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Macrophytes in shallow lakes: relationships with water, sediment and watershed characteristics

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Abstract

We examined macrophyte-environment relationships in shallow lakes located within the Prairie Parkland and Laurentian Mixed Forest provinces of Minnesota. Environmental variables included land cover within lake watersheds, and within-lake, water and sediment characteristics. CCA indicated that sediment fraction smaller than 63 μm ($f_{<63}$), open water area, turbidity, and percent woodland and agricultural cover in watersheds were significant environmental variables explaining 36.6% of variation in macrophyte cover. When Province was added to the analysis as a spatial covariate, these environmental variables explained 30.8% of the variation in macrophyte cover. CCA also indicated that pH, $f_{<63}$, percent woodland cover in watersheds, open water area, emergent vegetation area, and organic matter content were significant environmental variables explaining 43.5% of the variation in macrophyte biomass. When Province was added to the analysis as a spatial covariate, these environmental variables explained 39.1% of the variation in macrophyte biomass. The $f_{<63}$ was the most important environmental variable explaining variation for both measures of macrophyte abundance (cover and biomass) when Province was added as a spatial covariate to the models. Percent woodland in watersheds, turbidity, open water area, and Ca+Mg explained 34.5% of the variation in macrophyte community composition. Most species showed a negative relationship with turbidity and open water area except for *Potamogeton richardsonii*, *Stuckenia pectinata*, and filamentous algae. Our study further demonstrates the extent to which macrophyte abundance and community composition are related to site- and watershed-scale variables including lake morphology, water and sediment characteristics, and percent land cover of adjacent uplands.

Keywords

aquatic macrophyte; canonical correspondence analysis; multivariate; land cover; ordination; sediment; shallow lake

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1. Introduction

Macrophyte community composition and distribution varies with climate, hydrology, substrate type, and nutrient availability (Cronk and Fennessy, 2001) and can be influenced by geology, land use, and water and sediment chemistry (Moyle, 1945; Stewart and Kantrud, 1972; Barko and Smart, 1986; Barko et al., 1991; Koch, 2001; Loughheed et al., 2001; Hansel-Welch et al., 2003; del Pozo et al., 2011). Factors influencing the growth and distribution of aquatic macrophytes have long been of interest to ecologists (Pearsall 1920; Misra 1938; Moyle, 1945; Peltier and Welch, 1970; Barko et al., 1986). Several studies have examined relationships between macrophytes and various environmental variables. Macrophyte relationships with water chemistry variables (Hunter et al., 1986; Grillas, 1990; Bini et al., 1999; Heegaard et al., 2001; Meerhoff et al., 2003; Capers et al., 2010; Akasaka and Takamura, 2011; O'Hare et al., 2012) and surrounding land use have been studied in various aquatic ecosystems (Crosbie and Chow-Fraser, 1999; Loughheed et al., 2001; del Pozo et al., 2011; Akasaka et al. 2010; Sass et al., 2010; Alahuhta et al. 2012). Water transparency, nutrient concentrations, and land use were found to play a role in macrophyte distribution and abundance (Bini et al., 1999; Akasaka et al., 2010; Alahuhta et al., 2012). Physical and chemical characteristics of sediments also play a major role in macrophyte distribution (Misra, 1938). However, few studies have considered macrophyte relationships with sediment characteristics (Chambers and Prepas 1990; Grillas, 1990; Crosbie and Chow-Fraser 1999; Loughheed et al., 2001; Mikulyuk et al., 2011), although sediment organic matter, particle size (Chambers and Prepas, 1990; Crosbie and Chow-Fraser, 1999; Loughheed et al., 2001), and sediment texture (Mikulyuk et al., 2011) were reported to play a role in macrophyte distribution and abundance.

Studies of macrophyte-environment relationships have used various techniques to assess aquatic macrophytes and most have reported measurements of diversity, richness, frequency, and community composition (Chambers and Prepas, 1990; Crosbie and Chow-Fraser, 1999; Magee et al., 1999; Loughheed et al., 2001; Akasaka et al., 2010; Sass et al., 2010; Akasaka and Takamura, 2011; Mikulyuk et al., 2011; O'Hare et al., 2012). Some studies have also reported various measures of macrophyte abundance (Grillas, 1990; Meerhoff et al., 2003; del Pozo et al., 2011; Mikulyuk et al., 2011; Netten et al., 2011; Alahuhta et al., 2012). We considered two measures of abundance, percent cover and biomass for each species. We also considered presence/absence of species as a measure of community composition. Most studies of macrophyte-environment relationships focused on lakes which were often much deeper than the shallow lakes in our study (Heegaard et al., 2001; Capers et al., 2010; Mikulyuk et al., 2011; O'Hare et al., 2012; Alahuhta et al., 2012) while other studies chose to specifically exclude shallow lakes (Sass et al., 2010).

Our study focused on shallow lakes which are defined as lakes that do not stratify for long periods, mix frequently, have intense sediment-water interaction, and are mostly colonized by macrophytes (Scheffer, 2004; Heiskary and Wilson, 2005). Different patterns of variation in nutrients, chlorophyll-a, and transparency are known for shallow lakes compared to deeper, stratified lakes (Heiskary and Wilson, 2005) and plant communities in shallow lakes often function in ways that affect whole lake ecosystems (Scheffer 2004). For example, aquatic macrophytes are believed to exert large proximate influence over shifts between clear macrophyte- and turbid, phytoplankton-dominated regimes in shallow lakes (Scheffer and Jeppesen, 1998; Bayley et al., 2003; Zimmer et al., 2009). These shifts often occur over a short time period (within 1 year) or sometimes over several years (Bayley et al., 2007) and factors inducing these regime shifts are often unidentified. Questions about the role of macrophytes in such regime shifts led to the current study, which aims to clarify influences on plant communities in these dynamic systems.

We assessed macrophyte abundance and community composition of 38 shallow lakes of varying turbidities in two different ecological provinces in Minnesota, to determine the role of environmental variables in the variation of macrophyte abundance and community composition. We considered a unique combination of predictor variables in our study, which included watershed features (land cover within the lake watershed and lake watershed area), within-lake aspects (basin area, open water area, and emergent vegetation area), water characteristics (pH, Ca and Mg concentrations, turbidity, chlorophyll-a), and sediment characteristics (organic matter content and particle size). We hypothesized that land cover within watersheds, along with water and sediment characteristics play a role in macrophyte abundance and community composition in shallow lakes.

2. Materials and methods

2.1. Description of study sites

We studied 38 shallow lakes in two different ecological provinces of Minnesota, sampled during August 9–19, 2010 and August 8–17, 2011. Five of these lakes did not contain any macrophytes and so were not included in the analysis, leaving 33 study lakes. These included 11 lakes in the Laurentian Mixed Forest Province (LMF) and 22 lakes in the Prairie Parkland Province (PP) (Figure 1). The PP lakes were sampled in 2010 (5 west-central lakes), and in 2011 (17 south-western lakes). No LMF lakes were sampled in 2011. The LMF Province includes areas of conifer forest, mixed hardwood and conifer forests, and conifer bogs and swamps (Minnesota Department of Natural Resources 1999). Tallgrass prairie and areas of wet prairie were dominant in the PP province prior to settlement of this region but agriculture is now the dominant land use. The LMF lakes occurred within the Itasca moraine and Erskine moraine, and the PP lakes within the Big Stone moraine and Altamont moraine (Ojakangas and Matsch, 1982; Lusardi, 1997). Parent materials of these provinces included glacial till or outwash. Soils in the LMF Province included very permeable soils formed on loamy sediments overlying sandy and gravelly sediments on glacial outwash, and fine loamy and poorly drained organic soils overlying loamy glacial deposits. Soils in the PP Province included well drained and poorly drained soils that formed in calcareous glacial or loamy till (Soil Survey Staff, 2012).

2.2. Vegetation assessment

We used two methods to assess macrophyte abundance in study lakes. First, we estimated percent cover for each macrophyte species using an acrylic glass-bottom cylinder (scope) at 10 locations (each about 0.5 m²) in each lake, approximately equidistant from each other, and at least 4 m from shore (Figure 2). When macrophyte species could not be identified through the scope, samples were retrieved with an extension arm tool, placed in plastic bags with lake water, and transported in coolers on ice to our laboratory for later identification. The objective of the scope was to employ a method that was effective, efficient, and less invasive than raking. However, usefulness of this approach was limited by depth and turbidity in some lakes. Macrophyte biomass in each study lake was also determined using a weighted plant rake at 15 locations along 5 transects. To collect macrophytes for mass estimates, a plant rake was cast at each location and dragged along the lake bottom for approximately 3 m. Macrophytes were retrieved from the plant rake, placed in buckets, and weighed on spring scales. The proportion of each species per rake sample was determined and then multiplied by the resulting wet weights (g sample⁻¹) to estimate biomass of each species at each of the 15 locations. Finally, cover data (scope) and mass estimates (rake) were combined creating a single community composition matrix based on presence/absence of species observed or raked. In all cases, macrophytes were identified to the lowest taxonomic level (typically species) when possible. We included filamentous algae and *Chara* spp. in the analysis of all macrophyte data.

2.3. Within-lake and watershed variables

Lake watershed area (LWA), basin area (BSN), emergent vegetation area (EVA), open water area (OWT), and the land cover proportions (woodland, grassland, shrubland, corn and soybeans, hay and grains, total agriculture) for the watershed of each lake were derived from digitized features determined using aerial photographs and GIS software (methods summarized by Hanson et al., 2012). Basin area included open water and emergent vegetation area, lake watershed area included the entire land area draining to the outlet of the study lake. Shrubland referred to the area with mixed grasses, shrubs, and trees. Woodland referred to forested area with >75% mature trees. Total agriculture was the sum of the percent cover attributed to corn and soybeans, hayed areas and small grain fields. Lakes in the LMF Province were located where forest was the dominant land cover (>40%), whereas lakes in the PP Province occurred where dominant land cover was cultivated land (>79%) (Minnesota Geospatial Information Office Staff, 1999). This coincided with our land cover data, which indicated that LMF lakes occurred in watersheds dominated by woodland while PP lakes occurred in watersheds dominated by agriculture. We sampled lakes within watersheds of 8–1384 ha, with 1.8–59 ha basin area (Table 1). Lake depth average $\pm$ standard deviation was 1.2 ± 0.6 m for the PP Province and 1.8 ± 1.0 m for the LMF Province.

2.4. Water and sediment variables

At the approximate location where macrophyte cover was determined, water samples were collected directly above the vegetation beds by placing sample bottles approximately 25 cm below the water's surface for each lake. A portion of each water sample was used to measure turbidity using a HACH® portable turbidimeter (Model 2100P), and pH using a VWR Symphony SP90M5 portable multimeter. The remaining water samples were filtered (0.45- μ m pressure filter, Pall Corporation Supor® –450) and preserved with 0.1 ml (2 drops) of concentrated nitric acid for multi-element analysis. Chlorophyll-a (Chl-a) concentrations for each lake were determined in July of the same year using methods described by Zimmer et al. (2009). Ca and Mg concentrations (mg l^{-1}) were determined using a Spectro Genesis Inductively Coupled Plasma Optical Emission Spectrometer (ICP-OES). Percent recovery rates were calculated using the expected and measured values of a certified reference water standard (EnviroMAT Ground Water, High, ES-H-2), and were greater than 90%. Alkalinity has been reported to have strong correlations with Ca and Mg in lake waters (Stallard, 1980; Roberts et al., 1985; Heegaard et al., 2001), and so we used the sum of the mmol l^{-1} of Ca and Mg (Ca+Mg) as an indicator of alkalinity.

A sediment corer adapted from Madsen et al. (2007) was used to collect sediment samples at approximately the same locations where the macrophytes were surveyed and the water samples collected. Samples were transported in a cooler with ice to the lab, placed in paper bags, and oven-dried until constant weight at 60°C, crushed, and homogenized. These dried samples were reserved for organic matter (OM) via loss-on-ignition, particle size and multi-element analysis. OM of sediment samples was determined by again drying the samples in an oven at 105°C for two hours, weighing, and then ashing in a furnace at 360°C for two hours. After ashing, the remaining sample material was cooled, weighed and then passed through a 63- μ m sieve under running water. The weight of sample that passed through the sieve was considered the fraction of sediment smaller than 63 μ m (<63). Results of the multi-element analysis for both water and sediments are reported elsewhere (Kissoon, 2012).

2.5. Statistical analysis

Environmental variables were transformed using log or arcsine transformations prior to statistical analysis to increase homogeneity of variance, and macrophyte variables (cover and biomass) were relativized by maxima to reduce the influence of highly abundant species

and then arcsine transformed to improve normality (McCune and Grace, 2002). Environmental variables included water variables (pH, turbidity, Chl-a, and Ca+Mg), sediment variables (OM and $f < 63$), within-lake variables (open water area and emergent vegetation area), and watershed variables (lake watershed:basin area, %grassland, %shrubland, %woodland, %corn and soybeans, %hay and grains, and %total agriculture). A General Linear Model with a nested design was used to determine significant differences between provinces and among lakes within provinces ($p < 0.01$) for macrophyte, water, and sediment variables using Minitab® statistical software (Minitab® 15 ©2006 Minitab Inc.). Indicator Species Analysis was carried out in PC-ORD using the Dufrêne and Legendre (1997) method to determine significant indicator species for provinces ($p < 0.05$).

We used direct gradient analysis to relate macrophyte characteristics to environmental features of lakes and watersheds. Preliminary Detrended Correspondence Analysis (DCA) indicated that unimodal gradient analysis (CCA) was appropriate for analysis of the macrophyte cover and biomass data because the gradient lengths were > 4.0 standard deviations and RDA was deemed appropriate for analysis of macrophyte community composition because the gradient lengths were < 4.0 standard deviations (ter Braak and Šmilauer, 2002). Prior to analysis rare macrophyte species (species that occurred in less than three lakes) were deleted from macrophyte matrices to reduce dataset sparsity (McCune and Grace, 2002; Peck, 2010). Relationships between environmental variables and macrophyte abundance (cover and biomass) were assessed using Canonical Correspondence Analysis (CCA) in CANOCO (©2005 CANOCO Version 4.5). Strength of relationships between environmental variables and macrophyte community composition were assessed using redundancy analysis (RDA). Previous studies have used these methods to investigate species-environment relationships with good results (Toivonen and Huttunen 1995; Heegaard et al. 2001; Loughheed et al. 2001; Petry et al. 2003; Dodkins et al. 2005; Hanson et al. 2009; Capers et al. 2010; Sass et al. 2010; O'Hare et al. 2012). We conducted global tests using all explanatory variables (water, sediment, and watershed variables) before proceeding with forward selection procedures (Blanchet et al. 2008). For CCA, forward selection procedures with Monte Carlo permutation tests (499 permutations) were used to identify significant environmental variables using an alpha level of 0.05, and these were included in final models. For RDA, forward selection procedures were conducted using the vegan package in R with double stopping criteria to identify environmental variables using an alpha level of 0.05 and adjusted r^2 (0.33) of the global test (Borcard et al. 2011; R Core Team, 2012). Further analysis was carried out to partition sources of variation attributed to spatial (Province) and environmental components independent of each other using partial Canonical Correspondence Analysis (pCCA) or partial redundancy analysis (pRDA) according to methods by Borcard et al. (1992). All environmental variables had low variance inflation factors (< 20) which indicated that they did not correlate with each other and therefore contributed uniquely to the analysis (ter Braak and Šmilauer, 2002). However, Chl-a and turbidity were highly correlated and so only turbidity was included with the other environmental variables. Macrophyte species excluded from indicator species analysis, CCA, and RDA because of their sparsity (occurred in less than 8% of lakes in this study) included *Bidens beckii*, *Brasenia schreberi*, *Drepanocladus* spp., *Elodea canadensis*, *Heteranthera dubia*, *Nitella* spp., *Nuphar* spp., *Nymphaea* spp., *Potamogeton gramineus*, *Potamogeton praelongis*, and *Ruppia occidentalis*.

3. Results

3.1. Differences between provinces and among lakes

Results of a nested ANOVA showed that total macrophyte cover and biomass varied significantly between provinces and among lakes within provinces. Lakes in the LMF Province had greater total macrophyte cover and lower total macrophyte biomass than did

those in the PP Province ($p < 0.01$) (Table 1). Species richness varied among the lakes with the most macrophyte species (12 species) in one PP lake, and a single species in one LMF lake and three PP lakes. *Stuckenia pectinata* was the most common macrophyte occurring in >60% of the lakes. Other prevalent macrophytes included *Ceratophyllum demersum* and *Chara* spp. which occurred in >30% and filamentous algae, *Myriophyllum sibiricum*, *Najas flexilis*, *Potamogeton pusillus*, *P. richardsonii*, and *P. zosteriformis* occurred in >20% of our study lakes. Results of the indicator species analysis showed that filamentous algae, *P. richardsonii* and *Stuckenia pectinata* were significant indicators of the PP Province while *P. amplifolius*, *P. natans*, *Sagittaria cristata*, and *Utricularia vulgaris* were significant indicators of the LMF Province (Table 2).

Results of a nested ANOVA showed that turbidity, pH, Ca+Mg, and OM varied significantly between provinces and also among lakes within provinces (Table 1). Turbidity, pH, and Ca+Mg were higher in PP lakes, while OM was greater in LMF lakes. The f_{63} varied significantly between provinces, but was similar among lakes within provinces. Lakes in the PP Province had significantly higher f_{63} compared to lakes in the LMF Province. Pearson correlations showed that turbidity and Chl-a correlated negatively with total macrophyte cover ($r > -0.500$, $p < 0.001$). Turbidity correlated positively with pH ($r = 0.547$, $p < 0.001$) and Chl-a ($r = 0.874$, $p < 0.001$), and pH correlated positively with f_{63} ($r = 0.552$, $p < 0.001$) and Ca+Mg ($r = 0.617$, $p < 0.001$).

3.2. Relationships between macrophyte abundance and environmental variables

We conducted a CCA to identify environmental variables associated with macrophyte cover. CCA indicated that f_{63} , percent woodland, open water area, turbidity, and percent agriculture were significant sources of variance in macrophyte cover, and together these explained 36.6% of the variation across the two provinces (Figure 3, Table 3). CCA supported results of the indicator species analysis by indicating that certain species were associated with specific provinces. For example, *Chara* spp., *Myriophyllum sibiricum*, *Utricularia vulgaris*, *Sparganium americanum*, *Najas flexilis*, and *Sagittaria cristata* cover were positively associated with lakes in the LMF province and with percent woodland in watersheds. *P. zosteriformis*, *Ceratophyllum demersum*, and *Lemna trisulca* exhibited greater cover in lakes with high f_{63} . In contrast filamentous algae, *P. pusillus*, *Stuckenia pectinata*, and *P. richardsonii* were more widespread (higher cover values) in lakes with high turbidity, high percent agricultural cover in adjacent uplands, and large open water areas and such lakes usually occurred in the PP Province. We also conducted pCCA to estimate the variation in macrophyte cover attributable to our environmental variables while controlling for Province. Results of the pCCA showed that f_{63} , percent woodland, open water area, turbidity, and percent agriculture explained 30.8% of macrophyte cover variation (Table 3). Province as a covariable accounted for 4.6% and covariance (shared variance) accounted for 5.7% of the variation while the remaining 58.9% of the variance was unexplained. When we added Province as a spatial covariate to the model, the variance explained by f_{63} and percent woodland decreased and the variance explained by open water area, turbidity, and percent agriculture increased. However, f_{63} remained the most important variable explaining 11.3% of the variation in macrophyte cover.

We also used CCA to identify environmental variables associated with variation in macrophyte biomass. Results of this CCA indicated that pH, f_{63} , percent woodland, open water area, emergent vegetation area, and OM were all significant sources of variance in macrophyte biomass, and collectively these explained 43.5% of the biomass variation (Figure 4, Table 3). *P. zosteriformis*, *Lemna trisulca*, and filamentous algae biomass were positively associated with pH, while *Stuckenia pectinata* was associated with pH and open water area. *Chara* spp., *Utricularia vulgaris*, and *Najas flexilis* biomass were positively associated with lakes in watersheds dominated by woodland and high OM. We also used a

pCCA to determine the variation in macrophyte biomass attributed to the environmental variables while controlling for Province. Results of this pCCA showed that pH, sediment ≤ 63 , percent woodland, open water area, emergent vegetation area, and OM explained 39.1% of the variation in macrophyte biomass (Table 3). Province as a covariable explained 6.6% and covariance explained 4.4% of the variation while the remaining 49.9% of the variance was unexplained. When we added Province as a spatial covariate to the model, the variance explained by ≤ 63 , percent woodland, open water area, and organic matter increased, while the variance explained by pH and emergent vegetation area decreased. Lake pH went from being the most important environmental variable explaining 13% of the variation to the least important variable explaining only 2.6% of the variation. With Province as a covariable ≤ 63 became the most important environmental variable, explaining 10.1% of the variation in macrophyte biomass.

3.3. Relationships between macrophyte community composition and environmental variables

We used RDA to identify environmental variables associated with variation in macrophyte community composition. Results of this RDA showed that percent woodland, turbidity, open water area, and Ca+Mg were significant sources of variance, and collectively explained 34.5% of the variation (Figure 5, Table 4). Turbidity and open water area were positively associated with *P. richardsonii*, while Ca+Mg was associated with the presence of *Stuckenia pectinata* and filamentous algae. Lakes within watersheds dominated by woodland were positively associated with the presence of *Potamogeton amplifolius*, *P. natans*, *Sagittaria cristata*, *Sparganium americanum*, *Utricularia vulgaris*, and *Najas flexilis*. We also conducted pRDA to estimate the variation in macrophyte community composition attributed to the environmental variables while controlling for Province. Results of a pRDA showed that percent woodland, turbidity, open water area, and Ca+Mg together explained 23.5% of the variation in macrophyte community composition independent of Province (Table 4). The covariable, Province explained 2.7% and covariance explained 11% of the variation while the remaining 62.8% of the variance was unexplained. When we added Province as a spatial covariate to the model, turbidity became the most important environmental variable explaining 13.8% of the variation in macrophyte community composition. Percent woodland was no longer significant after we added Province to the model, indicating that percent woodland was probably correlated with Province. Province and percent woodland in watersheds were not significant sources of variation in this pRDA model.

4. Discussion

Our study builds on earlier works assessing relationships between aquatic macrophytes and environmental variables (Heegaard et al., 2001; Loughheed et al., 2001; Meerhoff et al., 2003; Akasaka et al. 2010; Capers et al., 2010; Sass et al., 2010; Akasaka and Takamura, 2011; del Pozo et al., 2011; O'Hare et al., 2012; Alahuhta et al. 2012) and indicates the extent to which macrophyte cover, biomass and community composition in shallow lakes are related to a unique combination of site- and watershed-scale variables including lake morphology, water and sediment physiochemical characteristics, and cover types of adjacent uplands. Our study differs from these earlier works of macrophyte-environment relationships in several ways. First, our study used multiple methods of measuring macrophyte abundance. Alahuhta et al. (2012) used both the rake and equipment similar to our scope but they only reported species frequency and cover estimates. Second, most of these earlier works focused on deeper lakes whose plant communities function differently from those in shallow lakes (Scheffer, 2004; Heiskary and Wilson, 2005). However, the macrophyte-environment relationships reported are similar to our findings and so our study may not only be of local interest but could be relevant to other shallow lakes and aquatic ecosystems in different parts of the world. Third, we included watershed-scale variables,

which were considered in few studies examining macrophyte-environment relationships (Crosbie and Chow-Fraser, 1999; Heegaard et al., 2001; Lougheed et al., 2001; Mikulyuk et al., 2011). Finally, we included two quantitative sediment variables; organic matter content and particle size, which reportedly play an important role in macrophyte growth (Misra, 1938) but have only been considered by a few earlier works (Grillas, 1990; Prepas and Chambers, 1990; Lougheed et al., 2001).

4.1. Relationships with sediment and water characteristics

Sediment composition is an important influencing factor for aquatic macrophyte growth (Barko and Smart, 1986; Husband and Hickman, 1989; Chambers and Prepas, 1990; Lehmann et al., 1997; Bini et al., 1999). Lake sediment κ_{63} was our most important environmental variable explaining considerable variation in both macrophyte cover and biomass. Few other studies have reported relationships between sediment particle size and macrophyte abundance (Chambers and Prepas, 1990; Crosbie and Chow-Fraser, 1999; Lougheed et al., 2001). Sediments with a finer particle size distribution were prevalent in the PP lakes, which may be attributed to the geology (Ojakangas and Matsch, 1982) and land-use patterns within the PP Province. Runoff from agricultural or cultivated lands here is probably contributing fine grain particles to these prairie lakes (Lougheed et al., 2001). Similarly, Crosbie and Chow-Fraser (1999) and Lougheed et al. (2001) also found that wetlands in agriculture-dominated watersheds contained more fine grain sediments (silts and clays) which tend to bind with nutrients more than do sandy sediments (Golterman, 1995). Particle size influences sedimentation processes and the capacity to bind elements (Håkanson and Jansson, 1983), thus impacting macrophyte growth and abundance (Lougheed et al., 2001). We observed low macrophyte cover ($<5\%$) in some clear lakes ($<6 \mu\text{g L}^{-1}$ Chl-*a*) with sandy sediments (κ_{63} : $<35\%$). The poor macrophyte growth observed in lakes with sandy sediments may be due to low nutrient availability, low organic matter, and low rates of nutrient diffusion and exchange (Barko and Smart, 1986). Finer grain particles are more prone to disturbance and resuspension and thus can contribute to increased water turbidity and subsequent light limitations for macrophyte growth (Engel and Nichols, 1994; Hamilton and Mitchell, 1997). Open water area was also an important environmental variable explaining variation in macrophyte cover, biomass, and community composition. Zimmer et al. (2003) also reported that open water influenced macrophyte species richness and abundance in shallow lakes and we observed that open water area was positively associated with turbidity and κ_{63} . A combination of high clays and silts and greater surface area may make larger lakes especially susceptible to resuspension of sediments by wind and waves and resulting high turbidity. Intense interactions between lake sediments and overlying waters may increase translocation of sediment-bound nutrients leading to increased phytoplankton biomass (Engel and Nichols, 1994; Scheffer 2004).

Widespread submerged macrophyte growth is known to coincide with clear conditions and deeper light penetration in shallow lakes (Faafeng and Mjelde, 1998; Scheffer and Jeppesen, 1998; van den Berg et al., 1998; Bini et al., 1999). Hansel-Welch et al. (2003) reported that changes in macrophyte community structure were influenced by water clarity and abundance of filamentous algae in a large, shallow lake in Minnesota. Low water clarity and extensive growth of filamentous algae are usually associated with land use impacts (del Pozo et al., 2011). Negative relationships between macrophyte abundance and lake turbidity have been reported in many studies (Lougheed et al., 2001; Hansel-Welch et al., 2001; Zimmer et al., 2009) and we also found negative correlations between turbidity and Chl-*a* with macrophyte abundance. Lakes with turbid waters and nutrient-rich sediments tend to be dominated by emergent vegetation and some submersed species that can tolerate low light and high nutrient levels (Stuckey, 1975). *P. richardsonii* and *Stuckenia pectinata* have been proposed as possible indicators of nutrient enriched, turbid conditions (Stuckey, 1975), and both

species were common in our turbid study lakes. Filamentous algae and *P. richardsonii* tend to indicate high nutrient levels in lakes (Mackie, 2004) and both taxa were significant indicators of lakes in the PP province.

Water chemistry has long been viewed as the greatest influence on macrophyte distribution in Minnesota (Moyle, 1945) and water quality patterns reflect nutrient inputs, sedimentation due to surrounding land use (Lougheed et al., 2001), and underlying geology (Moyle, 1945). We found that turbidity, pH, and Ca+Mg also were important water variables explaining variation in macrophyte abundance and community composition. In Minnesota, alkalinity is influenced by the surface and underlying geology and it is an important factor influencing macrophyte distribution throughout the state (Moyle, 1945). Heegaard et al. (2001) also reported that alkalinity and Ca and Mg concentrations influenced macrophyte distribution in lakes in Ireland.

4.2. Relationships with land cover in watersheds

We found that turbid lakes were dominant in the PP province in Minnesota where agriculture was also dominant. Other studies have found similar relationships between turbid waters and agriculture-dominated watersheds (Crosbie and Chow-Fraser, 1999; Lougheed et al., 2001). Turbid waters tend to have high Chl-a and high pH due to increased algal photosynthetic rates (Prowse and Talling, 1958). Atkinson et al. (2011) reported significantly higher suspended solids, pH, alkalinity, and soluble reactive phosphorus for wetlands in agricultural areas compared to those in non-agricultural areas. Nilsson and Håkanson (1992) also reported higher pH and alkalinity for lakes in areas dominated by cultivated land. Similarly, higher pH and Ca+Mg were observed in PP lakes, which occurred within agriculture-dominated watersheds indicating the possible influence of land use on the lake water chemistry.

Land cover within watersheds played a role in macrophyte abundance and community composition. Percent woodland cover in watersheds explained significant variation in both macrophyte abundance and community composition and percent agriculture explained variation in macrophyte cover. However, the percent variation explained by these land cover variables were small (<10%). Similarly, other studies have reported relationships between land use and macrophyte abundance and community composition (Lougheed et al., 2001; Sass et al., 2010; Mikulyuk et al., 2011). When Province was added as a spatial covariate to our model for community composition, percent woodland cover in watersheds was no longer a significant source of variance, indicating that percent woodland cover was correlated with Province. In our macrophyte biomass model, we observed a positive association between percent woodland cover and organic matter content, indicating a possible link between land cover within the watershed and sediment composition. Percent woodland cover was also negatively associated with turbidity, open water area, and Ca+Mg while percent agriculture cover was positively associated with turbidity. Other studies have reported similar relationships between water and land use variables (Crosbie and Chow-Fraser, 1999; Lougheed et al., 2001; Sass et al., 2010).

Macrophytes contribute to the nutrient and sedimentation dynamics of shallow lake ecosystems since they sequester nutrients from both the water and sediments (Clarke and Wharton, 2001) and mobilize nutrients from the sediments via root uptake, senescence, and by altering the pH and redox status of sediments (Barko and James, 1998). Macrophyte growth can also be influenced by the physical and chemical characteristics of waters and sediments (Moyle, 1945; Crosbie and Chow-Fraser, 1999; Lougheed et al., 2001; del Pozo et al., 2011). Changes in the water and sediment quality will subsequently lead to changes in the macrophyte community composition (Stewart and Kantrud, 1972). In our study, variation in macrophyte community composition and abundance were explained by a

combination of water, sediment, lake morphology, and land cover variables. Land cover within the watershed can impact water and sediment characteristics (Fraterrigo and Downing, 2008), which in turn can influence macrophyte communities (Crosbie and Chow-Fraser, 1999). However, in our study the lack of a land cover continuum or gradient may have masked the true contributions of land cover in explaining variation in macrophyte abundance and community composition. Differences in geology between the two ecological provinces likely influenced the physical and chemical characteristics of the water and sediments. The impacts of natural and anthropogenic activities in lake watersheds on the water and sediment chemistry and subsequent impacts on macrophyte communities in shallow lakes should receive further investigation to enhance our understanding of macrophyte community dynamics in these systems.

5. Conclusions

In contrast to earlier works of macrophyte-environment relationships, our study 1) focused on shallow lakes, 2) presented two different measures of macrophyte abundance, and 3) considered a unique combination of predictor variables at site- and watershed-scales. Although, our study focused on shallow lakes, the macrophyte dynamics and species-environment relationships could be applied to other aquatic systems in different parts of the world. Our findings indicated that macrophyte communities are controlled by a suite of site- and watershed-scale factors in shallow lakes. This indicates that strategies for rehabilitation should focus on both lake and watershed-scale measures to help achieve conservation of plant communities and water quality characteristics in these ecosystems. A combination of water, sediment, and watershed variables, which reflect the geology and land use of the watersheds and lake morphological variables influenced macrophyte abundance and community composition in shallow lakes. Lake sediment particle size was the most important variable that explained variation in macrophyte abundance. In addition to sediment particle size, turbidity, open water area, percent agriculture cover, and percent woodland cover explained variation in macrophyte cover and pH, open water area, extent of emergent vegetation area, percent woodland cover and organic matter explained variation in macrophyte biomass. Variation in macrophyte community composition was explained by turbidity, open water area, Ca+Mg, and percent woodland cover in watershed.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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Highlights

- Site- and watershed-scale variables influence macrophyte abundance and community composition.
- Lake morphology, water and sediment characteristics, and land cover in watersheds play a role in macrophyte communities.
- Sediment particle size plays a key role in aquatic macrophyte abundance.

Fig. 1.
Map of Minnesota showing the shallow lake study sites sampled in 2010 and 2011.

Fig. 2. Diagram showing (a) side and (b) top perspectives of the field of view of the acrylic glass-bottomed cylinder used to determine macrophyte cover in shallow lakes (different letters represent different species identified in the field of view).

Fig. 3.

Ordination plot of CCA of macrophyte cover constrained by environmental variables (environmental variables (in bold): fraction of particles smaller than 63 μm ($f<63$), percent woodland (WDL), open water area (OWT), turbidity, percent agriculture (AG); macrophyte or algae species (●) (occurred in >9% of shallow lakes sampled): *Ceratophyllum demersum* (Ced), *Chara* spp. (Csp), filamentous algae (Fa), *Lemna trisulca* (Lt), *Myriophyllum sibiricum* (Ms), *Najas flexilis* (Nf), *Potamogeton pusillus* (Ppus), *Potamogeton richardsonii* (Pr), *Potamogeton zosteriformis* (Pz), *Sagittaria cristata* (Sag), *Sparganium americanum* (Spg), *Stuckenia pectinata* (Spec), *Utricularia vulgaris* (Uv); Provinces: Prairie Parkland (Δ), Laurentian Mixed Forest ($\square$)).

Fig. 4.

Ordination plot of CCA of macrophyte biomass constrained by environmental variables (environmental variables (in bold): pH, fraction of particles smaller than 63 μm ($f<63$), percent woodland (WDL), open water area (OWT), emergent vegetation area (EVA), organic matter (OM); macrophyte or algae species (●) (occurred in >9% of the shallow lakes sampled): *Brasenia schreberi* (Bras), *Ceratophyllum demersum* (Ced), *Chara* spp. (Csp), filamentous algae (Fa), *Lemna trisulca* (Lt), *Lemna minor* (Lm), *Myriophyllum sibiricum* (Ms), *Najas flexilis* (Nf), *Potamogeton amplifolius* (Pam), *Potamogeton natans* (Pn), *Potamogeton richardsonii* (Pr), *Potamogeton zosteriformis* (Pz), *Sagittaria cristata* (Sag), *Stuckenia pectinata* (Spec), *Utricularia vulgaris* (Uv); provinces: Prairie Parkland ($\square$), Laurentian Mixed Forest ($\triangle$)).

Fig. 5. RDA of macrophyte community composition variables constrained by environmental variables (environmental variables: percent woodland (%WDL), turbidity, open water area (OWT), Ca+Mg; common macrophyte or algae species (occurred in >9% of shallow lakes sampled): *Ceratophyllum demersum* (Ced), *Chara* spp. (Csp), filamentous algae (Fa), *Lemna minor* (Lm), *Lemna trisulca* (Lt), *Myriophyllum sibiricum* (Ms), *Najas flexilis* (Nf), *Potamogeton amplifolius* (Pam), *Potamogeton natans* (Pn), *Potamogeton pusillus* (Ppus), *Potamogeton richardsonii* (Pr), *Potamogeton zosterformis* (Pz), *Sagittaria cristata* (Sag), *Sparganium americanum* (Spg), *Stuckenia pectinata* (Spec), *Utricularia vulgaris* (Uv); Provinces: Prairie Parkland (Δ), Laurentian Mixed Forest ($\square$)).

Table 1

Average $\pm$ standard deviation for macrophyte, water, sediment, and watershed variables for each ecological province († indicates the significantly higher value between provinces for a particular variable ($p<0.01$); *did not test for differences for Chl-a, within-lake and watershed variables since only average data for each lake was available).

Variables	Province	Prairie Parkland (n=22)	Laurentian Mixed Forest (n=11)
Macrophyte variables	Total macrophyte cover (%)	57 $\pm$ 48	67 $\pm$ 46 †
	Total macrophyte biomass (g rake sample $^{-1}$)	558 $\pm$ 638 †	348 $\pm$ 634
Water variables	pH	9 $\pm$ 1 †	8 $\pm$ 1
	Turbidity (NTU)	18 $\pm$ 20 †	2 $\pm$ 2
	*Chl-a (μ g l $^{-1}$)	65 $\pm$ 80	4 $\pm$ 4
	Ca+Mg (mmol l $^{-1}$)	3 $\pm$ 2 †	0.9 $\pm$ 1
Sediment variables	OM (%)	10 $\pm$ 5	26 $\pm$ 16 †
	f<63 (%)	91 $\pm$ 15 †	67 $\pm$ 28
*Within-lake variables	Basin area (ha)	25 $\pm$ 18	7 $\pm$ 3
	Open water area (ha)	19 $\pm$ 16	4 $\pm$ 2
	Emergent vegetation area (ha)	5 $\pm$ 7	3 $\pm$ 3
*Watershed variables	Lake watershed area (ha)	351 $\pm$ 374	80 $\pm$ 72
	Lake watershed:basin area	17 $\pm$ 19	16 $\pm$ 19
	Grassland	22 $\pm$ 26	6 $\pm$ 7
	Shrubland	1 $\pm$ 2	2 $\pm$ 5
	Woodland	2 $\pm$ 3	83 $\pm$ 10
	Corn and Soybeans	39 $\pm$ 21	0 $\pm$ 0
	Hay and Grains	25 $\pm$ 20	0 $\pm$ 0
	Total Agriculture	64 $\pm$ 26	0 $\pm$ 0

Table 2

Indicator values and p-values for macrophytes in each ecological province as determined by indicator species analysis in PC-ORD (Monte Carlo test of significance of observed indicator value for macrophytes, 4999 permutations, $p < 0.05$; ns = not significant).

Species	Province with maximum observations	Indicator Value	p-value
<i>Ceratophyllum demersum</i>	Prairie Parkland	40.4	Ns
<i>Chara spp.</i>	Laurentian Mixed Forest	28.5	Ns
Filamentous algae	Prairie Parkland	54.5	0.0060
<i>Lemna minor</i>	Prairie Parkland	27.3	Ns
<i>Lemna trisulca</i>	Prairie Parkland	20.5	Ns
<i>Myriophyllum sibiricum</i>	Laurentian Mixed Forest	14.9	Ns
<i>Najas flexilis</i>	Laurentian Mixed Forest	44.5	Ns
<i>Potamogeton amplifolius</i>	Laurentian Mixed Forest	27.3	0.0314
<i>Potamogeton natans</i>	Laurentian Mixed Forest	45.5	0.0012
<i>Potamogeton pusillus</i>	Prairie Parkland	24.2	Ns
<i>Potamogeton richardsonii</i>	Prairie Parkland	40.9	0.0296
<i>Potamogeton zosteriformis</i>	Laurentian Mixed Forest	20.8	Ns
<i>Sagittaria cristata</i>	Laurentian Mixed Forest	37.9	0.0256
<i>Stuckenia pectinata</i>	Prairie Parkland	69.1	0.0008
<i>Sparganium americanum</i>	Laurentian Mixed Forest	14.5	Ns
<i>Utricularia vulgaris</i>	Laurentian Mixed Forest	43.6	0.0214

Table 3

Results of CCA models of macrophyte cover and biomass using environmental variables and pCCA models of macrophyte cover and biomass using environmental variables and covariables (determined by manual forward selection procedure with Monte Carlo permutation tests according to ter Braak and Šmilauer 2002 ($p < 0.05$); variance proportions calculated according to Borcard et al. (1992); forward selection with Monte Carlo permutation tests ($p < 0.05$)).

Species Matrix	Variance Class	Variables	CCA			pCCA		
			% Variance explained	p-value	% Variance explained	p-value	% Variance explained	p-value
Macrophyte cover	Environmental	$\leq 63 \mu\text{m}$	12.4	0.002	11.3	0.002	0.002	0.002
		% Woodland	9.0	0.002	0.3	0.036	0.036	0.036
		Open water area	7.2	0.002	8.8	0.002	0.002	0.002
		Turbidity	4.3	0.016	5.0	0.016	0.016	0.016
	Covariable	% Agriculture	3.7	0.046	5.4	0.032	0.032	0.032
		Province			4.6	0.028	0.028	0.028
	Covariance				5.7			
	Total		36.6		41.1			
Macrophyte biomass	Environmental	pH	13	0.002	2.6	0.008	0.008	0.008
		$\leq 63 \mu\text{m}$	9	0.034	10.1	0.030	0.030	0.030
		% Woodland	7.4	0.022	8.6	0.034	0.034	0.034
		Open water area	6.7	0.020	7.5	0.014	0.014	0.014
	Emergent vegetation area		4.9	0.012	4.6	0.032	0.032	0.032
		Organic matter	2.5	0.008	5.7	0.028	0.028	0.028
	Covariable	Province			6.6	0.010	0.010	0.010
					4.4			
	Covariance							
	Total		43.5		50.1			

Table 4

Results of RDA models of macrophyte community composition using environmental variables and pRDA models of macrophyte community composition using environmental variables and covariables (determined by manual forward selection procedure with Monte Carlo permutation tests according to ter Braak and Šmilauer 2002 ($p<0.05$); variance proportions calculated according to Borcard et al. (1992); forward selection with Monte Carlo permutation tests ($p<0.05$)).

Species Matrix	Variance Class	Variables	RDA		pRDA	
			% Variance explained	p-value	% Variance explained	p-value
Macrophyte community composition	Environmental	%Woodland	15.1	0.002	2.4	0.324
		Turbidity	12.6	0.002	13.8	0.002
		Open water area	3.9	0.022	3.9	0.018
	Covariable	Ca+Mg	2.9	0.024	3.4	0.044
		Province			2.7	0.306
		Covariance			11	
Total		34.5		37.2		