

## Aquatic macrophytes in Adirondack (New York) lakes: patterns of species composition in relation to environment

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A study of aquatic vegetation of 31 small, dilute, and unproductive lakes in the Adirondack Mountains of New York shows that macrophyte species composition is primarily related to variation in pH and associated factors. Among the lakes, surface water pH ranged from 4.5 to 7.8; conductivity ranged from 11.9 to 58.7  $\mu\text{S}/\text{cm}$ . Relationships between aquatic vegetation and environmental factors were studied using detrended correspondence analysis (DCA). Submersed and floating-leaved taxa were analyzed separately from emergent taxa. Correlations between DCA axis 1 and pH-related factors (pH, alkalinity, Ca, Mg, Na, Al, conductivity, elevation) were strong for both submersed plus floating-leaved and emergent taxa. No significant correlations were found with water color, transparency, or trophic status indicators (total P and chlorophyll *a*). Between-lake variation in composition of aquatic vegetation in Adirondack lakes follows a pH "complex-gradient." Influences of elevation, morphometry, and substrate are secondary. Our results indicate that acidification of softwater lakes could be accompanied by significant changes in aquatic macrophyte assemblages.

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Une étude de la végétation aquatique de 31 petits lacs, dilués et improductifs dans les Montagnes de l'Adirondack de New York a établi une relation primaire entre la composition des espèces de macrophytes et la variation dans le pH et les facteurs qui y sont associés. Parmi les lacs, le pH de l'eau de surface était situé entre 4,5 à 7,8 et la conductivité entre 11,9 et 58,7  $\mu\text{S}/\text{cm}$ . Les relations entre la végétation aquatique et les facteurs écologiques ont été étudiées à l'aide d'analyses d'ordination (AO). Les taxons à feuilles submergées – flottantes ont été analysés séparément des taxons émergents. Les corrélations entre l'axe 1 de l'AO et les facteurs reliés au pH (pH, alcalinité, Ca, Mg, Al, conductivité, élévation) étaient fortes pour les taxons à feuilles submergées – flottantes et pour les taxons émergents. Aucune corrélation n'a été trouvée avec la couleur ou la transparence de l'eau ni avec les indicateurs de statut trophique (P total et chlorophylle *a*). La variation «entre lacs» de la composition de la végétation aquatique des lacs de l'Adirondack suit un gradient complexe de pH. Les influences de l'élévation, de la morphométrie et du substrat sont secondaires. Nos données indiquent que l'acidification des lacs d'eau douce pourrait être accompagnée de changements importants dans les assemblages de macrophytes aquatiques.

[Traduit par la revue]

### Introduction

Comparative studies of aquatic macrophyte vegetation among basins differing in limnological characteristics are valuable in understanding aquatic vegetation–environment relationships (Hutchinson 1975). These studies allow identification of the major environmental gradients controlling composition and structure of aquatic macrophyte communities. In addition, they provide specific information on the distributions of aquatic plant species with respect to chemical and other environmental variables. This information is useful in suggesting and (or) corroborating mechanistic ecophysiological and population studies of aquatic plants. Data from comparative studies also find application in paleolimnological reconstructions based on macrofossils of aquatic macrophytes (Birks 1973, 1980).

Comparative macrophyte studies have pointed to water chemistry as a major influence on composition and structure of aquatic vegetation (Hutchinson 1975). Alkalinity, pH, and ionic composition and concentration (as represented by composite indices of hardness, conductivity, or salinity) have been identified as important chemical factors underlying variation in macrophyte community composition. These variables are all significantly interrelated and may comprise a single envi-

ronmental "complex-gradient" (Whittaker 1967) influencing aquatic vegetation.

Nearly all comparative studies to date have been in regions of circumneutral to hardwater lakes (Lohammar 1938; Moyle 1945; Swindale and Curtis 1957; Spence 1964, 1967; Birks 1973; Crowder *et al.* 1977), regions of circumneutral lakes characterized by wide variations in ionic concentration and trophic status (Seddon 1967, 1972), or areas in which water quality ranges widely from acidic to very hard or even saline (Iversen 1929; Iversen and Olsen 1943; Pip 1979; Hellquist 1980; Kadono 1982). Macrophyte studies in regions of predominantly softwater lakes are few in number and mostly limited in their conclusions with respect to chemical gradients. The five New Hampshire lakes studied by Collins and Likens (1969) vary widely in elevation, size, and morphometry. Wile and Miller (1983) and Yan *et al.* (1985) conducted extensive botanical and chemical surveys of softwater lakes in south-central Ontario, but interpretation of their data is at least partly confounded by high concentrations of heavy metals in many of their study sites near Sudbury. Catling *et al.* (1986) have recently demonstrated a pH-related gradient in composition of macrophyte communities among softwater lakes in Nova Scotia. A detailed study of nine lakes in northern New York (Roberts *et al.* 1985) provides information on chemical influences on macrophyte community structure. However, the small number of sites limits interpretation of between-site differences in species composition.

The paucity of comparative macrophyte studies of lakes at

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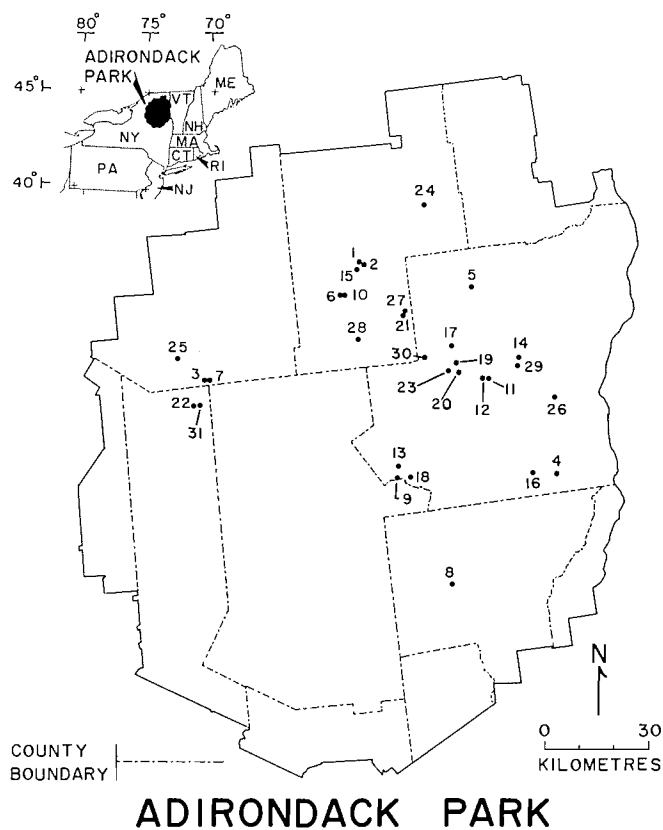


FIG. 1. Map of the Adirondack Park, NY, showing locations of study lakes. Lake names corresponding to map numbers are listed in Table 1. Inset: Map of northeastern United States, showing location of Adirondack Park.

the lower end of the pH–alkalinity–conductivity complex-gradient is a serious deficiency. Vegetational variation occurring along broad, “master” environmental gradients (e.g., highly acidic to highly alkaline waters) can mask significant trends occurring at finer scales (Peet 1980). It remains to be determined whether the chemical factors responsible for vegetational differences among alkaline–hardwater lakes and between softwater and hardwater lakes exert a significant influence at the restricted scale of dilute, softwater lakes. This question is especially relevant in light of recent chemical changes induced by acid deposition on softwater systems in northeastern North America.

We present and discuss results of an investigation of aquatic macrophyte composition of 31 small, dilute lakes in the Adirondack Mountains of northern New York (U.S.A.) (Fig. 1; Tables 1, 2). Objectives of the study were (i) to describe the aquatic macrophyte floras of the lakes, (ii) to assess the chemical and (or) other factors responsible for between-lake differences in species composition and richness, and (iii) to evaluate the potential consequences of lake acidification for aquatic macrophyte composition.

### Regional setting

The Adirondack Mountains consist of a large, highly dissected geologic dome in northern New York (Fig. 1). Elevations range from 30 to >1500 m. Bedrock consists of a variety of Proterozoic metamorphic and igneous rocks (Buddington 1953; Isachsen and Fisher 1970). Surficial materials include bedrock, coarse-textured tills of varying thickness, and coarse outwash. Regional climate is character-

ized by cold, snowy winters and cool, wet summers (Mordoff 1949). Temperature and precipitation vary substantially with elevation (Kudish 1975).

The region is largely undeveloped and forested. Forest composition varies with elevation and soil texture (Heimberger 1934; Braun 1950; Holway *et al.* 1969; Nicholson *et al.* 1979). Forests below 300–400 m consist of hemlock, white pine, northern hardwoods (sugar maple, beech, yellow birch), and temperate hardwoods (oaks, hickories, elms, ashes, basswood). From 300–400 m to ~800 m, forests are dominated by hemlock, white pine, northern hardwoods, and red spruce. Subalpine red spruce – balsam fir – paper birch forest occurs from ~800 to ~1250 m. Vegetation above 1250 m consists of sub-alpine balsam fir forest, with alpine tundra above ~1480 m.

Lakes and ponds are numerous in the Adirondack region. Lakes are typically dilute and unproductive (Berg 1966; Charles 1982; Driscoll and Newton 1985); many have been affected by acid precipitation (National Research Council 1986).

The 31 study lakes were selected to represent a wide variety of conditions among small Adirondack lakes. All have undeveloped watersheds (i.e., no permanent structures, paved roads, etc.). (Heart Lake has a lodge and outbuildings near its east shore, but the rest of the watershed is undeveloped.) Three of the lakes (Bog Pond, East Copperas Pond, and Washbowl Pond) are bog ponds ringed by floating *Sphagnum* mats. With the exception of two (Elk Pass Bog Pond and Elk Pass West Pond), the lakes used in this study comprise a subset of the 38 lakes studied by Charles (1982, 1985) and Smol *et al.* (1984).

Previous studies of aquatic macrophytes in Adirondack lakes include the floristic surveys of Muenscher (1930, 1931, 1932, 1933, 1934, 1935), Burnham (1917), and Hedy (1942), detailed investigations at Lake George (Boylan and Sheldon 1975; Ogden *et al.* 1976; Sheldon and Boylen 1977, 1978; Stross 1979), Lake Colden (Hendrey and Vertucci 1980), and Silver Lake (Singer *et al.* 1983) and a vegetational study of nine midelevation lakes (Roberts 1985).

### Methods

Botanical surveys were conducted during the summers of 1979 (15 June – 4 August) and 1980 (15 July – 30 August). The principal objective of the surveys was to catalog the entire aquatic species complement of each lake. Each lake was surveyed thoroughly from a canoe or inflatable boat. The entire perimeter of each lake was covered in a zig-zag pattern, with frequent transects made toward the basin center. Aquatic macrophytes were observed and collected in shallow water directly from the boat or by wading, and in deeper water by means of a grappling hook and line or by diving with a face mask. Specimens of each emergent, floating-leaved, and submersed species were collected. Distribution patterns of species within each lake in relation to substrate type, depth, bottom slope, and influent streams were noted.

All plant specimens were identified by S. T. Jackson based on standard taxonomic references and comparisons with herbarium specimens. Determinations of all specimens of *Potamogeton*, *Sparganium*, *Sagittaria*, *Lysimachia*, *Hypericum*, and *Utricularia* were checked by C. B. Hellquist. Nomenclature of vascular plants, bryophytes, and charophytes follows Fernald (1950), Ketchledge (1980), and Wood (1965), respectively. Exceptions are *Juncus pelocarpus* f. *submersum* Fassett, *Hypericum ellipticum* f. *aquaticum* Fassett and *Potamogeton pusillus* var. *tenuissimus* Mert. & Koch. No effort was made to distinguish species of *Sphagnum* or *Nuphar*. *Nuphar* species within the region include *N. advena*, *N. variegatum*, and *N. microphyllum*. Sterile forms not identifiable with certainty to any genus were categorized on the basis of morphology into operational taxonomic units (e.g., unknown monocot 1). Voucher specimens of each species from each lake have been deposited in the Indiana University Herbarium.

Limnological sampling was carried out monthly during May–August of 1978 and May, June, and August of 1979. Chemical data from surface-water samples were used in this study, except for chlorophyll *a* and total P concentrations, which were determined from com-

TABLE 1. Lakes examined in this study. Lake numbers correspond to map numbers in Fig. 1. pH values refer to summer-average (1978–1979) air-equilibrated surface pH

No.	Lake name	pH	Elevation (m)	Surface area (ha)
1	Bear Pond	5.0	499	22.6
2	Bog Pond	5.4	498	0.8
3	Cat Mountain Pond	5.1	526	8.4
4	Clear Pond	7.2	432	8.9
5	Copperas Pond (Fish Creek)	7.8	546	9.2
6	Copperas Pond (Wilmington Notch)	7.3	480	8.3
7	Cowhorn Pond	6.0	530	8.5
8	Crane Mountain Pond	6.5	793	5.6
9	Dunk Pond	7.5	474	6.8
10	East Copperas Pond	4.5	480	3.6
11	Elk Pass Bog Pond	5.1 <sup>a</sup>	1024	0.1
12	Elk Pass West Pond	5.1 <sup>a</sup>	1024	0.3
13	Frank Pond	6.6	517	10.3
14	Giant's Washbowl	7.2	695	1.7
15	Green Pond	6.2	493	7.9
16	Gull Pond	7.2	319	5.2
17	Heart Lake	6.6	661	11.2
18	Huntley Pond	7.8	482	15.7
19	Lake Arnold	4.8	1150	0.4
20	Lake Tear of the Clouds	4.6	1320	0.3
21	Little Pine Pond	7.7	478	2.1
22	Little Shallow Pond	7.3	515	2.2
23	Livingston Pond	5.5	850	0.8
24	Mountain Pond	4.7	482	1.8
25	Nicks Pond	5.2	515	5.5
26	Parch Pond	6.9	460	5.6
27	Pine Pond	7.0	475	18.1
28	Rock Pond	6.8	486	10.8
29	Round Pond	7.0	527	9.1
30	Upper Wallface Pond	5.0	948	5.5
31	Washbowl Pond	4.5	515	1.6

<sup>a</sup>pH values for lakes 11 and 12 are air-equilibrated pH of surface samples obtained 28 May 1981.

posite lake-average water samples. Methodological details of water sampling and analysis are available in Charles (1982). All limnological analyses were conducted or supervised by D. F. Charles.

Alkalinity, pH, conductivity, true color, and total P data were from averages of all samples collected in 1978 and 1979. Cation and anion concentrations were from August 1979 samples. Chlorophyll *a* concentrations were averages of 1979 samples. Epilimnion temperature and Secchi disc depth were averages of August 1978 and August 1979 determinations.

A Fisher Acumet 425 pH meter with separate glass and reference electrodes, accurate to 0.01 pH unit, was used to measure pH both before and after aeration. All pH measurements were made at ambient temperature in the laboratory, usually less than 12 h (maximum 24 h) after sample collection. pH data used in this study were from air-equilibrated pH measurements. Alkalinity was determined using a Gran plot technique (Schofield 1978) based on Gran (1952). Conductivity was measured with a YSI model 31 conductivity meter. Conductivity measurements were temperature compensated.

Samples for cation analyses were spiked with LaCl and stored at 4°C. Cation concentrations were determined with a Jarrell-Ash 800 atomic absorption spectrophotometer. Anion concentrations were measured with a Technicon Auto-Analyzer II. Total Al was analyzed using the technique of Dougan and Wilson (1974).

Samples for total P determination were kept frozen until analyzed. They were digested in an autoclave by persulfate oxidation (Menzel and Corwin 1965). Measurements of soluble reactive P followed the method of Murphy and Riley (1962). Chlorophyll *a* concentrations were determined by the technique of Strickland and Parsons (1972), with corrections for pheopigments after Lorenzen (1967).

Indirect ordinations of the macrophyte presence-absence data were carried out using detrended correspondence analysis (DCA) (Hill and

Gauch 1980; Gauch 1982). Emergent taxa were analyzed separately from submersed and floating taxa. Pearson product-moment correlations between each of the first two DCA axes and environmental variables were carried out to determine the ecological factors associated with the variation in vegetation identified by the ordination. Elk Pass Bog Pond and Elk Pass West Pond were excluded from these analyses because water chemistry data other than pH were not available.

Our data analysis is based entirely on presence-absence data, which we justify by the following arguments. For this study, we define the community of interest as the aquatic macrophyte populations of an entire lake. Our main objective was to examine variation in community composition among different lakes. Within a lake, macrophyte populations often vary considerably in distribution and abundance on small spatial scales ( $10^{-1}$ – $10^1$  m) (Carpenter and Titus 1984). In such heterogeneous communities, a large number of quantitative samples would be required to characterize each community accurately. A species list of each lake can be obtained with much less effort and expense and, at the same time, provides a useful characterization of the communities (Pielou 1984). Nearly all comparative macrophyte studies involving more than 10 lakes have been based solely on presence-absence data (Iversen 1929; Lohammar 1938; Iversen and Olson 1943; Moyle 1945; Spence 1964, 1967; Seddon 1967, 1972; Birks 1973; Crowder *et al.* 1977; Pip 1979; Hellquist 1980; Kadono 1982; Wile and Miller 1983; Yan *et al.* 1985; Catling *et al.* 1986).

## Results

### *Submersed and floating-leaved macrophytes*

A total of 45 submersed and floating-leaved taxa were col-

TABLE 2. Mean, median, and range of selected characteristics of 29 Adirondack study lakes. Data for Elk Pass Bog Pond and Elk Pass West Pond are not included

Characteristic	Mean	Median	Maximum	Maximum
Surface area (ha)	6.4	5.6	0.1	22.6
Maximum depth (m)	9.3	9.0	0.8	21.0
Volume development <sup>a</sup>	1.23	1.20	0.48	2.44
Shoreline development <sup>a</sup>	1.4	1.3	1.0	2.6
Elevation (m)	619	515	319	1320
Watershed area (ha)	48	33	5	251
pH	—	6.5	4.5	7.8
Alkalinity ( $\mu\text{equiv./L}$ )	83	33	-31	408
Conductivity ( $\mu\text{S/cm}$ at 25°C)	28.6	24.0	11.9	58.7
Color, true (Pt-Co units)	18	15	3	58
Color, Forel-Ule	13	13	5	22
Secchi, disc depth (m)	4.9	4.6	0.8	10.1
Total P ( $\mu\text{g/L}$ ) <sup>b</sup>	12.7	7.6	3.3	62.8
Chlorophyll <i>a</i> ( $\mu\text{g/L}$ ) <sup>c</sup>	5.4	2.3	0.3	32.6
Calcium ( $\mu\text{equiv./L}$ )	149	120	22	448
Magnesium ( $\mu\text{equiv./L}$ )	47	35	15	145
Sodium ( $\mu\text{equiv./L}$ )	26	23	5	75
Potassium ( $\mu\text{equiv./L}$ )	7	7	1	15
Sulfate ( $\mu\text{equiv./L}$ )	119	120	50	180
Chloride ( $\mu\text{equiv./L}$ )	9	9	<2	24
Nitrate ( $\mu\text{equiv./L}$ )	2	<1	0	33
Iron ( $\mu\text{g/L}$ ) <sup>d</sup>	—	<100	<100	500
Manganese ( $\mu\text{g/L}$ )	16	15	0	70
Aluminum, total ( $\mu\text{g/L}$ )	78	29	5	673
Aluminum, ( $\mu\text{equiv./L}$ ) <sup>e</sup>	5	<1	0	58
Epilimnion temperature (°C)	21.5	22	15	26

<sup>a</sup>Definitions and calculations follow Hutchinson (1957, p. 166).<sup>b</sup>Maximum total phosphorus concentration for nonbog lakes was 22  $\mu\text{g/L}$ .<sup>c</sup>Maximum chlorophyll *a* concentration for nonbog lakes was 10  $\mu\text{g/L}$ .<sup>d</sup>Concentrations of total Fe were below detection limits (100  $\mu\text{g/L}$ ) for 23 of the 29 lakes.<sup>e</sup>Equals sum of charges from  $\text{Al}^{3+}$ ,  $\text{Al}(\text{OH})^{2+}$ , and  $\text{Al}(\text{OH})_3$ , calculated from total Al based on methods of Cronan (1978). Most concentrations are probably overestimated because this technique does not account for Al bound to organics or fluoride.

lected from the 31 lakes (Fig. 2). Of these, 19 (42% of total) occurred in only one or two lakes. Nearly all of these infrequent species were restricted to circumneutral lakes ( $\text{pH} > 6.5$ ). Three taxa, *Isoetes muricata*, *Nuphar* spp., and *Eriocaulon septangulare*, occurred in more than 50% of the study lakes; the latter two taxa were found in >75% of the lakes. Mean and median frequencies of occurrence of all species were 6 and 4 lakes, respectively.

Number of species per lake ranged from 1 to 23; mean and median species richness both equaled 8. Five lakes contained only one species, either *Nuphar* (4 lakes) or *Eriocaulon septangulare* (1 lake). These lakes all had restricted littoral zones poorly suited for macrophyte vegetation. Two (East Copperas Pond and Washbowl Pond) were bog ponds with steep sides and highly colored water. Mountain Pond was a small, deep, acidic kettle pond with steep sides, high volume development (1.2), and low shoreline development (1.1). Clear Pond and Copperas Pond (Wilmington Notch) were larger, circumneutral ponds with high volume development (1.5 and 1.4, respectively), high average depth (9.2 and 9.8 m), low shoreline development (1.2 in both cases), and steep sides. Substrates in the restricted shallow areas of these two ponds consisted variously of boulders, sands, and gravels, sunken logs, and (or) coarse terrigenous organic debris (wood, leaves, needles). The impoverished floras of these five lakes thus appeared to be controlled ultimately by basin morphometry. These lakes varied widely in water chemistry, color, and trophic status (Charles 1982). Because they each shared only a

single, more or less ubiquitous species with other lakes in the data set, they provided no information on nonmorphometric influences on macrophyte vegetation. These five sites were deleted from the data matrix before DCA ordination.

Sample scores for DCA axis 1 correlated significantly with several lake characteristics, most strongly with pH and alkalinity (Table 3; Figs. 3, 4). Most of these variables were significantly intercorrelated (Charles 1982, 1985); all except K were significantly correlated with pH (Table 3). The significant correlation with  $\text{NO}_3$  resulted entirely from three high-elevation lakes, each of which had very high DCA values and very high  $\text{NO}_3$  concentrations.  $\text{NO}_3$  did not occur in detectable amounts at most of our study sites (Table 2), including several with high DCA scores. We regard the  $\text{NO}_3$  correlation as ecologically insignificant.

Two variables correlated with DCA axis 1, elevation and epilimnion temperature, were nonchemical. Both pH and epilimnion temperature showed strong negative correlations with elevation in the study lakes (Charles 1982, 1985). All study lakes above 800 m elevation were acidic ( $\text{pH} < 6.0$ ) (Table 1; Charles 1982). To filter out potential effects of elevation-related climatic factors on the macrophyte floras, we deleted all lakes above 800 m elevation from the data matrix and repeated the ordination. The resulting DCA axis 1 scores correlated significantly with pH, alkalinity, conductivity, and Ca but not with elevation, total P, or total Al (Table 3).

The predominant pattern along the pH complex gradient was a progressive disappearance of individual species as pH

Fig. 2. Occurrences of submersed and floating-leaved aquatic macrophyte taxa in Adirondack study sites. Sites are arranged in order of decreasing pH.

In explaining this variation, PCA axis 2 scores did not correlate significantly with any of the variables listed in Table 3, and inspection of sample and species distributions along DCA axes 2 and 3 did not reveal any meaningful trends. Several species showed clear preferences for particular substrate texture and composition. *Lobelia dortmanna*, *Juncus pelocarpus* f. *submersum*, and *Myriophyllum tenellum* were nearly always observed rooted in sands or sandy silts. *Nitella flexilis*, *Chara vulgaris*, *Najas flexilis*, *Drepanocladus fluitans*, and most species of *Potamogeton* were restricted to fine

decreased (Fig. 2). Twenty-seven species (60% of total) were restricted to circumneutral (pH > 6.0) lakes. Of the 18 taxa found in acidic (pH < 6.0) lakes, only two, *Potamogeton confervoides* and *Spartanium* cf. *angustifolium* (sterile form), were not observed in any of the circumneutral lakes. The fruiting form of *Spartanium angustifolium*, however, occurred in many circumneutral lakes (Fig. 2).

TABLE 3. Linear correlations of lake characteristics with axis 1 sample scores for detrended correspondence analysis (DCA) of submersed and floating-leaved vegetation, and with lakewater surface pH. Two separate DCAs are included, one using the entire data set and the other a subset consisting of all lakes < 800 m elevation

Lake characteristic	Correlation ( $r$ ) with DCA axis 1		Correlation ( $r$ ) with lakewater pH
	All lakes	Lakes < 800 m	
pH	-0.87**	0.43*	—
p(alkalinity)	0.86**	0.69**†	-0.97**
pCa	0.73**	-0.52**	-0.87**
pMg	0.80**	—	-0.88**
pNa	0.55**	—	-0.77**
pK	0.38**	—	-0.16
Fe	0.25	—	—
Mn	0.42*	—	-0.63**
Total Al	0.79**	-0.15	0.56**
Al	0.78**	—	-0.58**
Total P	-0.32	0.18	-0.25
SO <sub>4</sub>	-0.28	—	0.36*
NO <sub>3</sub>	0.74**	—	0.31*
Conductivity	-0.59**	0.62**	0.68**
True color	0.13	—	-0.19
Secchi disc depth	0.32	—	-0.05
Chlorophyll $a$	-0.08	—	-0.32
Elevation	0.79**	-0.25	-0.51*
Epilimnion temperature	-0.51**	—	0.48**
Volume development	0.22	—	-0.11

NOTE: Relationships for which correlations were not calculated are denoted by dashed lines. The negative log<sub>10</sub> of some characteristics was used to make curvilinear relationships more nearly linear. No close relationships were excluded because they were nonlinear. pX refers to the negative log<sub>10</sub> of characteristic X.

\*, significant at  $P < 0.05$ ; \*\*, significant at  $P < 0.01$ ; †, correlation with alkalinity, not based on negative log<sub>10</sub>.

organic muds. Between-lake variation in the areal extent and depth distribution of these and other substrate types probably had a significant effect on macrophyte composition. Assessment of this effect in our set of study sites, however, would have required more detailed information on substrate distribution than we had available.

Evaluation of elevation-related climate influences was complicated by three factors: (i) all of our study lakes above 800 m elevation were acidic (Table 1), (ii) total Al concentrations were significantly higher in the high-elevation acid lakes (128–673  $\mu\text{g/L}$ ) than in the low-elevation acid lakes (32–126  $\mu\text{g/L}$ ) (Charles 1982), and (iii) comparisons were based on small samples sizes of both high-elevation and low-elevation acid lakes (6 and 4 lakes, respectively). Five species present in low-elevation, low-Al acid lakes were absent from all or most of the high-elevation acid lakes: *Utricularia purpurea*, *Potamogeton epihydrus*, *P. oakesianus* a (occurred at 850 m), *Sparganium angustifolium*, and *Lobelia dortmanna* (occurred in Lake Colden at 843 m (Hendrey and Vertucci 1980)). *Nymphaea odorata* and *Brasenia schreberi* can be added to this group; although neither occurred in any of our acidic study lakes, both were observed in acidic low-elevation Adirondack lakes by Roberts *et al.* (1985). *Sparganium angustifolium* was probably not limited by elevation or Al; a submersed sterile form tentatively assigned to this species occurred as high as Lake Tear of the Clouds (1320 m elevation; 673  $\mu\text{g/L}$  total Al). This sterile form was restricted to acidic lakes but not to high elevations; it occurred in Bog Pond and (515 m; 32  $\mu\text{g/L}$  total Al) and Nicks Pond (515 m; 59  $\mu\text{g/L}$  total Al).

Species richness correlated significantly with pH ( $r = 0.5$ ,  $P < 0.01$ ) (Fig. 5). Deletion of the five single-species lakes

strengthened the correlation somewhat ( $r = 0.55$ ,  $P < 0.01$ ). Species richness did not correlate significantly with elevation ( $r = -0.13$ ) or surface area ( $r = 0.32$ ).

Species richness at Copperas Pond (Fish Creek) was higher than at any other site. This may have resulted in part from ease of dispersal into the pond. Copperas Pond drains through a short, open channel into Fish Creek, which in turn connects a vast network of lakes and ponds. Most of the taxa occurring in Copperas Pond (Fish Creek) were also observed growing in Fish Creek. All of the other study sites either do not have outlets or drain into small, fast-flowing streams poorly suited for macrophyte growth.

#### Emergent macrophytes

Four lakes contained no emergent macrophytes. The remaining 27 lakes had a total of 33 emergent taxa (Fig. 6). Most emergent taxa were sporadic in occurrence: 12 species (36% of total) occurred in only one lake and 24 species (73% of total) were found in three or fewer lakes. These infrequent species were not restricted to any particular segment of the pH gradient. One species, *Dulichium arundinaceum*, occurred in nearly half the study lakes (14 occurrences). Mean and median frequencies of occurrence were 3 and 2 lakes, respectively.

Emergent species richness ranged from 0 to 9. Mean and median species richness equaled 3 and 2, respectively. As in the case of submersed and floating-leaved taxa, ponds with restricted littoral areas (bog ponds, kettles, steep-sided basins) contained few or no emergent macrophyte taxa.

DCA axis 1 scores for the entire data set correlated significantly with pH, alkalinity, Ca, conductivity and elevation (Table 4). The correlation with elevation was substantially

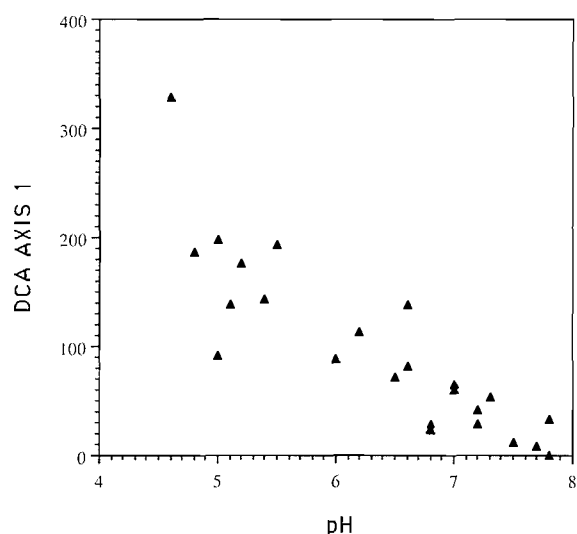


FIG. 3. Scatter diagram of surface lakewater pH versus DCA axis 1 sample scores for submersed and floating-leaved taxa from 24 lakes with two or more taxa.

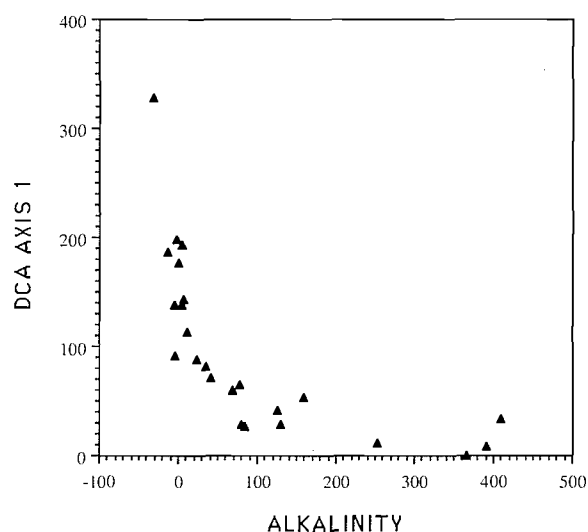


FIG. 4. Scatter diagram of surface lakewater alkalinity ( $\mu\text{equiv./L}$ ) versus DCA axis 1 sample scores for submersed and floating-leaved taxa from 24 lakes with two or more taxa.

weaker than with the chemical variables. Total P and total Al did not correlate significantly with DCA axis 1 (Table 4). Overall, correlations between ordination scores and lake characteristics were weaker for the emergent vegetation than the submersed and floating-leaved vegetation (Table 3).

The ordination and correlations were repeated for the subset of lakes at  $<800$  m elevation. DCA axis 1 scores did not correlate significantly with elevation (Table 4). Significant correlations were obtained for pH alkalinity, Ca, conductivity, and total P (Table 4). The two bog ponds (Bog Pond and East Copperas Pond) had the highest DCA axis 1 scores and total P concentrations and accounted entirely for the significant correlation with total P. DCA ordination of all sites at  $<800$  m containing more than one emergent species (thus excluding East Copperas Pond and others) yielded significant correlations with pH, alkalinity, Ca, and conductivity but not with total P, elevation, or total Al. Correlations with all variables except

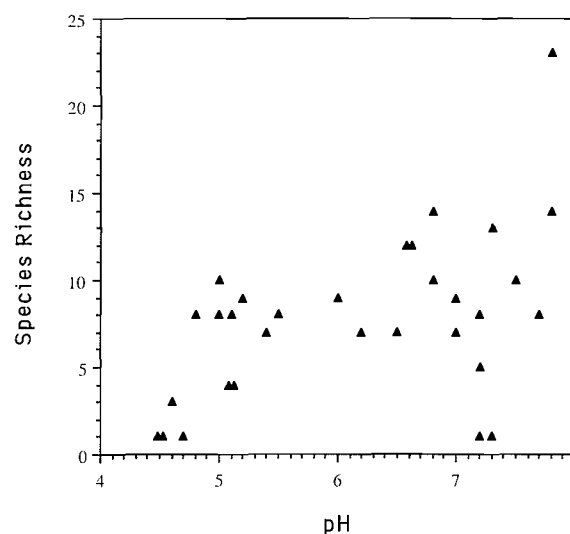


FIG. 5. Scatter diagram of pH versus species richness of submersed and floating-leaved aquatic macrophytes. All 31 study sites are included.

total P were of similar strength regardless of whether lakes with only one emergent species were included in the ordination.

DCA axes 2 and 3 did not reveal significant secondary patterns in distributions of emergent taxa.

Composition of emergent vegetation differed substantially between high-elevation and low-elevation acid lakes, in contrast to submersed and floating-leaved vegetation. Only *Dulichium arundinaceum* occurred at both low-elevation acid lakes and high-elevation sites. All other emergents of low-elevation acid lakes (*Sparganium americanum*, *S. chlorocarpum*, *Eleocharis acicularis*, *Glyceria borealis*, *Pontederia cordata*, *Utricularia cornuta*) were absent from sites above 800 m. This pattern may have resulted from climatic differences, to which emergent plants may be more sensitive than submersed plants. Alternatively, it may have been an artifact of the small sample size (6) of high-elevation lakes.

Emergent species richness (all sites) correlated significantly with pH ( $r = 0.36$ ,  $P < 0.05$ ) and surface area ( $r = 0.68$ ,  $P < 0.01$ ) but not with elevation ( $r = 0.14$ ) or shoreline development ( $r = 0.19$ ). Species richness among sites with at least one emergent species correlated significantly with surface area ( $r = 0.62$ ,  $P < 0.01$ ) but not with pH ( $r = 0.30$ ).

## Discussion

The dominant environmental gradient influencing composition of the aquatic macrophyte vegetation of these lakes was pH related. Compositional variation among lakes was reflected in the DCA axis 1 scores, which correlated strongly with pH and associated chemical variables (alkalinity, conductivity, Ca, Mg), for both submersed plus floating-leaved and emergent vegetation. Macrophyte composition showed no relationship with trophic status indicators (chlorophyll *a*, total P), water color, or transparency. Our data indicated that elevation related factors (temperature and (or) Al) and basin morphometry (areal extent, slope, and substrate composition of littoral zone) had some influence on macrophyte assemblages. These effects, however, were secondary to the pH complex-gradient.

These results compare favorably with similar studies in

	pH	7.8	7.8	7.5	7.3	7.3	7.2	7.2	7.2	7.0	7.0	6.8	6.8	6.6	6.6	6.5	6.2	6.0	5.5	5.4	5.2	5.1	5.1	5.1	5.0	5.0	4.8	4.5
Species Richness	4	6	6	2	1	1	4	2	9	6	4	4	7	6	5	2	2	1	4	1	1	3	2	7	5	2	1	
<i>Eleocharis smallii</i>	•																											
<i>Callitriche verna</i>		•																										
<i>Bidens</i> cf. <i>comosa</i>			•																									
<i>Eleocharis</i> sp. 1			•																									
<i>Elatine minima</i>									•																			
Unknown monocot 1									•																			
<i>Carex</i> cf. <i>rostrata</i>		•					•			•																		
<i>Hypericum ellipticum</i> f. <i>aquaticum</i>										•																		
<i>Sagittaria latifolia</i>		•	•							•																		
<i>Menyanthes trifoliata</i>		•									•																	
<i>Typha latifolia</i>		•							•		•																	
<i>Equisetum fluviatile</i>	•		•	•						•	•																	
Unknown monocot 2												•																
<i>Lycopus uniflorus</i>						•										•												
<i>Utricularia resupinata</i>									•					•	•													
<i>Onoclea sensibilis</i>															•													
<i>Hypericum boreale</i> f. <i>callitrichoides</i>								•								•												
<i>Calamagrostis canadensis</i>														•			•											
<i>Ranunculus reptans</i>																		•										
<i>Sparganium chlorocarpum</i>			•						•	•				•				•				•						
<i>Juncus filiformis</i>																												
<i>Pontederia cordata</i>	•							•						•					•						•			
<i>Sparganium americanum</i>	•	•	•										•												•			
<i>Glyceria borealis</i>				•						•						•	•								•			
<i>Utricularia cornuta</i>								•					•						•						•			
<i>Eleocharis acicularis</i>														•				•							•			
<i>Polygonum amphibium</i>																									•			
<i>Juncus pelocarpus</i>										•				•												•		
<i>Glyceria canadensis</i>										•																•		
<i>Lysimachia terrestris</i>								•			•	•		•	•	•									•			
<i>Dulichium arundinaceum</i>								•		•	•	•		•	•			•		•	•		•	•	•	•	•	
<i>Juncus brevicaudatus</i>																			•				•	•		•	•	
<i>Calla palustris</i>																				•								•

FIG. 6. Occurrences of emergent aquatic macrophyte taxa in Adirondack study sites. Sites are arranged in order of decreasing pH.

regions with much broader variation in water chemistry (Moyle 1945; Swindale and Curtis 1957; Spence 1967; Seddon 1972; Crowder *et al.* 1977; Kadono 1982). Several of these studies have identified conductivity as the principal descriptor of the chemical gradient controlling macrophyte composition (Swindale and Curtis 1957; Seddon 1972; Crowder *et al.* 1977). Seddon (1972) and Crowder *et al.* (1977) regard conductivity as an index of trophic status. In our study, however, vegetational composition was more strongly correlated with pH than conductivity. In addition, conductivity was not related to trophic status in softwater lakes (Charles 1982, 1985).

Crowder *et al.* (1977) did not apply numerical ordination to their data, and Seddon (1972) analyzed his data using principal components analysis, which can yield contrasting results to those of DCA (Gauch 1982). To compare our results with those of Crowder *et al.* (1977) and Seddon (1972) more directly, we conducted separate DCA ordinations of the submersed plus floating-leaved macrophyte data provided in their papers. We used all 50 species and all 21 sites of Crowder *et al.* (1977, Table II) in ordinating their data. The data set we used from Seddon's study consisted of the 36 submersed and floating-leaved species occurring in the 22 lakes for which

chemical data were provided in the paper (Seddon 1972, Table 2). We correlated DCA axis 1 for each data set with conductivity and pH. Conductivity and pH values for the Crowder *et al.* (1977) sites were obtained from Table I of their paper. Conductivity and pH values for Seddon's sites were identified by matching points between Fig. 2 and Figs. 5 and 7 in Seddon (1972). The correlations for Seddon's data were strong with both pH ( $r = 0.78$ ,  $P < 0.01$ ) and conductivity ( $r = 0.82$ ,  $P < 0.01$ ). Similarly, the data of Crowder *et al.* yielded significant correlations with both pH ( $r = -0.84$ ,  $P < 0.01$ ) and conductivity ( $r = -0.80$ ,  $P < 0.01$ ). Thus, pH and conductivity appear to be of equal value in describing vegetational variation among circumneutral to hardwater lakes (e.g., Wales, southeastern Ontario), whereas pH is more useful in softwater regions such as the Adirondacks. The restricted range of conductivity among softwater lakes (e.g., Table 2) is probably responsible for the difference.

We conclude that the chemical gradient underlying compositional variation among our Adirondack softwater sites is the tail end of a broad pH complex-gradient that extends to highly alkaline waters. At the scale of environmental variation observed in Adirondack lakes, the main factors associated with



TABLE 4. Linear correlations of selected lake characteristics with axis 1 samples score for DCA of emergent vegetation. Two DCAs are included, one consisting of the entire data set and the other a subset comprising all lakes <800 m elevation

Lake characteristic	Correlation ( <i>r</i> ) with DCA axis 1	
	All lakes	Lakes <800 m
pH	-0.55**	-0.62**
p(alkalinity)	-0.52**	0.57**
pCa	-0.58**	0.63**
Total Al	-0.30	0.13
Total P	-0.23	0.58
Conductivity	0.52**	-0.50*
Elevation	0.42*	0.12

NOTE: pX refers to the negative log<sub>10</sub> of characteristic X. \*\*, significant at  $P < 0.05$ ; \*, significant at  $P < 0.01$ .

vegetation variation are pH, alkalinity, Ca, Mg, and perhaps Al. In regions where the gradient is broader, or at least where the hardwater portion is represented, conductivity and trophic status become more prominent.

The pattern of progressive disappearance of species (rather than replacement) along the Adirondack pH complex-gradient is similar to that observed by Seddon (1972) among Welsh lakes. Diatom and chrysophyte assemblages show a similar pattern in our study sites (Charles 1985; Smol *et al.* 1984). Seddon (1972) proposed that, for aquatic macrophytes, this pattern results from differential tolerances of softwater conditions among species. The rarity of many characteristic softwater species in hardwater lakes was attributable to interspecific competition (Seddon 1972).

The broad tolerance of species characteristic of acidic and softwater lakes is well documented (Hutchinson 1975); all are at least occasionally observed in circumneutral to hardwater lakes. Of all the acid-lake taxa found in the present study, only *Potamogeton confervoides* was not observed in circumneutral lakes. However, it has been collected from circumneutral New England lakes (Hellquist 1980; Hellquist and Crow 1980). Observations at one of our study sites, Livingston Pond, illustrate the tolerance of acid-lake species to more neutral conditions. The pond was limed by the New York Department of Environmental Conservation in the fall of 1979. Preliming (1978–1979) pH was 5.5; postliming (May 1981) pH was 7.2. We observed no change in species composition in Livingston Pond between the summers of 1979 and 1980. Relative abundance and spatial distribution of macrophyte species did not change, with one exception. *Utricularia vulgaris*, which was abundant on gentle slopes <1 m deep in 1979, was rare throughout the pond in 1980.

Although our data are consistent with Seddon's (1972) hypothesis, confirmation cannot be provided by comparative studies such as ours. Mechanistic studies are required to understand the causal basis for variation of vegetation along environmental gradients. Studies of the physiological ecology of aquatic macrophytes are beginning to provide some understanding of the differential tolerances to softwater and acidic conditions (e.g., Sondergaard and Sand-Jensen 1979; Barko and Smart 1981; Raven 1981; Roelofs *et al.* 1984; Wetzel *et al.* 1984, 1985; Grisé *et al.* 1986). Several recent experimental studies have examined the role of interspecific competition in influencing distributions of aquatic macrophytes

(McCreary *et al.* 1983; Titus and Stephens 1983; Wilson and Keddy 1986a, 1986b). Similar studies designed specifically to test competitive exclusion of softwater species by hardwater species in hardwater lakes are required to provide a rigorous test of the competition component of Seddon's (1972) hypothesis. Moeller (1985) has recently proposed a physiologically based alternative hypothesis, which may partially account for sporadic occurrences of many acidic and softwater macrophyte species in hardwater lakes.

Distributions of most species in our data set with respect to pH, alkalinity, and conductivity are within the ranges reported in previous floristic studies (Iversen and Olsen 1943; Moyle 1945; Seddon 1972; Crowder *et al.* 1977; Pip 1979; Hellquist 1980; Hellquist and Crow 1980, 1981, 1982, 1984; Crow and Hellquist 1981, 1982, 1983, 1985; Wile and Miller 1983; Catling *et al.* 1986). Six species in our study occurred beyond the pH and alkalinity ranges reported by Crow and Hellquist (1981, 1983) and Hellquist and Crow (1981, 1982). These species and the minimum pH and alkalinity values at which they occurred in our study are *Sparganium americanum* (pH 5.0; alkalinity  $-5 \mu\text{equiv./L}$ ), *S. angustifolium* (5.0;  $-5 \mu\text{equiv./L}$ ), *S. chlorocarpum* (5.1;  $-5 \mu\text{equiv./L}$ ), *Sagittaria graminea* (5.0;  $-2 \mu\text{equiv./L}$ ), *Eriocaulon septangulare* (4.8;  $-13 \mu\text{equiv./L}$ ), and *Myriophyllum tenellum* (5.0;  $-2 \mu\text{equiv./L}$ ). *Sparganium angustifolium* may occur at pH and alkalinity as low as 4.6 and  $-31 \mu\text{equiv./L}$ , respectively, if the sterile submersed form we observed at Lake Tear of the Clouds belongs to this species.

The strong response of aquatic macrophyte composition to the lower end of the pH complex-gradient indicates that as lakes acidify owing to natural processes (Whitehead *et al.* 1986) or industrial acid deposition (National Research Council 1986), species composition of aquatic vegetation should change. In the Adirondacks, this compositional change would consist of disappearance of acid-intolerant species (e.g., *Najas flexilis*, *Nitella flexilis*, *Potamogeton pusillus*, *P. natans*, *P. amplifolius*) and probably invasion by acid-tolerant species as well (e.g., *Sphagnum* spp., *Potamogeton confervoides*). This is supported by other comparative studies in the Adirondacks (Roberts *et al.* 1985) and Ontario (Yan *et al.* 1985). Long-term monitoring in Europe has documented substantial compositional changes in response to industrial lake acidification (Grahn 1977; Roelofs 1983).

In many European lakes, a major element of acidification-related vegetational change has been the development of extensive populations of submersed *Sphagnum* and consequent reductions of populations of other species (Grahn 1977). Submersed *Sphagnum* occurred at only four of our acid lakes, all at elevations >900 m. *Sphagnum* populations at all these sites were sparse, and there was no evidence that they were expanding at the expense of other aquatic species. Roberts *et al.* (1985) reported that *Sphagnum* was not a major component in five low-elevation Adirondack acid lakes. Any changes in vegetation resulting from acid deposition in the Adirondacks to date have differed qualitatively from those observed in Europe.

Whether acidification-related changes in composition of aquatic macrophytes are accompanied by reduction in species richness is unclear. Roelofs (1983) reports a substantial reduction in species richness in recently acidified Netherlands lakes. In contrast, tracheophyte species richness in 39 Ontario lakes is uncorrelated with pH (Yan *et al.* 1985). Although we obtained a statistically significant correlation between submersed and floating-leaved species richness and pH, there

is considerable scatter in the relationship (Fig. 5). Other factors (morphometry, substrate) undoubtedly influence species richness.

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