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ENVIRONMENTAL FACTORS AFFECTING BIOMASS AND DISTRIBUTION OF *STUCKENIA PECTINATA* IN THE HERON LAKE SYSTEM, MINNESOTA, USA

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Abstract: The Heron Lake System historically has been an important resource for waterfowl in Southern Minnesota, USA. In the early 1900s, the system was a major nesting, feeding, and staging area for breeding and migrating waterfowl mainly due to the extensive growth of sago pondweed, *Stuckenia pectinata*. In recent years, the abundance of *S. pectinata* has decreased dramatically. We conducted a study from 2002 through 2003 to identify factors limiting the success of *S. pectinata*. Distribution and biomass of *S. pectinata* differed significantly over the years of this study. Biomass was related to environmental factors, including water transparency and water temperature early in the season. Water transparency during May (time of early growth) had a negative relationship with maximum biomass at each site over all years. Water temperature had a positive relationship with increases in seasonal biomass yield of *S. pectinata* in the Heron Lake System.

Key Words: *Stuckenia pectinata*, environmental factors, temperature, water transparency, distribution, biomass

INTRODUCTION

Shallow lakes that contain an abundance of submersed vegetation often have clear water and can support a diverse population of both plants and animals (Hansel-Welch et al. 2003). However, shallow lakes may become degraded by excessive nutrient inputs from sewage effluent, agriculture, or internal loading caused by fish foraging and excretion. Degraded lakes often are turbid and lack macrophyte abundance and diversity (Hansel-Welch et al. 2003). Changes in a lake's plant community can be a result of the destruction of all or some of the existing vegetation by pathogens, herbivores, or humans. Changes in the physical or chemical conditions within shallow lakes, such as water levels and or nutrient loading, influence the growth of submersed macrophytes (van der Valk 1981). One important submersed species influenced by these changes is sago pondweed (*Stuckenia pectinata* (L.) Börner).

Stuckenia pectinata can have a substantial role in freshwater ecosystems by providing food and cover for animals and also influencing the physical and chemical aspects of the water and sediment (Carpenter and Lodge 1986). Specifically, *S. pectinata* serves as a direct food source for many species of waterfowl, most notably diving ducks and swans, and indirectly as a rich environment for aquatic invertebrates (Baldassarre and Bolen 1994). Seeds, tubers, and vegetative parts of *S. pectinata* are all eaten by waterfowl (Kuehn and Holmes 1963). In fact, Martin and Uhler (1939) stated that, ''sago pondweed is probably the most important single waterfowl food plant on the continent and is responsible for about half, or more, of the total food percentage credited to the genus *Potamogeton* [*Stuckenia*].'' The importance of *S. pectinata* is so great that,

in North America, continental migration pathways of some species of waterfowl can be determined by the locations of large bodies of water dominated by the plant (Kantrud 1990). However, abundance of *S. pectinata* has decreased drastically over the past few decades in wetlands that have historically been locations of substantial use by migrating and staging waterfowl (Kantrud 1990). Environmental factors such as light availability, water clarity, water temperature, and water depth can be attributed to this decline.

Light availability may be the primary environmental factor limiting submersed macrophyte colonization and biomass (Barko et al. 1986, Scheffer 1998, Case and Madsen 2004). Many plants such as *S. pectinata* grow from over wintering tubers found in bottom sediments. Tubers provide energy to shoots as they grow upward toward the lake surface, without the need for photosynthesis. Shoots continue towards the lake surface until carbohydrate reserves are exhausted, which usually takes 16–23 days after tuber sprouting (Hodgson 1966). For survival, a critical level of light must be reached prior to depleting the carbohydrate reserves in the tuber. Turbid conditions have a negative impact on the biomass of *S. pectinata* (Kantrud 1990) and other species of submersed macrophytes. Shallow lakes with a loose bottom, little or no submersed plants, and a long fetch experience turbidity caused by frequent resuspension due to wind and wave action (Blom et al. 1994). Similarly, wind and wave energy influence the distribution of solar radiation within the water column, resulting in changes in water temperature.

Water temperature influences plant performance, especially photosynthetic rates (Pilon and Santamaria 2002a). Increased water temperature results in increased overall biomass of submersed macrophytes, including *S. pectinata* (Barko et al. 1982, van Dijk and van Vierssen 1991, van Dijk et al. 1992). However, high water temperatures (>25 °C) reduce photosynthetic rates (Barko et al. 1982, Spencer 1986, Madsen and Adams 1989, Pilon and Santamaria 2002a), propagule germination (Scheffer 1998), and shoot elongation (Spencer 1986, Madsen and Adams 1988) of *S. pectinata*. Likewise, biomass of *S. pectinata* is reduced during periods of cooler temperatures due to lower photosynthetic rates (Scheffer 1998). Water temperature also has a regulatory effect on phenology and resource allocation to propagules (Kantrud 1990). For example, *S. pectinata* allocates more resources to aboveground biomass when water temperatures are warmer (Spencer 1986, Madsen and Adams 1988, Madsen 1991).

Above-ground biomass of *S. pectinata* increases with water depths between 30 and 46 cm (Robel 1961,1962). However, *S. pectinata* biomass decreases at water depths >46 cm, with complete exclusion of the plant at depths greater than 100 to120 cm (Robel 1962). During periods of increased water depth, irradiance levels are reduced (Pilon and Santamaria 2002b), resulting in differences in biomass of *S. pectinata* (Case and Madsen 2004). Similarly, greater irradiance levels result in increased overall biomass, while decreased light leads to a reduction in biomass and an earlier peak biomass (Barko et al. 1982, van Dijk and van Vierssen 1991, van Dijk et al. 1992).

Effects of environmental factors on *S. pectinata* have received considerable attention; van Dijk and van Vierssen (1991) studied the survival of *S. pectinata* under different light conditions (artificial shade) in a controlled environment. They concluded that a negative correlation exists between annual biomass production and daily mean photon densities; where maximum biomass was reached earlier in the growing season under low photon densities. Similarly, van Dijk et al. (1992) studied the impact of light climate history on *S. pectinata* biomass under controlled settings using artificial shade techniques. Results from the study demonstrated that the above and below-ground biomass of *S. pectinata* was less, the growing season was shorter, and the maximum above-ground biomass was less at higher levels of shading. Pilon and Santamaria (2002a) reported that total biomass of *S. pectinata* cultured in experimental tanks strongly increased between 10 and 15°C and leveled off at 25°C. Similarly, there was a reduction in shoot length at higher temperatures and an increase in the number of shoots produced per plant. Pilon and Santamaria (2002b) reported that low irradiance resulted in a decrease in biomass yield in *S. pectinata* cultured in experimental tanks. Case and Madsen (2004) studied the correlation between sediment characteristics and shoot and tuber presence in the Heron Lake System. They found a positive correlation between the amount of silt in the sediment and the presence of *S. pectinata* shoots. Similarly, there was a negative correlation between the amount of sand in the sediment and the presence of *S. pectinata* shoots. Tuber location and density were not correlated with either water-depth or sediment characteristics.

The majority of these past studies have been short-term, spatially limited, or both. They were conducted in controlled environments or small experimental plots and were largely focused on the effects of differing light conditions on *S. pectinata* biomass. Case and Madsen (2004) studied *S. pectinata* on a whole lake scale but did not study the effects of environmental factors on *S. pectinata* biomass. The objective of this study was to determine the effects of environmental factors (e.g., light availability, water transparency, water depth, and water temperature) on the biomass and distribution of *S. pectinata* at the long-term and whole-

lake scales. We predicted that increased light levels that reach *S. pectinata* will increase whole-lake plant distribution and biomass. Likewise, increased water temperatures will result in increases in *S. pectinata* biomass. In contrast, greater water depths will result in lower whole-lake distribution and biomass of *S. pectinata* because of the negative effects of water depth on light availability.

MATERIALS AND METHODS

Site Description

The present study was conducted in the Heron Lake System from May 2002 through October of 2003. In addition, we used data from an identical study conducted during 2001 (Case and Madsen 2004). The Heron Lake System is located in Jackson County, Minnesota (Lat.43.72333° N Long.95.2325° W) and is composed of four water bodies. For this study, we sampled South Heron Lake, North Heron Lake, and Duck Lake; North Marsh was not sampled because it dries annually. The four lakes have a mean depth of less than 1.5 m and a combined surface area of approximately 32 km^2. South Heron Lake (12.2 km^2) is a long narrow body of water with meandering shorelines and many sandy points. Two sampling locations (A and B) were selected for South Heron Lake due to the differences in sediment and depth characteristics in the northern and southern portions of the lake. Site A was located in the southern portion that is deeper and has sediments composed of silt and clay (Case and Madsen 2004). Site B was located in the northern bay of the lake and has sediments composed of sand (Case and Madsen 2004). North Heron Lake (13.5 km^2) had only one sample site due to the flat morphology of the lake and the relatively uniform silt composition of the sediment. Likewise, Duck Lake (1.9 km^2) had only one sample site because of the small surface area of the lake. Each sampling location was approximately one hectare.

The Heron Lake System has a large watershed ratio (37:1 watershed: lake surface). The large percentage of agricultural land that surrounds the lakes and large amounts of sewage effluent from neighboring communities result in nutrient loading and poor water quality (Case and Madsen 2004). Poor water quality in the system is exacerbated by sediment resuspension resulting from the large fetch of each lake.

Vegetation Distribution

To document the change in distribution of *S. pectinata* among lakes and between years, surveys of aquatic vegetation were conducted in July of 2002 and 2003 on South Heron, North Heron, and Duck Lakes. Aquatic macrophyte distribution was determined using a point intercept survey method using a 300-m grid following methods outlined by Madsen (1999). The grid was constructed using ArcView GIS software and maps of the Heron Lake System to obtain Universal Transverse Mercator (UTM) coordinates. A grid of 200-m was used on Duck Lake. North Heron Lake was not surveyed in 2002 due to low water levels, the greater portion of the lake was not accessible by boat to complete a plant survey.

A Garmin GPSMAP76 Versatile Navigator (Olathe, KS) was used to navigate to each sampling point on the lakes using the UTM coordinates. A total of 292 points were sampled during each sampling event, 156 on South Heron Lake, 98 on North Heron Lake, and 38 on Duck Lake. At each sample point, a rake was used to determine the presence or absence of aquatic macrophyte species at these points. Plant species were identified using Crow and Hellquist (2000) as the taxonomic reference. Water depth was measured at each point using a 2.54-cm-diameter PVC pipe marked in centimeters up to a length of two meters.

Seasonal Biomass

To assess seasonal biomass of *S. pectinata* among sites and between years, we collected above-ground and below-ground biomass samples annually from four sites in the Heron Lake System. Biomass is defined as the mass per unit area of living plant material (i.e., above-ground and below-ground plant structures) (Roberts et al. 1985, Madsen 1993). Sample sites for *S. pectinata* were selected based on previous year's plant stands and were determined using aerial photographs of the lakes.

Thirty biomass samples were collected every three weeks at each site between May and September 2002 and 2003 for a total of 1530 samples. Plant samples were collected using a 0.018 m^2 (15.24-cm-diameter) PVC coring device. The coring device was placed at least 20 cm into the lake sediment following methods outlined by Madsen (1993). Core samples were rinsed through a 19-L pail with a 0.25-cm^2 wire mesh bottom to separate plants from sediment. Biomass samples obtained from the pail were then placed into 3.79-L Ziploc® bags. Plants were stored in a cooler and transported to the lab. In the lab, plant biomass was washed and divided into tuber, roots and rhizomes, shoots, and inflorescences. Plant parts were dried for at least 48 hours at 55 °C to a constant mass using a VWR Scientific1390FM (Cornelius, OR) constant temperature oven and then weighed to ± 0.0001 g using a Mettler Toledo AB104-S (Greifensee, Switzerland). Mass data

were used to estimate annual biomass, maximum biomass, and tuber biomass.

Environmental Data

To evaluate relationships between environmental factors and *S. pectinata* biomass, environmental measurements (water depth, water transparency, and water temperature) were taken when biomass samples were collected. Environmental data were collected every three weeks during biomass sampling. Water depth was measured with each biomass sample at each of the four sites. Water transparency was measured using a secchi disk once during each biomass sampling period at each of the four sites. Likewise water temperature was taken once at each site during every biomass sampling period using an YSI (Yellow Springs, OH) 5238 probe; data were recorded at 0.25-m intervals from the water surface to the lake bottom.

Tuber Survey

To evaluate tuber biomass and abundance among lakes and between years, we conducted surveys on South Heron, North Heron, and Duck Lakes. Surveys were conducted in October of each year when tuber production was completed. Tubers were sampled using every other point of the 300-m grid used for the vegetation survey. Tubers were sampled at all 38 points on Duck Lake to obtain more than 30 samples. Tubers were not sampled on North Heron Lake in 2003 due to extremely low water levels. Only half of South Heron Lake was sampled in 2003 because of low water.

Tubers were collected using a 0.018-m^2 PVC coring device placed at least 20 cm into the sediment (Madsen 1993). Tubers were gathered by rinsing the sediment core in a 19-L pail with a 0.25-cm^2 wire mesh bottom. The tubers found at each location were put into Whirl Pac bags, labeled with the date and UTM coordinates, and placed into a cooler for transportation to the lab.

In the lab, tubers were washed, counted, and dried to a constant mass at 55 °C for 48 hours in a VWR Scientific 1390FM (Cornelius, OR) constant temperature oven. Dry mass of the tubers was found to the nearest ± 0.0001 g using a Mettler Toledo AB104-S (Greifensee, Switzerland) analytical balance.

Statistical Analyses

Data collected by Case and Madsen (2004) were also used in this study to provide a longer time frame for analysis. Level of significance was $p = 0.05$ for all analyses.

Vegetation Distribution. The change in distribution of *S. pectinata* were determined using McNemar's Test (dichotomous response) (Stokes et al. 2000) to account for repeated measures in the sampling design. The McNemar's test for two time points was used to analyze survey data from North Heron and Duck Lakes because only two years of data were collected. A pairwise comparison was made of the three years for South Heron Lake using McNemar's test for repeated measures. We estimated the percent frequency of occurrence of *S. pectinata* for each lake by dividing the number of points at which *S. pectinata* was observed by the total number of points for the given lake and multiplied by 100.

Seasonal Biomass. Seasonal biomass for a given month was determined by calculating the mean of all the biomass samples collected for that month. Seasonal biomass was then plotted over time to observe when maximum biomass was attained for each site in a given year. Maximum biomass was used to determined correlations between May water depth, water temperature, and water transparency. A pairwise comparison of least squares means was conducted to assess differences in biomass between years. Biomass is reported as g m^{-2}.

Environmental Data. A regression model was developed using the mixed procedure method in SAS (Littell et al. 1996) to evaluate possible relationships between May water depth, water temperature, water transparency, and year with maximum biomass of *S. pectinata*. A similar model was developed to determine if relationships exist between seasonal biomass and seasonal fluctuations in water depth, water temperature, and water transparency. These models account for dependence between measurements taken on the same sites over time by modeling the correlation autoregressive of the model.

Tuber Survey. We evaluated changes in tuber abundance using a Chi square. A repeated measures test was not used because the same points were not revisited in all years. Tuber density (N m^{-2}) and biomass (g m^{-2}) were calculated to assess total seasonal tuber biomass; these data were not statistically analyzed and are reported in this paper.

RESULTS

Vegetation Distribution

The distribution of *S. pectinata* varied in South Heron Lake ($X^2 = 37.44$, d.f. = 1, $p < 0.01$) between 2001 and 2002; ($X^2 = 56.01$, d.f. = 1, $p < 0.01$); and ($X^2 = 7.81$, d.f. = 1, $p = 0.01$) between 2001 and 2003. North Heron Lake *S. pectinata* distribution was different between 2001 and 2003 ($X^2 = 40.16$, d.f. = 1, $p < 0.01$). Likewise, the distribution of *S. pectinata*

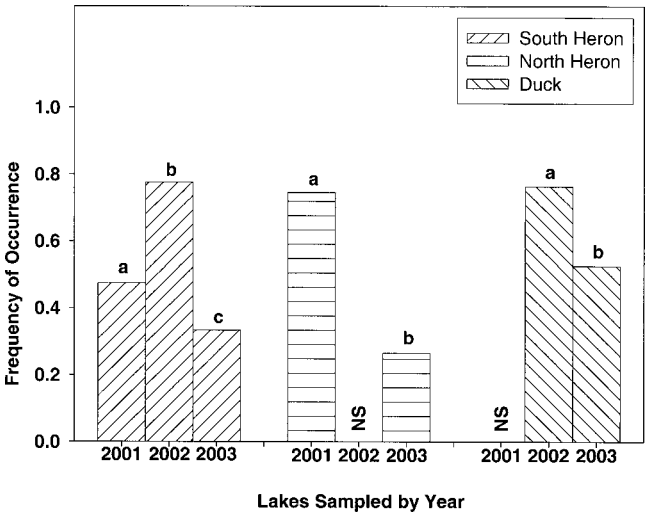

Figure 1. The frequency of occurrence (proportion of total sites sampled) of *S. pectinata* within South Heron, North Heron, and Duck lakes for three vegetation surveys 2001–2003. Letters above bars indicate a significant difference in *S. pectinata* occurrence between years for a given lake at the p=0.05 level of significance using McNemar's Test for repeated measures. Times when no samples were taken are indicated by NS.

in Duck Lake was also different between 2002 and 2003 (X^2 = 4.76, d.f. = 1, p = 0.03). A more widely distributed *S. pectinata* population was observed in 2002 for South Heron and Duck Lakes with a percent frequency of occurrence of 77.60% and 76.30% respectively (Figure 1).

Seasonal Biomass

The greatest seasonal biomass of *S. pectinata* was observed in 2002 (Figure 2). Seasonal biomass in 2002 was different than seasonal biomass observed in 2003 at the four sites (t = 2.84, d.f. = 54, p = 0.01); however, 2002 was not different from 2001. Maximum biomass was also higher in 2002 for each site (Figure 2). A marginally significant difference was observed for maximum biomass between 2002 and 2003 (t = 3.68, d.f. = 2, p = 0.06); however, there was no difference between 2001 and 2002. Maximum biomass was 91.80 g m^{-2}, 93.01 g m^{-2}, 60.47 g m^{-2}, and 63.18 g m^{-2} for South Heron A, South Heron B, North Heron, and Duck, respectively (Figure 2).

Environmental Data

Seasonal biomass of *S. pectinata* was not related to water depth at any of the sample sites (t = −0.59, d.f. = 54, p < 0.55) (Table 1). Likewise, maximum biomass was not associated with May water depths at the sample sites (t = 1.08, d.f. = 2, p = 0.39) (Table 2).

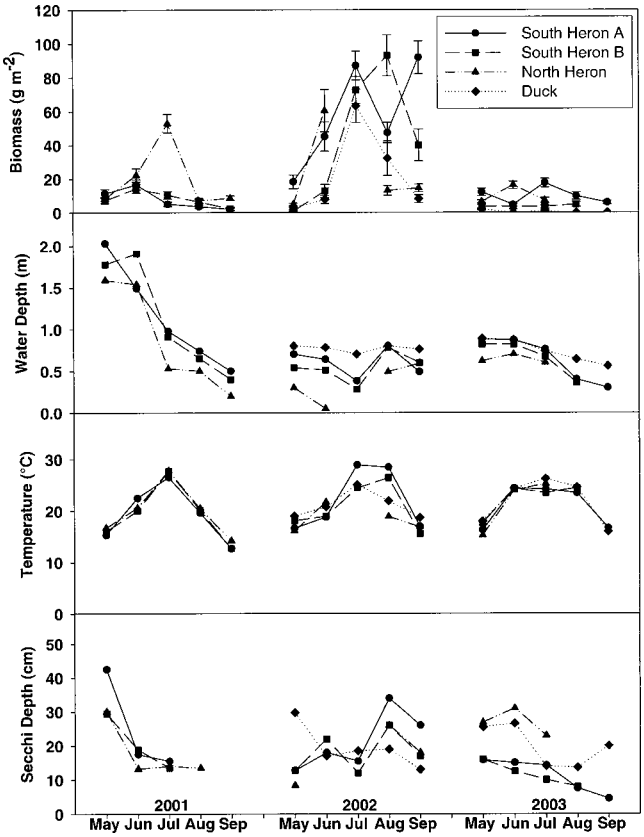

Figure 2. Total mean monthly biomass (±1 SE of *S. pectinata*), mean monthly depth measurements, mean monthly temperature readings, and mean monthly secchi depths from the four sampling sites within the Heron Lake System 2001–2003.

Water depths were lowest in 2002 for the sites on South Heron and North Heron Lakes (Figure 2). Water depths in Duck Lake fluctuated little between years, with water depths staying between 0.80 to 0.90 m.

Water temperature was positively related to seasonal biomass at each site (t = 2.41. d.f. = 54, p = 0.02) (Table 1). However, there was no relationship between May water temperatures and maximum biomass at each site (t = 1.21, d.f. = 2, p = 0.35) (Table 2). Water temperatures in 2002 stayed cooler in May and June for each site (Figure 1).

Water transparency was not associated with seasonal biomass of *S. pectinata* (t = 0.04, d.f. = 54, p = 0.97) (Table 1). However, May water transparency was negatively associated with maximum biomass (t = −4.28, d.f. = 2, p = 0.05) (Table 2). Secchi disk depths increased as water depths increased in each year (Figure 1).

Tuber Survey

The abundance of tubers varied among lakes (X^2 = 14.40, d.f. = 2, p < 0.01). However, abundance did

Table 1. The equation for the mixed procedures regression model for seasonal biomass of *S. pectinata*. The r^2 coefficient for the model is 0.39.

Effect	Year	Estimate	Standard Error	Df	t Value	P Value
[1]Intercept		−16.53	14.55	1	−1.14	0.45
[1]Depth		−6.36	10.73	54	−0.59	0.56
[1]Temperature		1.31	0.54	54	2.41	0.02
[1]Secchi		1.27	33.69	54	0.04	0.97
[2]Year	2001	16.00	9.16	54	1.75	0.08
[2]Year	2002	32.45	7.21	54	4.50	0.01
[2]Year	2003	5.96	6.55	54	0.91	0.36

[1] Regression coefficients generated by the model.
[2]Least squares means generated by the model.

not vary among years (X^2 = 1.66, d.f. = 2, p = 0.43). Tuber abundance in South Heron Lake was not different among years (X^2 = 3.25, d.f. = 2, p = 0.20). Abundance of tubers in North Heron Lake was different in 2001 and 2002 (X^2 = 4.23, d.f. = 1, p = 0.04). Duck Lake tuber distribution was not different in 2002 and 2003 (X^2 = 1.89, d.f. = 1, p = 0.17). The greatest density and biomass of tubers was found in 2003 for South Heron and Duck Lakes (Table 3). North Heron Lake had the greatest tuber density and biomass in 2002 (Table 3).

DISCUSSION

Stuckenia pectinata is an integral component within the Heron Lake ecosystem, such that understanding its abundance and distribution over space and time is important. *Stuckenia pectinata* constitutes a major source of food for waterfowl and important habitat structure for many aquatic invertebrates. The success of *S. pectinata* in the Heron Lake System is strongly related to environmental constraints imposed on the population. The results of this study indicate that *S. pectinata* biomass is strongly related to water transparency and water temperature. Environmental factors early in the growing season have a significant impact on the maximum biomass attained by *S. pectinata* and ultimately its distribution within the Heron Lake System.

Vegetation Distribution

The differences in the distribution of *S. pectinata* on a given lake can be attributed to the variability in water depths over the years. During times of high water (2001 and 2003), light intensities at the deeper sites limited *S. pectinata* colonization and forced plants to colonize the shallow sites where light could penetrate to the bottom. However, *S. pectinata* growing in these shallow sites was then limited by sediment texture and wave action (Case and Madsen 2004). Anderson (1978) found that light intensity imposed limits on pondweed colonization, and factors such as water depth, turbidity, and substrate texture combined to affect light availability to *S. pectinata* plants. Indeed, Case and Madsen (2004) showed that the success *S. pectinata* growing in shallow sites was limited by high wave energy and poor sediment texture (high concentration of sand). A negative correlation existed between the amount of sand in the sediment and the presence of *S. pectinata* shoots (Case and Madsen 2004). Aquatic macrophytes that grow in sediments with greater sand composition are more susceptible to uprooting by wave action (Doyle 1999) and thus reductions in standing biomass.

Environmental Factors and Biomass

Water temperatures in the Heron Lake System had a positive correlation with seasonal biomass of *S. pec-*

Table 2. The equation for the mixed procedures regression model for maximum biomass of *S. pectinata*. The r^2 coefficient for the model is 0.80.

Effect	Year	Estimate	Standard Error	DF	t Value	P Value
[1]Intercept		−16.16	36.75	1	−0.44	0.74
[1]Depth		26.58	24.63	2	1.08	0.39
[1]Temperature		2.68	2.22	2	1.21	0.35
[1]Secchi		−1.82	0.43	2	−4.28	0.05
[2]Year	2001	29.95	19.52	2	1.53	0.26
[2]Year	2002	77.99	12.48	2	6.24	0.02
[2]Year	2003	14.07	9.98	2	1.41	0.29

[1] Regression coefficients generated by the model.
[2] Least squares means generated by the model.

Table 3. Mean (±1 SE) tuber density (N m^{-2}), mean tuber weight (g), and tuber biomass (g m^{-2}) of *S. pectinata* in the Heron Lake System for three years 2001–2003. Times when no samples were taken are indicated by NS.

	Year		
	2001	2002	2003
South Heron Lake			
Mean Tuber Density (N m^{-2})	26 ± 7.04	56 ± 19.23	73 ± 21.09
Mean Tuber Weight (g)	0.06 ± 0.01	0.08 ± 0.03	0.11 ± 0.05
Mean Tuber Biomass (g m^{-2})	1.79 ± 0.54	4.66 ± 1.55	8.25 ± 2.88
North Heron Lake			
Mean Tuber Density (N m^{-2})	41 ± 10.55	105 ± 21.32	NS
Mean Tuber Weight (g)	0.07 ± 0.04	0.04 ± 0.02	NS
Mean Tuber Biomass (g m^{-2})	3.18 ± 0.99	4.32 ± 1.20	NS
Duck Lake			
Mean Tuber Density (N m^{-2})	NS	23 ± 6.50	32 ± 16.45
Mean Tuber Weight (g)	NS	0.05 ± 0.01	0.13 ± 0.04
Mean Tuber Biomass (g m^{-2})	NS	1.37 ± 0.42	4.44 ± 2.15

tinata. Warmer temperatures early in the season allowed for greater tuber germination and shoot elongation, resulting in increased seasonal biomass for 2002. Temperatures between 10 and 15 °C were shown to promote the greatest shoot elongation (Pilon and Santamaria 2002a), and maximum biomass attained when water temperatures are between 15 and 25°C (Van Dijk and van Vierssen 1991). Similarly, increases in temperatures were correlated to an increased number of shoots per plant and can correspond to increases in tuber production (Pilon and Santamaria 2002a), ultimately resulting in greater *S. pectinata* distribution and biomass.

Stuckenia pectinata biomass in the Heron Lake System was significantly influenced by the poor water clarity observed throughout the study. Maximum biomass was inversely related to water clarity during the time of early plant growth. The poor water clarity was a direct result of the intense wave energy and long fetch of the three lakes. The frequent resuspension of bottom sediments reduced light availability to *S. pectinata* during the time of early growth, which resulted in reductions in maximum biomass. Thus, it is necessary to have favorable environmental conditions from germination until leaves are photosynthetically active. Hodgson (1966) stated that the time of early growth is the most crucial time for adequate light transmission and, therefore, the time when water depth and turbidity are most critical.

Although water depth did not have a significant influence on *S. pectinata* biomass in this study, one can be certain that water depth is related directly to water clarity and indirectly to the biomass of *S. pectinata*. Water depths were greater at all sites in May and June in both 2001 and 2003. These years also had the lowest maximum biomass. In May of 2002, water depth at all sites was less and maximum biomass of *S. pectinata* was greater. The increase in biomass is attributed to greater light availability based on work conducted by Robel (1961, 1962). A critical level of light is needed for photosynthesis of all aquatic vegetation. At greater depths, this critical level may not be reached and macrophyte colonization may be limited because of insufficient photosynthetic activity (Case and Madsen 2004). During years of greater water depths, the Heron Lake System has had biomass of *S. pectinata* that was greatly reduced (Case and Madsen 2004). However, in a similar shallow lake system, water depth had the least significant effects on changes in the plant community (Hansel-Welch et al. 2003); for this reason, water depth alone may not account for all of the variability in the biomass of *S. pectinata*. Light availability as a function of depth and water clarity early in the growth cycle should result in greater production and a more widely distributed population of *S. pectinata*.

Tuber Survey

Stuckenia pectinata tubers in the Heron Lake System were found in areas of previous plant growth. Tubers in North Heron Lake were found along the same range of elevations as the *S. pectinata* shoots. In a previous study, tubers in South Heron Lake were found in a narrower range of elevations than the *S. pectinata* shoots, indicating that tubers are only formed under more optimal conditions (Case and Madsen 2004). The low production of tubers may limit the distribution of *S. pectinata* in following years to areas of high tuber density. Production of tubers would occur

only in those high density locations, which may explain why there was not a difference in the abundance of tubers among years because new *S. pectinata* beds were not established. Similarly, reduced production of tubers can be a symptom of light stress (van Dijk et al. 1992, Doyle 2000). Plants subjected to low levels of light tend to allocate more resources towards shoots and leaves than to tubers (Madsen 1991). The production of tubers in the Heron Lake System is poor due to the reduced biomass of light stressed plants. Plants grown at low irradiance allocate a higher proportion of dry matter to shoots, at the expense of roots and rhizomes (Pilon and Santamaria 2002b), and may explain why tuber production in the Heron Lake System is poor.

Conclusions

The distribution and biomass of *S. pectinata* in the Heron Lake System is limited by water temperature and water clarity. Light availability during the first four to six weeks of growth is critical for shoot elongation and greater plant biomass. Water depths below 0.50 m in May and June should aid *S. pectinata* plants in overcoming high turbidity and rapid light extinction within the water column. The lesser depths should also allow for a greater dispersion of *S. pectinata* throughout the three lakes by allowing light penetration to more areas of the lakes. Lesser water depths and increased light availability will allow *S. pectinata* to allocate more resources to tuber production in the fall prior to senescence. Greater allocation of resources to tubers results in greater plant and tuber biomass yield (Santamaria and Rodriguez-Girones 2002).

Stuckenia pectinata was the only submersed macrophyte found in South and North Heron Lakes during 2001 (Case and Madsen 2004) and in the present study. The low biomass of *S. pectinata* and lack of species diversity in this system should be of concern. Therefore, it is imperative that conditions within the system be improved for continued *S. pectinata* growth and to aid in the restoration of other aquatic plant species. We propose that the optimal water depth for the growth of *S. pectinata* is less than 0.50 m during germination (May–June). Shallow depths at this time will aid *S. pectinata* in overcoming light deficiencies and facilitate an increase in water temperatures. Increases in water temperature should promote tuber germination and shoot elongation until photosynthesis begins. Management objectives in the Heron Lake System should be directed towards improving light availability through techniques to increase water transparency. Plantings of emergent vegetation along shorelines can solidify bottom sediments and offer some sheltered areas for the growth of submersed macrophytes.

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LITERATURE CITED

Anderson, M. G. 1978. Distribution and production of sago pondweed (*Potamogeton pectinatus* L.) on a northern prairie marsh. Ecology 59:154–160.

Baldassarre, G. A. and E. G. Bolen. 1994. Waterfowl Ecology and Management. John Wiley and Sons, New York, NY, USA.

Barko, J. W., M. S. Adams, and N. L. Clesceri. 1986. Environmental factors and their consideration in the management of submersed aquatic vegetation: a review. Journal of Aquatic Plant Management 24:1–10.

Barko, J. W., D. G. Hardin, and M. S. Matthews. 1982. Growth and morphology of submersed freshwater macrophytes in relation to light and temperature. Canadian Journal of Botany 60:877–887.

Blom, G., E. H. S. van Duin, and L. Lijklema. 1994. Sediment resuspension and light conditions in some shallow Dutch lakes. Water Science Techniques 30:243–252.

Carpenter, S. R. and D. M. Lodge. 1986. Effects of submersed macrophytes on ecosystem processes. Aquatic Botany 26:341–370.

Case, M. L. and J. D. Madsen. 2004. Factors limiting the growth of *Stuckenia pectinata* (Sago Pondweed) in Heron Lake, Minnesota. Journal of Freshwater Ecology 19:17–23.

Crow, G. E. and C. B. Hellquist. 2000. Aquatic and Wetland Plants of Northeastern North America. 2 Vol. University of Wisconsin Press, Madison, WI, USA.

Doyle, R. D. 1999. Effects of waves on the early growth of *Vallisneria americana*. U.S. Army Corps of Engineers, Rock Island, IL, USA. Environmental Report 12.

Doyle, R. D. 2000. Effects of sediment resuspension and deposition on plant growth and reproduction. U.S. Army Corps of Engineers, Rock Island, IL, USA. Environmental Report 28.

Hansel-Welch, N., M. G. Butler, T. J. Carlson, and M. A. Hanson. 2003. Changes in macrophyte community structure in Lake Christina (Minnesota), a large shallow lake, following biomanipulation. Aquatic Botany 75:323–337.

Hodgson, R. H. 1966. Growth and carbohydrate status of sago pondweed. Weeds 14:263–268.

Kantrud, H. 1990. Sago Pondweed (*Potamogeton pectinatus* L.) A Literature Review. U.S. Fish and Wildlife Service, Northern Prairie Wildlife Research Center, Jamestown, ND, USA.

Kuehn, J. H. and R. Holmes. 1963. Availability and use of sago pondweed by ducks in Thief Lake, Minnesota. Minnesota Department of Conservation, Division of Game and Fish. Section of Research and Planning. Fish and Wildlife Surveys Unit, St. Paul, MN, USA.

Littell, R. C., G. A. Milliken, W. W. Stroup, and R. D. Wolfinger. 1996. SAS® System for Mixed Models. SAS Institute Inc., Cary, NC, USA.

Madsen, J. D. 1991. Resource allocation at the individual plant level. Aquatic Botany 41:67–86.

Madsen, J. D. 1993. Biomass techniques for monitoring and assess-

ing control of aquatic vegetation. Lake and Reservoir Management 7:141–154.

Madsen, J. D. 1999. Point and Line intercept methods for aquatic plant management. U.S. Army Engineer Research and Development Center, Vicksburg, MS, USA. APCRP Technical Notes Collection (TN APCRP-M1–02).

Madsen, J. D. and M. S. Adams. 1988. The germination of *Potamogeton pectinatus* tubers: environmental control by temperature and light. Canadian Journal of Botany 36:23–31.

Madsen, J. D. and M. S. Adams. 1989. The light and temperature dependence of photosynthesis and respiration in *Potamogeton pectinatus* L. Aquatic Botany 36:23–31.

Martin, A. C. and F. M. Uhler. 1939. Food of game ducks in the United States and Canada. U.S. Department of Agriculture, Washington, DC, USA. Technical Bulletin 634.

Pilon, J. and L. Santamaria. 2002a. Clonal variation in the thermal response of the submerged aquatic macrophyte *Potamogeton pectinatus*. Journal of Ecology 90:141–152.

Pilon, J. and L. Santamaria. 2002b. Clonal variation in morphological and physiological responses to irradiance and photoperiod for the aquatic angiosperm *Potamogeton pectinatus*. Journal of Ecology 90:859–870.

Robel, R. J. 1961. Water level depth and turbidity in relation to growth of sago pondweed. Journal of Wildlife Management 25: 436–438.

Robel, R. J. 1962. Changes in submersed vegetation following a change in water level. Journal of Wildlife Management 26:221–224.

Roberts, M. J., S. P. Long, L. L. Tieszen, and C. L. Beadle. 1985. Measurement of plant biomass and net primary production. p. 1–19. *In* J. Coombs, D. O. Hall, S. P. Long, and J. M. O. Scurlock (2 ed.). Techniques in Bioproductivity and Photosynthesis. Pergamon Press, Maxwell House, Fairview Park, Elmsford, NY, USA.

Santamaria, L. and M. A. Rodriguez-Girones. 2002. Hiding from swans: optimal burial depth of sago pondweed tubers foraged by Bewick's swans. Journal of Ecology 90:303–315.

Scheffer, M. 1998. Ecology of Shallow Lakes. Chapman and Hall, London, UK.

Spencer, D. F. 1986. Early growth of *Potamogeton pectinatus* L. in response to temperature and irradiance: morphology and pigment composition. Aquatic Botany 26:1–8.

Stokes, M. E., C. S. Davis, and G. G. Koch. 2000. Categorical Data Analysis Using the SAS® System, second edition. SAS Institute Inc., Cary, NC, USA.

van der Valk, A. G. 1981. Succession in wetlands: a Gleasonian approach. Ecology 62:688–696.

van Dijk, G. M., A. W. Breukelaar, and R. Gijlsrta. 1992. Impact of light climate history on seasonal dynamics of a field population of *Potamogeton pectinatus* L. during a three year period (1986–1988). Aquatic Botany 43:17–41.

van Dijk, G. M. and W. van Vierssen. 1991. Survival of a *Potamogeton pectinatus* L. population under various light conditions in a shallow eutrophic lake (Lake Veluwe) in the Netherlands. Aquatic Botany 39:121–129.

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