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ENVIRONMENTAL INFLUENCES ON PLANT SPECIES COMPOSITION IN GROUND-WATER SEEPS IN THE CATSKILL MOUNTAINS OF NEW YORK

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Abstract: Ground-water seeps in the Catskill Mountains are important water sources for streams and often have different chemistry than nearby surface water. Many studies have shown correlations between water chemistry and plant species composition in wetlands, but there are no such studies in the Catskill Mountain ground-water seeps. The objective of this study was to identify the chemical and physical environmental variables that most strongly influence plant species composition in seeps. Environmental variables and plant species abundance were measured at 33 seeps. TWo-way INdicator SPecies ANalysis with analysis of variance and Canonical Correspondence Analysis showed that plant species composition is determined primarily by water depth and alkalinity/acidity complex gradients. Growing season changes in water chemistry were not shown to influence the plant community.

Key Words: wetlands, wetland vegetation, seeps, springs, bryophytes, Catskill Mountains, indirect gradient analysis

INTRODUCTION

Ground water is an important water source for streams, especially during the summer when the quantity of surface water diminishes (Williams and Pinder 1990, Likens and Bormann 1995, Rice and Bricker 1995). Ground-water hydrologic flowpaths differ from surface waters and therefore differ in chemistry, even on sites with relatively unreactive bedrock (Rice and Bricker 1995). For example, hydrologic characterization at Hubbard Brook Experimental Forest (HBEF) models two types of waters, dilute surface water and ''salty'' ground water (Likens and Bormann 1995). In the eastern United States, ground waters usually are less acidic and have higher alkalinities than surface waters due to ground-water/bedrock reactions, which yield base cations such as Ca^{2+} and Mg^{2+}.

Ground-water discharge areas, or seeps, typically occur at the bases of steep slopes where the ground surface intersects the water table. Frequently, seeps are caused by an aquiclude, an impermeable layer of rock or clay in the hill. Aquicludes inhibit downward movement of water to the water table but allow horizontal movement to the ground surface. Seeps can also develop when ground water reaches the surface through faults or fractures in impermeable rock (de Blij and Muller 1993). In the Catskill Mountains of New York State, many seeps flow throughout the summer and have well-developed channels approximately 0.5–5 m wide. Channels with high velocity flow usually have cobble substrates with very little sand, silt, or clay. Often, these cobbles are covered with mat-forming mosses such as *Brachythecium rivulare* BSG. and *Bryhnia novae-angliae* (Sull. & Lesq. ex. Sull) Grout; these moss mats are usually the most common substrate for vascular plants in the seep. Channels with low velocity flow often have muddy substrates with less exposed cobble; these channels often have dense populations of herbaceous species such as *Impatiens capensis* Meerb., *Laportea canadensis* (L.) Wedd., or *Eupatorium rugosum* Houttuyn.

Specific environmental conditions are known to affect plant community characteristics in many types of wetlands. For example, a strong relationship between water chemistry and species composition has been shown in peatlands (Jeglum 1971, Karlin and Bliss 1984, Johnson and Leopold 1994, Walbridge 1994, Anderson et al. 1995, Anderson et al. 1996). Ionic con-

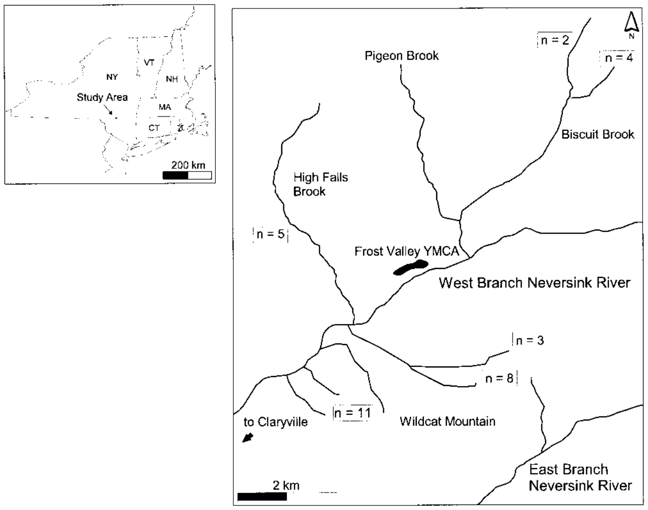

Figure 1. Locations of study areas (in boxes) and number of seeps sampled in each area. Approximate location of study region on inset map.

centrations, especially pH, Ca^{2+}, and Mg^{2+}, affect species composition in moderately to strongly minerotrophic peatlands (Karlin and Bliss 1984, Motzkin 1994). Because there have been few studies of vegetation/environment relationships in seeps and none in the Catskill Mountains, we characterize the environmental factors that are correlated with plant species composition in Catskill ground-water seeps. Knowledge of the effects of seep water on vegetation is important for a basic understanding of these systems; this knowledge will also be useful to watershed managers responsible for prioritizing sites for protection, especially if bioindicators of flow regimes or water chemistry can be found.

METHODS

Site Description

This study was conducted at the Frost Valley YMCA camp, Ulster County, New York, USA (41°59' N, 74°31' W) and at the headwaters of Biscuit Brook (both branches) and High Falls Brook. All seeps are at headwaters of brooks that flow into the West Branch of the Neversink River (Figure 1).

The Catskill Mountain region has bedrock consisting primarily of interbedded layers of shales, sandstones, and conglomerates. Quartz and metamorphic rocks make up approximately 78% and 16% of the mineral and rock fragments; therefore, the bedrock is relatively unreactive (Murdoch and Stoddard 1993). The study area has a ''step-riser'' topography that results from uneven weathering of the bedrock layers (Kudish 1979).

Soils are primarily silt loams and bouldery silt loam inceptisols (Tornes 1979) with low to moderate cation exchange capacities (Murdoch and Stoddard 1993). Soils at the study site are in the Arnot-Oquaga-Lackawanna association, which was derived from glacial till consisting of fragments of regional bedrock (reddish sandstones, siltstones, and shale). The Arnot and Oquaga soils are both moderately to excessively well drained. The Arnot soil has a depth of 25 to 50 cm; the Oquaga soil has a depth of 50 to 100 cm. The Lackawanna soil is very bouldery and has a root-restrictive fragipan at a depth of 43 to 92 cm (Tornes 1979).

Mean annual precipitation is 119 cm. Mean January temperature is −4.2° C; mean July temperature is 21.5° C (Tornes 1979). The elevation range for the study site is approximately 550 m to 900 m.

The forests at the study sites include species typical of the Catskill Mountains. The canopy is dominated by *Fagus grandifolia* Ehrh., *Betula alleghaniensis* Britton, and *Acer saccharum* Marsh.; associated tree species include *Tsuga canadensis* (L.) Carr., *Prunus serotina* Ehrh., *Acer rubrum* L., *Fraxinus americana* L., and *Tilia americana* L. Subcanopy species include saplings of the above tree species, and *Acer pensylvanicum* L., *Hamamelis virginiana* L., *Ilex montana* (T. & G.) A. Gray, *Ostrya virginiana* (Mill.) K. Koch, and *Viburnum alnifolium* Marsh. Common herbs include: *Dryopteris intermedia* (Muhl.) A. Gray, *Dennstaedtia punctilobula* (Michx.) Moore, *Lycopodium lucidulum* Michx., *L. annotinum* L., *Laportea canadensis, Tiarella cordifolia* L., *Trillium erectum* L., *Trientalis borealis* Raf., and *Oxalis acetosella* L. Nomenclature for mosses follows Crum (1983), for liverworts follows Schuster (1974), and for vascular plants follows Gleason and Cronquist (1991).

Vegetation Sampling

Seeps were selected for sampling based on the following criteria: 1) the presence of an extensive water chemistry data set from ongoing hydrologic investigations by the United States Geological Survey; 2) high or low pH, relative to previously sampled seeps, to include as large a range of site conditions as possible; and 3) a high abundance of plant species not encountered in previously sampled seeps. Seeps with continuous flow throughout most of the summer were preferentially selected over similar ''ephemeral'' seeps.

Vegetation was sampled in 10 × 20 m plots placed so that the seep channel bisected the long axis of the plot (the 20 m side). Initially, 2 or 3 plots were placed along the seep channel, with the center of the first plot placed 15 m downstream from where the seep first discharged above ground and the centers of the downstream plots 10–25 m apart from the previous plot, depending on channel length. It became apparent that the vegetation was homogenous along a given seep channel, so only one plot was established on subsequently sampled seeps. Forty-five plots were established on 33 seeps. Percent cover of herbaceous species, bryophytes, and woody seedlings < 0.5 m tall was estimated in eight 0.5×1 m quadrats placed in a continuous line approximately in the center of the seep channel and within the 10×20 m plot. The herbaceous species on the banks of the seep channel were not sampled because they were dry and occupied by typical upland herbs as described in the site description. Plant cover was visually estimated and recorded in a cover classification system ranging from 1 to 5 with the following values: 1 = 1–5% cover, mean value = 2.5%; 2 = 5–25% cover, mean value = 15%; 3 = 25–50% cover, mean value = 35.5%; 4 = 50–75% cover, mean value = 62.5%; 5 = 75–100% cover, mean value = 82.5%; p = present but less than 1% cover, mean value = 0.1% (Barbour et al. 1987). The relative cover of each species was calculated as a percentage of the sum of all species' cover in the plot; thus, an individual species relative cover value ranged from 0 to 100 with a sum of 100 for each plot. Estimating cover of the mosses *Brachythecium rivulare* and *Bryhnia novae-angliae* was difficult because they have very similar appearances in the field and often grow together in mixed mats on cobbles in the seep channel. The cover of the two-species mixture was estimated as with other species. To estimate the relative proportions of the two species in the mixture, the mats were removed from four 0.25×0.25 m quadrats in each 10×20 m plot and allowed to dry at room temperature. After drying, the appearance of the two species became less similar, and they could be identified macroscopically with confidence. The relative proportions of each species in the 0.25×0.25 m quadrats were then estimated and the mean proportion was calculated for each plot. The mean relative proportions were multiplied by the relative cover of the two-species mixture to get an estimate of each species' cover in the 10×20 m plot.

The diameter of all woody stems ≥ 1.5 m tall in the 10×20 m plot was measured at breast height (dbh) and recorded by species. Canopy stems were defined as having a dbh > 5 cm; subcanopy stems were defined as having a dbh ≤ 4.9 cm.

Environmental Sampling

Surface-water pH and conductivity (Cond) were analyzed in a laboratory from seep-water samples collected from the center of each vegetation plot. Samples were collected monthly between May 1996 and September 1996 and in April 1997. Because all plots had not been set up for the entire study period, some plot sample data are missing. The number of samples per month is as follows: May–18; June–20; July–34; August–45; September–41 (4 seeps were dry); April (1997)-43. In each quadrat, the typical substrate height above or below the water table was measured and expressed as a plot mean height above water table (MHAWT). Percent open water (%OW) was estimated in each of the quadrats using the same cover classes as for vegetation cover; a plot mean was calculated. Percent slope and aspect of each plot were estimated with a clinometer and compass, respectively. Canopy basal area (Can BA) and subcanopy density (Sub den) data were collected as part of the vegetation sampling (see above). Water samples were collected in August 1996, and the concentrations of major ions were measured by the following methods: NH_4^+—Wescan Ammonia Analyzer; Cl^-, NO_3^-, SO_4^{2-}—Dionex Ion Chromatograph; Ca^{2+}, Mg^{2+}, Na^+, K^+, Al—Spectro-Analytical Instruments Model FMA-07 Inductively Coupled Plasma-Atomic Emission Spectrometer. Detailed chemical analyses were conducted only once since preliminary research showed high correlations between pH and ions. The quantity of light (μ einsteins/m^2/sec) was measured using a LI-COR model LI-185B Quantum/Radiometer/Photometer. Measurements were made at 0.5 m above the ground at four equally spaced points in the seep channel, and the readings were expressed as percent full sun (PFS), which was measured in nearby open fields. To minimize temporal variability, all light measurements were taken between 1000 and 1400 hrs during two weeks of August 1996 on sunny or uniformly cloudy days.

Data Analysis

Plot Classification. The TWINSPAN program (TWo-way INdicator SPecies Analysis; Hill 1979) was used to divide the seep herb-layer data into a hierarchy of vegetation community types, or classes, based on presence/absence of species. All dichotomies through the third division level were retained if the resulting groups had greater than four sampling plots in them. This classification facilitates descriptions of the seeps based on their vegetation and allows the differences in vegetation to be correlated to the measured environmental variables as described below.

Analysis of Variance (ANOVA). ANOVA was performed between environmental variables of the two resulting groups at each retained TWINSPAN dichotomy to show which variables differed between the two groups (Jongman et al. 1987, Anderson et al. 1995). ANOVA was also used to compare means of environ-

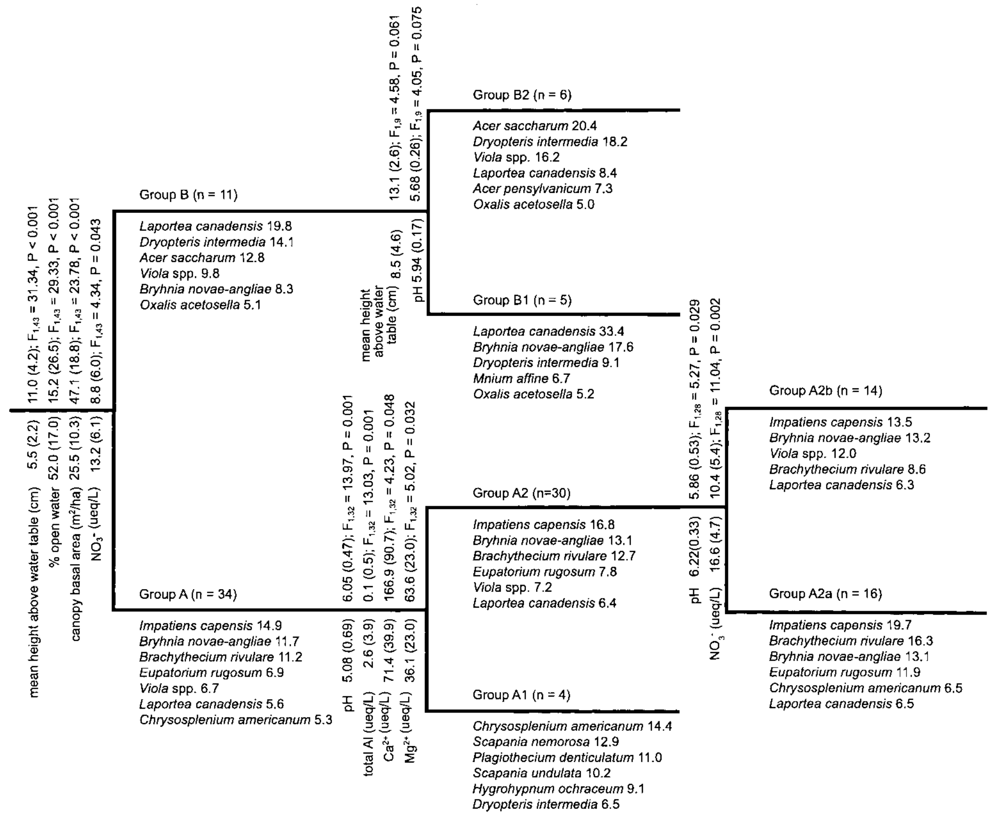

Figure 2. Dominant species, mean relative cover, and significantly different environmental variables between TWINSPAN groups. Significantly different environmental variables (mean (standard deviation)), F, and P values are listed at each dichotomy. Dominant species had mean relative cover greater than or equal to 5.0.

mental variables for the final TWINSPAN groups. For variables with significant differences as shown by the ANOVA, Tukey's Tests were used to identify the groups with significantly different means ($p \leq 0.05$) (Jongman et al. 1987, Suren 1996).

Canonical Correspondence Analysis. Investigations of species' responses to environmental variables were conducted using canonical correspondence analysis (CCA) with the program CANOCO 3.1 (ter Braak 1987–1992). The forward selection option for environmental variables was used. Forward selection is useful in identifying a few environmental gradients that are associated with differences in species composition and in reducing multicollinearity in the environmental data set (Palmer 1993). All environmental variables, except pH, were log-transformed prior to CCA to reduce skewness in frequency distributions (Palmer 1993) and to reduce variance dependence on the mean (Jongman et al. 1987).

RESULTS

Plot Classification

The TWINSPAN resulted in four retained divisions, with five final groups of seep herbaceous communities (Figure 2). The first dichotomy had one group, labeled group A, which was dominated by (i.e., high mean relative cover) *Impatiens capensis, Bryhnia novae-angliae, Brachythecium rivulare,* and *Eupatorium rugosum.* Group B was dominated by *Laportea canadensis, Dryopteris intermedia, Acer saccharum* seedlings, *Viola* spp. (mostly *V. cucullata* Aiton and *V. macloskeyi* F. Lloyd), and *Bryhnia novae-angliae.* The ANOVA of environmental data of the two groups identified four variables that differed significantly, including mean height above water table, percent open water, canopy basal area, and NO_3^-. Group B was further divided into a group dominated by *Laportea canadensis, Bryhnia novae-angliae,* and *Dryopteris intermedia* (group B1) and a group dominated by *Acer saccharum* seedlings, *Dryopteris intermedia,* and *Viola* spp. (group B2). There were no significant differences in environmental data at $P \leq 0.05$, but the mean height above water table was significantly different at $P = 0.06$, and pH was different at $P = 0.075$.

Group A was separated into a group (A1) with four plots dominated by prostrate plants *Chrysosplenium americanum* Schwein, the liverworts *Scapania undulata* (L.) Dumort and *S. nemorosa* (L.) Dumort, and the mosses *Hygrohypnum ochraceum* (Turn. *ex* Wils.),

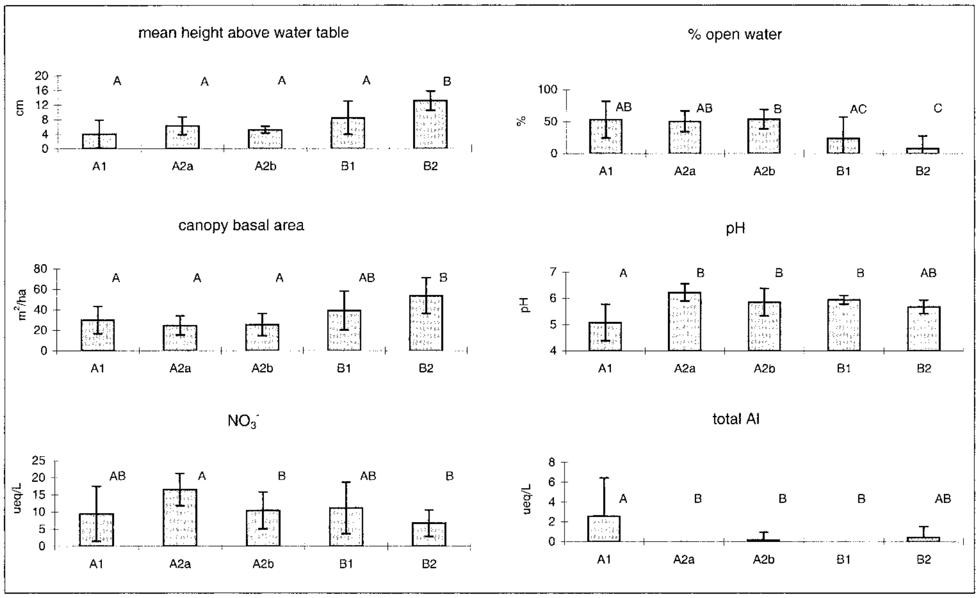

Figure 3. Environmental variables (mean height above water table, % open water, canopy basal area, pH, NO_3^-, and total Al) with significant difference between the five final herb layer TWINSPAN groups (columns). Significance determined by Tukey's Studentized Range (HSD) Test with confidence limit differenced (CLDIFF), $P < 0.05$. Groups with different letters are significantly different. Error bars denote 1 SD.

and *Plagiothecium denticulatum* (Hedw.) BSG.; and a group (A2) of 30 plots dominated by taller vascular herbaceous plants *Impatiens capensis* and *Eupatorium rugosum* and the mosses *Brachythecium rivulare* and *Bryhnia novae-angliae.* Group A2 had a higher pH, higher Ca^{2+}, higher Mg^{2+}, and lower total Al than group A1.

The fourth dichotomy separated group A2 into two groups of approximately equal numbers of plots (Figure 2). These two groups shared many dominant species, including *Impatiens capensis, Bryhnia novae-angliae, Brachythecium rivulare,* and *Laportea canadensis,* although group A2a had higher values for *Brachythecium rivulare, Impatiens capensis, Eupatorium rugosum,* and *Chrysosplenium americanum,* while group A2b had more *Viola* spp. For the environmental data, group A2a had higher pH and higher NO_3^-.

Environmental Relationships Between the Five Final Groups

ANOVA of the five retained TWINSPAN groups indicated six variables with significant differences between the groups: mean height above water table, percent open water, canopy basal area, pH, NO_3^-, and total Al (Figure 3).

Canonical Correspondence Analysis

Forward selection of environmental variables in CCA showed that seven variables described the variation in the species data. The selected variables were percent open water, pH, Mg^{2+}, conductivity, mean height above water table, NH_4^+, and percent full sun. The first axis (eigenvalue = 0.51) was most strongly correlated with percent open water (negatively), pH (negatively), and mean height above water table (positively) (Figure 4). The second axis (eigenvalue = 0.40) was most strongly correlated with pH and mean height above water table (both negatively), suggesting that the second axis is related to the first, a common problem with reciprocal averaging-based ordination techniques. The third axis (not shown) (eigenvalue = 0.24) was negatively correlated with Mg^{2+} and positively with conductivity, representing an ionic gradient. The fourth axis (not shown) (eigenvalue = 0.18) was most strongly correlated with NH_4^+.

The only ions entered into forward selection were NH_4^+ and Mg^{2+}. Other ions may not have been selected because all, except NH_4^+, Cl^-, and SO_4^{2-}, were correlated with pH (not shown), and thus, variation in vegetation associated with ions may be adequately summarized by pH and/or Mg^{2+}. NH_4^+ was the sixth variable entered into forward selection; it may be required to summarize the variation in the data because it was not correlated with any of the entered ion-related variables (pH, Mg^{2+}, and conductivity).

The position of species on the first two axes of the CCA diagram was most strongly correlated with percent open water, mean height above water table, and pH. A species optimum for an environmental variable,

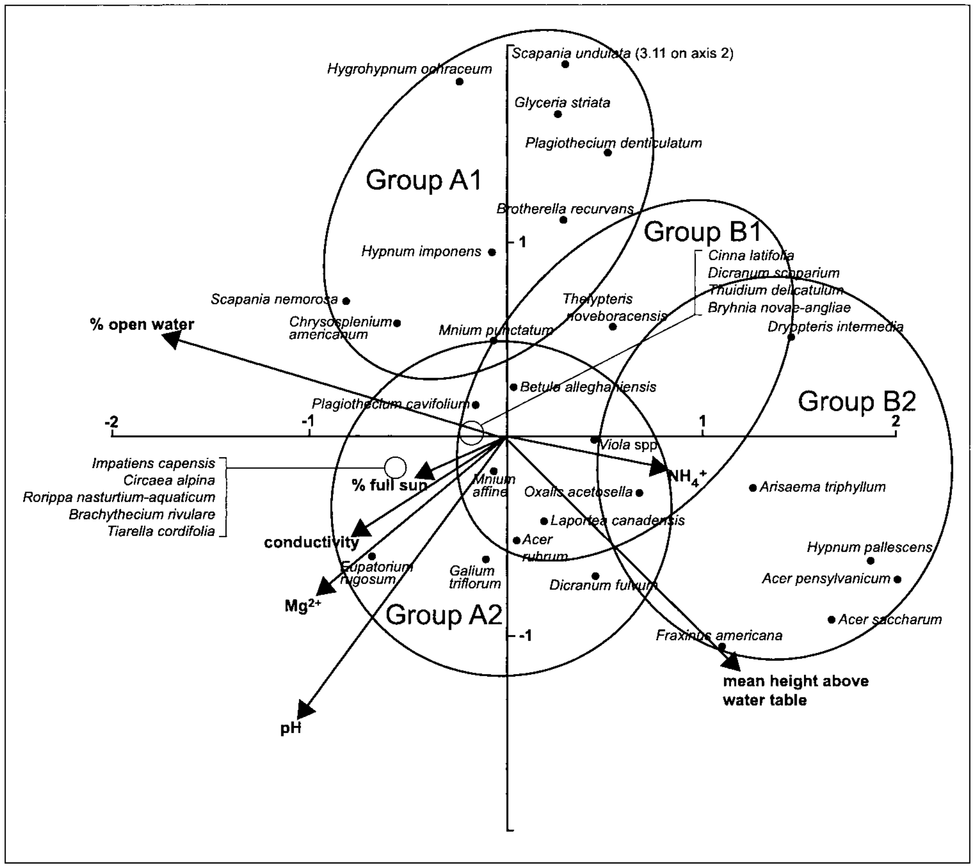

Figure 4. Canonical Correspondence Analysis of all species with forward selection of environmental variables. The approximate locations of the four major plot groups are shown in rings. Groups A2a and A2b are not shown for clarity. Eigenvalues are as follows: axis 1, 0.51; axis 2, 0.40; axis 3, 0.24; axis 4, 0.18.

relative to other species, can be estimated by visualizing a perpendicular line from that species label to the environmental vector, with values of the environmental variable increasing towards the variable label or the vector's arrow-head.

The seedlings of the upland tree species, *Acer pensylvanicum, A. saccharum,* and *Fraxinus americana* were found in the area of lowest percent open water, mid-range pH, and highest mean height above water table. The bryophytes *Scapania undulata, Hygrohypnum ochraceum, Plagiothecium denticulatum* and the grass *Glyceria striata* (Lam.) A. Hitchc. were found in the area of medium percent open water, lowest pH, and lowest mean height above water table. *Oxalis acetosella, Dicranum fulvum* Hook., *Laportea canadensis, Acer rubrum,* and *Galium triflorum* Michx. were in the area of low percent open water, high mean height above water table, and mid-range pH. There was a cluster of the species *Cinna latifolia* (Trevir.) Griseb., *Thuidium delicatulum* (Hedw.) BSG., *Dicranum scoparium* Hedw., *Impatiens capensis, Tiarella cordifolia, Rorippa nasturtium-aquaticum* (L.) Hayek, *Brachythecium rivulare, Bryhnia novae-angliae,* and *Circaea alpina* L. in the region of mid- to low percent open water, mean height above water table, and high pH.

DISCUSSION

Plant Species Distributions

Hydrologic characteristics, including percent open water and substrate height above the water table, as well as chemical characteristics including pH and concentrations of ions such as Ca^{2+}, Mg^{2+}, and NO_3^- are correlated with plant species composition in Catskill Mountain ground-water seeps. Other less strongly correlated variables that are significantly different among the groups of the TWINSPAN dichotomies are canopy basal areas and Al concentrations. Additional variables that entered into the CCA equation include conductivity, NH_4^+, and percent full sun.

Percent open water and mean height above water table may be viewed as components of a complex gradient of water quantity or depth. A complex gradient is a series of environmental variables that change together along some primary gradient (Whittaker 1966).

Percent open water is an estimate of the amount of submerged substrate unavailable for occupation by terrestrial plants (only two submerged plant species were encountered in the study, *Fontinalis antipyretica* Hedw., which occurred in only one plot and was therefore not in the data analysis, and *Hygrohypnum ochraceum*). The mean height above water table is an estimate of the water level relative to the rooting zone of the vascular plants and the ramets of the bryophytes. This measurement is analogous to floodplain elevation used in many riparian vegetation studies, although on a much smaller spatial scale. Several studies in many types of wetlands have shown a significant vegetation-water quantity or depth relationship, where water quantity has been measured as percent standing water, peat moisture, degree of soil saturation, floodplain elevation, depth of water, height above water table, or microtopography. These studies include peatlands (Glaser et al. 1990, Vitt et al. 1990, Anderson et al. 1995, Anderson et al. 1996), fens (Bernard et al. 1983, Motzkin 1994, Walbridge 1994), riparian wetlands (Bell 1974, Bell and del Morel 1977, Barnes 1978, Bell 1980, Harris 1986, Menges 1986), and swamps (Parsons and Ware 1982, Paratley and Fahey 1986).

Because there have been very few studies of seep vegetation in the United States, riparian studies must be used for comparisons. This comparison is valid because streams often have hydrologic regimes and vegetation similar to the seeps. Riparian vegetation composition is correlated primarily with floodplain elevation or height above the water table, which is a complex gradient determining flood frequency, flood duration, and water-table depth (Menges 1986). The grade, or slope, of a stream can influence the stream width, water depth, and velocity. Higher velocity streams have increased sediment transport, which can directly affect vegetation through physical disturbance and can indirectly affect vegetation by determining soil texture (Hupp 1982). Hupp (1982) found that a higher stream gradient caused an increase in channel width, a decrease in water depth, and the formation of a braided channel. At the Catskill study sites, the higher slope channels were usually narrower, had deeper channels, and were less braided than lower slope channels. The water velocities were greater, which resulted in less cobble and soil substrate and more exposed bedrock in the channel.

Many riparian studies have shown the influence of floodplain elevation on vegetation. In the present study, the lower mean height-above-water-table ranges were occupied by plants with adaptations to tolerate flowing water such as being small statured, prostrate, and/or being firmly attached to the rock substrates (*Hygrohypnum ochraceum, Scapania undulata, Scapania nemorosa, Plagiothecium denticulatum, Plagiothecium cavifolium* (Brid.) Iwats., *Chrysosplenium americanum,* and *Rorippa nasturtium-aquaticum* (Figure 4)). Channels with gentle slopes had lower water velocities, which resulted in less soil removal and fewer exposed cobbles in the channel. These gentle-sloped channels also had the only submerged aquatic plants in the study, *Hygrohypnum ochraceum* and *Fontinalis antipyretica. Circaea alpina,* a small upright plant, also grows at lower levels on moss covered cobbles (Haber 1977); perhaps the moss mats provide a firm and erosion resistant substrate for the plants rhizomes. Robach et al. (1996) found that *Rorippa nasturtium-aquaticum* grew best in water that did not freeze during the winter, such as ground-water streams; this species also occurs in Catskill Mountain seeps that flowed throughout the winter.

Several studies have shown that bryophytes are distributed in vertical zonation patterns along a stream elevation (relative to water level) gradient, from aquatic species to upland species. This patterning is related to species tolerance to decreasing humidity away from the water (Glime 1970, Craw 1976, Vitt et al. 1986, Muotka and Virtanen 1995, Virtanen 1995, Suren 1996), physical damage from flowing water and sediments (Craw 1976, Kimmerer and Allen 1982, Suren 1996), and light intensity (Glime 1970).

The bryophyte floodplain elevational pattern in the Catskill Mountain seeps is similar to that shown in other studies. Muotka and Virtanen (1995) found that *Hygrohypnum ochraceum* and *Scapania* spp. were in the lowest elevations above the water surface. *Scapania undulata* was at lower mean heights above the water table than *Scapania nemorosa* (Figure 4), as shown by Glime (1970) and described by Schuster (1974). *Brachythecium rivulare* was most abundant at low-mid heights above the water table and is classified as an emergent (Vitt et al. 1986) and as a facultative aquatic (Virtanen 1995). Virtanen (1995) considered *Mnium punctatum* Hedw. to be a ''terrestrial species of moist and wet habitats'' and *Mnium affine* Bland. *ex* Funck. to be a ''herb rich forest species.'' In the study area, *M. punctatum* appeared to occur in wetter areas than *M. affine,* but *M. affine* was usually only found in seep areas, not in the surrounding forest as described by Virtanen. Many of the bryophyte species included in the analysis are often found in upland forests on moist decaying wood (*Thuidium delicatulum, Hypnum imponens* Hedw.), tree roots (*Hypnum pallescens* (Hedw.) P.-Beauv.), or rocks (*Dicranum fulvum*) (Crum 1983). These species were usually on the moss-covered cobbles close to the water, but occasionally high local abundance may have been due to the presence of the preferred substrate in sampling quadrats rather than to any of the variables measured in the study.

The grasses, *Cinna latifolia, Glyceria striata,* and *Poa* spp., had their greatest importance at the low- to mid- mean height above water table, as in Menges and Waller (1983) and Menges (1986). Apical meristems of perennial forbs may be damaged by moving water at the lower floodplain elevations, while the basal meristems and overall morphology of grasses make them more tolerant of flowing water (Menges and Waller 1983).

In the low- to mid-range of mean height above the water table, three tall herbs had large relative cover values: *Impatiens capensis, Laportea canadensis,* and *Eupatorium rugosum.* Barnes (1978) found that *L. canadensis* had its greatest frequency at lower floodplain elevations, *I. capensis* at higher elevations, and *E. rugosum* at mid- to high elevations, while Menges and Waller (1983) found that *I. capensis* was more frequent at lower floodplain elevations and *L. canadensis* at higher elevations. The results from this study are sililar to those of Menges and Waller (1983); *I. capensis* was most abundant at the lowest MHAWT, *L. canadensis* was most abundant at the highest MHAWT, and *E. rugosum* was most abundant in the middle. Several additional factors may be associated with the relative abundances of *I. capensis* and *L canadensis.* For example light, may be a determining factor; Menges and Waller (1983) consider *L. canadens*is a ''light generalist,'' meaning it can exist in varied light conditions, while *I. capensis* is a ''high light specialist.'' In field observations, it was noted that *I. capensis* was usually less than 30 cm tall on sites with a denser tree canopy, but it was approximately 1 m tall on open-canopy sites. Simpson et al. (1985) also found that it had greater height and biomass on full-sun sites. Differences in competitive abilities and site-colonization strategies may also influence the abundances of *I. capensis* relative to *L. canadensis. Impatiens capensis* is an annual ''competitive ruderal'' (Menges and Waller 1983), and each year the population must be reestablished by seeds, thus it is susceptible to local extinction. It may be poor at site colonization because the large seeds may depend on water for dispersal (Winsor 1983). *Laportea canadensis* is a competitive species that can reproduce either by seed or by clonal growth (Menges and Waller 1983). *Impatiens capensis* was most often growing on moss-covered cobbles, while *L. canadensis* was more often on soil. *Laportea canadensis* may not survive on the moss-covered cobbles because it needs deeper substrate for its larger root system. If it is able to survive on the cobbles, clonal expansion would be inhibited by the small size of the cobbles and the flowing water between them.

Water pH and ion concentrations may be viewed as components of a complex alkalinity/acidity gradient. This complex gradient includes variables such as pH, alkalinity, acidity, hardness, and base cation concentrations (Vitt and Chee 1990, Motzkin 1994, Anderson et al. 1995), but in this study, additional ions such as NO_3^-, K^+, and Na^+ were positively correlated with pH while total Al was negatively correlated. Alkalinity/acidity complex gradients have been correlated with plant species composition and abundances in many types of wetlands, including near-ombrotrophic peatlands (Vitt and Slack 1975, Karlin and Bliss 1984, Glaser et al. 1990, Vitt et al. 1990, Anderson et al. 1995, Anderson et al. 1996), minerotrophic fens (Vitt and Chee 1990 (for bryophytes), Motzkin 1994, Walbridge 1994), riparian wetlands (Dunn and Stearns 1987 (for trees)), and swamps (Parsons and Ware 1982).

Most studies of environment-vascular plant species composition relations in riparian wetlands have not focused on water chemistry but rather on components of the floodplain elevation complex gradient, light, and soil characteristics (Bell 1974, Bell and del Morel 1977, Barnes 1978, Bell 1980, Menges and Waller 1983, Harris 1986, Menges 1986, Dunn and Stearns 1987). In contrast, there are many water chemistry-bryophyte species composition studies. Water chemistry may be more important for riparian bryophytes that obtain most of their nutrients from water than for terrestrial vascular plants that use soil nutrients. In headwater streams, such as the study seeps, bryophytes are often closer to the water and may be the only streamside vegetation (Vitt et al. 1986). In streams of western Canada, Vitt et al. (1986) found that the first axis of a detrended correspondence analysis ordination was correlated with Ca, Mg, and soil texture and the second axis was correlated with soil texture and height relative to the water surface. *Brachythecium rivulare* was considered a calciphile; it also occurred in the high Ca^{2+} and pH seeps in our study (Figure 4). Muotka and Virtanen (1995) also found *Brachythecium rivulare* in streams with high pH and *Scapania* spp. and *Hygrohypnum ochraceum* in the streams with low pH, as in our study seeps.

Seep Biogeochemistry

NO_3^- and pH were positively correlated, although they were expected to be negatively related since NO_3^- is often associated with episodic decreases in pH and acid neutralizing capacity (e.g., Murdoch and Stoddard 1993). NO_3^- is positively correlated with all ions except NH_4^+ and total Al; thus, sites with a high NO_3^- often have even higher concentrations of the base cations Ca^{2+} and Mg^{2+}, which results in an increase in pH. The positive correlations between pH and conductivity and also between conductivity and NO_3^- are further evidence for this high ion concentration/high pH relationship. Acidic anions, such as NO_3^- and SO_4^{2-}, may increase the decomposition rate of rocks, which would cause an increase in base cation concentrations (Rice and Bricker 1995, van Dam and Mertens 1995). The high NO_3^-/high pH relationship may be caused by the temporal aspects of ground-water recharge. It has been shown that there are two separate ground-water systems in the area of the Frost Valley site, one shallow and one deep (Burns et al. 1998). The shallow system may be dry during the summer, except for shortly after storms, while the deeper system flows throughout the year. The deeper system has a residence time of 6 to 22 months and is recharged during the early spring (late February–March) and autumn (August–November) seasons (Burns et al. 1998). Since the vegetation is dormant during most of the recharge period, most of the NO_3^- is available to pass into the deeper ground water. Later in the year, the NO_3^- is discharged in ground-water seeps that emanate from the hillside and quickly channelize, thus largely avoiding the plants' rooting zones. The NO_3^- concentrations in stream water during the summer are clearly associated with the presence of such seep zones. Thus, it is possible that forest soils could be nitrogen-limited in the Catskill Mountains during the summer, while Catskill Mountain stream concentrations of NO_3^- are above detection, since seeps are acting as a NO_3^- source (Burns et al. 1998).

While this study focused on the effect of water chemistry on plant distribution, it is apparent that vegetation can significantly affect water chemistry in the seep zones. The seep zones are areas of denitrification and vegetation uptake of NO_3^- during the growing season, thus reducing surface-water NO_3^- concentrations as the water travels across the seep zone (Burns 1998). Denitrification can be an important process, especially in seep channels with slow water-flow rates and high organic matter accumulation (Burns 1998), but most of the seeps in the study area had rapid flow rates and low organic matter accumulations. These seeps usually had dense mats of the mosses *Brachythecium rivulare* and/or *Bryhnia novae-angliae* and much vascular vegetation; thus, plant uptake may also be an important process in reducing seep-water NO_3^- concentrations. This reduction of NO_3^- could have a significant impact on water quality since most of the seeps with dense vegetation are fed by deep ground water and therefore flow throughout the year and may have elevated NO_3^- concentrations. Uptake by vegetation may be low if the water flows too rapidly past the plants or if the cobble substrate is above the water level, isolating the plant roots and moss mats from direct contact with the water. Plant biomass may only serve as a short-term nitrogen sink since the aboveground portions of the plants die each year and nutrients are re-released to the water. The effects of seep vegetation on nitrogen retention and transformation are complex and require further investigation.

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