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Statistical classification of vegetation and water depths in montane wetlands

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ABSTRACT

Relationships between water depths and density of submergent vegetation were studied in montane wetlands using statistical techniques based on clustering and an extension of regression trees. Sago pondweed (*Stuckenia pectinata*) was associated with lower average water depths than water milfoil (*Myriophyllum sibiricum*). We detected a nonlinear relationship when average water depths were used to predict percent cover in *S. pectinata*, with depths of 30–40 cm, producing the highest predicted average percent cover of *S. pectinata*; higher and lower depths resulted in lower percent cover predictions. For *M. sibiricum*, higher water depths were monotonically associated with higher average percent cover. To foster more *S. pectinata* and less *M. sibiricum*, managers might employ water control structures to reduce water depths below 1 m, using both temporary drawdowns and average depths of 30–40 cm. Other species responded less markedly to water depth variation. Should decreased water depths become more common, these results suggest an increase in *S. pectinata* and a decrease in *M. sibiricum*. Published in 2012. This article is a US Government work and is in the public domain in the USA.

KEY WORDS submergent plant; water depth; montane wetlands; *Stuckenia pectinata*; *Myriophyllum sibiricum*; cluster analysis; regression trees

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INTRODUCTION

Intermountain West wetlands provide important habitat for migratory birds and other wetland-dependent wildlife. Similar to wetland habitats in other regions of North America, agriculture and development have resulted in the loss of approximately 57% of Intermountain West wetlands to drainage (Ratti and Kadlec, 1992). The significance of this loss is magnified due to the region's largely arid landscape. This scenario has led to the preservation and active management of some of the Intermountain West's largest montane wetland complexes as national wildlife refuges (NWR) (e.g. Alamosa-Monte Vista NWR, Grays Lake NWR, Malheur NWR, Red Rock Lakes NWR, and Ruby Lake NWR). However, management of these habitats is hindered by the relative scarcity of information on the ecology of montane wetlands. Consequently, it is difficult to predict the response of these habitats to management actions intended to improve habitat quality for migratory birds.

The complex nature of a wetland system involves linkages among the biotic and abiotic factors that drive wetland characteristics and their spatial and temporal patterns. An understanding of montane wetland ecology should be based on several elements, including hydrology, soils, herbivory, and management activities. We agree with the broad review of Wilcox and Nichols (2008) that water level variation not only affects species diversity in wetlands, but is also a driving force for specific species. Greater understanding of montane wetland ecology would therefore improve the ability of managers to make sound, science-based decisions regarding management of these important flyway resources. Refuge management of wetland complexes can be hampered by a lack of knowledge about such ecological processes, although it is understood that hydrology is pivotal and we suspect that groundwater plays a role in many settings.

Ecological theory related to the interaction between geomorphology, hydrology, and wetland ecology in prairie pothole wetlands has been well described for emergent plants (Moyle, 1945; van der Valk, 1989; Glaser *et al.*, 1990). Plant distribution has been linked to groundwater discharge (Rosenberry *et al.*, 2000), average recharge flux (Sebestyen and Schneider, 2004), water chemistry (Glaser *et al.*, 1990; Drexler and Bedford, 2002), and type of water presence (i.e. groundwater, seasonal surface, or permanent surface water; Goslee *et al.*, 1997). Additionally, Lodge *et al.* (1989) found a positive relationship between groundwater velocity and submersed macrophyte biomass. *Stuckenia pectinata* has been shown to have

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limited coverage in areas with high water depths and insufficient light for colonization (Wersal *et al*., 2006; Case and Madsen, 2004). Hansel-Welch *et al.* (2003) identified light attenuation as 'the best single environmental variable for explaining the variance in the plant community' at their shallow lake study site in Minnesota. Madsen *et al.* (2006) also found that *S. pectinata* successfully grew in clay sediments rather than in sand and silt sediments.

Although several recent studies have been conducted on the distribution and growth of submergent vegetation, wetlands in the Northern Rocky Mountains have not been intensively studied, especially regarding submergents in high-altitude settings. First-order controls on wetland plant species distributions, groundwater–surface water interactions, and hydrodynamics remain poorly understood. Furthermore, little is known about the interactions among these factors. The broad principles elucidated from many years of intensive research in prairie marshes seem at least partially applicable to montane landscapes because some similar plant communities exist, but even in the prairies, ecological questions continue to arise (Seabloom and van der Valk, 2003). On the other hand, the concept of ecological sieves functioning in relation to hydroperiods and drought induced successional cycles (van der Valk, 1981) is likely valid in many landscapes, including montane wetlands. In our experiences, we have observed that montane wetlands are not as subject to the severe turbidity issues reviewed by Kantrud (1990) and Korschgen (1989) for prairie pothole and other wetlands in catchments dominated by agricultural production and wetland drainage. Similarly, the interaction of carp (*Cyrprinus carpio*) and turbidity as an influence to submergent persistence and growth in high elevation wetlands does not seem to be a major ecological issue (Bouffard and Hanson, 1997). As our knowledge of the multiple factors affecting the presence and vigor of submergent plants increases, we will be able to consider how individual variables interact with the life history of the plants to result in the plant communities that develop and change over time. Foremost in this study, we postulate that water depths are key for understanding the ecology of submergent plants in North American montane wetlands.

Here, we report on a study conducted within Red Rock Lakes NWR in southwest Montana, which encompasses the largest, natural wetland complex in the Northern Rockies. We explored the relationship between wetland water depths and submerged aquatic plant communities. Our basic premise was that a greater preponderance of *S. pectinata*, and less *Myriophyllum sibiricum*, would be found in the shallower habitats of the lake areas within the extensive sedge (*Carex* spp.) marsh (arbitrarily dubbed ponds) than in the open water (lake) areas of Lower Red Rock Lake proper. Keith (1961) observed that *M. sibiricum* occupied a wide range of water depths in Alberta impoundments, but *S. pectinata* preferred depths less than 0.8 m. Our hypotheses emanated from our *a priori* field observations and from the more quantitative work of Anderson (1978) who demonstrated inverse relationships between water depths and *S. pectinata* and *M. sibiricum*. *S. pectinata* has long been recognized as an important resource for wetland birds around the world, especially waterfowl (Anderson and Low, 1976; Kantrud, 1990; Earnst, 1994; Cox and Kadlec, 1995; Bolen, 2000; Sandsten *et al*., 2005; Shaltout and Al-Sodany, 2008). Waterfowl eat the leaves and turions, the latter an excellent source of protein and carbohydrates. Moreover, the fine-structured leaves of *S. pectinata* provide habitat for a higher diversity and greater biomass of aquatic invertebrates than *M. sibiricum* (Krull, 1970). Field observations of waterfowl behavior at Red Rock Lakes NWR prior to the initiation of this study led us to hypothesize that the use of *M. sibiricum* was lower relative to *S. pectinata*.

We were interested in understanding patterns of responses in submergent plant communities in relation to hydrology, especially of those plants considered by local waterfowl managers to be important waterfowl foods. Kantrud's (1990) thorough review of *S. pectinata* habitat requirements remains a standard in the field and was essential in the development of our research. During our preliminary reconnaissance, we routinely detected site-specific groundwater discharge in the wetlands and posited that discharge is a key ecological process in this wetland system. Greenwood *et al.* (2011) found differences in groups of patterns of discharge between years both in terms of long-term and higher-frequency variation, suggesting a very complicated underlying groundwater system in the area. Although relationships between hydrological patterns, soils, and vegetation will be the final target of our research, the current study focuses on linking wetland water depths observed in a network of specific stilling wells with submergent vegetation growth as one ecological process. We are not aware of work examining the nuances of hydrologic characteristics on these two plants of primary interest in montane environments. Therefore, we examined the following specific questions:

1. What are the principal patterns in the responses of vegetation species and water depths across sites and years?
2. Is the variation in the canopy cover of *S. pectinata (*Sago pondweed) related to annual average water depths?
3. Is the variation in the canopy cover of *M. sibiricum* (water milfoil) related to annual average water depths?

From 2003 through 2005, we focused on comparing 32 randomly selected wetland sites; 16 were ponds and 16 were lake areas. Hydrologic data were collected using stilling wells. Wetland plant data were collected from visual observation. We have chosen to use statistical techniques based on clustering methodology and an extension of regression trees (Breiman *et al*., 1984; Sela and Simonoff, 2011) because we did not have *a priori* quantitative information on the multivariate relationships that may exist among the parameters.

STUDY AREA

In Southwestern Montana, USA, Red Rock Lakes NWR is part of a high mountain valley, known as the Centennial

Valley. The wetland hydrologic data that we collected are in the valley bottom at an elevation of approximately 2014 m. The most outstanding ecological feature of this wetland complex is its size, extending over 10 000 ha and including Upper and Lower Red Rock Lakes and Swan Lake. Several types of wetlands exist in the complex, with permanent and semipermanent lacustrine aquatic beds and semipermanent and seasonal palustrine emergent wetlands being the most prominent. Much of the Red Rock Lakes NWR is a federally designated wilderness with limited access; so detailed climatic, hydrologic, and soil data are rare.

The Centennial Valley has a continental climate with cold summers and a short growing season (National Oceanic and Atmospheric Administration Western Regional Climate Center, 2005, station no. 244820). At Lakeview (adjacent to the wetlands studied), the annual average temperature is 1.7 °C. The average maximum temperature during July is 24.8 °C, and the average minimum temperature during January is -17.8 °C. The average annual precipitation in the study area ranges from approximately 127 cm in the high country of the Centennial Mountain Range to 38 cm on the valley floor (United States Soil Conservation Service, 1977; Amend *et al.*, 1986; Montana Natural Resources Information System, 2005). Evaporation determined with a class A pan evaporation is approximately 89 cm per year (Dingman, 1994).

METHODS

Site selection

The primary ecological questions examined in this study relate to understanding differences between what we locally termed open water sites (hereafter lake plots) and palustrine pond (hereafter ponds) habitats. The latter were somewhat distinct, open water sites within a larger matrix of emergent vegetation dominated by beaked sedge (*Carex utriculata*). Under the study of Cowardin *et al.* (1979) in wetland classification system, these habitats are all aquatic beds within either lacustrine or palustrine wetlands having permanent or semipermanent water regimes. By the nature of such wetlands, water depths varied from being dry at some times in most ponds to nearly 2 m at a few lacustrine sites. Sixteen study sites were selected within each of the two habitat types (lakes and ponds). The sites were selected to present similar opportunities for waterfowl to utilize the sites from a vertical and horizontal habitat structure perspective. Components of surface and groundwater hydrology (e.g., surface water depth, vertical groundwater gradients, water chemistry, etc.) were considered part of the suite of underlying independent variables and were not used as criteria for selecting locations.

To sample ponds, we began by selecting palustrine emergent semipermanent wetlands (PEMF) from the National Wetland Inventory (U. S. Fish and Wildlife Service, 2004) that met three criteria: (1) Ponds had to be at least 2500 m^2 in area; (2) They could not be contiguous with the open water area of Lower Red Rock Lake, itself; and (3) They must be at least 200 m apart. Eighty-five ponds met these criteria, and 16 were randomly chosen for study. We similarly selected lake sites within the open water habitat of Lower Red Rock Lake. The main distinction between lake and pond sites was size of open water area, and in fact, sites were chosen to be as similar in all other aspects as possible. We used previously established random points (Paullin, 1973) within the large, lacustrine portion of the complex. Plots (50 m × 50 m) were established using these random points as the northeast corner of each plot so that they (1) did not include emergent vegetation and (2) were at least 200 m apart from each other. Thirty-four lake plots met these criteria, and 16 were randomly selected (Figure 1).

Hydrology

Piezometers made of 3.8-cm diameter plastic pipe were placed at the northeast corner of each of the plots as part of a larger project. The pipes functioned in this study either as reference points from which to manually make repeated water depth measurements or, stilling wells mounted directly on the outside of the piezometer pipe. When stilling wells were present, temperature compensating capacitance rods with integrated digital data loggers were utilized to automatically record water levels. Manual measurements were taken periodically to correct for instrument drift.

Vegetation

Vegetation surveys were conducted once annually in late summer on each of the study sites to quantify composition by canopy cover of submerged aquatic vegetation. Each 2500 m^2 lake plot was divided into 25 10 m × 10 m quadrats, creating a 5 × 5 grid of quadrats. The quadrats were then surveyed from a canoe with each transect bisecting lengthwise a group of five quadrats aligned linearly north to south. We began by surveying all 25 quadrats, which was found to be too time intensive. Therefore, we eliminated two transects and surveyed the first, third, and fifth north–south transects for the remaining 15 plots. For each quadrat, Braun-Blanquet cover classes (Mueller-Dombois and

Figure 1. Red Rock Lakes study area map with lake (circle) and pond (triangle) sites.

Ellenberg, 1974) were used to estimate the percent canopy cover for each submergent species present. Because of the differences in the area and shape of ponds, vegetation characterization differed slightly between plots and ponds. Foot surveys across small ponds were conducted and cover classes were assigned. However, for larger ponds, where this was not logistically feasible, 10 m × 10 m quadrats were sampled along transects. Two transects per pond were surveyed, with the first beginning at the piezometer and progressing in the cardinal direction that paralleled the long axis of the pond. The second transect was then placed so as to run parallel to, but not overlap, the first and to allow the greatest number of quadrats. The average percent cover of the species was used in the analyses.

Statistical methods

Three separate cluster analyses were performed for the 32 sites across the 3 years (2003–2005). The three analyses were conducted for exploratory purposes with different groups of the vegetation species so as to consider the relationships among the rare and more prominent species. The *k*-means algorithm in a statistical package called R was used for all cluster analyses (R Development Core Team, 2010). The *k*-means algorithm begins with arbitrary cluster centers and partitions the data so that the within-cluster sum of squares of individuals to their closest cluster is minimized (Manly, 2005). A cluster analysis was performed for

1. The average water depth, average percent coverage of *S. pectinata*, *Chara vulgaris*, *Ranunculus subrigidus* and *M. sibiricum*. These species were those of primary interest to local waterfowl managers. The first three were considered of highest value, and the latter's presence was thought to be opposed to the first one.
2. The average water depth, average percent cover of *S. pectinata*, *C. vulgaris*, *M. sibiricum*, and *R. subrigidus*, the average percent cover for all of the pondweeds except *S. pectinata*, and the sum of the average percent cover of all of the *Potamogetons* and *Stuckenias*. The pondweeds comprise three genera in this ecosystem: *Potamogeton*, *Stuckenia*, and *Zannichellia*, with the latter not common. We wished to know if any taxonomically similar species to *S. pectinata* might have similar water depth niches to it and be responding similarly as part of these plant communities.
3. The average water depth, the average percent cover of *S. pectinata*, *M. sibiricum*, and *R. subrigidus*, and the average percent cover for all of the *Potamogetons* except *S. pectinata*. This analysis was similar to the second one, but we wished to limit it to a smaller suite of species of interest (those thought to be the most prominent and important waterfowl vegetative foods) to simplify the interpretation of the results of the analyses.

The pondweeds considered in the analyses are *S. filliformis*, *S. pectinata*, *S. vaginata*, *Potamogeton friesii*, *P. foliosis*, *P. praelongus*, *P. richardsonii*, and *P. zosteriformis*. The groupings of the average percent cover for all the pondweeds except *S. pectinata* and the sum of the average percent cover for all the *Potamogetons* and *Stuckenias* were chosen on the basis of what is locally thought to be the plants' value to waterfowl along with postulated life history responses to water conditions. Four observations were excluded from each cluster analysis because certain ponds were dry during the survey period (three in 2003 and one in 2005), and therefore, submergents were absent.

In each of the three cluster analyses, the within sums of squares was optimally minimized using three groups. However, because there are groupings of sites, two clusters were used to explore the patterns in the two primary groups of observations and whether these groups are related to the distinction of the sites (i.e. lake or pond) habitats. Because of the exploratory nature of this research, no integrity of the study was lost by selecting two clusters versus three clusters.

Regression trees are an attractive method for predicting the effect of water depth on the average percent cover; however, they fail to account for systematic differences between sites and years, attributing effects to variation in water depth that may actually be due to site and year effects. Sela and Simonoff (2011) developed an extension of regression trees for longitudinal data or repeated measurements over time called RE-EM trees. This methodology was used to predict each of the average percent cover of *S. pectinata* and *M. sibiricum* using water depth as the predictor across the 3 years (2003–2005), while accounting for site and year effects. Regression trees are nonparametric models based on estimated, recursive binary splits of the data set using the explanatory variable (s) to optimally predict a quantitative response variable. Regression trees allow for threshold and nonlinear effects. RE-EM trees not only contain a typical predictive tree model but also incorporate random effects to adjust the tree for systematic variation that may exist on the basis of the design of the study. These models are estimated using a modification of the R package RE-EM tree (Sela and Simonoff, 2009) to estimate mixed models with crossed random effects using a package in R (lme4) to fit linear mixed-effects models (Bates and Maechler, 2009). These methods provide techniques for valid application of regression trees for clustered and correlated data that are generated by longitudinal or spatial-temporal designs.

The model for an observation of site i ($i = 1, \ldots, 32$) in year j ($j = 1,2,3$) is $PercentCover_{ij} = \alpha + f(Depth_{ij}) + \gamma_i + \eta_j + \varepsilon_{ij}$, where α is the intercept, $f(Depth_{ij})$ is the regression tree component of the model based on water depth, $\gamma_i \sim N(0, \sigma_\gamma^2)$ is the random site effect, $\eta_j \sim N(0, \sigma_\eta^2)$ is the random year effect, and $\varepsilon_{ij} \sim N(0, \sigma_\varepsilon^2)$ is the residual random error. This model adjusts the trees that are based on water depth, the fixed effect, to account for systematic differences between the sites and between the years, inducing correlation within site across years and within year across sites. The resulting trees then explain the variation in percent cover on the basis of variation in water depth around the mean for each site and year. Both trees were cross-validated, pruning the tree to the size of the simplest tree within one standard error of the tree with the minimum cross-validation score. The cross-validation process was repeated, and the most frequently selected tree size is reported.

RESULTS

The first cluster analysis considered variables for the average water depth, average percent coverage of *S. pectinata*, *C. vulgaris*, *M. sibiricum*, and *R. subrigidus*. The two clusters are summarized in Table 1. The first cluster contained only lake observations across the 3 years. The second cluster has nine lake and 44 pond sites across the 3 years. The nine lake observations in the second cluster had lower water depths and moderate average percent cover compared with the other lake sites. The water depth and the average percent cover for *M. sibiricum* is higher in the first cluster than in the second cluster. The average percent cover for both *S. pectinata* and *R. subrigidus* is higher in the second cluster than in the first.

The second cluster analysis was conducted with the variables average water depth, average percent cover of *S. pectinata*, *C. vulgaris*, *M. sibiricum*, and *R. subrigidus*, the average percent cover for all *Potamogeton spp*.(labeled *P*. other), and the sum of the average percent cover of all *Potamogeton spp*. and all *Stuckenia spp*. (labeled *P*. all). The two clusters obtained from this analysis are summarized in Table 2. Forty-three lake observations made up the first cluster. Five lake observations and 44 pond observations made up the second cluster. The first cluster contains sites with larger water depths, small average percent cover for *S. pectinata*, and large average percent cover for *M. sibiricum*. The second cluster has smaller water depths than the first cluster, large average percent cover for *S. pectinata*, and small average percent cover for *M. sibiricum*. The first cluster has the smallest average percent cover for *C. vulgaris*, *R. subrigidus*, and the average percent cover of all of the *Potamogetons* and *Stuckenias* (*P*. all) are smaller than the second cluster. The average percent cover for all *Potamogetons* and *Stuckenias* except *S. pectinata* (*P*. other) is smaller for the first cluster than the second cluster.

The final cluster analysis included variables for the average water depth, the average percent cover of *S. pectinata*, *M. sibiricum*, *R. subrigidus*, and the average percent cover for all *Potamogeton spp*.(labeled *P*. other) across the years 2003–2005. The numbers of observations and averages for each variable are presented in Table 3. The first cluster contains lake observations (39) and no pond values, whereas the second cluster contains all of the measured pond observations (44) and nine lake measurements. The first cluster contains sites with high water depths and greater percent average cover of *M. sibiricum* and *P*. other than the second cluster. The second cluster contains sites with lower water depths and greater *S. pectinata* and *R. subrigidus* than the first cluster.

In contrasting the three cluster analyses, we see that the differences between observations are mainly related to whether the sites are ponds or lakes, with distinct water depths and vegetation patterns associated with each type of site. For the assessment of the impacts of differences in the

Table I. Cluster results from cluster analysis for water depth, *S. pectinata*, *C. vulgaris*, *M. sibiricum*, and *R. subrigidus*.

Cluster	Number of observations	Water depth (cm)	*S. pectinata*	*C. vulgaris*	*M. sibiricum*	*R. subrigidus*
1	39	67.50 (2.6)	0.78 (0.2)	0.75 (0.3)	50.38 (2.5)	0.02 (0.01)
2	53	31.25 (2.7)	33.65 (5.1)	2.46 (0.9)	2.03 (0.8)	9.31 (3.4)

The number of sites and the averages (standard errors) of the variables across 3 years (2003–2005). Plant data are presented as percent cover.

Table II. Cluster results from cluster analysis for water depth, *S. pectinata*, *C. vulgaris*, *M. sibiricum*, *R. subrigidus*, *P*. other and *P*. all.

Cluster	Number of observations	Water depth (cm)	*S. pectinata*	*C. vulgaris*	*M. sibiricum*	*R. subrigidus*	*P*. other	*P*. all
1	43	65.30 (3.0)	0.83 (3.0)	0.68 (3.0)	47.27 (3.0)	1.23 (1.2)	9.57 (1.7)	10.39 (1.7)
2	49	30.22 (2.4)	36.30 (4.5)	2.66 (0.8)	0.81 (0.4)	9.01 (3.0)	4.26 (1.8)	40.55 (5.3)

The number of sites as well as the averages (standard errors) of the variables across 3 years (2003–2005). Plant data are presented as percent cover.

Table III. Cluster results from cluster analysis for water depth, average percent cover of each of *S. pectinata*, *M. sibiricum*, *R. subrigidus*, and average percent cover for all of the pondweeds except *S. pectinata*.

Cluster	Number of observations	Water depth (cm)	*S. pectinata*	*M. sibiricum*	*R. subrigidus*	*P*. other
1	39	67.50 (3)	0.78 (0.3)	50.3 (2.9)	0.02 (0.01)	10.46 (1.8)
2	53	31.25 (2.3)	33.65 (4.4)	2.03 (0.7)	9.31 (2.9)	4.00 (1.7)

The number of sites as well as the averages (standard errors) of the variables across 3 years (2003–2005). Plant data are presented as percent cover.

average water depth on changes in vegetation, methods that first account for the average depths of vegetation at a site are considered using the RE-EM trees. Additionally, inter-annual variation of water depth and other factors may need to be considered and accounted for in modeling the distributions of vegetation cover.

Regression trees adjusted to account for the spatial-temporal aspects of the responses between the $n = 32$ sites and across the 3 years (2003–2005) were used to predict the average percent cover for each of *S. pectinata* and *M. sibiricum* using water depth as a predictor. Spatial-temporal variation is accounted for by including crossed random site and year effects. The pruned tree for *S. pectinata* contained four terminal nodes. Four nodes were also found for *M. sibiricum*. The results for both trees are given in Figure 2 and Table 4, which also contain estimated standard errors for the estimated percent cover at the terminal tree nodes. Both tree models had important amounts of variability explained by the additions of random site and year effects, with the year random effect more important for the *M. sibiricum* responses than the *S. pectinata* responses (sago pondweed tree: $\hat{\sigma}_{\gamma}^2 = 485.1$, $\hat{\sigma}_{\eta}^2 = 14.4$, and $\hat{\sigma}_{\varepsilon}^2 = 171.8$; water milfoil tree: $\hat{\sigma}_{\gamma}^2 = 178.4$, $\hat{\sigma}_{\eta}^2 = 104.8$, and $\hat{\sigma}_{\varepsilon}^2 = 177.25$). This suggests that water *M. sibiricum* might be more responsive to climate differences that are not tied to water depth than *S. pectinata*, which has a minimal year random effect once the water depth effect is incorporated in the model. The tree results show that the average percent cover for *S. pectinata* is smallest with higher average water depths and that depths between 30.3 and 39.6 cm produced the highest average percent cover. The average percent cover for *M. sibiricum* is small with lower water depths and seems to increase as a monotonic function of the average water depth. As an example to read the tree, note that the lowest predicted percent cover from the tree is −5.6, which means for water depths below 14, the percent cover is 5.6% lower than the predicted average value for that combination of site and year.

DISCUSSION

These results support our hypothesized linkages between water depths and variation in species composition, and are consistent with those of Anderson (1978) for a large wetland in Manitoba. On the basis of the cluster analysis results, we see that there were differences in the lake and pond sites in both water depths and types of submergent

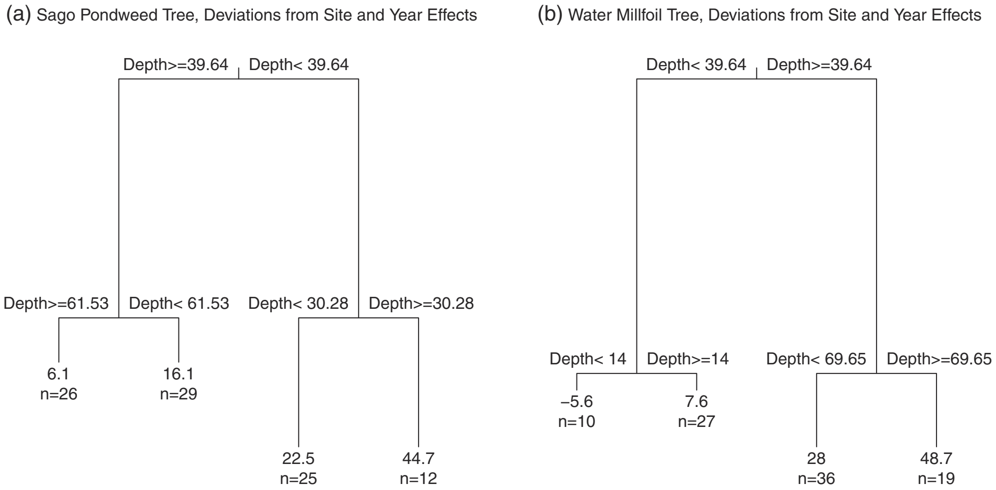

Figure 2. Estimated cross-validated regression RE-EM trees for (a) *S. pectinatus* and (b) *M. exalbescens*, adjusted for random site and year effects. For any observation, the predicted tree value can be found with the binary splits on the basis of the observed water depth for site in a particular year.

Table IV. Regression tree results from two analyses using water depth, site, and year as predictors, and using *S. pectinata* and *M. sibiricum* as the responses.

Response	Number of observations	Water depth (cm)	Predicted average percent cover
S. pectinata	26	≥61.53	6.10 (6.6)
	29	[39.64, 61.53)	16.11 (5.3)
	12	[30.28, 39.64)	44.73 (7.4)
	25	<30.28	22.50 (6.0)
M. sibiricum	10	<14	−5.62 (8.7)
	27	[14, 39.64)	7.63 (7.1)
	36	[39.64, 69.65)	28.04 (6.9)
	19	≥69.65	48.69 (7.9)

Predicted percent cover (standard error) adjusting for random site and year effects are presented.

vegetation. Except for a few observations, lake sites had greater water depths, whereas pond sites were shallower. It is clear that *S. pectinata* prefers shallower habitats than *M. sibiricum*, with the latter always more prominent in deeper water. Growing season average water depths of approximately 40 cm generally seemed to segregate *S. pectinata* from *M. sibiricum*. However, we recognize that plant life history is complex, and hasten to point out that other factors, such as the timing of particular water-depth highs or lows, also may be driving plant community composition. We recognize, for example, that low water depths are the symptom of prolonged dry conditions, which may affect wetland ecology and wetland species via means other than water depth. If so, average water depths could be a surrogate for another factor(s) related to composition and density of submergent vegetation. Similarly, the regression tree analysis indicates that the average water depths' range of 30–40 cm is ideal for *S. pectinata*. This interpretation is based on only 3 years of observations, and given the complexities of linkages between hydrologic variables and ecosystem response, such an inference would benefit from additional years of data collection. We also recognize that there may be a lag in vegetation response, which would require longer-term observations.

Pond and lake sites with lower water depths are weakly associated with higher average percent cover of *R. subrigidus*. Likewise, *C. vulgaris* was associated with lower water depths. In both these cases, however, neither plant was broadly distributed in the system at high percent coverage. Plus, *C. vulgaris* is well adapted to waters of high calcium concentrations. More controlled studies would be necessary to separate multivariate predictors. Higher average percent cover of all *Potamogeton spp*. and *Stuckenia spp*. (labeled *P*. other) appears to be associated with higher water depths, but we recognize, *post hoc*, that this group represents many plants with different life histories that likely confound the interpretation. *Potamogetons* and *Stuckenias*, as a group, did not appear to exhibit a strong preference for shallow water, as postulated.

The ecological theory of Gleasonian sieves presented by van der Valk (1981) as a way to interpret the underlying causality of species assemblages for emergents in prairie wetlands, as related to drought and deluge periods, is standing the test of time. The germination of species is known to be related to the timing of drawdown, whether due to climatological patterns or to management manipulations. We suggest that Gleasonian sieves may also be a useful conceptual model for understanding submergent communities in relation to water depth. Unfortunately, it is more difficult to demonstrate unequivocally because less is known about the life history mechanisms by which submergents react to water depth and its change.

These results were generated using exploratory cluster analysis techniques and a novel adaptation of regression trees for data collected from a complex design using crossed random effects to account for the spatial-temporal effects on the average percent cover responses. The regression tree methodology has the benefit of being able to accommodate nonlinear effects, as were detected in the *S. pectinata* tree while providing a tree that is easy to understand for examining the relationship between water depth and vegetation percent cover. Adjusting trees for correlating aspects of the study design such as was performed here may be of interest in other similar situations, expanding the range of situations where trees may be legitimately considered.

CONCLUSIONS

If managers of montane wetlands in the Northern Rockies, similar to those we studied at Red Rock Lakes NWR, desire to have greater amounts of *S. pectinata* and lesser amounts of *M. sibiricum*, employing water control structures to lower water depths should produce that result. Managers should consider lowering water depths below 1 m, and recognize that a depth of 30–40 cm might be optimal. Water levels in semipermanent wetlands are dynamic by definition, and holding water levels constant at any one particular depth is likely counter to fostering natural wetland processes. Our qualitative observations in several of the ponds are in agreement with those of L. Fredrickson (personal communication, February, 2003) who has indicated that robust vigor, especially of turion development in *S. pectinata*, is directly related to the occurrence of low water depths the previous summer. Investigating occasional, complete drawdowns late in the growing season followed by controlled water depths of less than 40 cm should be informative to managers across the range of these plants, not only in southwest Montana.

The effect of climate change, as currently being experienced in the Northern Rocky Mountains (Pederson *et al*., 2009), on wetland water depths is equivocal due to the poorly understood relationships between climate change, groundwater discharge, and wetland water depths. Changing snow-melt phenology and soil-frost conditions also affect surface runoff to montane wetlands and complicate the response of wetland stage due to exchange with groundwater. If one makes the relatively simplistic assumption that wetland water depths will decrease under a warming climate, we would look for an increase in *S. pectinata* and a decrease in *M. sibiricum*. Because our results expand those of Anderson's (1978), especially in terms of geographic, geologic, climatologic, and ecological range, we encourage additional studies that would further our understanding of eco-physiological causality in relation to water depths, as well as more multivariate perspectives. This, then, would allow the more definitive application of Gleasonian sieves as ecological theory for predicting submergent plant communities. Ultimately, this would allow a conceptual model for applying adaptive management in relation to wetland management recommendations for waterbird habitats. Additionally, the other factors, including hydraulic gradients, water clarity, wave amplitude, fetch, soil compositions, presence and types of fish, and waterfowl use, also may be related to the distribution of wetland vegetation; the incorporation of these and other variables would contribute to the predictive power of this conceptual model. Although our study was focused in southwest Montana, we suggest that incorporating our results into a more widely applicable ecological model is appropriate and builds on the prior work of others.

We recommend the use of cluster analysis to explore relationships across different aspects of the multivariate patterns between wetland vegetation and water depths. RE-EM trees are useful for exploring specific relationships between individual response variables and sets of predictors while accounting for systematic differences that occur across locations, years, or both. These techniques provide a simple and numerically stable method for estimating models that account for spatial-temporal correlations and allow for complex relationships between a set of predictor variables and the response variable.

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