HABITAT DIFFERENCES AMONG SEVEN SPECIES OF *MYRIOPHYLLUM* (HALORAGACEAE) IN WISCONSIN AND MICHIGAN

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ABSTRACT

Thirty-five *Myriophyllum* (milfoil) habitats in Wisconsin and the Upper Peninsula of Michigan were evaluated to determine differences in habitat characteristics between two groups of species. Habitats of three "northern" species (*M. alterniflorum*, *M. farwellii*, and *M. tenellum*) differed significantly from the habitats of four "widespread" species (*M. heterophyllum*, *M. sibiricum*, *M. spicatum*, and *M. verticillatum*) for five of nine water and sediment variables analyzed. Habitats of the northern milfoil species were poor in silt and clay, and were characterized by acid to neutral pH and low levels of calcium and sediment ammonium nitrogen. Habitats of the widespread species had higher proportions of silt and clay, neutral to alkaline pH, and high concentrations of both calcium and sediment ammonium nitrogen. These results support the generalization that northern milfoil species are associated with soft water oligotrophic habitats, whereas widespread milfoil species occur in hard water eutrophic habitats.

INTRODUCTION

The specific influence of the habitat on the distribution of aquatic vascular plants has long been a topic of contention. In his treatise on the classification of aquatic plant communities, Pearsall (1918) stated that ". . . just as there are terrestrial plant communities of organic and inorganic soils, there are also aquatic communities of these habitat types." He later concluded that submerged aquatic plant distributions depended more on sediment variables than on lake water chemistry or physical conditions of the habitat (Pearsall 1921). Conversely, Spence (1964) and Seddon (1972) argued that water chemistry rather than sediments was the determining factor that governed aquatic plant distribution. Although he considered that water chemistry may be an important determinant of aquatic plant distributions, Moyle (1945) suggested that sediments and the

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physical nature of the water also greatly influenced local species distributions. Because the mineral composition of natural waters is directly influenced by the type and composition of the underlying sediments and watershed (Rodhe 1949, Stumm & Morgan 1981), it is evident that both substrate and water composition ultimately determine the types of aquatic plant communities present and thus the particular species found within them.

In North America, aquatic plant species have been categorized as "northern," "southern," "widespread," etc. depending on their present distribution pattern (Stuckey 1971). Although these designations might imply differential climatic tolerances, the different distribution patterns cannot be adequately explained on the basis of latitudinal climatic gradients alone. Climatic conditions seem to be less influential on the distributions of submersed aquatic plants, owing in part to their wide temperature tolerances (Les 1986). Stuckey (1983, 1993), however, suggested that the absence of certain aquatic plant species from the "prairie peninsula" was perhaps due to warming climatic conditions of the xerothermic period. Although one might expect these "missing" species to be mainly those with northern distributions (which presumably would be less adapted to warmer temperatures), this was not the case. Stuckey (1983, 1993) observed that plants absent from the prairie peninsula included species distributed mostly north of, mostly south of, and equally north and south of the prairie peninsula. Most of the aquatic species absent from the prairie peninsula were typically plants of acidic soft water habitats (Stuckey 1993).

Water hardness and pH have long been implicated as major determinants of freshwater plant and animal distributions (Edmondson 1944, Wetzel 1983). Different levels of tolerance to water hardness and pH have been suggested by submersed aquatic plant "associations" (Spence 1964). Interspecific differences in tolerance to water hardness have also been shown for congeneric species of *Eleocharis* (Moyle 1945), *Potamogeton* (Lohammar 1938), *Sagittaria*, *Scirpus* (Curtis 1971), and *Myriophyllum* (Hutchinson 1970).

Lake habitats are categorized as "soft" or "hard" water depending on whether their water is derived from the drainage of acidic or calcareous deposits (Wetzel 1983). Calcareous hardwater lakes are buffered strongly at pH values above 8, whereas soft water lakes are more poorly buffered with pH values less than 7 (Wetzel 1983). In the upper Great Lakes region, there is a general north-south geographic orientation to lake hardness. Acidic-soft lake waters overlie granitic and igneous bedrock in northern Wisconsin and the western Upper Peninsula of Michigan, whereas alkaline-hard lake waters predominate over limestone bedrock in the southern portions of these states (Curtis 1971, Dorr & Eschman 1970, Martin 1965, Wilson 1939). Therefore, the distributions of many "northern" or "widespread" aquatic plant species in the Great Lakes region may result from their specific tolerance to water hardness rather than their adaptation to particular climatic factors.

Because aquatic plants often display different chemical tolerances (Moyle 1945), various authors have considered the importance of aquatic macrophyte communities as indicators of environmental conditions (e.g. Curtis 1971, Seddon 1972, Stuckey 1971, 1975, Swindale & Curtis 1957). Stuckey (1971, 1975) associated habitat conditions and the geographic distributions of freshwater macrophytes, concluding that species with northern distributions generally occupy oligotrophic habitats, whereas those that are widespread geographically exist under more eutrophic conditions.

We are interested in investigating the nature of morphological and physiological adaptations in the water milfoil genus *Myriophyllum* (Haloragaceae). Interspecific differences in submerged leaf shape in *Myriophyllum* have been associated with geographical distribution and habitat differences (Gerber & Les, 1994); however, the habitats of milfoil species have not been quantified adequately. The purpose of this study was to analyze quantitative habitat data and to assess the association of habitat variables with the distributional patterns of seven *Myriophyllum* species found in the upper Great Lakes region. This comparison provides us with critical base-line information to facilitate our study of habitat-linked adaptations in the genus.

MATERIALS AND METHODS

We separated seven *Myriophyllum* species into two groups based on their present geographical distributions and published habitat descriptions (Aiken 1981, Beal 1977, Ceska & Warrington 1976, Correll & Correll 1972, Crow & Hellquist 1983, Fassett 1930a, 1930b, Hutchinson 1975, Muenscher 1944, Reed 1977, Voss 1985): 1) a "northern" group including *Myriophyllum alterniflorum* DC, *M. farwellii* Morong, and *M. tenellum* Bigelow; and 2) a "widespread" group including *M. heterophyllum* Michaux, *M. sibiricum* Komarov, *M. spicatum* L., and *M. verticillatum* L.

We selected 35 different sites (5 sites/species) in Wisconsin and the Upper Peninsula of Michigan for study of habitat variables (Fig. 1). Voucher specimens were collected from each site and are deposited in the University of Wisconsin-Milwaukee herbarium (UWM).

Water and sediment samples were collected within or adjacent to *Myriophyllum* plant beds, from each site during August/September 1993. In the field, water samples were collected at a depth of 0.25 m, filtered (0.45μm), and stored on ice for later analyses. Light measurements were taken at all sites at depths of 0, 0.5, 1, and 1.5 m, when possible, to calculate extinction coefficents. Generally speaking, extinction coefficient values $< 1\ m^{-1}$ indicate clear water and those $> 6\ m^{-1}$ indicate turbid water (Wetzel 1983). In the lab, water pH and conductivity measurements were made at 24°C using an Orion Research digital ionalyzer/501. Water ammonium-nitrogen analysis followed a modified Koroleff (1983) method. Water calcium levels were determined by atomic absorption on an Instrumental Laboratory aa/ae spectrophotometer following Standard Methods (1989). In the field, two sediment cores were collected from each site. Pore water was extracted from one sediment core, filtered (0.45 μm), and stored on ice for later analysis. In the lab, the second core was dried and used for particle size analysis (%sand, %silt, %clay) following the hydrometer method of Gee & Bauder (1986). Hydrometer readings were taken at 30 sec and 7 hr. Organic matter was determined by heating ground sediment samples (2 g) to 250°C for 1 hr (Liegel et al. 1980). Pore water ammonium-nitrogen analysis was modified from the Solorzano (1969) phenol-hypochlorite method.

Analysis

We used pH vs. calcium plots to determine the influence of each related factor on *Myriophyllum* distributions. By placing lines as boundaries around the "envelope" of plotted points (Hutchinson 1970) for each geographic species group, the general importance of each factor (calcium vs. pH) was determined. All water and sediment variables were ln transformed to normalize distributions (Sokal & Rohlf 1981). We tested for significant differences between the northern and widespread groups for four water (ammonium-nitrogen, calcium, extinction coefficient, and pH) and five sediment (ammonium-nitrogen, % clay, organic matter, % sand, and % silt) variables using a nested analysis of variance (ANOVA). The 35 collection sites were nested within the seven species and the species were nested within the two geographic groups. We then analyzed the water and sediment

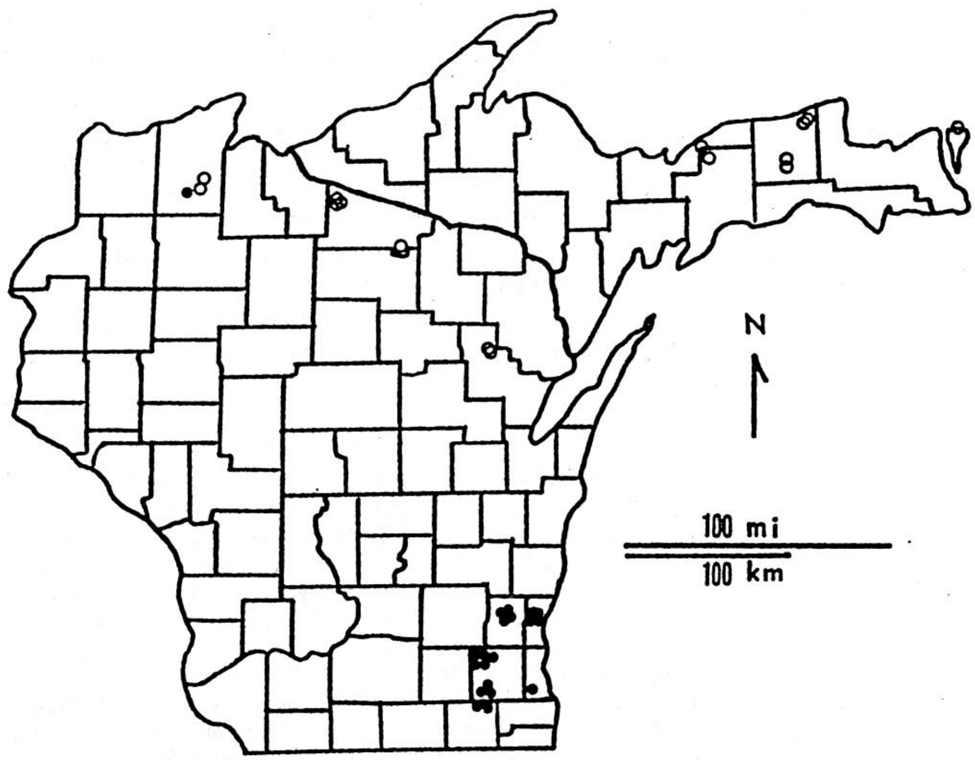

FIGURE 1. Wisconsin and Upper Peninsula of Michigan showing site localities. Open circles are northern species sites, and solid circles are widespread species sites.

variables for significant differences among the seven *Myriophyllum* species using one-way ANOVA and Tukey post hoc tests.

RESULTS

The pH vs. calcium plots indicated that the northern species group (Fig. 2) was generally restricted by water calcium concentration. Within the northern group, one site with *Myriophyllum alterniflorum* had high calcium levels relative to the other northern sites. Conversely, the widespread species group (Fig. 2) seemed to be restricted by pH but had a wide range of calcium tolerance, with the exception of one *M. sibiricum* site with high pH.

The lakes with northern *Myriophyllum* species differed significantly ($p < 0.05$) from lakes with widespread species in five water (calcium, pH) and sediment (ammonium-nitrogen, % silt, % clay) variables (Table 1). Similarly, significant interspecific differences were found for water calcium levels, pH, and sediment ammonium-nitrogen levels (Table 2). However, no interspecific differences were found for % silt and % clay possibly due to the small sample sizes.

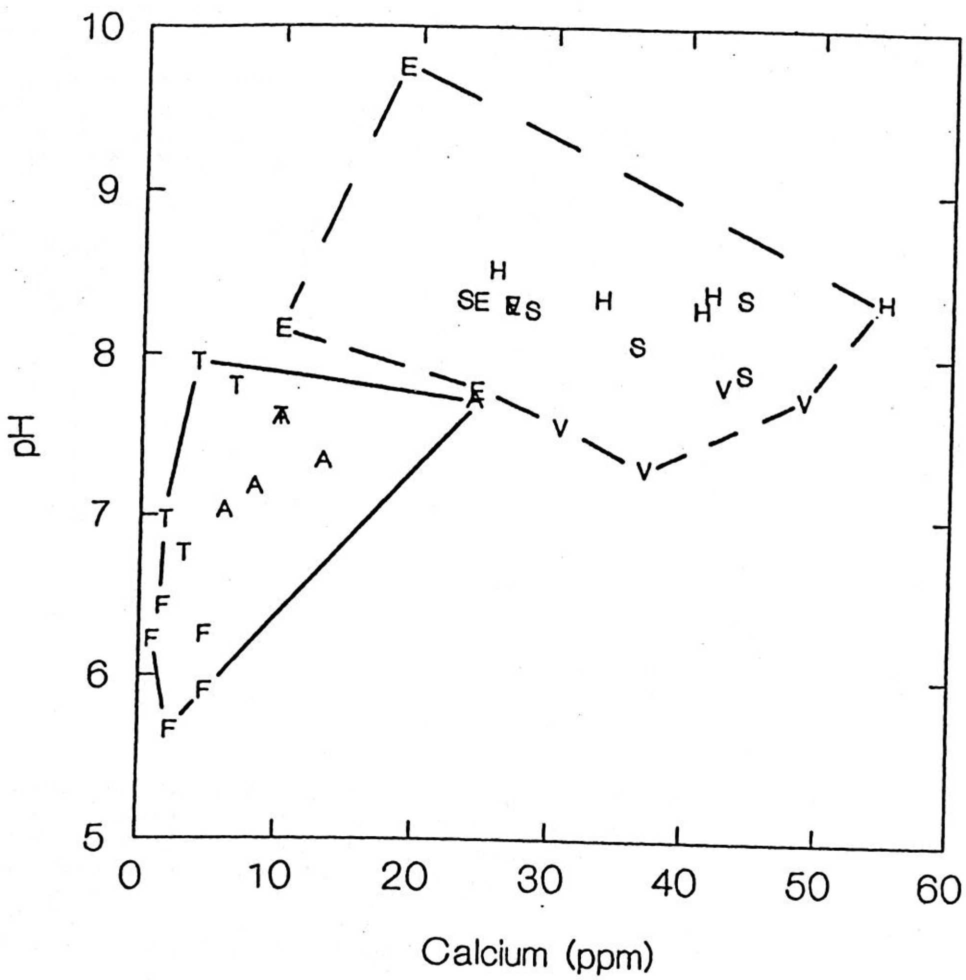

FIGURE 2. Water pH vs. calcium plots for 35 sites in Wisconsin and Upper Peninsula Michigan. The solid line designates the envelope for the northern species group; the dotted line for the widespread species. A = *Myriophyllum alterniflorum*, E = *M. sibiricum*, F = *M. farwellii*, H = *M. heterophyllum*, S = *M. spicatum*, T = *M. tenellum*, V = *M. verticillatum*.

No significant differences were found for extinction coefficients or sediment organic matter between the northern and widespread groups (Table 1); however, significant interspecific differences were found (Table 2). Particle size analysis could not be performed on sediment samples from three sites due to large amounts of organic matter. Light extinction coefficients and organic matter were highly variable for the northern group. *Myriophyllum alterniflorum* and *M. tenellum* were essentially found in clear water lakes with sandy sediments whereas *M. farwellii* grew in brown-stained waters (see Table 2) on organic sediments; however, some exceptions were found. One site with *M. alterniflorum* had brown-stained water and two sites with *M. farwellii* had relatively clear

TABLE 1. Summary of nested ANOVA of nine habitat variables compared between lakes inhabited by northern or widespread *Myriophyllum* species. Means are given as the antilog of the transformed variable. Ca = ppm aqueous calcium, EC = extinction coefficient (m^{-1}), N(aq) = μM aqueous ammonium-nitrogen, N(sed) = μM pore water ammonium-nitrogen, OM = % organic matter.

	Northern Mean (N)		Widespread Mean (N)		F (ANOVA)	Significance
N(sed)	35.37	(15)	325.71	(20)	40.227	p = 0.001
Ca	4.92	(15)	31.16	(20)	20.836	p = 0.006
% silt	5	(13)	16	(19)	14.987	p = 0.012
% clay	4	(13)	8	(19)	11.279	p = 0.020
pH	6.92	(15)	8.18	(20)	8.014	p = 0.037
% sand	82	(13)	66	(19)	6.170	p = 0.056
N(aq)	1.39	(15)	0.80	(20)	2.591	p = 0.168
OM	3.06	(15)	6.69	(20)	1.011	p = 0.361
EC	1.31	(15)	1.10	(20)	0.166	p = 0.700

TABLE 2. Water and sediment variables of 35 sites are seven *Myriophyllum* species. Results are the antilog of the mean (± 1 SD) of five sites/species (* = 4 sites; ** = 3 sites). Values were significant (ANOVA, $p < 0.05$) for Ca, N (sed), pH, OM, and EC (means with same lower case letters were not significant). Ca = ppm aqueous Ca, EC = extinction coefficient (m^{-1}), N (aq) = μM aqueous ammonium-nitrogen, N (sed) = μM pore water ammonium-nitrogen, OM = %organic matter. Alt = *M. alterniflorum*, Far = *M. farwellii*, Ten = *M. tenellum*, Sib = *M. sibiricum*, Het = *M. heterophyllum*, Spi = *M. spicatum*, Ver = M. verticillatum.

	Northern			Widespread			
	Alt	Far	Ten	Sib	Het	Spi	Ver
N (sed)	25(1)a	30(<1)a	59(1)ab	213 (<1)b	462 (1)b	507 (<1)b	225 (1)b
Ca	11.0bc (0.5)	2.5a (0.7)	4.4ab (0.7)	19.8cd (0.4)	38.2d (0.3)	34.3d (0.3)	36.3d (0.3)
% silt	15 (1)	8 (1)**	4 (<1)	14 (1)	12 (1)	17 (1)	26 (1)*
% clay	4 (<1)	6 (<1)**	3 (<1)	7 (1)	8 (1)	8 (<1)	8 (1)*
pH	7.37b (0.04)	6.09a (0.05)	7.40b (0.07)	8.44c (0.09)	8.38c (0.01)	8.19bc (0.02)	7.74bc (0.05)
% sand	73 (1)	80 (1)**	93 (<1)	75 (<1)	65 (<1)	66 (<1)	58 (<1)*
N (aq)	2.1 (0.7)	0.7 (0.4)	1.9 (0.6)	0.7 (1.0)	1.3 (1.2)	1.0 (1.4)	0.6 (1.1)
OM	1.4a (0.5)	15.2bc (1.6)	1.3a (0.4)	3.5ab (0.9)	4.7abc (1.2)	7.6abc (0.5)	16.0bc (1.2)
EC	1.0ab (0.8)	3.3b (1.0)	0.7a (0.4)	1.1a (0.3)	0.8a (0.3)	1.3a (0.2)	1.4ab (0.3)

TABLE 3. General environmental variables under which each *Myriophyllum* species (Spp) is found. Data from published sources and the present study. References (Ref.): Aiken 1981[1], Aiken et al. 1979[2], Almestrand & Lundh 1951[3], Ceska & Warrington 1976[4], Correll & Correll 1972[5], Crow & Hellquist 1983[6], Hutchinson 1970[7], 1975[8], Iversen 1929[9], Muenscher 1944[10], Reed 1977[11], Seddon 1972[12], Spence 1964[13], Swindale & Curtis 1959[14], Voss 1965[15], 1985[16]. Alt = *M. alterniflorum*, Far = *M. farwellii*, Ten = *M. tenellum*, Sib = *M. sibiricum*, Het = *M. heterophyllum*, Spi = *M. spicatum*, Ver = *M. verticillatum*.

Spp	Water	Sediment	Ref.
Alt	acidic-slightly alkaline pH; wide range of Ca tolerance	sandy; low NH_4^+	1, 6, 8, 9, 12-14, 16
Far	acidic pH; soft; brown-stained to clear	sandy; highly organic; low NH_4^+	3, 6, 10
Ten	acidic-slightly alkaline pH; soft	sandy; low NH_4^+	1, 10, 14–16
Sib	wide range of pH and Ca tolerance	sandy-muck; high NH_4^+	2, 5, 6, 10, 14, 16
Het	acidic-alkaline pH; wide range of Ca tolerance	silty-clay; high NH_4^+	6
Spi	Wide range of pH tolerance; hard	sandy-muck; high NH_4^+	2, 3, 6, 7, 9, 11–13
Ver	slightly acidic-slightly alkaline pH; wide range of Ca tolerance	silty-muck; high NH_4^+	2, 3, 7, 8

water. These observations help to clarify the large intraspecific variances found for both of these species.

No significant differences were found for water ammonium-nitrogen or sediment sand content between the northern and widespread groups or among species (Tables 1 & 2). Temporal variations in water ammonium-nitrogen levels occur in eutrophic lakes, whereas these levels are generally low throughout the year in temperate oligotrophic lakes (Wetzel 1983). Water ammonium-nitrogen levels were low at all of the sites, probably because samples were collected late in the growing season. Large variances in sediment sand content were found among the sites (especially for the widespread group). Because numerous sediment collection sites were in urban areas, the large variance in sand content may have been due to anthropogenic input.

DISCUSSION

Hutchinson (1975) has stressed that "The most important chemical dichotomy in the ecology of the plants of freshwaters is that of soft and hard waters." In Wisconsin, limestone and calcareous lake sediments are generally confined to the south, whereas insoluble sandy sediments predominate in the north. Waters above these sediments form a gradient from soft, cold waters in the north to hard, warm waters in the south (Fenneman 1902, Juday 1914, Curtis 1971, Wilson 1939). Aquatic plant communities found within this region reflect this gradient (Curtis 1971), as do the congeneric species of *Myriophyllum*.

Clearly, lake water pH and calcium play important roles in the distribution of the seven *Myriophyllum* species examined in this study. In the upper Great Lakes region, milfoil species in the northern group were found at sites with low calcium concentrations and acid-neutral pH. Conversely, species in the widespread group were found at sites with high calcium concentrations and neutral-alkaline pH. As in our region, Swedish lakes show a similar geographical gradient of northern softwater lakes and southern hardwater lakes. Earlier studies of *Myriophyllum* in Swedish lakes demonstrated that *M. alterniflorum* generally occurred in low pH soft water lakes, whereas *M. spicatum* and *M. verticillatum* more typically occurred in harder water lakes with higher pH (Almestrand & Lundh 1951, Hutchinson 1970, 1975). However, Iversen (1929) and Spence (1964) have associated *M. alterniflorum* with moderately-hard to hard waters in Danish and Scottish lakes.

Hutchinson (1975) categorized *Myriophyllum* species into three water hardness groups. Despite his admitted lack of adequate data, he tentatively placed *M. alterniflorum*, *M. farwellii*, and *M. tenellum* among soft water species, and *M. verticillatum* with species of intermediate water hardness; *M. sibiricum* was included among the hard water species. Our data provide some evidence to corroborate Hutchinson's categorization of these species.

Explanations of *Myriophyllum* species distributions based solely on lake water pH and calcium concentrations may be misleading (Sculthorpe 1967). Bicarbonate concentrations and conductivity (associated with pH and calcium concentrations) are also low in soft waters. Higher levels of these four variables are found in hard waters (Hutchinson 1970, Sculthorpe 1967). Optimal photosynthetic rates have been observed for *Myriophyllum spicatum* in bicarbonate solutions; however, under acidic conditions limited rates were observed (Steeman-Nielsen, 1947). These findings led Spence (1967) to suggest that lake water alkalinity was a factor restricting the distribution of *M. spicatum*. Sediment variables, light, and water flow may all affect plant distributions (Sculthorpe 1967). Thus, we included other variables in addition to water pH and calcium concentration to identify habitat differences between northern and widespread species groups.

Physical texture rather than chemical composition is the primary influence of sediments on aquatic plant distributions (Sculthorpe 1967). Sediment texture and chemistry are interdependent; however, sandy (large particle size) or highly organic sediments are relatively nutrient-poor, and silt/clay sediments (small particle size) are relatively nutrient-rich (Hutchinson 1975). In the upper Great Lakes region, the northern species occur on sediments low in silt and clay where ammonium-nitrogen levels are low. Furthermore, the low pH and calcium levels found at these sites indicate that the northern species are restricted to oligotrophic habitats. Sites inhabited by the widespread species had significantly higher levels of silt, clay, and high ammonium-nitrogen levels. Those factors together with the relatively higher levels of pH and calcium indicate that widespread species are found in more meso- to eutrophic sites.

Water and sediment characteristics of the littoral zone are important factors that in part influence the distribution of rooted, submersed *Myriophyllum* species (Table 3). Interestingly, water pH and calcium characteristics of habitats with species in the northern group are similar in both the upper Great Lakes region and other sites in Europe and North America (Table 3). One exception is the higher calcium content of Scottish waters, compared with the upper Great Lakes region, where Spence (1964) found *Myriophyllum alterniflorum*. Conversely, water pH and calcium characteristics of habitats with species in the widespread group had a more restricted range in the Great Lakes region. Wider ranges of water pH and calcium levels were found when data from European and other North American regions were included.

Although the northern species are restricted to oligotrophic environments in the upper Great Lakes region, tolerance to water and sediment variables may only partially explain their confined distribution. Climate, plant competition, chances of geographical dispersal, and dispersal agents may also affect plant distributions (Aiken et al. 1979, Good 1953, Seddon 1972). While climate may greatly influence terrestrial plant distributions, submersed plants may be less susceptible to climatic extremes of terrestrial habitats, owing to the stable, well-buffered nature of aquatic habitats (Les 1986, Tiffney 1981).

Plant competition has previously been suggested as a factor in aquatic plant distributions, though evidence is indirect. *Isoetes lacustris* and *I. setacea*, confined mainly to oligotrophic habitats, have also been found in eutrophic habitats but are generally excluded from these areas due to their poor competitive ability (Sculthorpe 1967, Seddon 1965). Seddon (1965) found these species in restricted sites where other aquatics could not survive. Similarly, wide ranges of water solute tolerance for several species, including *Littorella uniflora*, were found by Seddon (1972); however, he suggested this species was restricted to nutrient-poor waters due to competition from other species.

Myriophyllum alterniflorum has a wide range of chemical tolerance (Iversen 1929, Seddon 1972, Spence 1964), but seems to be generally restricted to oligotrophic environments in the upper Great Lakes region. This habitat restriction may be due in part to competition; however, many factors can ultimately affect the distribution of one species as discussed above. Interestingly, only one site from this study (Frog Bay, Sugar Island, Chippewa Co., Michigan) was inhabited by both a northern (*M. alterniflorum*) and a widespread species (*M. sibiricum*).

In summary, this study provides data for the categorization of seven *Myriophyllum* species into northern and widespread groups by characterizing some of the typical habitat features in which they are found in Wisconsin and the UP of Michigan. This report also provides habitat data on *M. farwellii* which is rare in Wisconsin and Michigan. Because many aquatic species, including *Myriophyllum*, are overlooked by general collectors (Voss 1972), and limited habitat data for these specimens exist, further habitat analyses are encouraged to expand the base-line habitat data provided by this report.

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