J. Aquat. Plant Manage. 53: 54–63

Ecology and phenology of flowering rush in the Detroit Lakes chain of lakes, Minnesota

MICHELLE D. MARKO, JOHN D. MADSEN, R. A. SMITH, B. SARTAIN, AND C. L. OLSON*

ABSTRACT

Flowering rush, *Butomus umbellatus* L., has been an increasing problem in the Detroit Lakes chain of lakes for more than 40 yr. Flowering rush dominates ecosystems by crowding out native species, including hardstem bulrush, *Schoenoplectus acutus* (Muhl. ex Bigelow) A & D Löve, a vital part of native ecosystems. Furthermore, flowering rush creates boating hazards and hampers recreational activities on the lakes. The phenological differences between flowering rush and the native hardstem bulrush were examined as part of a project to determine best management practices for controlling this invasive species. Biomass allocation, plant height, carbohydrate allocation, and reproductive structures of flowering rush were examined in the Detroit Lakes system. Flowering rush and hardstem bulrush exhibited similar times of emergence, maximal growth, and senescence, thus requiring careful management to protect the native species. Hardstem bulrush was approximately 1 m taller than flowering rush during midsummer. Flowering rush continually formed rhizome buds as its primary mode of reproduction, and approximately one bud for every 2 g of rhizome, or 393 buds m^{-2}, were produced within the midst of a flowering rush bed. These high densities of rhizome buds could lead to further spread of flowering rush as well as require long-term treatment of this propagule bank. The number of leaves sprouting from rhizomes was greatest in midsummer in both 2010 and 2011. Throughout summer, 69% of the biomass of flowering rush plants was found below ground, indicating treatment efforts will need to target a reduction of belowground material, potentially over several years.

Key words: *Butomus umbellatus,* carbohydrate analysis, hardstem bulrush, invasive macrophyte, phenology, *Schoenoplectus acutus*.

INTRODUCTION

Flowering rush (*Butomus umbellatus* L.) is an invasive species native to Eurasia and was first discovered in North America in 1905 in Quebec (Les and Mehrhoff 1999). Flowering rush has spread across North America and forms problematic infestations in the St. Lawrence River region, Great Lakes region, and western United States (Anderson et al. 1974, Boutwell 1990, Brown and Eckert 2005). Flowering rush can form monotypic stands that crowd out native plants and interfere with recreational water use and water flow (Boutwell 1990, Jacobs et al. 2011). In the St. Lawrence River region, it was found to be more invasive than purple loosestrife (*Lythrum salicaria* L.; Lavoie 2003). The spread of flowering rush in irrigation ditches has affected water flow and become a management concern for native fish species, such as cutthroat and bull trout (Jacobs et al. 2011). One region in Minnesota, the Pelican River Watershed, has been struggling with flowering rush for over 40 yr as it has spread through the Detroit Lakes chain of lakes since the 1960s (T. Guetter, Pelican River Watershed District, pers. comm.). Since its introduction as an ornamental species in Lake Sallie (Becker County, Minnesota), different methods of mechanical and chemical controls have been employed ineffectively. Harvesting of flowering rush in the Detroit Lakes Chain in the 1990s and 2000s might have resulted in its spread within the watershed because the mechanical action resulted in dislodging rhizomes and rhizome buds, which are known to be a major factor in flowering rush dispersal (Hroudová et al. 1996).

Flowering rush is a perennial monocot from the Butomaceae family. The leaves of the plant are triangular in shape and vary in color from light to dark green. The leaves can be submersed or emergent. Both sexually reproducing diploid and asexually reproducing triploid biotypes are found throughout the United States (Eckert et al. 2000) with the triploid form dominating the regions around Minnesota (Lui et al. 2005). The triploid plants produce more aboveground and belowground biomass, more lateral rhizome buds, and taller flowering stalks (Hroudová and Zákravský 1993). Although there is mixed evidence that triploid plants can produce viable seeds in their native range (Hroudová and Zákravský 1993, Krahulcová and Jarolímová 1993), there is no evidence that triploid forms reproduce sexually in North America (Liu et al. 2005). Triploid plants are known to produce few flowers and many vegetative structures (Liu et al. 2005). The triploid form is able to grow in a wider range of conditions than the diploid form and thrives in fluctuating water levels (Hroudová et al. 1996). This advantage has led Liu and colleagues (2005) to suggest the spread of the triploid form is a result of its greater ecological tolerance.

Typically, flowering rush is found in water of less than 1.3 m; however, it has been documented growing in water deeper than 6 m (Parkinson et al. 2010). Water bodies with fluctuating water levels are particularly susceptible to infestation from flowering rush because the changes in depth can promote the spread of reproductive structures

---

*First, third, and fifth authors: Assistant Professor, Undergraduate Student, and Undergraduate Student: Biology Department, Concordia College, Moorhead, MN 56562. Second and fourth authors: Professor and Graduate Student, Geosystems Research Institute, Mississippi State University, Mississippi State, MS 39762-9627. Corresponding author's E-mail: marko@cord.edu. Received for publication August 20, 2013 and in revised form January 29, 2014.

(Hroudová et al. 1996). The shallow water allows for seed germination and production of aerial shoots from the rhizome (Hroudová et al. 1996); unfortunately, stable water levels do not lead to a decrease in stand density once flowering rush is established (Hroudová 1989). Limited information regarding the preferred habitat, growth form, and phenology of flowering rush, especially in North American lakes, is available. The relative allocation of biomass to aboveground leaves as well as to belowground material could impact its ability to spread, to compete with native vegetation, and to withstand environmental fluctuations. Given the amount of variation observed by the triploid form, it is important to characterize the ecology and phenology of the population within the Detroit Lakes area in order to determine the best management plan.

Phenological differences between invasive and native species can contribute to the success of the invaders (Wolkovich and Cleland 2011). Phenological studies have assisted in coming up with treatment solutions for many other aquatic invasive plants, including alligatorweed [*Alternanthera philoxeroides* (Mart.) Griseb.; Weldon et al. 1968], curlyleaf pondweed (*Potamogeton crispus* L.; Woolf and Madsen 2003), Eurasian watermilfoil (*Myriophyllum spicatum* L.; Madsen 1997), hydrilla [*Hydrilla verticillata* (L. f.) Royle; Madsen and Owens 1998], waterhyacinth [*Eichhornia crassipes* (Mart.) Solms; Madsen et al. 1993], and waterchestnut (*Trapa natans* L.; Madsen 1993). In this study, the ecology of flowering rush was compared to that of the native hardstem bulrush [*Schoenoplectus acutus* (Muhl. ex Bigelow) A. & D. Löve], which is a species that occupies a similar depth and habitat. It typically grows in waters less than 2 m deep, but has been found in deeper waters (Eggers and Reed 1997). Hardstem bulrush is widely regarded by fisheries biologists as a beneficial species in shallow littoral zones (Eggers and Reed 1997, Gardner et al. 2001). We studied the phenology and life history of flowering rush to better understand potential management options and timing for long-term control. We studied hardstem bulrush to determine whether there might be an advantageous time to control flowering rush when hardstem bulrush was not growing.

MATERIALS AND METHODS

This study was conducted in three lakes and a pond found in the Pelican River Watershed District from May 2010 to October 2011. These kettle lakes are connected by the Pelican River and include Detroit Lake, Lake Sallie, and Lake Melissa (Figure 1; Table 1). Detroit Lake can be further subdivided into Big Detroit and Little Detroit, which are partially separated by a sandbar; and Curfman Pond, which is connected to Big Detroit by a channel, giving a total of five water bodies (Wilcox 1907). All lakes have a mesotrophic or meso- to eutrophic trophic status and are lined with residential development (Table 1) (MPCA 2013). A survey by the Minnesota Department of Natural Resources in 2009 found 8.4 ha of flowering rush in Curfman Pond, 84 ha in Detroit Lake, 10 ha in Lake Sallie, and 4.0 ha in Lake Melissa. The asexually reproducing triploid form of flowering rush is the biotype that is currently plaguing the Detroit Lakes area (Liu et al. 2005).

Water quality parameters were taken over the course of 2010 and 2011 using a Hydrolab MS5[1] with depth, temperature, and dissolved oxygen sensors.[2] Water samples were collected on all sample days.

We initiated sampling in May 2010, and continued through October 2011. Four phenology plots were chosen before the sampling began on the Detroit Lakes Chain. Phenology plots were located on the southeastern shores of Little Detroit (1.8 ha, depth range 0.9 to 1.6 m), on the southwestern shore of Big Detroit (1.4 ha, depth range 0.6 to 1.6 m), on the eastern shore of Lake Sallie (1.8 ha, depth range 0.8 to 2.1 m) and on the eastern shore of Curfman Pond (1.3 ha, depth range 0.4 to 2.5 m) (Figure 1). These study sites were selected to be distributed between the main basins, have dense contiguous growth of flowering rush, and be areas that would not be a high priority for management in 2011. Hardstem bulrush plots were located on the southeastern shore of Little Detroit (1.5 ha, depth range 0.8 to 1.6 m), the northeastern shore of Lake Sallie (1.8 ha, depth range 0.8 to 2.7 m), the southwestern shore of Lake Melissa (1.2 ha, depth range 1.0 to 1.6 m), and along the eastern shore of a shallow island in the center of Curfman Pond (1.3 ha, depth range 0.2 to 1.6 m) (Figure 1). Dense hardstem bulrush stands were selected that were near flowering rush stands. Two sampling strategies were employed throughout this study, nondestructive and destructive, and sampling periods occurred every 3 wk during the summer and three times over the winter of 2010. Nondestructive sampling was used on the four flowering rush phenology plots and on four hardstem bulrush plots. During nondestructive sampling, 30 flowering rush and 20 hardstem bulrush sites measurements of plant height, leaf emergence out of water, and water depth were taken. We used nondestructive sampling techniques to be able to compare the phenology of flowering rush with a relatively rare and desirable native plant, hardstem bulrush. Hardstem bulrush is protected by the state natural resource agency, which did not allow destructive sampling of this species.

Destructive sampling of flowering rush involved the use of a 0.152-m-diam coring device constructed of polyvinyl chloride (PVC) pipe and/or metal pipe to suction plant mass up from the ground (Madsen et al. 2007). The samples were collected in the dense part of the flowering rush beds. This study was intended to describe typical phenology of flowering rush in the Detroit Lakes chain of lakes. A further study on phenology by depth will be reported in a separate study. Plants were thoroughly washed and separated into aboveground and belowground biomass. For each sample collected, rhizome buds, leaves, and ramets were counted and recorded. A flowering rush ramet is a single section of leaves growing from a rhizome. In some cases, there were several ramets per rhizome. Wet weights were recorded for aboveground and belowground biomasses for each sample. The separated samples were then dried in a forced air oven[3] at 60 C or lyophilized.[4] Dry weights were then recorded and the samples were ground into a fine powder using a

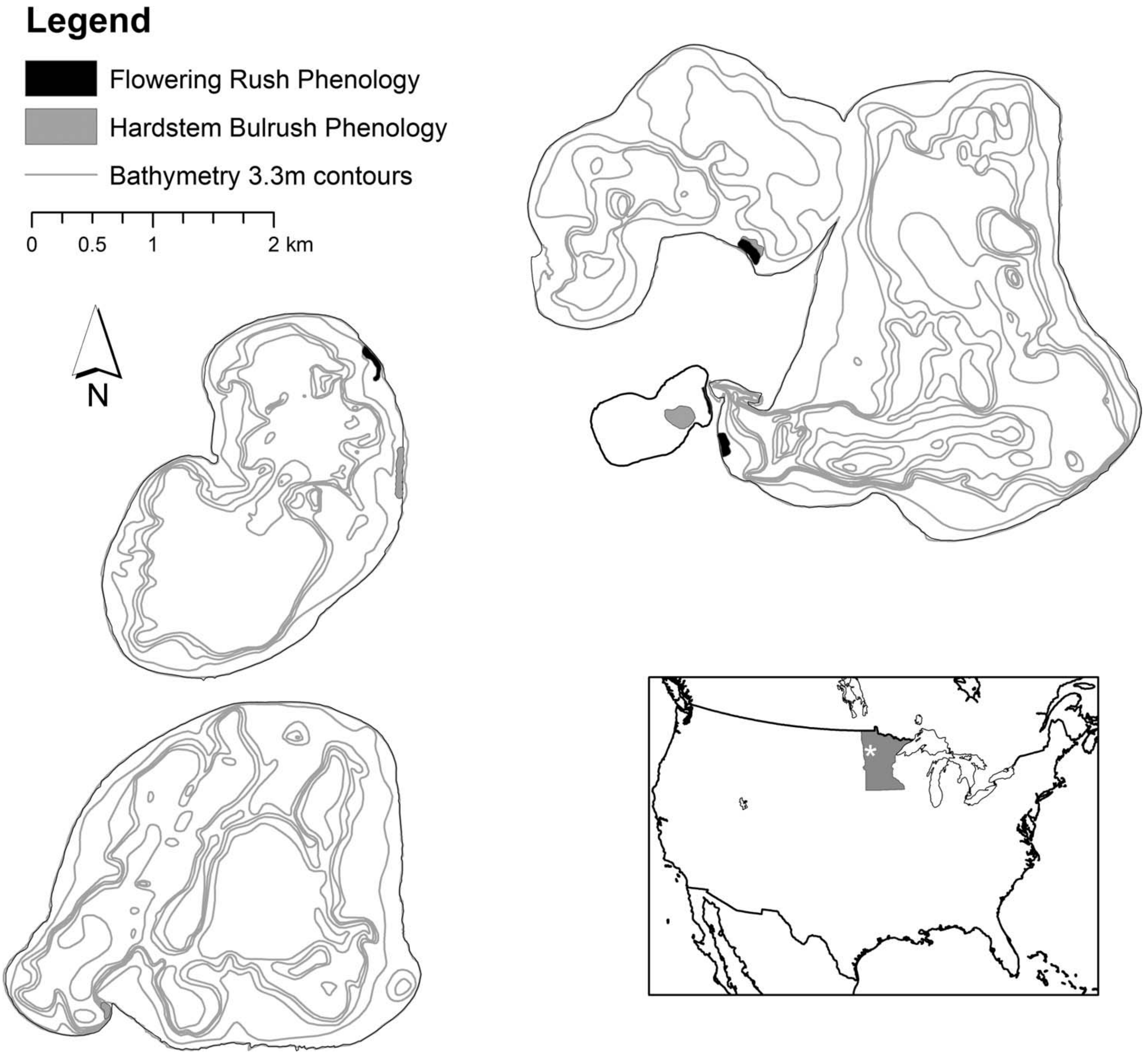

Figure 1. Detroit Lake chain of lakes including Detroit Lake (Big and Little), Curfman Pond, Lake Sallie, and Lake Melissa, and their location on the North America inset. Bathymetric contours at 3.3 m depth intervals are included in light gray. Flowering rush (black) and hardstem bulrush (gray) phenology plots are located within the littoral zone near shore. Arrows point to plots that are difficult to discern on this map.

blender[5] and Wiley Mini-mill[6] (mesh #60) for carbohydrate analysis.

Both starch and sugar samples were double-extracted with a methanol, chloroform, and formic acid solution. Soluble sugar standards were made using glucose. Starch standards were made using potato starch and glucose. Carbohydrate concentrations were determined using a spectrophotometer[7] at $\lambda = 422$ nm for both sugars (following Gent 1984 after Streeter and Jeffers 1979) and starch (Streeter and Jeffers 1979).

Data were tested for normal distribution (K-S test or Shapiro-Wilk test) and variance homogeneity (Levene's test). Extreme outliers were removed. A square root-transformation was performed with carbohydrate data that did not meet the tests for normality and homogeneity. For the nondestructive sampling variables of plant height and plant height above water, an analysis of covariance was used with depth as covariate, and species, lake, sampling date (date), and lake by date interaction terms as explanatory variables. The percentage of plants that had emergent leaves was

TABLE 1. AVERAGE SUMMER VALUES FROM 2010 AND 2011 FOR STANDARD PHYSICAL AND CHEMICAL PROPERTIES OF THE DETROIT LAKES CHAIN OF LAKES. MORPHOMETRIC DATA WERE AVAILABLE FROM THE MINNESOTA DEPARTMENT OF NATURAL RESOURCES LAKE FINDER APPLICATION (MDNR 2013). WATER QUALITY DATA WERE COMPILED BY MINNESOTA POLLUTION CONTROL AGENCY LAKE AND STREAM WATER QUALITY DASHBOARD (MPCA 2013). PARAMETERS OF TRANSPARENCY SUCH AS SECCHI DEPTH, CHLOROPHYLL-A, AND TOTAL PHOSPHOROUS REPRESENT 10-YR AVERAGES FOR EACH LAKE.

GPS location	Detroit Lake 46°47′N, 95°50′W	Curfman Pond 46°47′N, 95°51′W	Sallie Lake 46°46′N, 95°53′W	Melissa Lake 46°45′N, 95°54′W
Average area (ha)	1,248	47	741	749
Littoral zone (ha)	767	34.4	234	378
Max depth (m)	27.1	7.32	15.2	13.1
Transparency as Secchi depth (m)	3	3	2	3
Chlorophyll-a (μg L^{-1})	7	8	20	10
Total phosphorous (μg L^{-1})	21	24	35	20
Trophic state	Mesotrophic	Meso- to Eutrophic	Meso- to Eutrophic	Mesotrophic

analyzed by logistic regression using a Poisson distribution with species and date as explanatory variables. In order to show general trends in flowering rush phenology, for destructive sampling analyses data were combined by lake because no significant differences were found by site for aboveground material biomass (g dry weight m^{-2}) (F = 1.98, df = 3, $P > 0.1$), ramets m^{-2} (F = 2.15, df = 3, $P > 0.1$), leaves m^{-2} (F = 2.10, df = 3, $P > 0.1$), buds g^{-1} below ground (F = 0.26, df = 3, $P > 0.1$), ramets g^{-1} below ground (F = 1.01, df = 3, $P > 0.1$), and small differences by site were found for belowground biomass (g dry weight m^{-2}) (F = 2.95, df = 3, $P = 0.04$). Significant differences were found for the number of buds m^{-2} (F = 3.88, df = 3, $P = 0.0146$). The number of buds m^{-2} for Lake Sallie were lower than the number of buds m^{-2} for other lakes in 2010, but followed the same pattern as all lakes in 2011. However, because the purpose of this paper is to show general trends, data were averaged for comparisons with other data. Data were averaged by lake and analyzed using a one-way ANOVA with date as the explanatory variable and lake as replicates. Dry mass of plant materials were used in all analyses. Response variables assessed were ramets m^{-2}, ramets g^{-1} below ground, buds g^{-1} below ground, buds m^{-2}, leaves m^{-2}, buds $ramet^{-1}$, and buds $leaf^{-1}$. In order to determine the role of temperature and plant growth, a linear regression was used to compare water temperature with plant height above water. Square-root transformed carbohydrate response variables, starch, and sugar content, were analyzed using a two-way ANOVA with plant part (type), year, and type by year as explanatory variables. Significant differences were reported at $\alpha \leq 0.05$.

RESULTS AND DISCUSSION

Seasonal temperature patterns typical of northern temperate lakes were observed in 2010 and 2011 (Figure 2A). Plots remained well oxygenated all year long, except for late winter beneath the ice where oxygen fell to 55% oxygen saturation in Curfman Pond (Figure 2B). For all lakes, hardstem bulrush and flowering rush exhibited growth patterns closely matching lake warming and cooling (Figures 2A and 3). Plant height was significantly impacted by water depth (F = 438.11, df = 1, $P < 0.0001$), date (F = 387.10, df = 16, $P < 0.0001$), and the lake by date interaction (F = 18.60, df = 59, $P < 0.0001$). Both flowering rush and hardstem bulrush grew very rapidly in the spring. In early May 2011, when the water temperature was 11 to 12.5 C, flowering rush had just begun to sprout and plants were not observed during nondestructive sampling, but by mid-May of both years, when the water temperature was between 14 to 18 C, both flowering rush and hardstem bulrush had grown about 0.67 m (Figure 3). Height of flowering rush and hardstem bulrush above the water surface was positively correlated with spring water temperatures (flowering rush: F = 44.3, $P < 0.0001$; hardstem bulrush: F = 44.7, $P < 0.0001$). By the end of June both species had nearly reached their peak height, which they maintained until senescence in the fall (Figure 3). Lake Sallie flowering rush plants were slightly taller (1.76 m), than flowering rush plants from the other lakes (1.5 m), reflective of the deeper plant bed found in Lake Sallie (Figure 3). Hardstem bulrush was approximately 0.75 to 1 m taller than flowering rush for a majority of the growing season (F = 2093.40, df = 1, $P < 0.0001$) and reached a peak height of 2.5 m in all lakes (Figure 3). Throughout the growing season, hardstem bulrush had a significantly higher percent leaf emergence above water than flowering rush (date: $P < 0.0001$; species $P < 0.0001$) (Figure 4), which was consistent with the presence of both emergent and submersed flowering rush leaves. Hardstem bulrush typically grows as a fully emergent plant, whereas flowering rush can grow either submersed or emergent, and a proportion of the leaves remain submersed across all depths (Boutwell 1990). Flowers were first observed in study plots of hardstem bulrush on 9 June 2010 and last observed on 25 September 2010. No flowers were observed within flowering rush plots in either 2010 or 2011, although a few flowers were observed outside our study area. This absence of flowers is consistent with the allocation to vegetative structures observed in triploid populations (Lui et al. 2005). By mid-October in 2010 and 2011, flowering rush had senesced below the water surface, but some living leaves were still observed by biomass sampling (Figure 5B). In contrast, hardstem bulrush had not appeared to senesce by mid-October and was still close to its peak summer height (Figure 3). The timing of senescence for flowering rush corresponded with other reported values, even in its home range (Hroudová 1989). Although significant differences in plant height were observed between plots on different lakes (F = 4.20, df = 4, $P < 0.0047$), the pattern of sprouting, peak height, and senescence of flowering rush and hardstem bulrush appear to follow the same basic pattern on all lakes (Figure 3).

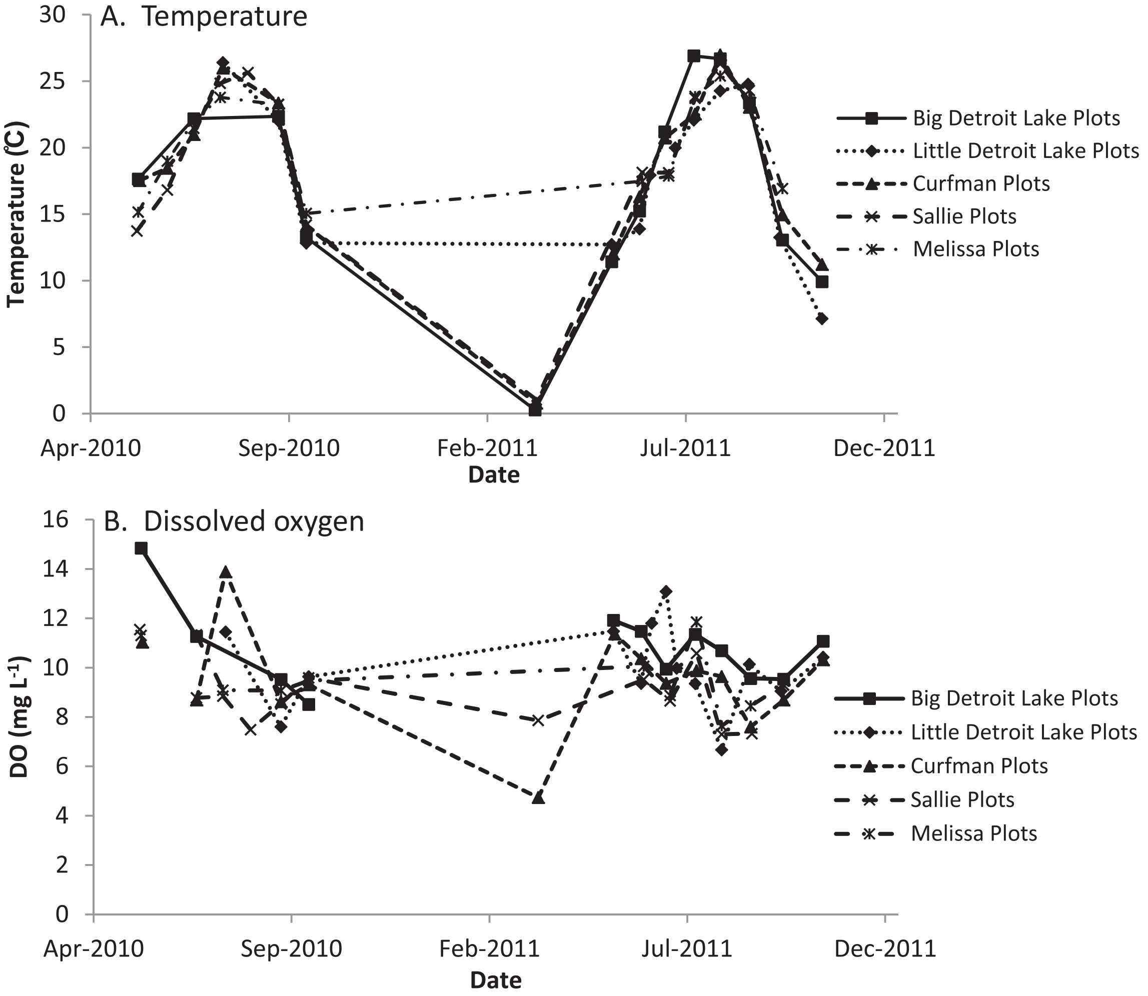

Figure 2. (A) Surface temperature (in C) and (B) dissolved oxygen content (mg L^{-1}) of Big Detroit, Little Detroit, Curfman Pond, Lake Sallie, and Lake Melissa in 2010 and 2011. Samples were taken in hardstem bulrush and flowering rush (plots) within each lake every 3 wk during the summer and twice over the winter.

The similarities observed in phenology were also observed in the biomass allocation to above- and belowground plant material. At its peak, within-bed biomass for aboveground flowering rush plants was 519 ± 50 g m^{-2} and belowground biomass was 1,052 ± 193 g m^{-2}. Although in the dense part of the flowering rush bed, these values were less than half the dense aboveground and belowground biomass produced by common reed, *Phragmites australis* (Cav.) Trin. ex Steud., another common invader (Wersal et al. 2013). Some significant differences were observed with aboveground biomass by date (F = 22.25, df = 17, $P < 0.0001$), with aboveground biomass being highest over the summer and absent over winter collections (Figure 5B). Belowground biomass was found to be largely consistent throughout the year (F = 0.95, df = 17, $P > 0.1$) with no major increases or decreases in biomass to correlate with leaf growth (Figure 5A). On average, 69% of the total June to August biomass was found to be belowground biomass, with some variation by date (F = 4.55, df = 17, $P < 0.0001$). This biomass allocation agrees with that found in populations in the Czech Republic where biomass was three to six times greater in belowground material than aboveground material (Hroudová 1989, Hroudová and Zákravský 1993, Hroudová et al. 1996).

Flowering rush is known to reproduce in four ways: the production of seeds, vegetative bulbils in the inflorescence, vegetative bulbils on the rhizome, and rhizome fragmentation with rhizome buds (Hroudová and Zákravský 1993). In our study, rhizome fragmentation and rhizome buds were the only observed method of reproduction, which is typical of the triploid biotype (Krahulcová and Jarolímová 1993). Flowers in the triploid biotype have been found to be self-incompatible, but viable seeds can be obtained from triploid crosses (Krahulcová and Jarolímová 1993). No viable seeds have been formed in triploid populations within the United States (Hroudová et al. 1996, Lui et al. 2005, Rice and Dupuis 2009). Total bud production in the Detroit Lakes chain was generally very high, with an average of 393 ± 22 buds m^{-2} (Figure 5C). Rhizome buds were in their highest density in midsummer and winter, but these differences were not significantly different (date: F = 1.17, df = 17, $P = 0.1$) (Figure 5C). Some differences in bud production were observed by lake, with Lake Sallie having significantly fewer buds m^{-2} than other lakes (Lake Sallie,

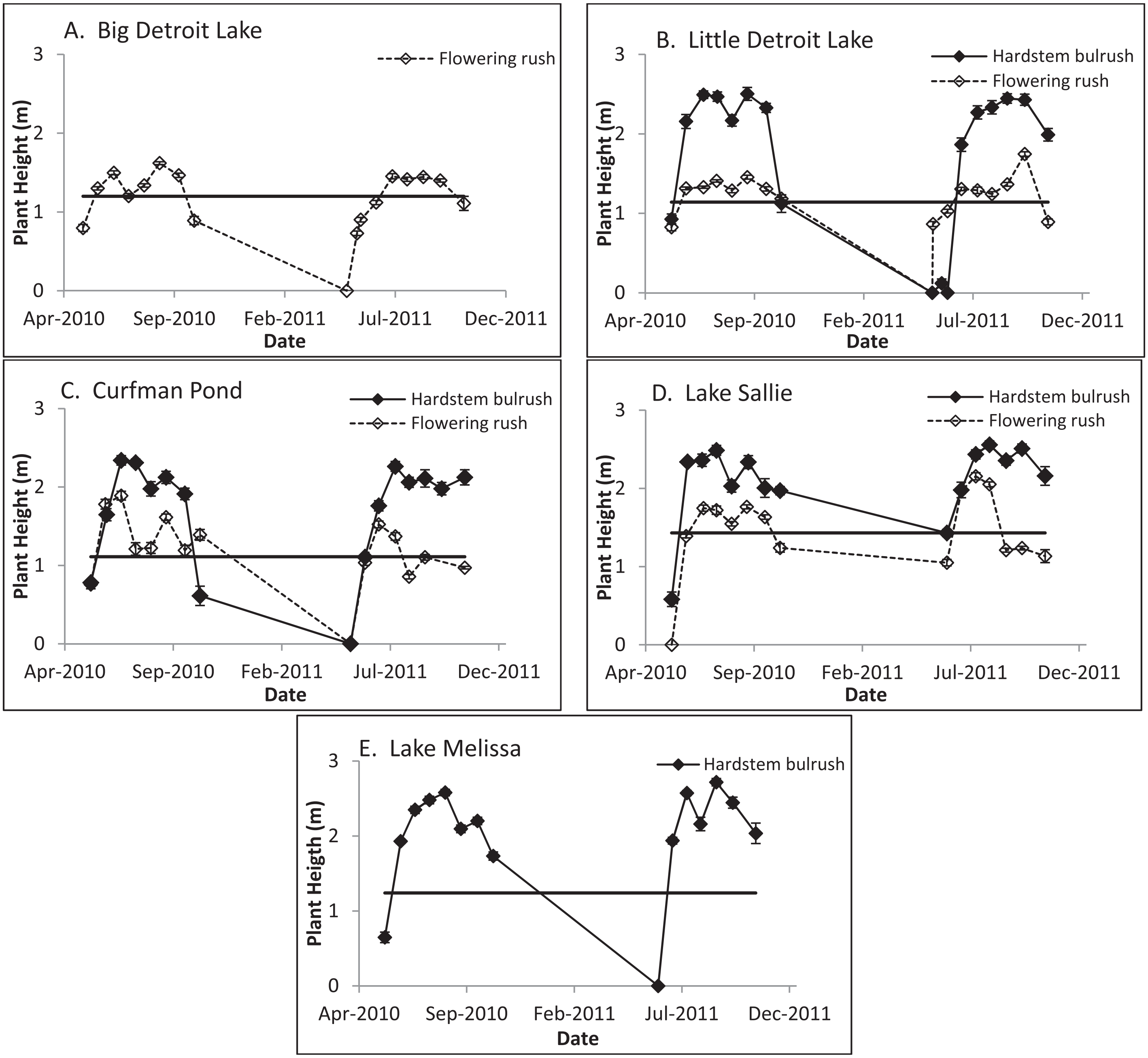

Figure 3. Mean (± 1 standard error) height (m) of flowering rush and hardstem bulrush for (A) Big Detroit Lake, (B) Little Detroit Lake, (C) Curfman Pond, (D) Lake Sallie, and (E) Lake Melissa for sampling periods in 2010 and 2011. Average water depth for each lake was indicated by the horizontal line through each graph.

297 ± 32 buds m^{-2}; Big Detroit Lake, 410 ± 31 buds m^{-2}; Little Detroit Lake, 415 ± 30 buds m^{-2}; Curfman Pond, 442 ± 30 buds m^{-2}; F = 3.88, df = 3, $P = 0.0146$). Rhizome bud size was not measured, and high values at certain times of the year might reflect the early stages of bud production or buds nearly ready to leaf out and become separate plants. Peak leaf and ramet production in midsummer corresponded with the rhizome bud abundance, indicating that midsummer was when rhizome buds become large enough to produce separate plants (leaf: F = 7.78, df = 6, $P = 0.0003$; ramets: F = 4.11, df = 17, $P < 0.0001$) (Figures 5C–E). Because plant density varied throughout a bed, we also compared bud production relative to belowground biomass and number of leaves. One rhizome bud was produced for every 2 g belowground biomass (0.504 ± 0.037 buds g^{-1} belowground biomass) or three buds for every two leaves (1.52 ± 0.276 buds $leaf^{-1}$). Variation in number of rhizome buds g^{-1} belowground biomass and rhizome bud $leaf^{-1}$ was observed over the study period (buds g^{-1} below ground: F = 2.34, df = 17, $P = 0.0104$; buds $leaf^{-1}$: F = 1.95, df = 17, $P = 0.0387$), with late summer exhibiting the greatest production of rhizome buds g^{-1} below ground. The number of

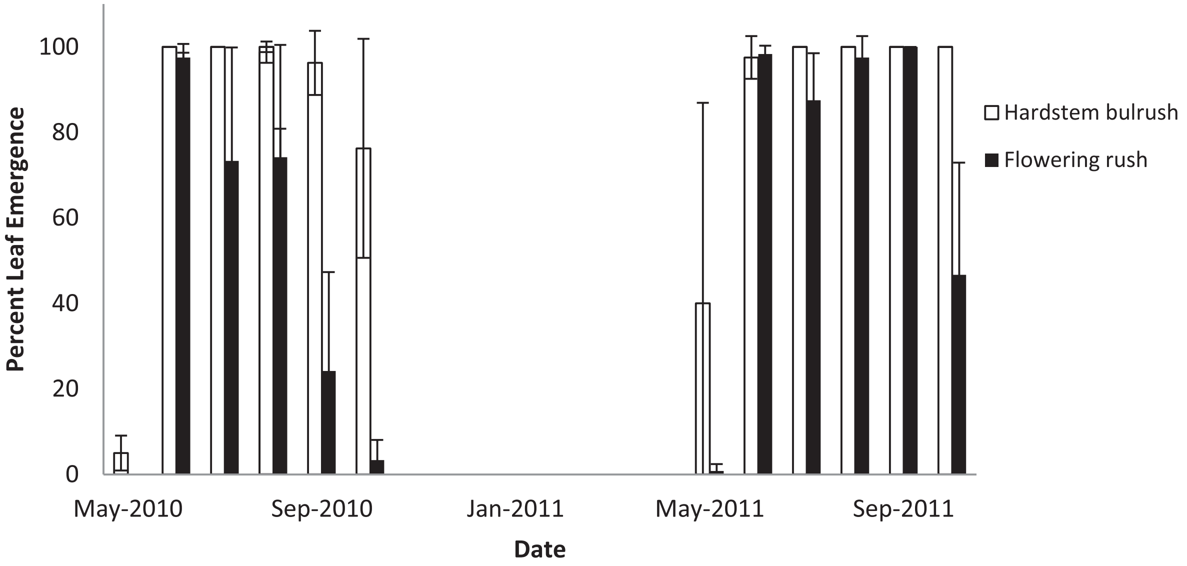

Figure 4. Mean (± 1 standard error) percentage of flowering rush and hardstem bulrush leaf emergence for 2010 and 2011.

rhizome buds g^{-1} did not differ among lakes (see Materials and Methods), indicating that regardless of local variations, for every 2 g of rhizome, a bud can be produced. This prolific bud production deserves further attention in order to identify the minimum size of rhizome needed to support a first bud, the amount of rhizome branching versus bud production, the size of bud that can produce a separate plant, the role of rhizome fragmentation versus bud production that is involved in bed density, and plant spread. It has been clearly established that rhizome fragmentation and buds are the primary mode of reproduction for the triploid biotype of flowering rush (Hroudová and Zákravský 1993, Liu et al. 2005). The high allocation of growth to belowground biomass and modification of reproductive systems away from sexual reproduction could promote local adaptations for colonization (Barrett et al. 2008). Further understanding of biology of rhizome bud production is essential for the long-term management of flowering rush.

Starch content was significantly different by plant part (type), year and day by year (type: F = 7.72, df = 3, $P < 0.001$l; year: F = 5.94, df = 1, $P = 0.0156$; day by year: F = 10.84, df = 1, $P = 0.0012$). Belowground rhizomes had significantly more starch (average 12 ± 1%) than aboveground leaves (average 5.1 ± 0.7%). A dip in belowground starch content occurred during late summer in both years, which might indicate an optimal time for treatment because this is when plants have their lowest energy reserves, and systemic herbicides would be translocated to belowground tissue (Figure 6). A similar strategy has been employed for both emergent (Wersal et al. 2011, 2013) and submersed (Madsen 1997) aquatic plants, and for terrestrial plants (Cyr et al. 1990). Glucose content differed by plant part, year, and day by plant part (type: F = 7.27, df = 3, $P < 0.001$; year: F = 8.91, df = 1, $P = 0.0032$; day by year: F = 3.48, df = 3, $P = 0.0168$). As expected, glucose content peaked in early spring in aboveground and belowground biomasses, indicating translocation from rhizomes. For most perennial species, starch is converted into sugars and translocated to the shoots to support early spring growth, until photosynthesis can supply nonstructural carbohydrate needs (McAllister and Haderlie 1986, Chapin et al. 1990). Aboveground biomass is found to have more glucose present compared to belowground biomass, reflective of photosynthesis in the shoots.

Control of flowering rush has been difficult due to its varied ecology (Rice and Dupuis 2009, Poovey et al. 2012). It grows emergent along shorelines to 6 m depth in a submersed form and thrives in areas with fluctuating water levels (Hroudová et al. 1996). Despite its heavy allocation to belowground material, which might indicate use of a systemic herbicide, Poovey and colleagues (2012) suggest using a contact herbicide requiring short exposure times due to varied habitats and growth forms of flowering rush. Northwestern Minnesota is a windy region, resulting in rapid mixing throughout the Detroit Lakes chain of lakes and maximum exposure times of 3 to 6 hr (J. Skogerboe, unpubl. data). In 2010, the Pelican River Watershed District initiated chemical control studies as part of this project. Early work with endothall resulted in little control of flowering rush, likely due to a small plot size and short exposure times (Madsen et al. 2012). Control has shifted to the use of diquat, which has resulted in decreases to aboveground (Madsen et al. 2012) and belowground (Madsen et al. 2013) biomass. Poovey and colleagues (2012) found that diquat, endothall, and flumioxazin reduced shoot biomass in aquaria experiments on both Minnesota and Idaho flowering rush populations. On emergent plants, imazamox and triclopyr have been effectively used to control shoot growth (Rice and Dupuis 2009).

The dense beds of flowering rush found across North America represent a considerable management challenge. Populations of diploid plants present in the Great Lakes and St. Lawrence River present the challenge of more genetic diversity and high reproductive output through sexual and asexual means (Liu et al. 2005). Triploid populations found

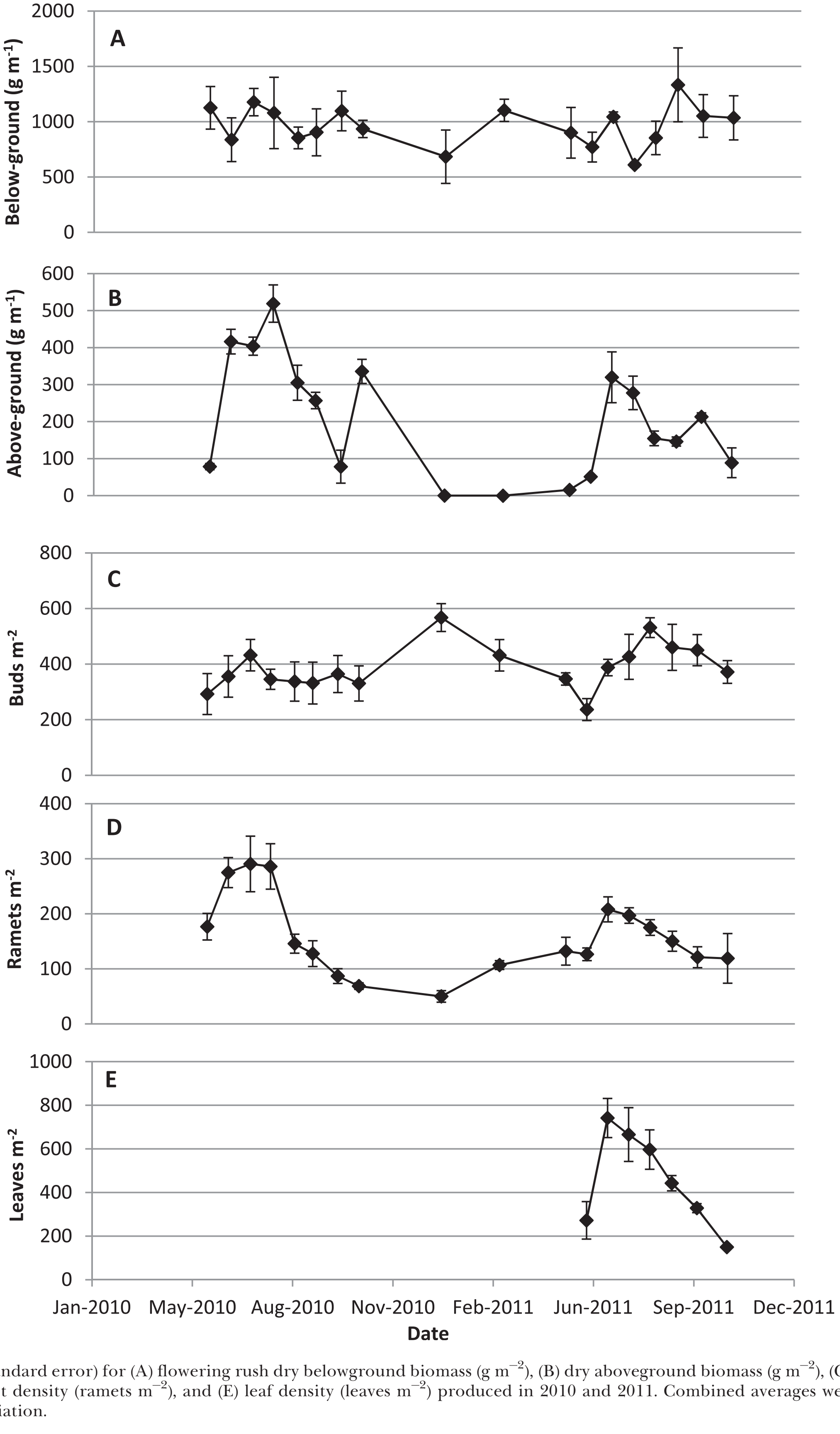

Figure 5. Mean (± 1 standard error) for (A) flowering rush dry belowground biomass (g m^{-2}), (B) dry aboveground biomass (g m^{-2}), (C) bud density (number of buds m^{-2}), (D) ramet density (ramets m^{-2}), and (E) leaf density (leaves m^{-2}) produced in 2010 and 2011. Combined averages were presented to better represent seasonal variation.

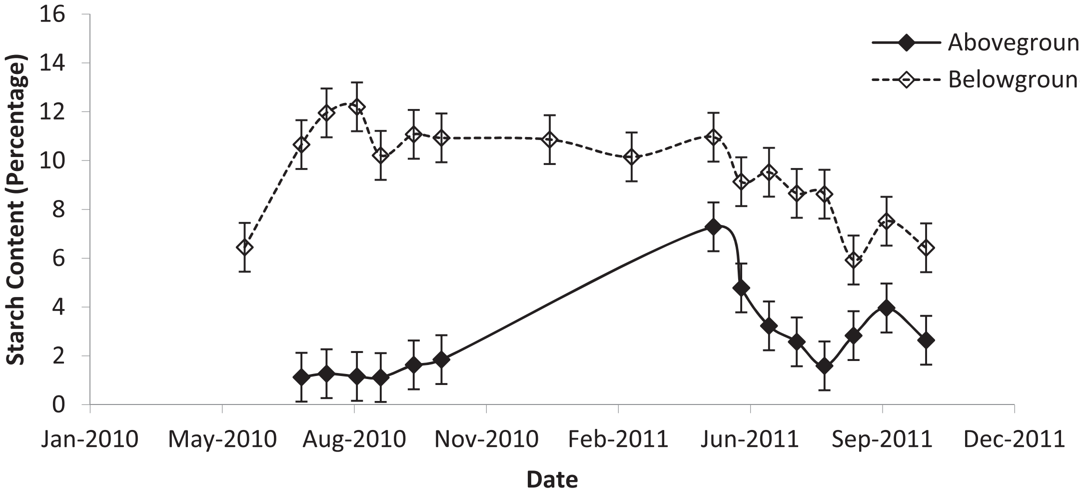

Figure 6. Mean percentage of dry weight (± 1 standard error) starch content in aboveground and belowground plant material.

in Minnesota, Montana, and Idaho lack the genetic diversity of the diploid plants, but proliferate through the production of extensive rhizomatous material and rhizome buds (Hroudová et al. 1996, Lui et al. 2005). Often found in threatened wetlands and along valuable shorelines, finding appropriate control methods is vital to protecting these resources (Boutwell 1990). The spread of flowering rush by rhizomes and rhizome buds represents a particular challenge in preventing spread. Notably, buds are abundant throughout the year, even in the winter, indicating a ready supply of new propagules each year and a need for long-term control. Future work is needed to determine when rhizome buds become separate plants, how they are spread, and what can be done successfully minimize the production of buds. Control options should seek to prevent the establishment of new plants and reduce the density of rhizome buds.

SOURCES OF MATERIALS

[1]Hydrolab MS5, Hach, Co., 5600 Lindbergh Dr., Loveland, CO 80539.

[2]Dissolved oxygen sensor, Luminescent Dissolved Oxygen, Hach Co., 5600 Lindbergh Dr., Loveland CO 80539.

[3]Forced air oven, Model 6, Thermo Fisher Scientific Inc., 81 Wyman Street Waltham, MA 02451.

[4]Lyophilizer, Model 77530, LabConco, 8811 Prospect Avenue, Kansas City, MO 64132.

[5]Blender, Ninja Professional, Euro-Pro Operating LLC, 4400 Bois Franc, Ville St-Laurent QC Canada H4S 1A7.

[6]Wiley Mini-mill, Thomas Scientific, P.O Box 99, Swedesboro, NJ 08085.

[7]Spectrophotometer, Biomate 3S, Thermo Fisher Scientific, 81 Wyman Street, Madison, WI 02451.

ACKNOWLEDGEMENTS

Funding for these studies was provided by the Pelican River Watershed District, with additional support from the Minnesota Department of Natural Resources Invasive Species Program, the Concordia College Fugelstad–Torstveit Endowment Research Fund, and NSF S-STEM grant # 0850132 to H. L. K. Manning of Concordia College. We would especially like to thank Tera Guetter and the Pelican River Watershed District for assistance in coordination and data collection. We thank the Minnesota Department of Natural Resources (DNR) for their continued support and use of resources for the project, including Chip Welling, Jay Rendall, Darrin Hoverson, Leslie George, and Jim Wolters. We thank Joshua Cheshier and Gray Turnage from Mississippi State University for assistance. We thank Concordia College students Samantha Dusek, Kristine Williams, Emily Salo, Jane Tolkinen, Kale Hermanson, Jordan Kosminskas, Nicole Lindor, Jennifer Renner, and many others for sample collection, processing, and analyses. We would also like to thank Dr. Bryan Bishop for providing GIS support, and Janet Thompson for coordinating many different specified tasks.

LITERATURE CITED

Anderson LC, Zeis CD, Alam SM. 1974. Phytogeography and possible origins of *Butomus umbellatus* in North America. Bull. Torrey Bot. Club 101:292–296.

Barrett SCH, Colautti RI, Eckert CG. 2008. Plant reproductive systems and evolution during biological invasion. Mol. Ecol. 17:373–383.

Boutwell, JE. 1990. Flowering rush: A plant worth watching. Aquatics 12:8–11.

Brown JS, Eckert CG. 2005. Evolutionary increase in sexual and clonal reproductive capacity during biological invasion in an aquatic plant *Butomus umbellatus* (Butomaceae). Am. J. Bot. 92:495–502.

Chapin FS, Schulze ED, Mooney HA. 1990. The ecology and economics of storage in plants. Annu. Rev. Ecol. Syst. 21:423–447.

Cyr DR, Bewley JD, Dumbroff EB. 1990. Seasonal dynamics of carbohydrate and nitrogenous components in roots of perennial weeds. Plant Cell Environ. 13:359–365.

Eckert CG, Massonnet B, Thomas JJ. 2000. Variation in sexual and clonal reproduction among introduced populations of flowering rush, *Butomus umbellatus* (Butomaceae). Can. J. Bot. 78:437–446.

Eggers SD, Reed DM. 1997. Wetland plants and communities of Minnesota and Wisconsin. Version 03SEP1998. U.S. Army Corps of Engineers, St. Paul District. Northern Prairie Wildlife Research Center Online, Jamestown, ND. http://www.npwrc.usgs.gov/resource/plants/mnplant/index.htm. Accessed January 12, 2014.

Gardner SC, Grue CE, Major WW, Conquest LL. 2001. Aquatic invertebrate communities associated with purple loosestrife (*Lythrum salicaria*), cattail (*Typha latifolia*), and bulrush (*Scirpus acutus*), in central Washington, USA. Wetlands 21:593–601.

Gent MPN. 1984. Carbohydrate level and growth of tomato plants. I. The effect of carbon dioxide enrichment and diurnally fluctuating temperatures. Plant Physiol. 76:694–699.

Hroudová Z. 1989. Growth of *Butomus umbellatus* at a stable water level. Folia Geobot. Phytotax. 24:371–385.

Hroudová Z, Krahulcová A, Zákravský P, Jarolímová V. 1996. The biology of *Butomus umbellatus* in shallow waters with fluctuating water level. Hydrobiologia. 340:27–30.

Hroudová Z, Zákravský P. 1993. Ecology of two cytotypes of *Butomus umbellatus*. II. Reproduction, growth and biomass production. Folia Geobot. Phytotx. 28:413–424.

Jacobs J, Mangold J, Parkinson H, Dupuis V, Rice P. 2011. Ecology and management of flowering rush (*Butomus umbellatus* L.). United States Department of Agriculture, Natural Resources Conservation Service, Invasive Species Technical Note No. MT-33. 9 pp. http://msuextension.org/publications/AgandNaturalResources/EB0201.pdf. Accessed January 13, 2014.

Krahulcová A, Jarolímová V. 1993. Ecology of two cytotypes of *Butomus umbellatus*. I. Karyology and breeding behavior. Folia Geobot. Phytotax. 28:385–411.

Lavoie C. 2003. Exotic plant species of the St. Lawrence River wetlands: A spatial and historical analysis. J. Biogeogr. 30:537–549.

Les DH, Mehrhoff LJ. 1999. Introduction of nonindigenous aquatic vascular plants in southern New England: A historical perspective. Biol. Invasions 1:281–300.

Lui K, Thompson FL, Eckert CG. 2005. Causes and consequences of extreme variation in reproductive strategy and vegetative growth among invasive populations of clonal aquatic plant, *Butomus umbellatus* L. (Butomaceae). Biol. Invasions 7:427–444.

Madsen JD. 1993. Waterchestnut seed production and management in Watervliet Reservoir, New York. J. Aquat. Plant Manage. 31:271–272.

Madsen JD. 1997. Seasonal biomass and carbohydrate allocation in a southern population of Eurasian watermilfoil. J. Aquat. Plant Manage. 35:15–21.

Madsen JD, Luu KT, Getsinger KD. 1993. Allocation of biomass and carbohydrates in waterhyacinth (*Eichhornia crassipes*): Pond-scale verification. Technical Report A-93-3. US Army Corps of Engineers Waterways Experiment Station, Vicksburg, MS. 42 pp.

Madsen JD, Owens CS. 1998. Seasonal biomass and carbohydrate allocation in dioecious hydrilla. J. Aquat. Plant Manage. 36:138–145.

Madsen JD, Sartain B, Turnage G, Marko MD. 2013. Herbicide Trials for Management of Flowering Rush in Detroit Lakes, Minnesota for 2012. Geosystems Research Institute Report 5059, Geosystems Research Institute, Mississippi State University, Mississippi State, MS. April 2013. 59 pp.

Madsen JD, Wersal RM, Marko MD, Skogerboe JG. 2012. Ecology and management of flowering rush (*Butomus umbellatus*) in the Detroit Lakes, Minnesota. Geosystems Research Institute Report 5054. Geosystems Research Institute, Mississippi State University, Mississippi State, MS. July 2012. 43 pp.

Madsen JD, Wersal RM, Woolf TE. 2007. A new core sampler for estimating biomass of submersed aquatic macrophytes. J. Aquat. Plant Manage. 45:31–34.

McAllister RS, Haderlie LC. 1986. Seasonal variations in Canada thistle (*Cirsium arvense*) root bud growth and root carbohydrate reserves. Weed Sci. 33:44–49.

MDNR (Minnesota Department of Natural Resources). 2013. Minnesota Department of Natural Resources LakeFinder Application. http://www.dnr.state.mn.us/lakefind/index.html. Accessed December 20, 2013.

MPCA (Minnsota Pollution Control Agency). 2013. Minnsota Pollution Control Agency Lake and Stream Water Quality Dashboard. http://cf.pca.state.mn.us/water/watershedweb/wdip/search__more.cfm?datatype=cmp. Accessed December 20, 2013.

Parkinson H, Mangold J, Dupuis V, Rice P. 2010. Biology, ecology and management of flowering rush (*Butomus umbellatus*). EB0201. Montana State University Extension, Bozeman, MT. 7 pp.

Poovey, AG, Mudge CR, Thum RA, James C, Getsinger KD. 2012. Evaluations of contact herbicides for controlling two populations of submersed flowering rush. J. Aquat Plant Manage. 50:48–54.

Rice PM, Dupuis V. 2009. Flowering rush: An invasive aquatic macrophyte infesting the headwaters of the Columbia River system. Center for Invasive Species Management. Department of Land Resources and Environmental Sciences, Montana State University, Bozeman, MT. 11 pp. http://www.weedcenter.org/research/docs/Flowering%20Rush%20white%20paper.pdf. Accessed January 17, 2014.

Streeter JG, Jeffers DL. 1979. Distribution of total non-structural carbohydrates in soybean plants having increased reproductive load. Crop Sci. 19:728–734.

Weldon LW, DeRigo HT, Blackburn RH. 1968. Control of alligatorweed with Dichlobenil. Proc. South. Weed Conf. 21:287–291.

Wersal RM, Cheshier JC, Madsen JD, Gerard PD. 2011. Phenology, starch allocation, and environmental effects on *Myriophyllum aquaticum*. Aquat. Bot. 95:194–199.

Wersal, RM, Madsen, JD, Cheshier, JC. 2013. Seasonal biomass and starch allocation of common reed (*Phragmites australis*) (Haplotype I) in southern Alabama, USA. Invasive Plant Sci. Manage. 6:140–146.

Wilcox AH. 1907. A pioneer history of Becker County, Minnesota. Pioneer Press Company, St. Paul, MN. 776 pp.

Wolkovich EM, Cleland EE. 2011. The phenology of plant invasions: A community ecology perspective. Front. Ecol. Environ. 9:287–294.

Woolf TE, Madsen JD. 2003. Seasonal biomass and carbohydrate allocation patterns in southern Minnesota curlyleaf pondweed populations. J. Aquat. Plant Manage. 41:113–118.