Habitat Relationships for Some Wisconsin Lake Plant Associations

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ABSTRACT

Depth, alkalinity, pH, and conductivity distributions; substrate preference; and turbidity tolerance were used to explain species groupings formed by association analysis for 62 species of Wisconsin lake plants. Three out of five plant groups could be largely explained by substrate. Turbidity tolerance helped define differences between hard and soft substrate species. Water chemistries explained species groupings within soft substrate species and among a group of plants that did not commonly associate with other species. The habitat factors and adaptations studied did not successfully explain a group of plants found in "mesic" water chemistries and varying substrate and turbidity conditions.

INTRODUCTION

In aquatic plant communities there are a number of biotic and abiotic factors that influence species interactions. Positive associations between species may occur from similarities of adaption and response to environmental conditions or from beneficial interactions such as mutualism or commensalism, favorable to one or both species. Negative associations may result from species preferring different habitats or from detrimental interactions such as resource competition or allelopathy.

Studies that relate aquatic plant groupings to habitat factors generally fall into two types. One type relates species groups in a single lake to within-lake habitat differences (Misra 1938, Spence 1967, Carpenter and Titus 1984, Nichols 1971, Schmid 1965, Sheldon and Boylen 1977, Wilson 1937 and 1941, and Rorslett 1987). These studies assume water chemistry is relatively constant and in-lake variables such as water depth, substrate type, fetch, sediment accumulation, light penetration, and water turbulence explain plant distribution. A second type concentrates on between-lake differences which generally means differences in water chemistry, but might also relate to water clarity or water temperature (Seddon 1972, Moyle 1945, Swindale and Curtis 1957, Pip 1979 and 1984, Olsen 1950, Kadono 1982 a and b, Hellquist 1980, and Lind 1976). Biotic relationships such as

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Table 1. Classification of lake plants based on interspecific associations and habitat preferences (after Nichols 1990 and 1992)

	ALKAL MEDIAN mg.L^{-1} as CaCO$_3$	COND. MEDIAN μmhos. cm^{-1}	pH MEDIAN	DEPTH MEDIAN (m)	SUB. PREF.[a]	TURB. TOL.[b]	CAN. AXIS I	CAN. AXIS II	RANGE[c]
TYPE 1 PLANTS									
Potamogeton strictifolius	92	200	7.7	1.10	3	-	-1.61	-1.36	M
Potamogeton gramineus	54	114	7.6	1.1	3	2	0.10	0.70	M
Najas flexilis	77	148	7.7	1.20	3	3	0.86	-0.38	M
Potamogeton pectinatus	140	287	8.1	1.50	2	2	1.81	-0.49	B
Potamogeton illinoensis	130	246	8.1	1.20	2	3	2.27	-0.18	M
Myriophyllum spicatum	153	337	8.4	1.70	2	3	2.54	-0.87	M
Scirpus validus	108	213	8.0	0.60	2	3	2.57	0.66	B
Average	**107.7**	**220.6**	**7.9**	**1.2**					
TYPE 2 PLANTS									
Eriocaulon aquaticum	11	31	6.8	1.20	3	3	-3.79	-0.58	L
Isoetes macrospora	22	55	7.2	1.80	3	-	-2.93	-0.28	L
Eleocharis acicularis	25	65	7.1	0.90	3	1	-2.16	-0.10	L
Potamogeton robbinsii	45	95	7.4	1.80	2	2	-1.95	0.55	M
Bidens beckii	45	91	7.4	1.20	1	3	-1.90	-0.14	L
Nuphar variegata	42	77	7.0	1	1	2	-0.75	-0.06	M
Nymphaea odorata	48	98	7.4	0.9	1	1	-0.17	0.14	B
Potamogeton praelongus	68	127	7.6	1.70	1	3	0.15	2.48	M
Polygonum amphibium	55	109	7.4	1	2	1	0.30	0.98	M
Potamogeton amplifolius	61	121	7.5	1.50	1	2	0.81	-0.08	M
Potamogeton richardsonii	64	127	7.5	1.50	2	2	0.91	-0.19	M
Myriophyllum verticillatum	94	188	7.7	1.50	2	3	1.24	0.69	B
Zosterella dubia	103	213	7.8	1.20	2	1	1.43	-0.60	M
Myriophyllum sibiricum	105	186	7.9	1.80	1	3	1.48	0.96	B
Vallisneria americana	70	136	7.6	1.20	3	1	1.60	-0.67	B
Potamogeton nodosus	155	316	8.2	0.90	2	1	2.69	-4.09	M
Average	**63.2**	**127.0**	**7.5**	**1.3**					
TYPE 3 PLANTS									
Myriophyllum farwellii	8	35	6.3	1.80	1	-	-2.86	0.49	L
Ceratophyllum echinatum	32	70	6.9	1.00	1	-	-2.84	0.39	L
Dulichium arundinaceum	26	66	7.0	0.60	1	1	-2.42	-0.82	L
Brasenia schreberi	31	69	7.0	1.00	2	1	-2.39	-0.18	L
Utricularia gibba	28	60	7.0	1.40	1	-	-2.02	-0.83	L
Sagittaria latifolia	42	90	7.2	0.75	1	1	-1.39	0.32	L
Sparganium chlorocarpum	8	82	7.2	0.85	1	-	-1.01	-0.45	L
Potamogeton pusillus	45	94	7.2	1.20	1	1	-0.76	0.26	M
Utricularia vulgaris	41	86	7.2	1.20	1	1	-0.55	0.38	M
Utricularia intermedia	40	99	7.2	1.20	1	-	0.23	-0.35	M
Potamogeton natans	93	191	7.8	0.90	2	2	1.37	0.65	B
Myriophyllum heterophyllum	125	234	7.8	2.00	2	-	2.29	0.20	M
Average	**45.7**	**97.9**	**7.2**	**1.2**					
TYPE 4 PLANTS									
Potamogeton diversifolius	15	58	7.4	1.20	1	-	-2.81	0.43	L
Typha latifolia	43	96	7.4	0.30	2	3	-0.45	-0.68	M
Sagittaria latifolia	43	90	7.3	0.20	2	2	0.27	0.10	M
Ranunculus longirostris	143	303	8.0	0.90	2	2	1.09	3.51	M
Wolffia columbiana	140	281	7.9	-	-	-	1.29	2.49	M
Potamogeton zosteriformis	91	178	7.8	1.50	1	3	1.30	0.33	B
Lemna trisulca	112	236	7.7	-	-	-	1.56	0.40	M
Ceratophyllum demersum	96	190	7.8	1.70	1	1	1.66	-0.08	B
Elodea canadensis	89	175	7.8	1.50	1	1	1.81	0.40	B
Spirodela polyrhiza	88	157	7.5	-	-	-	1.94	1.61	M
Potamogeton foliosus	104	185	7.8	0.60	1	1	2.80	-0.61	M
Lemna minor	117	238	7.8	-	-	-	2.85	-0.76	B
Potamogeton crispus	142	297	8.1	0.90	1	1	3.25	-1.47	M
Average	**93.9**	**191.0**	**7.7**	**1.0[d]**					

Table 1 (contd.)

TYPE 5 PLANTS , NON-ASSOCIATING SPECIES

Subtype A									
Lobellia dortmanna	14	36	7.0	1.50	3	-	-3.35	-0.16	L
Myriophyllum tenellum	15	43	6.9	1.80	3	-	-3.05	-0.58	L
Potamogeton epihydrus	22	60	6.8	1.10	2	2	-2.92	-0.38	L
Eleocharis robbinsii	28	59	6.8	1.20	1	-	-2.66	-1.03	L
Isoetes echinospora	22	58	7.0	1.50	2	-	-2.52	-0.33	L
Ranunculus flammula	28	59	7.0	1.80	3	-	-2.33	-1.05	L
Sagittaria graminea	32	72	7.1	0.60	2	-	-2.25	-0.84	L
Pontederia cordata	39	80	7.2	0.80	2	3	-1.66	0.33	M
Average	**24.9**	**58.3**	**7.0**	**1.3**					
Subtype B									
Najas marina	178	417	8.6	1.70	1	-	1.16	4.65	L
Potamogeton filiformis	73	94	8.2	1.50	2	-	1.22	-2.47	M
Scirpus americanus	65	127	8.0	0.65	2	3	1.35	-0.79	M
Zannichellia palustris	144	295	8.1	0.90	3	1	1.84	-2.29	M
Zizania aquatica & Z palustris	85	167	7.7	0.9	1	2	2.02	-0.52	M
Ranunculus trichophyllus	91	234	8.0	0.90	2	-	3.66	0.12	B
Average	**105.9**	**222.3**	**8.1**	**1.1**					

[a] Sub. pref.: 1-prefers soft substrate, 2-no substrate preference, 3-prefers hard substrate, - unknown or not appropriate
[b] Turb. tol.: 1-turbidity tolerant,, 2- turbidity preference indeterminate, 3-not turbidity tolerant, - unknown or not appropriate
[c] Range: L-limited, M-moderate, B-broad
[d] Does not include free floating species (*Lemnaceae*)

resource competition, allelopathy, or symbiotic relationships could also explain species groupings or lack thereof, but studies defining these relationships are limited and the results are not conclusive (Agami and Waisel 1985, Engel and Nichols 1984, Nichols 1984, Seddon 1972, McCreary et al. 1983, McCreary 1991, and Titus and Stephens 1983).

All factors, within-lake, between-lake, and biotic, might be needed to explain species groupings. In practice the number of parameters must be limited to a few which are believed to be important. Often parameter selection can be limited because parameters like water depth and sediment characteristics act as indicators for sets of interacting habitat variables including light, nutrient conditions, and mechanical disturbance (Anderson and Kalff 1988).

Nichols (1990) used interspecific association to objectively classify lake plants into five groups (Table 1). The goal of this study was to independently determine which habitat factors, if any, were important for explaining the groups formed by species association in the earlier study. This study builds on past studies by using both in-lake and between-lake habitat parameters to interpret species groupings.

METHODS AND MATERIALS

Nichols (1990) provided the list of species for this study. With the consolidation of some species caused by taxonomic revisions (Gleason and Cronquist 1991) and deletion of some species where data did not meet minimum criteria, 62 species were compared

Substrate preference, turbidity tolerance, depth, alkalinity, pH, and conductivity were the parameters selected for analysis. Nichols (1992) previously determined depth, substrate, and turbidity relationships (Table 1). Alkalinity, conductivity, and pH distributions were developed by combining the information in the Wisconsin Lake Plants Database (Nichols and Martin 1990) with herbarium records from the University of Wisconsin-Madison, -Milwaukee, -Oshkosh, -Stevens Point, and -LaCrosse and the Milwaukee Public Museum. The resultant database provided a list of lakes where each species occurred. A species had to occur in at least 20 lakes to be retained for this study. Most species occurred in far more than this minimal number but some rare species found in Nichols (1990) were eliminated from this study because they did not meet minimal criteria. Physical and chemical data for the lakes were collected during macrophyte sampling, were recovered from the Wisconsin Department of Natural Resources general waters file, or were found in the original data used for describing the limnological characteristics of Wisconsin lakes (Lillie and Mason 1983).

Boxplots (Reckow and Chapra 1983) were used to illustrate the water chemistry and depth distributions of each species. Distribution endpoints were either the maximum and minimum values or were trimmed to the positive and negative inner fence (Minitab 1991), whichever value was the least. This reduced outlier data and displayed the distribution of a species based on the "most typical" of approximately 90-100% of the distribution points (Minitab 1991). Although total distribution range is sensitive to the number of observations, it was used so that the ranges of habitat overlap could be studied. The total range problem is minimized by setting the minimum criteria and trimming to the inner fence. The average range (Range in Table 1) that the species occupied for the chemical parameters was also determined. This was done by calculating the percent of the maximum range for each of the three chemical parameters that a species occupied and then averaging the three values. A species was designated as having a limited range if it averaged less than 50% of the combined ranges, moderate range species averaged 50%-75%, and broad range species greater than 75% of the combined average ranges.

Canonical analysis (SAS 1989) was used to compare the minimum and maximum endpoints of the pH, alkalinity, and conductivity distributions for each species. This allowed the range overlap in chemical characteristics to be compared for each species. The habitat characteristics including the canonical axes which integrated alkalinity, pH, and conductivity were compared to the species grouping determined by association analysis (Nichols 1990) to see if and how the groups related to the selected habitat parameters.

RESULTS

Substrate preference, turbidity tolerance, and depth

Substrate preference sorted out two plant types, those that preferred hard substrate or showed no substrate preference (Type 1 plants), and those that preferred soft substrates or showed no substrate preference (Type 3 and 4 plants) (Table 2). Substrate preference could not explain Type 2 or Type 5 plants. In addition, there were no Type 1 plants that were turbidity tolerant and all Type 3 plants were turbidity tolerant or showed no turbidity preference (Table 3).

Depth distribution was very similar between groups. Plants do not appear to group by depth except that all the small, free floating species (*Lemnaceae*) are Type 4 plants.

Canonical analysis and water chemistry

The first canonical axis explained 78% of the variation and the first two axes explained 94% of the variation in water chemistry data. The first axis correlated with median alkalinity (n=62, r=0.84), conductivity (n=62, r=0.80), and pH (n=62, r=0.85) which was expected since the canonical variate for each species is a linear combination of alkalinity, conductivity, and pH. Species with low Axis I values had low median pH, alkalinity, and conductivity values and vice versa.

Axis I, with one notable exception, separated the limited range species from the broad range species (Fig. 1). It also separated the Type 5 plants into two distinct groups (Type 5A and 5B, Table 1) - a group with low Axis I values and limited ranges and a group with higher Axis I values and moderate ranges. Axis II appeared to separate the moderate range species but the reason is unknown. This axis did not correlate well with any of the habitat parameters studied.

Results indicate that canonical analysis could separate the species into two to five somewhat arbitrary groups. However, these groups did not explain the species groupings based on association analysis (Fig. 2).

The difference between Type 3 and Type 4 plants, both preferring soft substrate, appears to be water chemistry. Type 3 plants are generally found at lower pH, alkalinity, and conductivity levels than Type 4 plants (Table 1). Water chemistries also appear to determine the distribution of Type 5A plants. This group is found in the lowest average pH, alkalinity, and conductivity conditions. All but one of these species has a limited range. Although water chemistry was not useful for defining all plant grouping, it appears that the Type 5A group is largely defined by water chemistry and water chemistry defines the difference between the Type 3 and Type 4 plants.

Najas marina is the exception to many of the previous discussions. It is a Type 5 species with a limited water chemistry distribution but has the highest median alkalinity, pH, and conductivity of any species studied. This contrasts with other limited range species which had low median alkalinities, pHs, and conductivities. While its Axis I values are not unusual, its Axis II value forms the high end point of the Axis II distribution (Fig.1).

Table 2. Substrate preference of species by plant type[a]

Plant type	Prefer soft substrate	No substrate preference	Prefer hard substrate	Unknown preference
1	---	4	3	---
2	6	6	4	---
3	9	3	---	---
4	6	3	---	4[b]
5A	1	4	3	---
5B	2	3	1	---

[a] Number of species in each category

[b] Mostly small free-floating species (*Lemnaceae*) where substrate preference is not appropriate.

Table 3. Turbidity tolerance of species by plant type[a]

Plant type	Turbidity tolerant	Indetermined tolerance	Not turbidity tolerant	Unknown
1	---	2	4	1
2	6	4	5	1
3	5	1	---	6
4	4	2	3	5[b]
5A	---	1	1	6
5B	1	1	1	3

[a] Number of species in each category

[b] Mostly small free-floating species (*Lemnaceae*) where turbidity tolerance is not appropriate.

DISCUSSION

Substrate preference appears to be a significant determinate of the species groupings shown by association analysis. Three groups are explained by substrate preference. Type 1 and Type 4 plants are found in similar water chemistry conditions but they are the most dissimilar plant groups in the association dendrogram (Nichols 1990). The primary difference between the groups is substrate preference. Type 1 plants are found in high alkalinity, pH, and conductivity waters with some species preferring hard substrates and not being turbidity tolerant. This group is probably a characteristic hard water, marl lake association.

Type 3 and Type 4 plants show a similar substrate relationship but are separated by water chemistry characteristics. Type 3 plants are found at lower pHs, alkalinities, and conductivities. They also tolerate turbid water or show no turbidity relationship. This group is probably a dystrophic lake flora where light limitation is caused by stained water rather than suspended materials. Type 4 plants are characteristic of soft bottom areas of lakes with higher pHs, alkalinities, and conductivities. These lakes are more nutrient rich so light limitation is likely caused by suspended materials such as algae or sediment.

Type 5 plants form two distinct groups which probably represent the two ends of the spectrum of lake plant types in Wisconsin. Type 5A is characteristic of low alkalinity, conductivity, and pH waters - generally a soft water, oligotrophic lake association. Many of the species in this group are "isoetid" species (Madsen and Sand-Jensen 1991) that have specialized mechanisms for dealing with limited growth resources, especially carbon, found in their typical habitat. Nutrient resources are very limited so it is not unusual that these species are not found associating with other species, at least on a scale used in this study.

The other end of the spectrum is the alkali or near-alkali association as discussed by Moyle (1945). This group is found in high carbonate waters and high sulphate also appears to be important. Moyle (1945) considers 50 $mg \cdot L^{-1}$ to be the minimum sulfate ion concentration for the alkali association habitat. This is difficult to determine in Wisconsin because these species are infrequent (Nichols and Martin 1990) and there is only a small region of southeastern Wisconsin where sulfate concentrations over 40 $mg \cdot L^{-1}$ occur (Lillie and Mason 1983). Type 5B species are found in this region of the state along with some rare finds of alkali

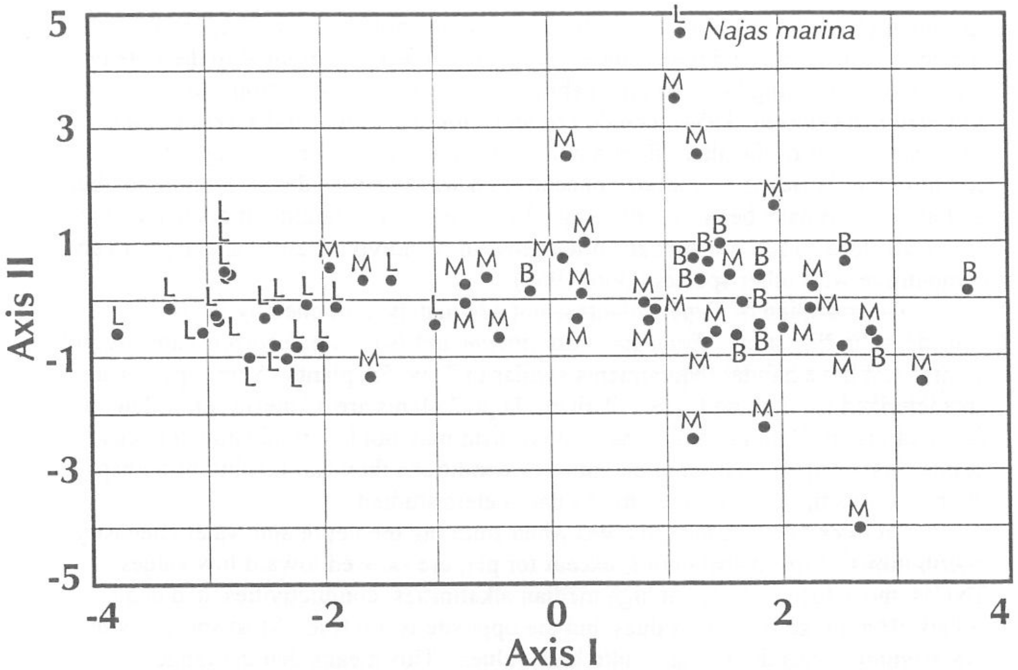

Figure 1. Species ranges displayed as limited, moderate, or broad on canonical axes.

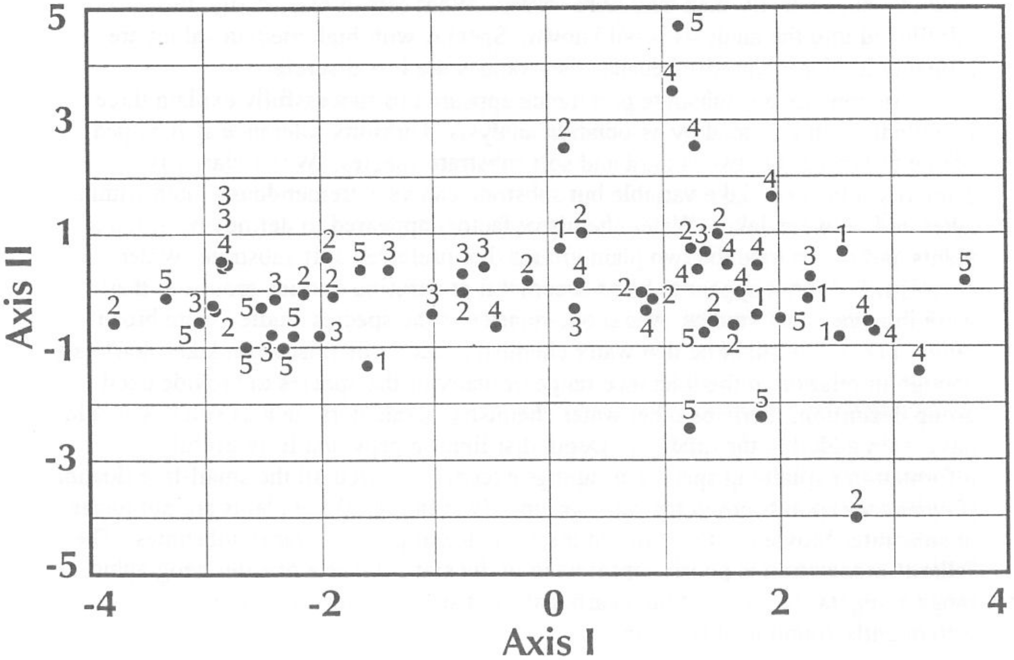

Figure 2. Species types 1-5 displayed on canonical axes.

species such as *Ruppia maritima*. These plants may not show association with other species because they and their typical habitat are poorly represented in the state or there may be limiting factors in the habitat that precludes association. Moyle (1945) and Stegman-Nielsen (1954) include *Potamogeton pectinatus* and *Myriophyllum spicatum* as part of the alkali flora but they are found over a broad range of conditions in Wisconsin. Sulfate concentration was not considered in this study but perhaps should have been. *Zizania* spp., Type 5B plants, should not be included in the alkali flora. They are annuals, often grow in monotypic stands, and are not very competitive with other species (Dore 1969).

The grouping of Type 2 plants is not adequately explained by factors considered in this study. *Eriocaulon aquaticum* and *Isoetes macrospora* are "isoetid plants" and have habitat requirements similar to Type 5A plants. Some species are characterized by floating leaves. Perhaps Type 2 plants are a "mesic" or middle-or-the-road group. Habitat conditions in Wisconsin may not be broad enough to clearly define this group in relation to the range of conditions they can inhabit, or perhaps their relationship is not defined by the parameters studied.

An interesting pattern emerges when studying the depth and water chemistry distributions. Most distributions, except for pH, are skewed toward low values. That is, most species found at high median alkalinities, conductivities, and depth values often range into low values, but the opposite is not true. Most species with low median values do not range into high values. This means that the range between the minimum values is much smaller than the range between maximum values. For example, minimum endpoints for alkalinity ranged from 1 to 137 $mg \cdot L^{-1}$ as $CaCO_3$, for conductivity from 1 to 276 $umhos.cm^{-1}$, and for depth from 0.1 to 0.9 m, while maximum values ranged from 39 to 364 $mg \cdot L^{-1}$, 72 to 856 $umhos.cm^{-1}$, and from 0.8 to 5 m respectively. This weights maximum values in the canonical analysis more heavily than minimum values. What sort of bias, if any, this introduced into the analysis is not known. Species with high median values are probably harder to classify because their ranges are less discrete.

In conclusion, substrate preference appeared to successfully explain three of five plant groups formed by association analysis. Turbidity tolerance also helped define differences between hard and soft substrate species. Water clarity is primarily a between lake variable but substrate can vary tremendously both within-lakes and between lakes. Water chemistry factors appeared to define one group of plants and to separate the two plant groups that preferred soft substrate. Water chemistries did not appear to be as successful at defining species groups as they were in some other studies. About one-quarter of the species studied were broad range species. It might be that water chemistry factors in Wisconsin lakes don't vary enough in relation to the tolerance range of many of the species to provide good group definition. Perhaps other water chemistry parameters such as sulfates should have been added to the analysis. Depth distribution provided little useful information explaining species groupings except it showed all the small-free floating (*Lemnaceae*) plants are in the same group. Even though these plants are not rooted in substrate, Moyle (1945) believed their relationship is to organic substrates. The "alkali" association is poorly represented in the state. Over a broader geographic range a vegetation exists at high carbonate and sulfate levels that is only infrequently found in Wisconsin.

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