Distribution and Biomass Allocation in Relation to Depth of Flowering Rush (*Butomus umbellatus*) in the Detroit Lakes, Minnesota

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The Detroit Lakes chain of lakes consists of five basins in northwest Minnesota adjacent to the town of Detroit Lakes. Flowering rush has been established in these basins since the 1960s. We evaluated the distribution of flowering rush in the five basins using a point intercept method, with 830 points distributed in a grid with points 150 m apart. These data were analyzed to determine whether invasive and native species frequencies were different between 2010 and 2011. We also assessed co-occurrence of flowering rush with native hardstem bulrush. The distribution of both flowering rush and hardstem bulrush was unchanged from 2010 to 2011. Flowering rush is invading areas with native plants and not establishing in unvegetated areas. Although flowering rush is found as deep as 4.5 m, it is most frequent at a depth of 1.3 m. We also examined the distribution of biomass and growth across a depth gradient from 0.3 to 3.0 m in 0.3-m intervals. At each 0.3-m interval, three biomass samples were collected at each of 10 transects for a total of 30 samples per depth interval or 300 biomass samples. At each point, leaf height, emergent leaf height, water depth, number of ramets, and number of rhizome buds were counted. Biomass samples were collected in a 0.018-m^2 core sampler, sorted to shoots and belowground biomass. We found that flowering rush height and biomass peaked at 1.3 m and declined with greater depth. Bud density was negatively related to water depth. Bud density averaged 300 buds m^{-2}, which was three times the average ramet density (100 ramets m^{-2}).
Nomenclature: Flowering rush, *Butomus umbellatus* L.; hardstem bulrush, *Schoenoplectus acutus* (Muhl. ex Bigelow) Á. & D. Löve.
Key words: Aquatic invasive species, aquatic macrophyte, biomass allocation, depth distribution, emergent plant, littoral zone plant.

Flowering rush (*Butomus umbellatus* L., Butomaceae) is an emergent invasive plant that has plagued the Detroit Lakes area, in particular, Detroit Lake, Lake Sallie, Lake Melissa, and Mill Pond (Becker County) since the 1960s. It is native to Europe and Asia and was first observed in the United States in 1928. It has likely had several introductions into the United States as an ornamental plant for water gardens. Currently two karyotypes are invasive to North America: an asexually reproducing polyploid (triploid) karyotype and a sexually reproducing diploid

karyotype (Lui et al. 2005). The asexually reproducing triploid karyotype is currently found in the Detroit Lakes area (Eckert et al. 2000; Poovey et al. 2012).

The two karyotypes, diploid and triploid, are native to Central Europe (Kirschner et al. 2004). The diploid populations tend to have a lower tolerance to high nutrient levels and are more restricted in their range. Diploids are self-compatible and form large numbers of both seeds and vegetative bulbils formed in the inflorescence. Triploid populations are self-incompatible and form fewer seeds and bulbils. Both karyotypes, however, form robust rhizomes with numerous rhizome buds. Isozyme analysis of samples from Central Europe found low genetic diversity within a population and higher diversity between populations or sites. In North America, both karyotypes are likewise found, with a preponderance of diploid plants in the eastern and Great lakes regions and a higher proportion of triploid populations in the west (Eckert et al. 2003).

Management Implications

Flowering rush is an invasive aquatic plant that has established in water resources across the United States and Canada. Flowering rush has been established in the Detroit Lakes (MN) since the 1960s and become a significant nuisance to shoreline residents and recreationists. In this study, we document that, although flowering rush can occur to depths of 4.5 m, it was most abundant to 1.3 m, so management efforts could be targeted from the shoreline to depths of 1.3 m. Flowering rush established in areas that already contained native aquatic plants, including hardstem bulrush, rather than establishing in areas without vegetation. Examining biomass allocation in depths from 0.3 to 3.0 m, biomass of shoots and density of ramets was highest in depths less than 1.0 m and decreased significantly beyond 1.3 to 1.6 m. Rhizome buds, the main propagule of flowering rush, had their highest densities from 0.3 to 1.6 m, averaging 200 to 300 buds m^{-2}, which translates into 2 to 3 million buds ha^{-1}. Management can be focused on water depths of 1 m or less to target the densest infestations of flowering rush, which will serve to reduce the pool of propagules for further spread or reinfestation.

Genetic analysis indicated that regular sexual recombination of both fertile and sterile populations is extremely low; therefore, vegetative propagation predominates, even with the diploid fertile karyotype. Eckert et al. (2003) maintain that the diploid karyotypes produce large numbers of both seed and vegetative propagules, whereas the triploid karyotype reproduces only by rhizome fragmentation. They posit therefore that the diploid karyotype should spread more rapidly than the triploid karyotype. They also indicate that the triploid populations were introduced independently of the diploid populations and were not derived from them. Lui et al. (2005) indicate that North America is being colonized by two distinct forms of flowering rush that are different in their reproductive strategy.

Flowering rush was introduced to North America at La Prairie, Quebec, along the St. Lawrence River around the turn of the 20th century (Countryman 1970). Les and Mehrhoff (1999) report 1905 as the first date of discovery in North America. Within two decades, Knowlton (1930) observed dense stands of flowering rush in the shallow flats of the St. Lawrence River. It then spread to the New York shore of Lake Champlain. Muenscher (1930) observed flowering rush on shallow flats of Lake Champlain. Other locations in North America include Connecticut, the Great Lakes region of the Midwest, Idaho, Montana, and Washington (Core 1941; Countryman 1970; Stuckey 1968). Gaiser (1949) found flowering rush in Lake St. Clair in 1938. Flowering rush spread to adjoining waterbodies in Ohio (Roberts 1972) and Indiana (Witmer 1964) through natural propagation.

Flowering rush has been dispersed in North America predominantly through the ornamental water garden trade (Les and Mehrhoff 1999). Waterfowl and wildlife consume the foliage, rhizomes, and bulbils, which may disperse the plants through their digestive tracts, or dislodge the plant from the sediment and allow for water transport (Hewitt 1942; Hroudová et al. 1996; Martin and Uhler 1939). Although some attribute spread to seed production, research in the native range indicated that reproduction from seed is not a high risk to spread, because germination occurs in the late spring when competition from vegetative plants is intense (Hroudová and Zakravský 2003). Furthermore, most plants in Central Europe are triploid, which rely on vegetative propagation. Nonnative populations in North America were found to have a higher allocation to both sexual and asexual reproduction, higher survival rates, and higher biomass production than populations native to Central Europe (Brown and Eckert 2005). The selection of plants for the ornamental trade inadvertently selected populations that would be more successful as invasives to waterways throughout North America. Although natural spread of propagules can certainly account for the continuing dispersal of this species, Gaiser (1949) reports with satisfaction the establishment of colonies in natural waterbodies using both purchased seed and transplanted rootstock, noting that flowering rush is very useful to muskrats for building lodges.

Delisle et al. (2003) utilized an intensive survey of regional herbarium specimens by decade to infer the spread of invasive species by comparing them with native species occurrences in the St. Lawrence River region. They found that the invasion curve of flowering rush is abrupt and significantly different from native species. They identified the most intense period of spread as 1922 to 1935, which is corroborated by observations by naturalists of the period (Knowlton 1930). They inferred a period of low water flows in the 1930s as a potential cause of the successful spread.

In Central Europe, flowering rush is considered to be a species of temporary aquatic habitats, areas with fluctuating water levels, and even the littoral zones of lakes and reservoirs (Hroudová 1989). Hroudová (1989) further reports that stands of flowering rush are most common in shallow waters from 0.6 to 0.8 m (2.0 to 2.6 ft). Hroudová (1989) investigated the ability of this plant to survive in stable water levels and found that an individual plant could produce 12 to 43 buds yr^{-1} over a 6-yr period of study. Although rhizome bud production was steady in stable water, falling water levels stimulated bud production.

Les and Mehrhoff (1999) report that flowering rush escaped from cultivation, forming a distinct community type in marshes along the St. Lawrence River. Lavoie et al. (2003) found extensive areas of dense flowering rush in the

St. Lawrence River, with flowering rush more common in the riverine portion than either the freshwater or brackish water estuary. Using extensive surveys of the St. Lawrence River before and after a water level fluctuation event, Hudon (2004) found that lowered water levels resulted in significantly less flowering rush aboveground biomass than before the event. While this appears to contradict the assertion that low-water events cause flowering rush to spread; in fact, the shift in abundance is due to sites transitioning from favorable water levels for growth to suboptimal low water (e.g., marsh), resulting in reduced abundance. In a regional survey of Great Lakes coastal wetlands, flowering rush was commonly found in coastal wetlands of Lakes Erie (50%) and Ontario (25%) (Trebitz and Taylor 2007). Hudon (2004) further reports that flowering rush proliferates in open water in depths of 0.3 to 3 m but persists in marsh habitats. Low-water events create more area for colonization.

Although the observation is commonly made that invasive plants reduce the diversity of native plant species (e.g., Mullin et al. 2000), surprisingly few studies actually document this competition as it is occurring (Boylen et al. 1999; Madsen et al. 1991). The next best thing is to document before and after the invasion has occurred. Witmer (1964) states that dense stands of flowering rush can cause the decline of native plant species. Roberts (1972) repeats the observation that dense flowering rush will displace native plants from sites previously occupied by the natives. Hudon (2004) found that flowering rush will tend to form monospecific and dominant beds, particularly during low-water events. She notes, however, that the tendency to form dominant stands was much more marked early in the invasion cycle (1920 to 1950) than since the 1950s, although it is still common in the St. Lawrence River. Lavoie et al. (2003) found that, although flowering rush may form dense stands, it has statistically less effect on native plant diversity than some other invasive plants, including common reed [*Phragmites australis* (Cav.) Trin. ex Steud] and reed canary grass (*Phalaris arundinacea* L.). They report that resistance to invasion is more a factor of native plant community density or cover than of native plant diversity.

Although much has been learned on the cytogenetics and reproduction of this species (Brown and Eckert 2005; Krahulcová and Jarolímová 1993; Thompson and Eckert 2004), more information is needed on the ecology of this species invading natural lakes. The purpose of this study was to (1) examine the distribution of flowering rush and native plants in a natural lake, (2) assess the co-occurrence of flowering rush with hardstem bulrush [*Schoenoplectus acutus* (Muhl. ex Bigelow) Á. & D. Löve] and potential displacement of the native bulrush, and (3) analyze the depth distribution of flowering rush biomass. Earlier research on the ecology and phenology of flowering rush

in this system documents the emergence of flowering rush and the native hardstem bulrush and their biomass allocation in dense beds of flowering rush (Marko et al. 2015).

Materials and Methods

Study Site Description. The Detroit Lakes are a series of five basins connected by water corridors. Three of these basins, Big Detroit Lake, Little Detroit Lake, and Curfman Pond, are contiguous and separated by areas of shallow water. The remaining two, Sallie Lake and Lake Melissa, are downstream of the other three basins and connected by a small stream. These lakes are near the city of Detroit Lakes (46.813333°N, 95.844722°W), MN, which is 74 km (46 mi) east of Fargo, ND. The lakes are mesotrophic to meso-eutrophic glacial kettle lakes. These lakes lie just east of the Big Stone moraine, which also marks the rapid transition from the forested eastern United States to the prairie, which stretches westward (Buell and Facey 1960). The watershed is primarily forested with sugar maple (*Acer saccharum* Marshall) and American basswood (*Tilia americana* L.) forests, numerous waterways, wetlands, small farm holdings, and an increasing network of residences (Buell and Facey 1960; Cowardin et al. 1998). Historically, the aquatic plant flora of the Detroit Lakes was dominated by slender naiad [*Najas flexilis* (Willd.) Rostk. & Schmidt], based on paleolimnological studies (Birks et al. 1976). After cultural eutrophication from domestic sewage and agricultural development, coontail (*Ceratophyllum demersum* L.), pondweeds (*Potamogeton* L. spp.), and spiral ditchgrass [*Ruppia cirrhosa* (Petagna) Grande] became dominant (Birks et al. 1976).

Distribution of Flowering Rush and Native Plants. The distribution of flowering rush and native plants was evaluated using a point intercept method in which a grid of 830 sampling points 150 m apart throughout the Detroit Lakes system (Figure 1) was generated using GIS from the shoreline to a depth of 7.7 m. A global positioning system (GPS) was used to navigate to each point (Madsen 1999). The points were surveyed in late July and early August of both 2010 and 2011. At each point, the presence or absence of all plant species was recorded, and depth was measured at that point, as per a point intercept method. All data were recorded on a GPS device (Trimble Yuma, Sunnyvale, CA). Species presence was examined by deploying a weighted plant rake on a rope. Depth was measured using either a sounding rod or an electronic depth finder. Because the lake level is maintained
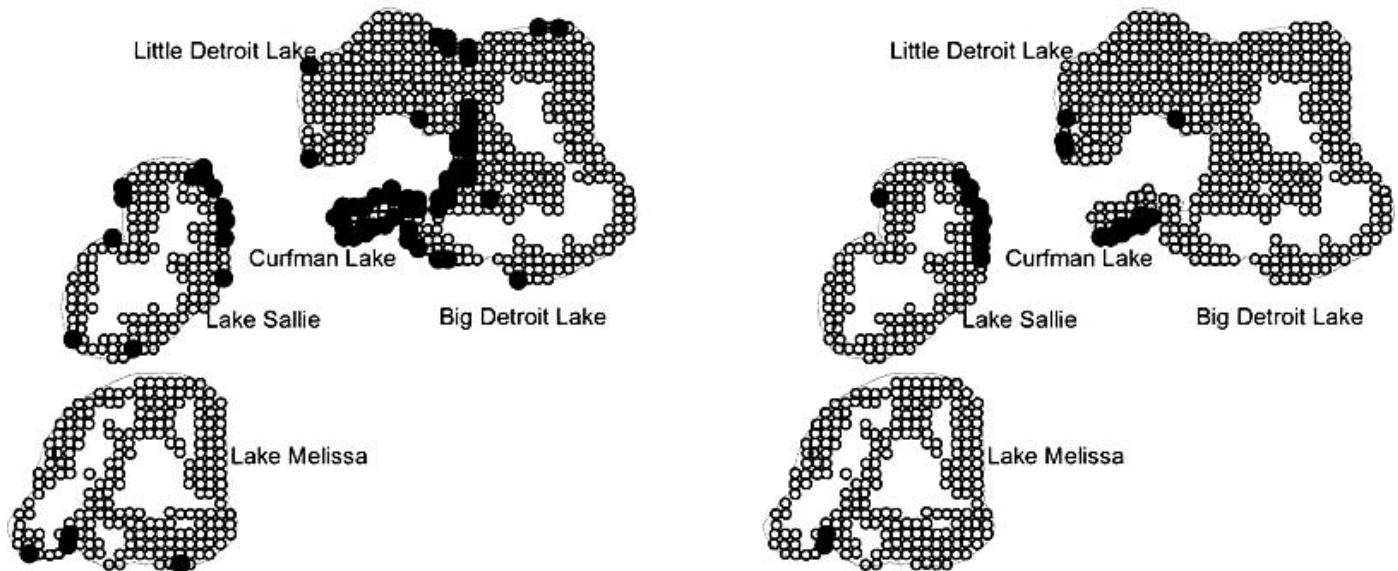
A. Flowering Rush

B. Hardstem Bulrush

Figure 1. Locations of (A) flowering rush and (B) hardstem bulrush in Detroit Lakes system from a survey in 2011. Open circles indicate survey points at which those species were absent, and closed circles indicate locations at which those species were present.

at a relatively fixed level, the purpose of repeating the survey was to collect additional data resolution and evaluate any potential interannual fluctuations.

For each basin, the frequency of occurrence was compared for 2010 and 2011 using a Cochran–Mantel–Haenszel test (Stokes et al. 2000; Wersal et al. 2010). An association analysis on flowering rush and native plant species was used to indicate whether the distribution of flowering rush was positively or negatively associated with either hardstem bulrush specifically, or the occurrence of native plant species in general (Madsen et al. 1994).

Analysis of Allocation with Depth. In midsummer of 2011, we sampled 10 transects around two adjoining basins (Big Detroit and Curfman Lakes) with a gradual slope from 0.3 to 3.0 m water depth (or maximum extent of flowering rush), with three samples at each 0.3-m depth interval. Samples at each depth interval were collected using a 15-cm (6-in)-diam core sampling device, with an area of 0.018 m^2 (0.19 ft^2) (Madsen 1993a; Madsen et al. 2007), and sorted into roots or rhizomes, submersed leaves, emergent leaves, and inflorescences. The number of rhizomes, ramets, rhizome buds, inflorescences, and bulbils was also recorded. Nondestructive observations were taken at each point to note plant height, water depth, height of leaf emergence, presence of inflorescences, and presence of

buds. Plants were washed, sorted into component parts noted above, and dried in a forced-air oven at 50 C (122 F) for at least 48 h. Plants were weighed and results converted to biomass (g dry weight [gDW] m^{-2}). Polynomial regression analysis was used to determine the relationship between water depth and flowering rush biomass or density. Regression models were sequentially fitted, beginning with a linear model. Polynomial terms were then added one at a time, and lack of fit determined using partial t tests.

Results and Discussion

Distribution of Flowering Rush and Native Plants. A total of 31 plant species were observed in the Detroit Lake system (Madsen et al. 2012), but only 19 were found at more than 1% of the points in the system (Table 1). The occurrence of some species was fairly static for both years within a given basin, whereas other species varied significantly between the two years. The most common species were found in all five basins (Table 1). Although a number of species are of interest for habitat and conservation, the focus of these discussions will be the invasive flowering rush and the native hardstem bulrush. Interannual differences can be due to a number of factors,

Table 1. Plant species percent frequency of occurrence in the Detroit Lake littoral zone system-wide for 2010 and 2011 based on point intercept surveys. Points are in water depths of 7.7 m or less. Only species of 1% frequency or greater are listed. P value given for comparison between years by a Cochran–Mantel–Haenszel statistic. An "X" in the column beneath the basin name indicates that the species was observed in that basin. A detailed analysis by basin is available elsewhere (Madsen et al. 2012).

Scientific name	Common name	2010	2011	P value	Big Detroit	Little Detroit	Curfman	Sallie	Melissa
Butomus umbellatus L.	Flowering rush	8.4	8.2	0.47	X	X	X	X	X
Ceratophyllum demersum L.	Coontail	25.3	17.8	< 0.0001	X	X	X	X	X
Chara L. spp.	Chara algae	57.9	55.4	0.17	X	X	X	X	X
Drepanocladus (Müll. Hal.) G. Roth spp.	Drepanocladus moss	3.4	6.0	0.0069	X	X	X	X	X
Elodea canadensis Michx.	Elodea	5.2	2.9	0.013	X	X	X	X	X
Lemna trisulca L.	Star duckweed	3.8	4.7	0.23	X	X	X	X	X
Myriophyllum sibiricum Komarov	Northern watermilfoil	20.9	17.7	0.057	X	X	X	X	X
Najas flexilis (Willd.) Rostk. & Schmidt	Slender naiad	20.5	22.2	0.22	X	X		X	X
Potamogeton foliosus Raf.	Leafy pondweed	1.7	4.2	0.0016	X	X		X	X
Potamogeton illinoensis Morong	Illinois pondweed	9.4	6.6	0.024	X	X	X	X	X
Potamogeton praelongus Wulfen	Whitestem pondweed	3.7	5.2	0.093	X	X	X	X	X
Potamogeton richardsonii (A. Bennett) Rydb.	Richardson's pondweed	8.9	10.7	0.12	X	X	X	X	X
Potamogeton zosteriformis Fern.	Flatstem pondweed	10.9	12.2	0.24	X	X	X	X	X
Ruppia cirrhosa (Petagna) Grande	Spiral ditchgrass	1.1	1.8	0.15	X	X		X	X
Ranunculus longirostris Godr.	Longbeak buttercup	1.8	1.8	0.57	X	X		X	X
Schoenoplectus acutus (Muhl. ex Bigelow) Á. Löve & D. Löve	Hardstem bulrush	3.0	2.4	0.28	X	X	X	X	X
Stuckenia pectinata (L.) Börner	Sago pondweed	17.4	13.6	0.019	X	X	X	X	X
Utricularia macrorhiza Le Conte	Common bladderwort	23.8	25.8	0.19	X	X	X	X	X
Vallisneria americana Michx.	Water celery	4.0	8.9	< 0.0001	X	X	X	X	X
No. of observations		833	830						

but no lake-wide management activity was pursued that could cause these particular changes in distribution.

System-wide, 11 of the 19 common species did not change in frequency between 2010 and 2011 (Table 1). Three species (elodea [*Elodea canadensis* Michx.], Illinois pondweed [*Potamogeton illinoensis* Morong], and sago pondweed [*Stuckenia pectinata* (L.) Börner]) decreased significantly in frequency, and five species (coontail, *Drepanocladus* sp., northern watermilfoil [*Myriophyllum sibiricum* Komarov], leafy pondweed [*Potamogeton foliosus* Raf.], and American eelgrass [*Vallisneria americana* Michx.]) increased in frequency.

Aquatic plant communities in lakes can be dynamic, with species increasing or decreasing without noticeable direct effect from human activity. These changes, therefore, are not necessarily the result of direct or indirect human efforts. Mean water temperature, length of growing season, and other environmental factors are major factors in driving the variation of individual species abundance and distribution (Mäemets et al. 2006). Lake aquatic plant communities may be quite stable for decades, or may

change progressively or rapidly depending on environmental variability and disturbance (Hobbs et al. 2012; Pot and ter Heerdt 2014). In prairie lakes, whether shallow or deep, these changes are often driven by water clarity and abundance of algae (Blindow et al. 2014; Hansel-Welch et al. 2003).

The frequency of flowering rush did not change in any of the five lakes between 2010 and 2011 (Table 1). The proportion of littoral zone covered was highest in Curfman Lake followed by Big Detroit Lake, although this was not tested statistically (Figure 1A; Table 1). Hardstem bulrush likewise did not change in frequency in the Detroit Lake system (Table 1). Proportion of littoral zone covered by hardstem bulrush was greatest in Curfman Lake, followed by Sallie Lake (Figure 1B; Table 1).

Flowering rush was found from the shore out to a depth of 4.5 m, with most plants found at 1.0 to 1.3 m depth (Figure 2). This represents a significant overlap with hardstem bulrush, which was found from shore to 1.5 m, with most plants found in 0.6 to 1.3 m water depth (Figure 2). Flowering rush and hardstem bulrush co-occur more
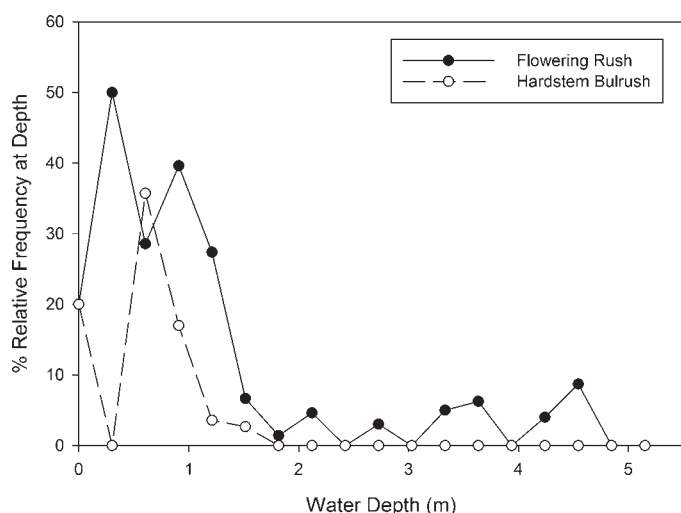
Figure 2. Frequency of points by depth (m) at which flowering rush and hardstem bulrush were present for all five basins in the Detroit Lake system in 2011.

often than a statistically neutral model would predict, with a correlation coefficient of 0.36 (Table 2). Management of flowering rush will involve interaction in habitats occupied by hardstem bulrush. In fact, most hardstem bulrush habitats in the Detroit Lake system have been invaded by flowering rush.

An analysis of the occurrence of flowering rush and the presence of any native plant species indicates that the vast majority of flowering rush occurs in the company of native plants (Table 3). Although there is a persistent meme that invasive plants only invade areas that are disturbed and have lost native plants (Alpert et al. 2000; Burke and Grime 1996; Maron and Marler 2007), this is not necessarily the case with flowering rush. Flowering rush establishes and succeeds in sites already inhabited by native plants, as seen with some other terrestrial (Stohlgren et al.

Table 2. Two-by-two table cross-tabulating the occurrence of flowering rush with hardstem bulrush from a 2011 survey of the Detroit Lake system. Number indicates the frequency of occurrence, and column or row totals on the edges indicate total presence or absence of the species. Numbers in parentheses are cell row percent frequencies. Chi-square test is significant at the P < 0.0001 level and a correlation coefficient of 0.36.

	Hardstem bulrush absent	Hardstem bulrush present	Total
Flowering rush absent	754 (99%)	8 (1%)	762 (92%)
Flowering rush present	53 (77%)	16 (23%)	69 (8%)
Totals	807 (97%)	24 (3%)	831 (100%)

Table 3. Two-by-two table cross-tabulating the occurrence of flowering with the occurrence of any native plant (Native cover) from a 2011 survey of the Detroit Lake system. Number indicates the frequency of occurrence, and column or row totals on the edges indicate total presence or absence of the species. Numbers in parentheses are row percent frequencies. Chi-square test is significant at the P < 0.0001 level and a correlation coefficient of 0.15.

	Native cover absent	Native cover present	Total
Flowering rush absent	202 (27%)	560 (73%)	762 (92%)
Flowering rush present	2 (3%)	67 (97%)	69 (8%)
Total	204 (25%)	627 (75%)	831 (100%)

1999, 2003), riparian (Quinn and Holt 2009), and aquatic (Capers et al. 2007) invasive plants. Managing invasive plants may assist in maintaining plant species diversity (Getsinger et al. 1997), and relying on diverse native plant communities to resist plant invasions without monitoring and management may not prove effective in the long term (Quinn and Holt 2009).

Analysis of Allocation with Depth. All data across transects were analyzed together; we did not analyze individual transects because biomass was highly variable. Total plant height, from the bottom to tip of the leaf, increased fairly linearly from 0.3 to 3.0 m water depth, but plant height increases more slowly at depths beyond 1.3 m (Figure 3A). Emergent plant height averaged around 40 cm above water level from 0.3 to 1.3 m water depth and then declined to almost zero below a depth of 1.6 m (Figure 3B). This result has significant implications for foliar applications of aquatic herbicides to flowering rush. Plants in water deeper than 1.3 m feet typically do not have leaf material extending above the water surface, yet plants can be found out to 3.0 m water depth or more. Further studies examining the ratio of leaf material above and below water are needed to provide an effective recommendation for the depth to which foliar applications should be made. Increased water depth resulted in increased leaf height in both common cattail (*Typha latifolia* L.) and southern cattail (*Typha domingensis* Pers.) but was compensated by increased allocation to leaves over rhizomes in common cattail and by decreased density and increased ramet size in southern cattail (Grace 1989).

Peak aboveground biomass of flowering rush (Figure 4A) was observed at a depth of 1.0 m, averaging almost 450 gDW m^{-2}. In plots ranging from 0.5 to 1.5 m,
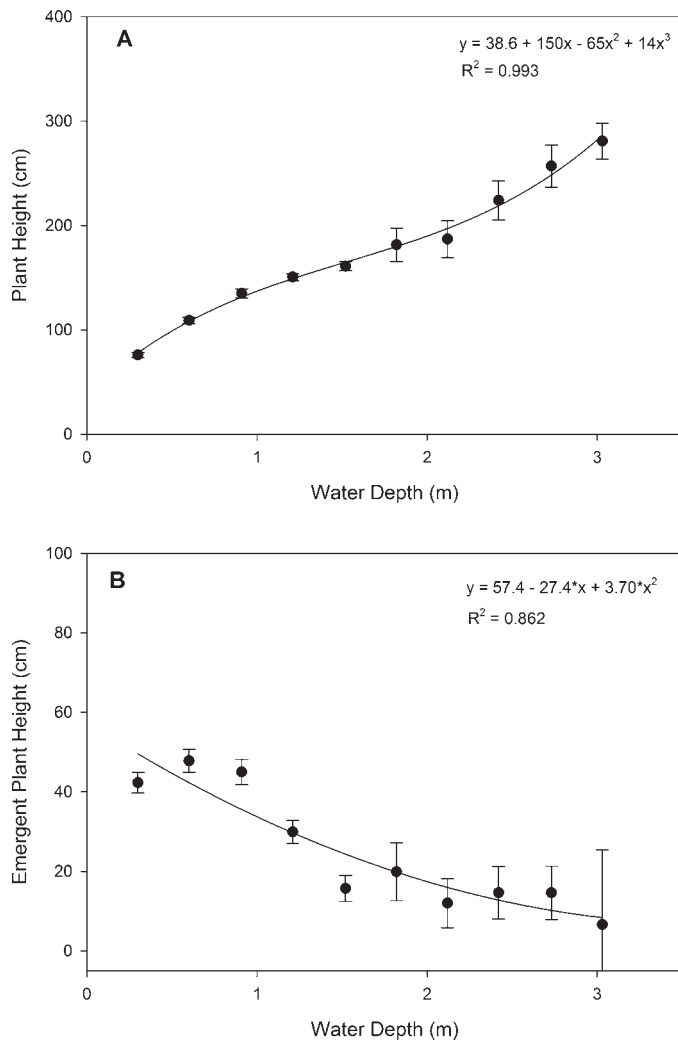
Figure 3. Flowering rush plant height (cm) for samples collected along depth transects in Detroit Lakes in 2011. (A) Flowering rush total plant height (cm from bottom to tip of leaf) by depth (m) and (B) flowering rush plant height (cm) above water surface ("emergent") by depth (m). Bars represent ± 1 standard error of the mean for a given depth.

Figure 4. Flowering rush biomass (g dry weight [gDW] m^{-2}) for biomass samples collected along depth transects in Detroit Lakes in 2011; (A) flowering rush aboveground biomass (gDW m^{-2}) by water depth (m); (B) flowering rush belowground biomass (gDW m^{-2}) by water depth (m). Bars represent ± 1 standard error of the mean for a given depth.

aboveground biomass was found to peak in July, reaching up to 500 gDW m^{-2} (Marko et al. 2015). Aboveground biomass was strongly but negatively related to water depth, particularly in water depths greater than 1.0 m. Aboveground biomass falls to less than 100 gDW m^{-2} at water depths of 1.6 m or greater. This would support the observation that nuisance problems are most common at water depths of 1.3 m or less.

Interestingly, belowground biomass almost linearly declined with depth from 0.3 to 3.0 m (Figure 4B). Water depth strongly reduced the stolon and sediment root production of parrotfeather [*Myriophyllum aquaticum* (Vell.) Verdc.] in a controlled experiment (Wersal and M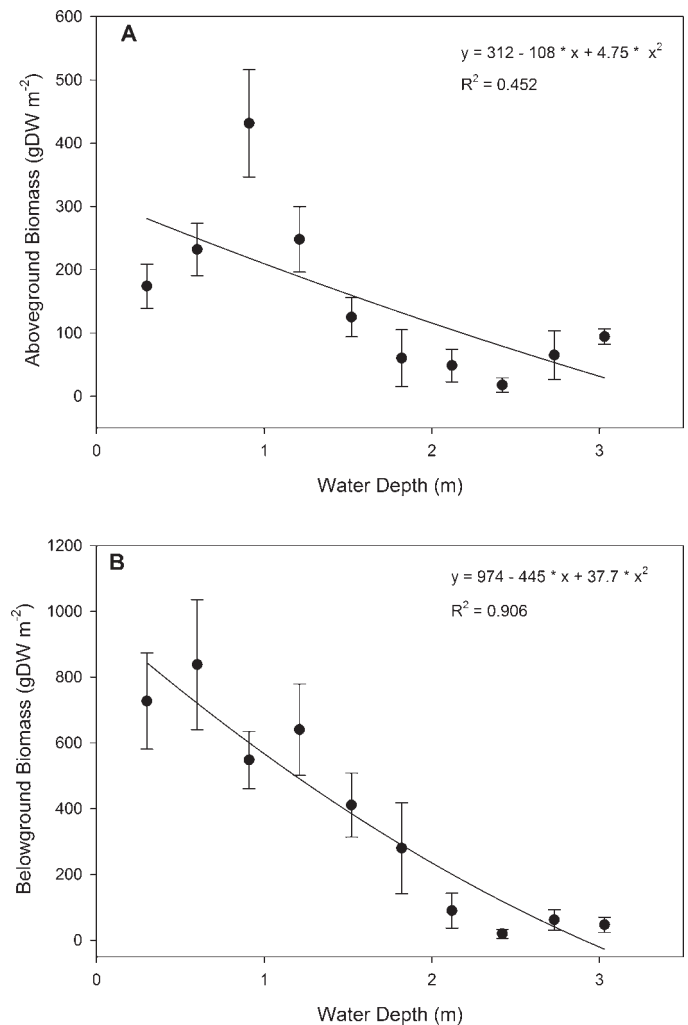adsen 2011). A flowering rush ramet is a single clump of leaves that grow from a bud. Although they look like distinct clumps above the sediment, they may or may not be connected by rhizomes below the sediment surface. Ramet density was strongly inversely related to water depth (Figure 5A), but this may also follow more of a broken stick model or sigmoid model, with relatively constant density in water depths from 0.3 to 1.3 m and a lower plateau of density at water depths of 1.6 m and greater. A similar response of reduced ramet density with increased water depth has been observed for blue cattail (*Typha* × *glauca* Godr. (pro sp.) [*angustifolia* or *domingensis* × *latifolia*]) (Waters and Shay 1992), common and narrowleaf (*Typha angustifolia* L.) cattails (Grace and Wetzel 1981), and southern cattail (Grace 1989).
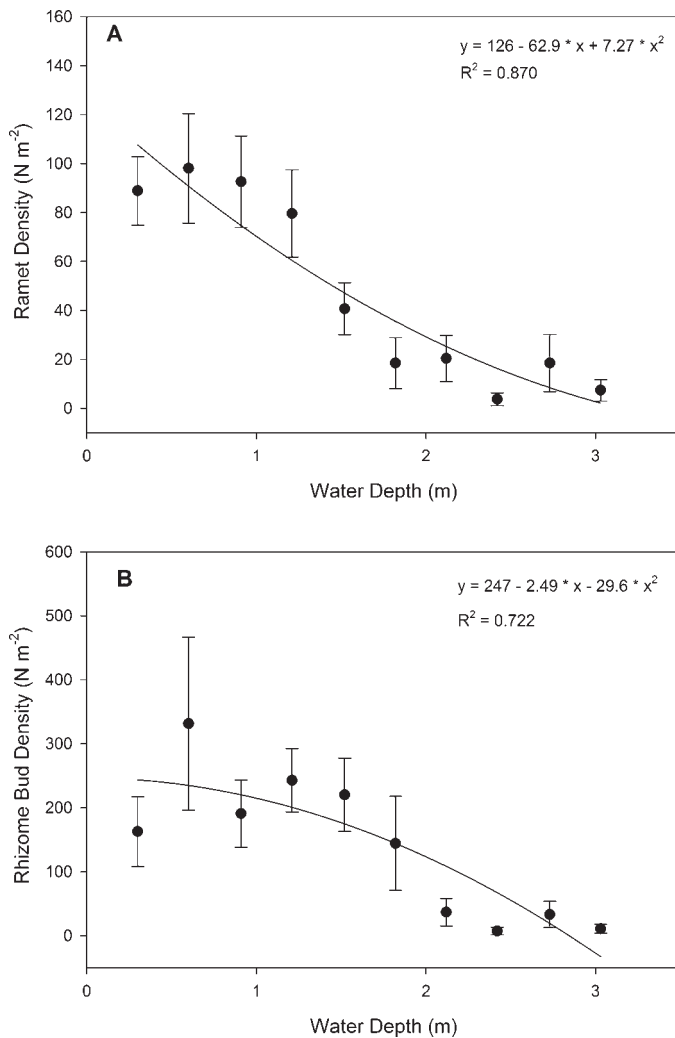
Figure 5. Flowering rush densities (N m^{-2}) for biomass samples collected along depth transects in Detroit Lakes in 2011; (A) flowering rush ramet density (N m^{-2}) by depth (m); (B) flowering rush bud density (N m^{-2}) by water depth (m). Bars represent $\pm$ 1 standard error of the mean for a given depth.

Through time, flowering rush can grow to very high densities that form a turf or mat of plants (Madsen et al. 2012). This mat may separate and float on the surface, or more commonly, sediments may accumulate and the plants grow above, causing a filling of the littoral zone. In some areas, the ramet bases were several feet above the hard-bottom base, which we determined using a sounding rod. Flowering rush may be an ecosystem engineer, causing the filling in of the margins of a lake (Jones et al. 1994, 1997; Wright and Jones 2006).

Rhizome density is highly variable, in part because rhizomes break easily, creating a large number of pieces (Madsen et al. 2012). These rhizome segments can initiate new growth and may act as propagules when dislodged by feeding waterfowl or wave action.

Unlike rhizome segments, flowering rush buds on the rhizome are not affected by breakage. Each bud represents a potential new ramet. Bud densities were negatively related to water depth, though bud densities were not significantly different in water depths between 0.3 and 1.6 m (Figure 5B). The mean number of buds was, in one depth range, more than 300 buds m^{-2}. Densities of more than 500 buds m^{-2} in late August 2011 were found in thick flowering rush plots ranging from 0.5 to 1.5 m depth (Marko et al. 2015). Bud densities and rhizome biomass were found to remain high over winter, indicating these buds are ready to disperse throughout the year when conditions are suitable (Marko et al. 2015). Little research has been done on the population biology, dormancy, or dispersal and spread of flowering rush, yet this has a significant potential effect on the development of early detection and rapid response strategies or other management approaches. In developing a coherent ecological strategy for managing invasive plants, overwintering and dispersal propagule(s) are the key (Madsen 2007). For waterchestnut (*Trapa natans* L.), this is the seed; for curlyleaf pondweed (*Potamogeton crispus* L.), it is the turion; for hydrilla [*Hydrilla verticillata* (L. f.) Royle], it is the subterranean and axillary turions (Madsen 1993b, 2007; Netherland 1997; Woolf and Madsen 2003). For triploid biotype flowering rush, the key propagule is the rhizome bud.

The study of biomass allocation demonstrated the relationship between water depth and biomass growth and allocation in Detroit Lake flowering rush and documented that flowering rush is most abundant in depths of less than 1.3 m.

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