



7-30-2002

A classification of aquatic plant communities within the Northern Rocky Mountains

John R. Pierce
Missoula, Montana

Mark E. Jensen
USDA Forest Service, Northern Region, Missoula, Montana

Follow this and additional works at: <https://scholarsarchive.byu.edu/wnan>

Recommended Citation

Pierce, John R. and Jensen, Mark E. (2002) "A classification of aquatic plant communities within the Northern Rocky Mountains," *Western North American Naturalist*: Vol. 62 : No. 3 , Article 1.
Available at: <https://scholarsarchive.byu.edu/wnan/vol62/iss3/1>

This Article is brought to you for free and open access by the Western North American Naturalist Publications at BYU ScholarsArchive. It has been accepted for inclusion in Western North American Naturalist by an authorized editor of BYU ScholarsArchive. For more information, please contact scholarsarchive@byu.edu, ellen_amatangelo@byu.edu.

A CLASSIFICATION OF AQUATIC PLANT COMMUNITIES WITHIN THE NORTHERN ROCKY MOUNTAINS

John R. Pierce¹ and Mark E. Jensen²

ABSTRACT.—A synecological study of aquatic macrophyte plant communities was conducted across northern Idaho and western Montana during the summers of 1997, 1998, and 1999. A total of 111 natural and man-made water bodies were sampled based on a stratification of environmental variables thought to influence plant species distribution (i.e., elevation, landform, geology, and water body size). Plant species foliar cover data were used to develop a hierarchical, floristic-based community type classification with TWINSPAN and DECORANA software. Six planmergent (conspicuous portion of vegetative plant body on the water surface) and 24 submergent (vegetative plant body found primarily underwater) community types were identified. Multivariate analysis indicated that all community types displayed significant differences in plant species composition, and the Sorenson's floristic similarity between communities averaged 10% for planmergent and 8% for submergent types. Canonical correspondence analysis was used to inspect relationships between abiotic factors and plant species abundance. Results of this analysis indicated some relationships between species distributions and abiotic factors; however, chance introduction of plant species to water bodies is a process considered to be equally important to the presence of the community types described.

Key words: aquatic plant communities, aquatic macrophyte vegetation, ecological classification, synecological study, vegetation classification.

Aquatic plant communities are widely distributed throughout the Northern Rockies, occurring in both natural and man-made water bodies of glaciated landscapes such as lakes, ponds, reservoirs, and low-velocity streams. The ecological value of these communities is twofold. First, they enhance a variety of processes in aquatic ecosystems such as oxygen production, substrate stabilization, nutrient cycling, improved water quality, and phytoplankton reduction (Nichols 1986, Scheffer 1998, Jurgens and Jeppeson 1997). Additionally, these communities provide habitat for aquatic fauna, nesting sites for waterfowl, and forage for large ungulates such as moose (Scheffer 1998, Lodge et al. 1997, Nichols 1986, Fraser et al. 1982).

Despite the importance of aquatic plant communities to ecosystem function and species habitat, they have received relatively little attention in the scientific literature. To date most research concerning mesic plant communities within the Northern Rockies has focused primarily on wetland and riparian types (Hansen et al. 1995); however, no classification system exists for aquatic plant communities. Even for the western United States, work on

aquatic plant community classification has been largely descriptive, with little supporting field data (Schuyler 1984, Sawyer and Keeler-Wolf 1995). The primary objective of this paper is to provide a quantitative classification of aquatic macrophyte plant communities for the United States portion of the Northern Rockies. The classification scheme presented is hierarchical and designed to nest within the national wetland and deep-water habitat system first proposed by Cowardin et al. (1979) and later modified for the Northern Rockies by Rabe and Chadde (1994). Specifically, our aquatic plant community classification describes important types at the subclass and dominant levels of these previous classification schemes. Our classification provides a much needed tool for future land management activities within lacustrine and riverine systems.

METHODS

Study Sites

We sampled 111 water bodies or sites across northern Idaho and western Montana during the summers of 1997, 1998, and 1999 (Fig. 1). Site selection was based on “subjective sampling

¹737 Locust, Missoula, MT 59802.

²USDA Forest Service, Northern Region, Missoula, MT 59807. Corresponding author.

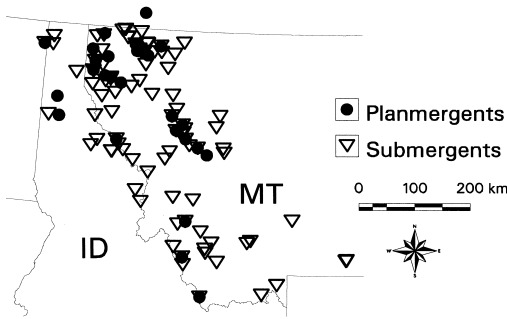


Fig. 1. Location of sampled water bodies used in developing a classification of aquatic plant communities for the Northern Rocky Mountains.

without preconceived bias” as described by Mueller-Dombois and Ellenberg (1974). Our objective was to describe representative aquatic plant communities for the study area. Accordingly, we stratified our sample to ensure that we characterized the following environmental factors that might influence species distributions: elevation (sites ranged from 628 to 2667 m), landform (valley bottoms to cirque basins), geology, and water body size. Six water bodies with less than 3-m visibility were visited but not sampled because we felt that the chance of missing a plant species or misreading associated measurements was too great in such situations.

Field Data

Sampling at each site was conducted along a water depth gradient that began where shoreline terrestrial vegetation ended and proceeded to a depth where aquatic plant species disappeared and the substrate was unvegetated. Sampling of the aquatic plant communities present along these transects was made within a 405-m² macroplot following ECO-DATA vegetation sampling procedures routinely used by the USDA Forest Service, Northern Region (USDA, Forest Service 1992). We sampled 169 macroplots in the 111 water bodies studied. The number of macroplots sampled along each water body transect ranged from 1 to 3, depending on the number of communities present at different depths. SCUBA equipment was used extensively in field sampling.

Vegetation information collected at each macroplot included a complete list of all macrophyte plants present, as well as their average height and foliar cover. Taxonomies used

in the identification of vascular plant species included Fassett (1940), Hitchcock and Cronquist (1973), Dorn (1984), Borman et al. (1997), and Douglas et al. (1994), in decreasing order of usage. We identified mosses and algae by the taxonomies of Lawton (1971) and Prescott (1978), respectively. Macrophyte plants were defined in this study as all vascular and moss species, as well as 2 genera of algae (i.e., *Chara* spp. and *Nitella* spp.). Voucher specimens were collected for each plant species within a macroplot with representative samples of each species deposited at the MRC in Missoula, MT.

Abiotic information collected at each macroplot included elevation; minimum and maximum water depth; water temperature, pH, and conductivity within 15 cm of the substrate bottom; and total nitrogen, organic carbon, and available phosphorus (USDA NRCS 1996) within a 15-cm-deep surface core of the water body substrate.

Data Analysis

In a previous hierarchical classification of aquatic plant communities, Schuyler (1984) identified 3 life form groupings: pleustophytes (free floating plants such as *Lemna* sp.), emergents (terrestrial wetland communities), and benthophytes (plants with their basal portion in or on the water body substrate). Of these life forms, we sampled only benthophytes in this study. Schuyler further broke down benthophytes into 2 growth form types or associations: submergents (vegetative plant body parts found primarily underwater) and planmergents (conspicuous portion of vegetative plant body on the water surface). In our classification we first split sample data into submergent and planmergent groupings. For each grouping we then analyzed data concerning macroplot species presence and abundance using TWINSPAN and DECORANA software (Hill 1979a, 1979b).

Two-Way INDicator SPecies ANalysis (TWINSPAN) was used to develop initial aquatic plant community classifications for the macroplots based on species lists and associated foliar cover values. TWINSPAN is a polythetic, divisive, hierarchical classification technique similar to the Braun-Blanquet classification method that emphasizes indicator species and the production of an arranged species-sample data matrix (Gauch 1982). Macroplots

were tentatively assigned to a community type based on their TWINSpan cluster assignment. Each macroplot was then inspected to see if it contained abundances of indicator plant species similar to those of other samples in its assigned community type. Macroplots displaying low similarity to other samples in their community type were reassigned to a different community type when appropriate. Detrended Correspondence Analysis (DECORANA; Hill and Gauch 1980), which produces a complementary ordination of species and samples to TWINSpan, was also used in the identification of sample outliers and final community type classification.

We used the multivariate statistical analysis program of SPSS (Norusis 1985) to detect floristic differences between community types and to identify indicator plant species for the classification. A Sorenson floristic similarity coefficient (Gauch 1982) was calculated between each community type to determine the number and abundance of plant species in common. Relationships between abiotic factors and plant species composition of macroplots were described using canonical correspondence analysis (CCA; ter Braak and Prentice 1988). CCA selected the linear combination of abiotic factors that best explained sample-species variability along 4 ordination axes. Significance of the regression between species and abiotic data was tested against the possibility of random association by comparing the *F*-ratio with 99 unrestricted Monte Carlo permutations of sampled data. Abiotic data were standardized to have a mean of zero and unit variance, and CCA species scores reflected weighted mean sample scores in this analysis.

RESULTS

Community Type Classification

We identified 24 submergent and 6 planmergent community types in this study (Table 1) using TWINSpan and DECORANA software (Hill 1979a, 1979b). This software, however, does not indicate whether such community types differ significantly in their vegetation composition. In testing the hypothesis that our plant communities differed in vegetation composition, we utilized 2 analysis procedures: multivariate analysis of species abundance (MANOVA) and percent similarity based

on species richness and abundance using Sorenson's similarity coefficient. Results of our MANOVA analysis indicated that all plant communities within the submergent and planmergent growth form groupings differed significantly from each other in average vegetation composition, as interpreted at a 95% confidence level. Additionally, these communities displayed low floristic Sorenson similarity scores, ranging from 0% to 37% (with an average of 10%) within planmergent community types, and 0% to 48% (with an average of 8%) within submergent community types. Given the fact that floristic similarity scores can range between 0% (no species in common) and 100% (all species and their abundance the same), we conclude that our classification of aquatic plant communities was effective in describing types with different floristic characteristics. A complete description of plant species constancy and cover, as well as floristic similarity, is available for our aquatic community types from the senior author.

A variety of plant species were effective in discriminating between the planmergent and submergent community types identified in this study. The plant species presented in our key to aquatic community types (Table 1) were also the primary indicator species of the TWINSpan and MANOVA analyses. These results suggest that forb species tend to have greater significance than graminoid, moss, or algal species in determining plant community types.

We used a foliar canopy cover of 10% or greater in our key to aquatic plant communities (Table 1) because this cover level was optimum in separating overall floristic differences between most of the community types studied. Canopy cover levels of 5%–20% have commonly been used in other classification keys for riparian and wetland communities (Youngblood et al. 1985, Hansen et al. 1995); accordingly, we felt that the 10% cover level used in this study was appropriate given previous research efforts. However, when using the key presented in Table 1, a person should first establish a visual depth transect to determine the number of plant communities present and their representative locals within a water body based on total species composition and abundance criteria. If this is not done, a community may be misidentified. For example, *Potamogeton praelongus* is primarily a deep-water

TABLE 1. Key to the 30 aquatic benthophyte plant communities identified in this study. (In using this key, observe the following procedure: If the majority of the photosynthetic biomass is at the water surface, select the first community type with 10% or more cover of the indicator species listed under the planmergent community types. If the majority of the photosynthetic biomass is below the water surface, select the first community type with 10% or more cover of the indicator species listed under the submergent community types.)

Code	Community type name	Sample size	Indicator species foliar cover	
			Average	Range
Planmergent				
NUPLUT	<i>Nuphar lutea</i>	20	31	10–60
BRASCH	<i>Brasenia schrebrii</i>	3	20	10–30
POLAMP	<i>Polygonum amphibium</i>	3	40	10–60
SPAANG	<i>Sparganium angustifolium</i>	2	15	10–20
POTNAT	<i>Potamogeton natans</i>	6	13	10–20
NYMODO	<i>Nymphaea odorata</i>	1	90	—
Submergent				
SCISUB	<i>Scirpus subterminalis</i>	4	33	10–70
POTPRA	<i>Potamogeton praelongus</i>	13	44	10–90
POTAMP	<i>Potamogeton amplifolius</i>	12	40	10–80
HIPVUL	<i>Hippuris vulgaris</i>	3	50	20–70
POTRIC	<i>Potamogeton richardsonii</i>	15	19	10–60
POTPEC	<i>Potamogeton pectinatus</i>	4	70	50–90
POTPUS	<i>Potamogeton pusillus</i>	11	35	10–90
POTFIL	<i>Potamogeton filiformis</i>	6	30	10–80
POTGRA	<i>Potamogeton gramineus</i>	1	20	—
POTFOL	<i>Potamogeton foliosus</i>	1	40	—
POTEPI	<i>Potamogeton epihydrus</i>	5	16	10–30
POTALP	<i>Potamogeton alpinus</i>	5	16	10–20
POTROB	<i>Potamogeton robbinsii</i>	5	42	10–90
POTCRI	<i>Potamogeton crispus</i>	2	75	60–90
ELEACI	<i>Eleocharis acicularis</i>	2	50	40–60
ISOBOL	<i>Isoetes bolanderi</i>	9	36	10–50
ELOCAN	<i>Elodea canadensis</i>	7	37	10–90
ELONUT	<i>Elodea nuttallii</i>	2	35	20–50
NITELL	<i>Nitella</i> spp.	5	36	20–60
CHARA	<i>Chara</i> spp.	18	69	10–90
HETDUB	<i>Heteranthera dubia</i>	1	20	—
RANAQU	<i>Ranunculus aquatilis</i>	1	20	—
MYRIOP	<i>Myriophyllum</i> spp.	1	10	—
DREEXA	<i>Drepanocladus exannulatus</i>	2	50	10–90

species; however, it sometimes can be found in shallow water with enough coverage to be keyed in Table 1, despite the fact that it may be found with much higher abundance at greater depths within the same water body. Ideally, a person should use both the key presented in Table 1 and the constancy/cover tables developed in this study in identifying different aquatic plant communities present within a given water body.

Canonical Correspondence Analysis

Results of our stepwise regression analysis indicated that different abiotic variables assumed different importance in explaining the cumulative amount of species-environmental variability within macroplot samples

from both the submergent and planmergent community types (Table 2). The abiotic variables listed in Table 2 accounted for 8% and 20% of the species-sample variability in our CCA analysis of submergent and planmergent community types, respectively. The species-environment relationship was significantly different from random for all 4 CCA axes ($P = 0.01$), accounting for 73% of all explained variation within submergent plant communities, and 77% of all variation within planmergent plant communities.

Ordination of species and environmental data along the first 2 CCA axes demonstrates different gradients between submergent and planmergent communities. For submergent community types, the 1st CCA axis was most significantly related to water conductivity

TABLE 2. Cumulative amount of total species—environmental variability accounted for by different abiotic variables based on a stepwise regression analysis.

Planmergent communities		Submergent communities	
Variable	Cumulative variance explained (%)	Variable	Cumulative variance explained (%)
Water-pH	17	Water-Conductivity	20
Sediment-Phosphorus	29	Sediment-Carbon	36
Water-Conductivity	40	Elevation	50
Sediment-Carbon	53	Water-Average depth	63
Sediment-Nitrogen	65	Water-pH	74
Elevation	76	Sediment-Nitrogen	85
Water-Max depth	89	Water-Max depth	91
Water-Average depth	100	Water-Min depth	96
		Sediment-Phosphorus	100

(interser correlation = 0.57) and elevation (interser correlation = -0.55). The 2nd CCA axis was primarily related to average water depth (interser correlation = 0.43). The 1st CCA axis for planmergent communities, however, was most strongly related to average water depth (interser correlation = 0.24) and elevation (interser correlation = -0.41). The 2nd CCA axis primarily described a water chemistry gradient of phosphorus (interser correlation = -0.64) and conductivity (interser correlation = -0.62). Descriptive statistics for selected abiotic and biotic variables are presented by community type in Tables 3 and 4.

DISCUSSION

Our classification of aquatic plant communities provides the first quantitative characterization of aquatic plant communities within the Northern Rocky Mountains. We used a floristic-based method for community type classification in this study. Ideally, we would have preferred to develop a site-potential classification for aquatic communities based on an understanding of seral community relations and indicator species associated with "climax" plant communities. Such classification schemes are important to land managers and have been widely used in the characterization of forest habitat types (Daubenmire 1952, 1968, Pfister et al. 1977) and rangeland sites (Hironaka et al. 1983, Mueggler and Stewart 1980, RISC 1983). We were unable to develop a site potential-based classification in this study simply because we do not understand the seral relations between the plant communities described. Accordingly, we thought it important to first describe communities according to floristic

similarities without undue concern regarding successional status. This approach resulted in a floristic-based classification of communities, which has been shown to approximate site potential-based classifications of habitat types in other research (Komarkova 1983, Jensen et al. 1988).

A factor that complicates seral plant community description in aquatic systems relates to concepts of island biology. Island biology as described by MacArthur and Wilson (1967) and Lomolino et al. (1989) states that the presence or absence of a species in an isolated environment or "island" is primarily a function of chance introduction, establishment, loss, and reintroduction. In our opinion, each of the water bodies in our study is an island. Accordingly, the aquatic macrophyte plants described are primarily dependent on birds, mammals, boats, and trailers for dispersal from one water body to another, unless they are downstream of another source area. Because of this, chance appears to play a major role in determining species presence or absence across our samples. Despite this fact, we were still able to discern general trends across the community types.

Planmergent communities were primarily restricted to ponds, small lakes, and sheltered bays of larger lakes. These communities have little tolerance for wave action and boat traffic and tend to be absent in areas of heavy recreational use. The POTNAT community type (ct) is considered to be the most resistant planmergent community to these types of disturbance. The POLAMP ct is unique in that it was always found in recently disturbed aquatic environments or in ones with naturally fluctuating water levels. The NUPLUT ct, the most

TABLE 3. Average values for selected abiotic attributes by planmergent and submergent community types.

Community types	Sample size	Elev. (m)	Slope (%)	Water depth (cm)		Water pH	Water conductivity ($\mu\text{S}/\text{cm}$)	Organic carbon (%)	N (%)	P (ppm)
				Min.	Max.					
Planmergent										
BRASCH	3	831	2	51.8	161.5	6.7	47	10.6	1.0	0.8
NUPLUT	20	1140	6	56.4	163.1	7.2	176	21.5	1.6	1.6
NYMODO	1	701	5	91.4	243.8	8.0	210	—	—	—
POLAMP	3	1449	5	51.8	143.3	7.3	240	14.9	1.3	1.7
POTNAT	6	1300	3	36.6	137.2	7.7	188	17.9	1.2	2.1
SPAANG	2	1710	11	45.7	91.4	7.5	35	12.1	1.0	0.4
Submergent										
CHARA	18	1316	15	207.3	484.6	7.8	279	10.8	1.1	0.9
DREXA	2	1908	80	152.4	457.2	7.7	10	8.5	0.8	2.7
ELEACI	2	1978	5	30.5	106.7	7.6	30	27.0	1.2	1.9
ELOCAN	7	1093	23	125	368.8	7.8	170	2.8	0.4	0.8
EIONUT	2	2030	1	106.7	320	7.4	60	—	—	—
HETDUB	1	1021	30	30.5	274.3	7.6	210	8.6	0.7	1.1
HIPVUL	3	1104	2	70.1	131.1	7.8	180	2.9	0.5	2.7
ISOBOL	9	1988	8	57.9	277.4	7.5	29	8.4	0.8	0.5
MYRIOP	1	1943	0	30.5	91.4	7.1	10	—	—	—
NITELL	5	1692	26	335.3	719.3	7.4	56	10.8	1.3	0.5
POTALP	5	1904	7	91.4	213.4	7.7	60	13.8	1.2	0.2
POTAMP	12	1275	28	118.9	347.5	7.3	99	13.2	1.0	0.7
POTCRI	2	1361	5	167.6	426.7	7.6	180	—	—	—
POTEPI	5	1866	7	121.9	243.8	7.4	16	20.0	1.8	0.2
POTFIL	6	1731	19	40.5	208.2	7.3	163	11.2	0.9	0.6
POTFOL	1	768	0	91.4	243.8	8.0	530	43.2	3.2	2.0
POTGRA	1	1113	150	61	426.7	8.0	370	4.1	0.3	0.6
POTPEC	4	1301	1	45.7	128	8.0	515	10.4	1.2	0.5
POTPRA	13	1371	12	256	502.9	7.5	148	10.9	1.0	0.6
POTPUS	11	1561	4	149.4	283.5	7.5	86	11.4	1.1	0.3
POTRIC	14	1355	12	91.4	265.2	7.6	153	3.8	0.4	1.5
POTROB	5	1234	14	256	554.7	7.1	80	8.7	0.9	2.3
RANAQU	1	1615	20	213.4	426.7	7.6	140	—	—	—
SCISUB	4	1041	3	91.4	198.1	7.8	382	12.4	1.1	1.6

widely observed planmergent community across the study area, occupied sites with relatively high organic carbon values (Table 3).

Across the submergent communities, we found that POTPRA and POTROB ct's consistently occupied the deepest substrate zones. CHARA and NITELL ct's (which are algal communities) were sometimes observed at deeper depths; however, they were just as commonly found in shallow depth environments (Table 3). NITELL and POTEPI ct's were found in water with a conductivity $<100 \mu\text{S}/\text{cm}$, while the CHARA ct was found where conductivity was $>100 \mu\text{S}/\text{cm}$. Plant communities most likely to be found in moving water were HIPVUL, POTPEC, and POTRIC.

From our transect data we found that macrophyte plant species diversity generally decreased with increasing depth. This same trend also occurred as elevation of water bodies increased. Segal (1971) also made similar

observations in his study of aquatic macrophytes, concluding that species diversity and community diversity decrease as the environment becomes more extreme. Our transect data also indicated that plant community diversity was often maximized within areas of water inflow into lakes and ponds. Additionally, the position of the thermocline was important to the zonation of aquatic communities, with most types stopping at this zone or experiencing an abrupt change in community composition.

Only 2 plant communities were named after nonnative species in this study. *Nymphaea odorata* is from North America; however, its native range is east of our study area (Fasset 1940). Usually when this species is found, its floating leaf canopy coverage is commonly so high that light is severely diminished beneath its canopy. Consequently, species diversity and abundance are greatly reduced when the NYMODO ct is present. The other nonnative

TABLE 4. Average values for selected vegetation attributes by planmergent and submergent community types.

Community types	Spp. richness	Community height (cm)	Foliar cover (%)				
			Graminoids	Forbs	Ferns	Moss	Algae
Planmergent							
BRASCH	4.0	—	13	33	0	0	27
NUPLUT	7.0	—	1	36	0	1	11
NYMODO	5.0	—	1	90	0	0	0
POLAMP	6.0	—	0	53	0	20	30
POTNAT	5.2	—	0	30	0	0	27
SPAANG	4.0	—	2	20	2	0	0
Submergent							
CHARA	3.0	15	0	2	0	2	69
DREEXA	1.0	4	0	0	0	50	0
ELEACI	3.5	6	40	0	0	2	0
ELOCAN	4.7	45	0	10	0	0	6
EIONUT	1.0	100	0	35	0	0	0
HETDUB	5.0	30	0	30	0	0	1
HIPVUL	4.0	30	0	80	0	0	0
ISOBOL	2.1	4	0	0	36	4	0
MYRIOP	1.0	10	1	10	0	0	0
NITELL	3.0	30	0	6	0	1	38
POTALP	3.0	15	16	34	0	0	18
POTAMP	3.2	100	0	44	0	0	0
POTCRI	3.5	180	0	90	0	0	0
POTEPI	3.0	20	1	22	9	12	0
POTFIL	3.4	40	4	30	0	0	16
POTFOL	5.0	60	0	60	0	0	3
POTGRA	5.0	30	0	30	0	0	60
POTPEC	2.5	60	0	70	0	0	42
POTPRA	3.0	300	0	56	0	0	8
POTPUS	5.3	70	2	55	0	1	21
POTRIC	5.5	120	1	39	0	0	15
POTROB	3.0	60	0	44	0	0	0
RANAQU	1.0	30	0	20	0	0	0
SCISUB	5.2	30	30	13	0	0	18

community we observed is named after *Potamogeton crispus*. This species was found only in reservoirs where it dominated the community type structure.

With regard to the genus *Myriophyllum*, the 2 species described were *M. verticillatum* and *M. sibiricum*. These species were rarely found in flower, making them difficult to identify. Because of this, we used only the genus name in our community type classification.

CONCLUSIONS

Our classification of aquatic plant communities within the Northern Rocky Mountains is by necessity largely descriptive. To date little, if any, attention has been given to describing synecological relations of these communities. Additionally, the autecological relations of many aquatic macrophyte plant species are also poorly understood.

Given the importance of these communities to aquatic system function and species habitat, it is imperative that more scientific studies be conducted. The sensitivity of these communities to eutrophication, boat use, altered flows, and introduced exotic species suggests that little time still remains for scientific study and maintenance of these systems. The permanent plots used in this study provide a needed baseline for future monitoring efforts. The classification developed in this study provides a useful communication tool for future land management activities within aquatic environments.

ACKNOWLEDGMENTS

Primary funding for this research was provided by the USDA Forest Service, Kootenai National Forest and the Wenatchee Forestry Sciences Lab. The authors wish to extend their

gratitude to Loren Bahls for algae identification, J. Timothy McGarvey and John Caratti for their assistance in data analysis, Jim Barber for spatial analysis, and Roland Redmond and Judy Tripp for their technical editing efforts. We also thank administrative officers of Glacier National Park for allowing us to sample within the park. Finally, the junior author wishes to acknowledge the unique efforts of John "Bog Man" Pierce in conducting the highly unusual sampling procedures involved in this work.

LITERATURE CITED

- BORMAN, S., R. FORTH, AND J. TEMTE. 1997. Through the looking glass—a field guide to aquatic plants. Wisconsin Lakes Partnership, University of Wisconsin Extension, Wisconsin Department of Natural Resources, Wisconsin Association of Lakes. 248 pp.
- COWARDIN, L.M., V. CARTER, F.C. GOLET, AND E.T. LA ROE. 1979. Classification of wetlands and deepwater habitats of the United States. Publication FWS/OBS79/31, U.S. Department of the Interior, Fish and Wildlife Service, Washington, DC. 103 pp.
- DAUBENMIRE, R. 1952. Forest vegetation of northern Idaho and adjacent Washington, and its bearing on concepts of vegetation classification. *Ecological Monographs* 22:301–330.
- _____. 1968. *Plant communities: a textbook of plant synecology*. Harper and Row, New York. 300 pp.
- DORN, R.D. 1984. *Vascular plants of Montana*. Mountain West Publishing, Cheyenne, WY. 276 pp.
- DOUGLAS, D.W., G.B. STRALEY, AND D. MEIDINGER. 1994. The vascular plants of British Columbia, part 4. *Monocotyledons*. Ministry of Forests Research Program. 257 pp.
- FASSETT, N.C. 1940. *A manual of aquatic plants*. McGraw-Hill. 382 pp.
- FRASER, D., B.K. THOMPSON, AND D. ARTHUR. 1982. Aquatic feeding by moose: seasonal variation in relation to plant chemical composition and use of mineral licks. *Canadian Journal of Zoology* 60:3121–3126.
- GAUCH, H.G. 1982. *Multivariate analysis in community ecology*. Cambridge University Press, New York.
- HANSEN, P.L., R.D. PFISTER, K. BOGGS, B.J. COOK, J. JOY, AND D.K. HINCKELY. 1995. Classification and management of Montana's riparian and wetland sites. *Miscellaneous Publication 54*. Montana Forest and Conservation Experiment Station, School of Forestry, University of Montana, Missoula. 646 pp.
- HILL, M.O. 1979a. DECORANA, a Fortran program for detrended correspondence analysis and reciprocal averaging. *Ecology and Systematics*, Cornell University, Ithaca, NY. Unpublished.
- _____. 1979b. TWINSPAN, a Fortran program for arranging multivariate data in an ordered two-way table by classification of the individuals and attributes. *Ecology and Systematics*, Cornell University, Ithaca, New York. Unpublished.
- HILL, M.D., AND H.G. GAUCH. 1980. Detrended correspondence analysis: an improved ordination technique. *Vegetatio* 42:47–58.
- HIRONAKA, M., M.A. FOSBERG, AND A.H. WINWARD. 1983. Sagebrush-grass habitat types of southern Idaho. *Bulletin 35*, University of Idaho Forest Wildlife and Range Experimental Station, Moscow. 44 pp.
- HITCHCOCK, C.L., AND A. CRONQUIST. 1973. *Flora of the Pacific Northwest*. University of Washington Press. 730 pp.
- JENSEN, M.E., L.S. PECK, AND M.V. WILSON. 1988. Vegetation characteristics of mountainous northeastern Nevada sagebrush community types. *Great Basin Naturalist* 48:403–421.
- JURGENS, K., AND E. JEPPESEN. 1997. Cascading effects on microbial food web structure in a dense macrophyte bed. Pages 262–273 in E. Jeppeson, M. Sondergaard, M. Sondergaard, and K. Christoffersen, editors, *The structuring role of submerged macrophytes in lakes*. Springer.
- KOMARKOVA, V. 1983. Comparison of habitat type classifications to some other classification methods. In: Moir and Hendzel, coordinators, *Proceedings of the workshop on southwestern habitat types*, April 1983, Albuquerque, NM.
- LAWTON, E. 1971. *Moss flora of the Pacific Northwest*. Hattore Botanical Laboratory, Nichinan, Miyazaki, Japan.
- LODGE, D.M., G. CRONIN, E. VAN DONK, AND A.J. FROELICH. 1997. Impact of herbivory on plant standing crop: comparisons among biomes, between vascular and nonvascular plants, and among freshwater herbivore taxa. Pages 149–174 in E. Jeppeson, M. Sondergaard, M. Sondergaard, and K. Christoffersen, editors, *The structuring role of submerged macrophytes in lakes*. Springer.
- LOMOLINO, M.V., J.H. BROWN, AND R. DAVIS. 1989. Island biogeography of montane forest mammals in the American Southwest. *Ecology* 70:190–194.
- MACARTHUR, R.H., AND E.O. WILSON. 1967. *The theory of island biogeography*. Princeton University Press, Princeton, NJ.
- MUEGGLER, W.F., AND W.L. STEWART. 1980. Grassland and shrubland habitat types of western Montana. *General Technical Report INT-66*, U.S. Department of Agriculture, Intermountain Forestry and Range Experimental Station, Ogden, UT. 154 pp.
- MUELLER-DOMBOIS, D., AND H. ELLENBERG. 1974. *Aims and methods of vegetation ecology*. John Wiley and Sons, New York. 547 pp.
- NICHOLS, S.A. 1986. Community manipulation for macrophyte management. Pages 245–251 in G. Redfield, J.F. Taggart, and L.M. Moore, *Lake and reservoir management. Volume II. Fifth Annual Conference and International Symposium of the North American Lake Management Society*, 13–16 November, Geneva, WI. North American Lake Management Society, Washington DC.
- NORUSIS, M.J. 1985. *Statistical package for the social sciences*. SPSS, Inc., Chicago, IL.
- PFISTER, R.D., B.L. KOVALCHIK, S.F. ARNO, AND P.C. PRESBY. 1977. *Forest habitat types of Montana. General Technical Report INT-34*, U.S. Department of Agriculture, Intermountain Forest and Range Experimental Station, Ogden, UT. 174 pp.
- PRESMOTT, G.W. 1978. *How to know the freshwater algae. The pictured key nature series*. Wm. C. Brown Company Publishers. 293 pp.

- RABE, E., AND S. CHADDE. 1994. Classification of aquatic and semiaquatic wetland natural areas in Idaho and western Montana. *Natural Areas Journal* 14:175–187.
- RISC. 1983. Guidelines and terminology for range inventories and monitoring. Report of the Range Inventory Standardization Committee. Society for Range Management, Denver, CO. 13 pp.
- SAWYER, J.O., AND T. KEELER-WOLF. 1995. A manual of California vegetation. California Native Plant Society. 471 pp.
- SCHEFFER, M. 1998. Ecology of shallow lakes. Chapman & Hall. 357 pp.
- SCHUYLER, A.E. 1984. Classification of life forms and growth forms of aquatic macrophytes. *Bartonia* 50: 8–11.
- SEGAL, S. 1971. Principles on structure, zonation and succession of aquatic macrophytes. *Hydrobiologia* 12:1–7.
- TER BRAAK, C.J., AND I.C. PRENTICE. 1988. A theory of gradient analysis. *Advances in Ecological Research*. 18:271–317.
- USDA FOREST SERVICE. 1992. Ecosystem inventory and analysis guide. U.S. Department of Agriculture, Northern Region, Missoula, MT.
- USDA NRCS. 1996. Soil survey laboratory methods manual. Soil survey investigations report 2, Version 3.0. U.S. Department of Agriculture, Natural Resources Conservation Service, Washington, DC. 693 pp.
- YOUNGBLOOD, A.P., W.G. PADGETT, AND A.H. WINWARD. 1985. Riparian community type classification of eastern Idaho–western Wyoming. R4-Ecol-85–01, U.S. Department of Agriculture, Forest Service, Intermountain Region, Ogden, UT. 120 pp.

Received 4 December 2000

Accepted 7 June 2001