Nishikawa, and K. Shibata. 1989a. Distribution of aquatic bryophytes in relation to water chemistry of the acid River Akagawa, Japan. Arch. Hydrobiol. 116:299–312.

Satake, K., T. Takamatsu, M. Soma, K. Shibata, M. Nishikawa, P.J. Say, and B.A. Whitton. 1989b. Lead accumulation and location in the shoots of the aquatic liverwort *Scapania undulata* (L.) Dum. in stream water at Greenside Mine, England. Aquat. Bot. 33:111–122.

Schuster, R.M. 1966. The Hepaticae and Anthocerotae of North America east of the 100th Meridion. Vol. 1. Columbia Univ. Press, New York.

Schuster, R.M. 1969. The Hepaticae and Anthocerotae of North America east of the 100th Meridion. Vol. 2. Columbia Univ. Press, New York.

Schuster, R.M. 1974. The Hepaticae and Anthocerotae of North America east of the 100th Meridion. Vol. 3. Columbia Univ. Press, New York.

Schuster, R.M. 1980. The Hepaticae and Anthocerotae of North America east of the 100th Meridion. Vol. 4. Columbia Univ. Press, New York.

Schuster, R.M. 1992a. The Hepaticae and Anthocerotae of North America east of the 100th Meridion. Vol. 5. Field Museum of Natural History, Chicago, IL.

Schuster, R.M. 1992b. The Hepaticae and Anthocerotae of North America east of the 100th Meridion. Vol. 6. Field Museum of Natural History, Chicago, IL.

Sheath, R.G., J.M. Burkholder, J.A. Hambrook, A.M. Hogeland, E. Hoy, M.E. Kane, M.O. Morison, A.D. Steinman, and K.I. Van Alstyne. 1986. Characteristics of softwater streams in Rhode Island: III. Distribution of macrophytic vegetation in a small drainage basin. Hydrobiologia 140:183–191.

Slack, N.G., and J.M. Glime. 1985. Niche relationships of mountain stream bryophytes. Bryologist 88:7–18.

Slack, N.G., D.H. Vitt, and D.G. Horton. 1980. Vegetation gradients of minerotrophically rich fens in western Alberta. Can. J. Bot. 58:330–350.

Smith, A.J.E. 1978. The moss flora of Britain and Ireland. Cambridge Univ. Press, London.

Smith, A.J.E. 1990. The liverworts of Britain and Ireland. Cambridge Univ. Press, New York.

Spence, D.H.N. 1975. Light and plant response in fresh water. *In* G.C. Evans et al. (ed.) Light as an ecological factor: II. Blackwell, Oxford.

Stokes, P.M. 1986. Ecological effects of acidification on primary producers in aquatic systems. Water Air Soil Pollut. 30:421–438.

Stotler, R., and B. Crandall-Stotler. 1977. A checklist of the liverworts and hornworts of North America. Bryologist 80:405–428.

Suren, A.M., and M.J. Winterbourn. 1992. The influence of periphyton, detritus, and shelter on invertebrate colonization of aquatic bryophytes. Freshwater Biol. 27:327–339.

Tyler, G. 1990. Bryophytes and heavy metals: a literature review. Bot. J. Linn. Soc. 104:231–253.

Vitt, D.H., and W. Chee. 1990. The relationship of vegetation to surface water chemistry and peat chemistry in fens of Alberta, Canada. Vegetatio 89:87–106.

Vitt, D.H., and J.M. Glime. 1984. The structural adaptations 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.

Wehr, J.D., M.G. Kelly, and B.A. Whitton. 1987. Factors affecting accumulation and loss of zinc by the aquatic moss *Rhynchostegium riparioides* (Hedw.) C. Jens. Aquat. Bot. 29:261–274.

Wehr, J.D., and B.A. Whitton. 1983. Accumulation of heavy metals by aquatic mosses: II. *Rhynchostegium riparioides*. Hydrobiologia 100:261–284.

Whitton, B.A., P.J. Say, and B.P. Jupp. 1982. Accumulation of zinc, cadmium and lead by the aquatic liverwort *Scapania*. Environ. Pollut. Ser. B 3:299–316.