

Synthesis of Upper Mississippi River System submersed and emergent aquatic vegetation: past, present, and future

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Abstract Altered hydrology resulting from the presence of locks and dams and erosive agricultural land use practices have created conditions that have impacted the growth, distribution, and survival of aquatic vegetation on the Upper Mississippi River System (UMRS). Three inter-related abiotic factors (light transparency, nutrients, and sedimentation) worsened by impoundment and erosive agricultural practices, have played a major role in widespread submersed macrophyte loss in the UMRS. Aquatic vegetation provides food and shelter for biota as well as impacting water quality. Successful efforts to restore aquatic macrophytes on the UMRS have

focused on habitat restoration construction projects and water-level management drawdowns. Currently, the status of aquatic vegetation varies within the UMRS, with most of the aquatic vegetation being found between lower Pool 4 (below Lake Pepin) and Pool 13. Although aquatic macrophytes have varied among locations over the past 17 years, an increase in aquatic plants was apparent in 2007 and 2008. Very little research regarding the role of moist soil and emergent vegetation and their responses to ecological factors has occurred within the UMRS. Future research efforts must continue to focus on understanding the ecological and anthropogenic impacts to all aquatic macrophytes within the landscape of one of the largest river systems in the world.

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Introduction

Aquatic vegetation has been widely recognized to benefit aquatic systems by providing food and shelter for fish, wildlife, and macroinvertebrates (Bellrose & Brown, 1941; Bellrose et al., 1979; Holland & Huston, 1984; Anderson & Day, 1986; Korschgen et al., 1988; Bowyer et al., 2005; Stafford et al., 2007). Submersed aquatic vegetation provides critical nursery habitat for young of the year northern pike

(Holland & Huston, 1984), and was shown to be the principal variable correlated with the density of most fish species on the Upper Mississippi River System (UMRS) (Johnson & Jennings, 1998). Macrophytes help stabilize aquatic sediments by reducing wave energy and current velocities, allowing suspended material deposition, reducing sediment resuspension, and improving water clarity (Madsen et al., 2001). Uptake of carbon and nutrients by aquatic vegetation inhibits nuisance algal blooms (Barko & Smart, 1981), and plays a critical role in the metabolism and energy flow within the ecosystem (Eckblad, et al., 1984; Barko et al., 1991).

Locks and dams were built during the 1930s throughout the UMRS which includes the Mississippi River from Minneapolis, Minnesota to Cairo, Illinois, and the Illinois River (Theiling & Nestler, 2010). These structures created permanent impoundments, flooding much of the lowlands and creating vast areas of shallow water. This new habitat initially allowed for the establishment and expansion of large vegetation beds (Green, 1960). Within the Upper Mississippi River National Wildlife and Fish Refuge located between Wabasha, Minnesota and Princeton, Iowa, a lush growth of vegetation persisted for three decades following dam construction, before aquatic macrophyte communities began to decline (Peck & Smart, 1986). Dams increased trapping efficiency of fine sediments in off-channel areas, particularly backwaters where flows substantially decreased from the main channel (Peck & Smart, 1986). As a result, flocculent substrates accumulated in backwaters. The increased sedimentation rates made rooting difficult (Barko & Smart, 1986) and buried submersed plant beds (Rogers, 1994). Wind- and boat-generated waves re-suspended loose substrate, increasing turbidity and decreasing light transparency (James et al., 2004). Despite the impairments experienced by most of the UMRS from increased rates of sedimentation, areas that were once too deep for aquatic vegetation in Pool 19 near Keokuk, IA, accumulated enough sediment to decrease water depths and allow for expanding populations of aquatic macrophytes through the 1970s and 1980s (Steffeck et al., 1985; Tazik et al., 1993).

Operation of the locks and dams on the Upper Mississippi System is conducted by four separate districts within the U.S. Army Corps of Engineers. Operational procedures differ among the districts.

Most notably, the Rock Island district locates the primary control points at the dam, whereas the St. Paul and St. Louis districts locate their control points mid-pool. Water-level fluctuations resulting from dam operation play a substantial role in aquatic macrophyte presence and abundance with scarce aquatic macrophytes in locations with considerable water-level variability (Lubinski et al., 1991; Theiling et al., 1996).

The Illinois River was also historically abundant in aquatic vegetation, particularly submersed aquatic vegetation, in the lower Illinois River and connected floodplain backwaters during the early 1900s (Kofoed, 1903). Beginning in 1915, beds of submersed aquatic vegetation began to disappear from the backwater lakes and the main-stem river following the diversion of Lake Michigan waters to the Illinois River (Richardson, 1921) and navigation dam construction (Bellrose et al., 1983). By the 1950s, submersed aquatic vegetation had almost completely disappeared from these habitats within the Illinois River (Mills et al., 1966; Sparks, 1984).

Submersed aquatic macrophytes

The amount of submersed aquatic vegetation (SAV) generally declines from upstream to downstream along the UMRS, with the greatest frequency of occurrence in Pools 4 through 13 (Yin et al., 2000, 2004). Likewise, species richness of SAV is reduced from 16 species in Pool 4 to 0 species in Pool 26 (Table 1) (Yin et al., 2000). Currently, the status of aquatic vegetation varies within the UMRS, with most of the aquatic vegetation remaining between lower Pool 4 (below Lake Pepin) and Pool 13. Aquatic vegetation is scarce or absent in many areas above and below this reach, and very few species are found in areas connected to the main stem of the Illinois River. In pools where it is known to occur, aquatic vegetation is most abundant in shallow backwaters. Lower Pool 4, and Pools 8 and 13, are considered successful areas of established submersed aquatic vegetation (Yin, 2008).

Abiotic influences

The following sections will focus on some of the more commonly studied parameters: light, nutrient

Table 1 Submersed and floating-leaved aquatic species occurrence documented by the Long Term Resource Monitoring Program (LTRMP), based on the LTRMP 2002 Annual Status Report (Yin et al., 2004)

Upper Mississippi River System location	Pool 4	Pool 5	Pool 7	Pool 8	Pool 12	Pool 13	Pool 26	Alton	La Grange
Submersed species									
<i>Ceratophyllum demersum</i>	x	x	x	x	x	x			
<i>Chara</i> spp.	x	x	x	x		x			
<i>Elodea canadensis</i>	x	x	x	x	x	x			
<i>Elodea nuttallii</i>									
<i>Heteranthera dubia</i>	x	x	x	x	x	x	x		
<i>Myriophyllum sibiricum</i>	x								
<i>Myriophyllum spicatum</i>	x	x	x	x	x	x			
<i>Najas flexilis</i>	x	x	x	x	x	x			
<i>Najas guadalupensis</i>						x	x		
<i>Najas minor</i>									
<i>Potamogeton crispus</i>	x	x	x	x	x	x			
<i>Potamogeton foliosus/pusillus</i>	x	x	x	x	x	x	x		
<i>Potamogeton nodosus</i>	x	x	x	x	x	x	x		
<i>Potamogeton pectinatus</i>	x	x	x	x	x	x	x		
<i>Potamogeton zosteriformis</i>	x	x	x	x		x			
<i>Potamogeton richardsonii</i>		x	x	x					
<i>Ranunculus longirostris</i>	x								
<i>Ranunculus</i> spp.			x						
<i>Utricularia macrorrhiza</i>	x		x	x					
<i>Vallisneria americana</i>	x	x	x	x	x	x			
<i>Zannichellia plaustris</i>	x	x		x		x			
Rooted floating-leaved species									
<i>Ludwigia peploides</i>							x		x
<i>Nelumbo lutea</i>	x	x	x	x	x	x	x		x
<i>Nuphar variegata</i>	x	x	x	x					
<i>Nymphaea odorata</i>	x	x	x	x	x	x			x

Sampled habitats include backwaters contiguous to the main channel, isolated backwaters, main channel borders, secondary side channels, impounded areas, and Lake Pepin; all of which are regularly influenced by either the Upper Mississippi or Illinois Rivers. Data collected in lakes near La Grange, IL are not influenced by the Illinois River and therefore not presented in this table but are available in Yin et al. (2004)

availability, sedimentation, and episodic drought and flood events that can devastate, or in some cases benefit, aquatic macrophytes.

Light

Light obstruction from turbidity and shading by other vegetative life forms such as filamentous algae, epiphytes, phytoplankton, and floating-leaved species, decrease submersed aquatic plant biomass as well as the maximum depth of plant rooting (Barko et al., 1986). Relatively few field experiments were

conducted on the UMRS that test light transparency and SAV presence and/or growth. However, in Lake Onalaska, Pool 7, UMRS, Kimber et al. (1995a, b) found that 9% of surface irradiance during the growing season was needed for seedling survivorship, bud production, and tuber production of *Vallisneria americana* Michx. The minimal light requirement for *V. americana* is relatively low compared to the wide range of 4–29% required among other SAV globally (Dennison et al., 1993). Yet 9% surface irradiance is also considerably higher than most algae and phytoplankton, requiring from 0.05 to 2% (Dennison et al.,

1993). Another light transparency measurement is turbidity, which measures suspended particles in the water column and blocks light. Biomass of *V. americana* was most abundant in sampled areas of Pool 8 when turbidity readings were <20 nephelometric turbidity units (NTU) (Kreiling et al., 2007). Likewise, according to data collected from the Long Term Resource Monitoring Program (LTRMP), submersed aquatic vegetation in side channels and main channel border areas of the Upper Mississippi River have a noticeably higher frequency of occurrence when turbidity measurements are below 20 NTU compared to areas above 20 NTU (Fig. 1). Specific field testing of light requirements for other SAV species on the UMRS are lacking. However,

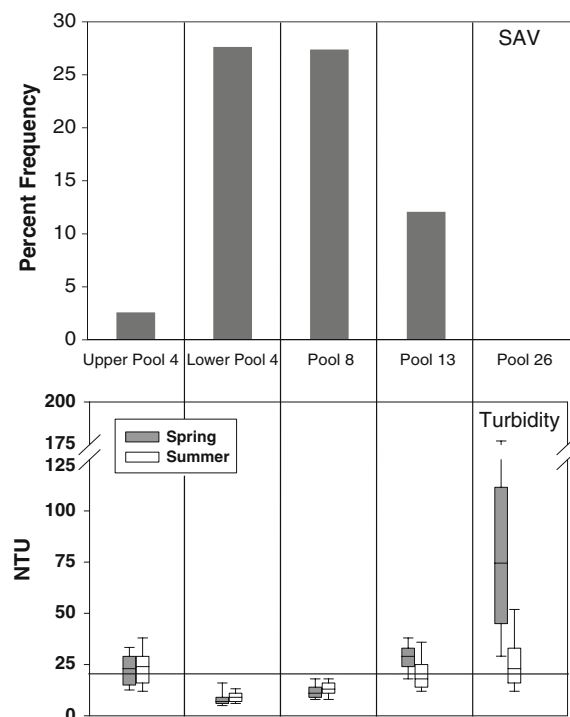


Fig. 1 The top portion of the graph represents mean percent frequency of occurrence of submersed aquatic vegetation (SAV) in side channels and main channel borders of the UMRS from 1998 to 2006. The bottom portion of the graph are box plots of spring and summer turbidity (in nephelometric turbidity units [NTU]) in the main channel from 1998 to 2006 of Long Term Resource Monitoring Program trend pools. A turbidity threshold of 20 NTUs has been suggested by the UMRCC (Upper Mississippi River Conservation Committee) Water Quality Technical Section. Upper Pool 4 is the area of pool above Lake Pepin and lower Pool 4 is the area below Lake Pepin

controlled laboratory experiments (Korschgen et al., 1997; Doyle, 2000; Doyle & Smart, 2001), computer modeling (Best et al., 2001), and field experiments from both national and international locations (Chambers & Kalff, 1985; Dennison et al., 1993; Carter et al., 1994) has provided extensive data for light requirements of other SAV species.

Nutrients

Submersed aquatic macrophytes can use both aqueous and sedimentary nutrient sources. Micronutrients calcium, potassium, magnesium, sulfate, sodium, and chloride are readily available in the water column (Barko et al., 1986). Sediments provide the primary source for nitrogen (N) and phosphorus (P) uptake for rooted macrophytes given the low concentrations in the water column (Barko et al., 1986). Although both N and P have the greatest potential for limiting macrophyte production, P is rarely limiting in many aquatic systems (Barko et al., 1991). However, P has remained a nutrient of interest because of its role in eutrophication.

Research at Lake Onalaska, Wisconsin, indicated that aquatic macrophytes preferred ammonium over other forms as a primary N source; with the greatest concentration of ammonium occurring in the sediment (Barko et al., 1991; Rogers et al., 1995a, b). Nitrogen can be limiting in infertile sediment. Lake Onalaska macrophytes depended on nutrient renewal through a continuous supply of sediment nutrients through sedimentation and other inputs to maintain healthy populations (Rogers et al., 1995a, b). Nutrients adsorbed onto sediment particles or in sediment pore water are taken up by rooted SAV and then released into the water column upon macrophyte tissue senescence, stimulating phytoplankton and algae production. As a result, macrophytes can be viewed as both a source of nutrients as well as a sink. Greater detail regarding nutrient cycling within the UMRS can be found in Houser & Richardson (2010).

Sedimentation

Agricultural land use practices on highly erodible land are a primary cause of sedimentation problems in the UMRS (Soballe & Weiner, 1999). Rates of sedimentation in some locations are 2 cm/year, which if sustained would completely fill some areas of the

UMRS within 50–100 years (Anderson & Day, 1986; Peck & Smart, 1986). Although moderate sedimentation provides nutrient renewal for aquatic macrophytes, excessive sedimentation can result in shading and eventual burial of the plants (Madsen et al., 2001). Sedimentation also provides a surge of nutrients that fosters eutrophication. Anoxic conditions in the surficial sediments increase the release of bound phosphorus into the water column (James et al., 1995), creating the potential for algal blooms. Sediment re-suspension not only contributes to an increase in turbidity and a decrease in light availability, but also can increase nutrient availability to phytoplankton, encouraging production and further exacerbating light attenuation (Madsen et al., 2001). Additional hypothesis driven research is needed for the UMRS to understand sediment and vegetation relationships.

Droughts and floods

Episodic events, such as floods and droughts, appear to coincide with significant SAV loss. Each of these extreme events have occurred in recent UMRS history; a severe drought from 1987 to 1989 (Kimber et al., 1995a, b; Rogers et al., 1995b; Rogers & Theiling, 1999) and the “Great Flood” of 1993 (Theiling, 1999). During the drought, a loss of SAV was documented in Pools 5, 7, 8, 9, 11, and 19 (Rogers, 1994). Fischer & Claflin (1995) documented declines in species richness and biomass from pre-(1975) to post-drought (1991) in Pool 8. Reasons for the rapid loss of SAV during the 3-year drought have yet to be determined, but may include one or both of the following: (1) increased nutrient concentrations in the water column due to low flows and high residence time may have triggered high densities of phytoplankton, epiphyton and filamentous algae (Vis et al., 2007), and (2) decreased nutrient concentrations in the substrate due to low runoff from agricultural landscapes (Rogers, 1994; Rogers et al., 1995a).

The Upper Mississippi River “Great Flood” of 1993 was one of the largest single flood events of the United States (Theiling, 1999). High discharge and current velocity can scour and uproot, or in areas of high deposition can bury aquatic macrophytes. Submersed aquatic vegetation in one Upper Mississippi River backwater, Big Lake of lower Pool 4, experienced a sharp reduction in SAV after the 1993

flood. During summer sampling in Big Lake, SAV was reduced from 63% frequency of occurrence along transects in 1992 to 42% in 1993 and 22% in 1994, a year after the flood (Yin et al., 2000). Although some areas like Big Lake experienced a decline in SAV, other areas may have benefited from the flood. The year following the flood, Spink and Rogers (1996) noted a decline in the invasive *Myriophyllum spicatum* L., and at least partial replacement by *V. americana* and *Zosterella dubia* (Jacq.) Small. in Lake Onalaska, Wisconsin. Increases in bed size and distribution also occurred for *V. americana* throughout the Upper Mississippi River. High water clarity and increased nutrients from sediment deposition were likely causes of high productivity during 1994 (Spink & Rogers, 1996).

Moist-soil and emergent vegetation

Moist-soil vegetation of the UMRS inhabits moist and saturated soil along channels, backwaters, and controlled water management units that are temporarily or seasonally flooded. Emergent macrophyte species are restricted to shallow water depths (<1 m) with limited current velocity (<0.3 m/s) (Peck & Smart, 1986). Organic matter accumulation, macro-invertebrates, and zooplankton increase with diverse emergent vegetation and are key food chain components for fish and waterfowl in the Upper Mississippi River (Flinn et al., 2005). Increased mallard (*Anas platyrhynchos* L.) use was related to increases in moist-soil vegetation in the Illinois River Valley, an important region for migratory waterfowl (Stafford et al., 2007).

Bowyer et al. (2005) describe the dominant moist-soil plants in Pool 25 UMRS and Chautauqua National Wildlife Refuge, Illinois River, following a draw-down. Plants dominant in Pool 25 were of the genus’ *Polygonum* L., *Echinochloa* P. Beauv., *Leptochloa* P. Beauv., *Cyperus* L., *Amaranthus* L., and *Eragrostis* Wolf., whereas dominant species of Chautauqua National Wildlife Refuge, Illinois River, were *Eragrostis hypnoides* (Lam.) BSP., *Leersia oryzoides* (L.) Swartz., *Cyperus erythrorhizos* Muhl., *Cyperus odoratus* L. (*C. ferruginescens*), *Sagittaria calycina* Engelm., and *Echinochloa walteri* (Pursh) Heller. (Bowyer et al., 2005). Clark and Clay (1985) documented *Sagittaria rigida* Pursh. and *Sagittaria*

latifolia Willd. in Pool 9 in open water and backwaters, with higher biomass and densities in open water than in backwaters due to shallow water and finer soil texture. The most extensive documentation of moist-soil and emergent plants identifies at least 55 common moist-soil and emergent species along Pool 19, Hancock County, Illinois (Henry, 1985). Recently, moist-soil vegetation has been suggested as an ecological indicator for optimal flood regime management that could be used to gauge naturalization of our highly modified river pulse (Changwoo et al., 2004).

Limited documentation throughout the UMRS exists regarding the presence and absence of moist-soil and emergent vegetation. Despite the species richness and importance of moist-soil and emergent vegetation for food and habitat along the UMRS, monitoring of the spatial distribution and coverage of moist-soil and emergent plant communities is minimal. Studies of the life histories and ecology of individual native species are lacking, although researchers have focused on the federally threatened decurrent false aster, *Boltonia decurrens* (T. & G.) A. Wood. (Mettler et al., 2001).

Hypothesis driven research for invasive species within the UMRS such as giant reed (*Phragmites australis* (Cav.) Trin.), purple loosestrife (*Lythrum salicaria* L.), and reed canary grass (*Phalaris arundinacea* L.) is minimal or lacking. Strefeler et al. (1996) studied the genetic diversity of *L. salicaria*, and noted that genetic introgression of this invasive from the native *Lythrum alatum* Pursh. may be a contributing factor to the spread of purple loosestrife through adaptive evolution. A study of interspecific competition between reed canary grass and *Echinochloa crusgalli* (L.) P. Beauv. indicated that *P. arundinacea* was more successful than *E. crusgalli* in fluctuating and submersed water conditions (Figiel et al., 1995). Low summer flows along the lower Chippewa River, Wisconsin, provided an environment for *P. arundinacea* that impacted moist-soil plant communities (Barnes, 1999).

Aquatic vegetation management

Aquatic macrophytes play a critical role in energy flow within aquatic systems by processing nutrients and oxygenating the surrounding habitat. Therefore,

they can be considered “biological engineers” that can resolve eutrophication problems (Byers et al., 2006; Caraco et al., 2006). This importance is reflected in the amount of focus and effort expended toward restoration of submersed aquatic vegetation.

Replanting

Efforts to replant SAV, particularly *V. americana* in the UMRS, have had some success (Kimber et al., 1995b). Korschgen & Green (1988) provide detailed restoration requirements for *V. americana* which include determining suitable habitat, harvesting winter buds from a nearby location, bud storage, preparing buds for spring planting, the planting effort itself, and fencing around the restoration site.

Habitat rehabilitation and enhancement projects

If river habitat conditions are not suitable for natural colonization or reintroduction efforts such as replanting, Habitat Rehabilitation and Enhancement Projects (HREPs), and water-level drawdowns are management options to consider. Federal and state agencies are attempting to restore fish and wildlife habitat through HREPs, which include construction of islands, bank stabilization, side channel modification, and backwater flow alteration (U.S. Army Corps of Engineers, 1997). Projects such as island construction can reduce wind fetch, wave action, and current velocity, factors which have been shown to have negative impacts on aquatic macrophyte establishment, growth, and persistence (Keddy, 1982; Best et al., 2001; Madsen et al., 2001). Many HREPs have been successful in increasing both aquatic macrophyte prevalence and species richness within the HREP area of influence (Yin & Langrehr, 2005; Langrehr et al., 2007). In Pool 8 during phase 2 of the HREP island construction projects, island construction was anticipated to influence approximately 275 ha, and in fact did increase aquatic macrophytes from 89 ha in 1998 to 156 ha in 2000 (Langrehr et al., 2007).

Drawdowns

Water-level drawdowns, which mimic the natural hydrograph and slowly reduce water levels following the annual spring pulse, are another restoration option

to enhance aquatic macrophyte growth. Reducing water levels expose shallow area substrates, enabling them to re-consolidate and thus reduce resuspension (Theiling et al., 1996). A reduced water level over slightly deeper aquatic areas improves light penetration and enhances aquatic macrophyte growth (Theiling et al., 1996). Small-scale drawdowns have been used extensively in water management units. These highly managed areas, separated from the negative impacts of the main river channel by levees, have successfully restored moist-soil vegetation and enhanced waterfowl habitat (Bowyer et al., 2005; Stafford et al., 2007).

Riparian areas above the dams, once seasonally exposed and oxygenated prior to construction of the locks and dams, are now perpetually flooded. However, pool-wide drawdowns have exposed substrates for the first time in over six decades. The primary goal of recent pool-wide drawdowns on the UMRS is to stimulate perennial emergent vegetation growth, while maintaining the 2.7 m (9 ft) navigation channel for commercial traffic. Drawdowns also can be an effective management tool for decreasing turbidity by stimulating macrophyte growth, which decreases current velocity causing suspended solids to settle out (Dieter, 1990; James & Barko, 1990, 1994; Madsen et al., 2001). Pool-wide drawdowns were first utilized in Pools 24, 25, and 26 during the summer of 1994 when water levels were lowered 0.18–0.46 m below ordinary stage (Woltemade, 1997). In 2001 and 2002, a pool-wide summer drawdown of 0.46 m (1.5 ft) was conducted in Pool 8, and another summer drawdown of 0.46 m (1.5 ft) in Pool 5 in 2005 (Woltemade, 1997). The second year of the drawdown in Pool 5 in 2006 was terminated early due to low water levels throughout the system. The dewatered area in Pool 8 included over 809 ha and in Pool 5 over 404 ha, but their zones of influence extended beyond the dewatered zone as light was able to reach areas that had been too deep in previous years. The areas influenced by the drawdowns showed an increase in shallow marsh annual and perennial vegetation of 182 and 240 ha, respectively, and an increase in SAV of 47 and 580 ha in Pools 8 and 5, respectively (Woltemade, 1997; River Resources Forum—Water Level Management Task Force, 2007). Plants dominant on the exposed substrates of Pool 8 were *Sagittaria* L. spp.

(primarily *S. latifolia*), *Cyperus* L. spp. (primarily *Cyperus esculentus* L.), *Heteranthera dubia* (Jacq.) MacMil., *L. oryzoides*, *E. hypnoides*, and *Lindernia dubia* (L.) Pennell (Kenow & Lyon, 2008).

Aquatic macrophyte composition is influenced by the timing and duration of receding water during the growing season (Fredrickson, 1991; Kenow & Lyon, 2008). Fredrickson (1991) determined which species would respond well to early, mid, or late season drawdowns in Missouri. Thus, river managers could use plant phenology to their advantage and time a drawdown to produce a desired outcome. For example, if preventing widespread establishment of an early germinating invasive species (e.g. *P. arundinacea*) is the goal, managers can time the drawdown to commence after the peak germination time of the invasive species. Or, efforts to re-establish a submersed plant important to waterfowl (*V. americana*) could plan a drawdown with long duration and possibly commence later in the season (Kenow & Lyon, 2008).

Biological indicators

SAV has been shown to be sensitive to water quality measures such as light and nutrients as well as sedimentation issues. As they are non-mobile and cannot flee from rapid environmental changes (Clayton & Edwards, 2006), SAV provides a mechanism for relating anthropogenic inputs to the health of the UMRS. As a result, SAV can reflect both the long-term trends and short-term episodes within the watershed (Nichols et al., 2000) and can serve as a potential biological indicator of turbidity, nutrient enrichment, and other water quality impairments. Aquatic vegetation indices are currently being developed for the upper impounded reach of the UMRS as an indicator of system health (Langrehr & Moore, 2008). Creation of biological indicators can be a key element in environmental policy development, as it can streamline ecological information (Moog & Chovanec, 2000). The development of such indicators can help reach ecological goals (meeting light and nutrient criteria) and can determine successful implementation of water quality initiatives and/or compliance with environmental laws (Moog & Chovanec, 2000).

Global issues

Since the building of the lock and dam system, the UMRS has witnessed many ecological stresses resulting in reduced aquatic macrophyte presence including: high sedimentation, increased sediment resuspension, high nutrient loading, high phytoplankton and metaphyton biomass, and reduced light transparency. This pattern of ecological change is not unique to the UMRS, and in fact reflects changes that led to the loss of aquatic macrophytes observed in other locations such as Chesapeake Bay, USA (Cercio & Moore, 2001), Bavarian lakes in Germany (Melzer, 1999), Rhine floodplain streams (Trémolières et al., 1994; Thiebaut & Muller, 1999), Danish lakes and streams (Sand-Jensen et al., 2000), and numerous other locations worldwide (Dennison et al., 1993).

Climate change is an issue of international importance, leading to alterations in temperature, rainfall intensity and frequency, and evaporation rates that will impact every ecosystem to some extent (Moss et al., 2003). How such climate changes impact aquatic macrophytes need to be considered. Analysis of long-term datasets can provide clues about climate change effects (Van Donk et al., 2003), such as the movement of exotic species northward. The LTRMP data of the UMRS may be valuable for determining the movement of plant species northward through long-term datasets.

Major threats to freshwaters worldwide include eutrophication, climate change, and invasion by exotic species. Chambers et al. (2008) believe these threats will lead to less aquatic macrophyte diversity and will threaten fish and wildlife diversity. Coordination and collaboration with researchers on other large river systems worldwide will help promote universal understanding of river functions and how submersed, emergent, and moist-soil vegetation are influenced by such functions.

Synthesis

Aquatic macrophyte presence and abundance was reduced on the UMRS overtime as impoundments aged due to the altered hydrology resulting from construction of the lock and dam system. Three key abiotic factors have had a major impact on growth

and survival of SAV. First, light transparency, a necessity for SAV growth and survival, has been limited by suspended solids in the water column along with shading by periphyton, epiphyton, and filamentous algae. Also, plant nutrients, N and P, are rarely limiting on the UMRS. However, N has been shown to be limiting during periods of drought when there is little nutrient renewal. Phosphorus remains a nutrient of interest because of its role in eutrophication and excessive algal growth. Finally, increases in sediment inputs from agricultural practices and other non-point sources have not only caused decreased water clarity, but have exacerbated eutrophication because of the P adsorbed onto the sediment particles. These three abiotic factors interact and have created a stressful environment for SAV growth and survival.

Floods cause both increases and decreases to UMRS vegetation. Flood benefits include nutrient cycling that increases productivity, resets plant communities, and provides connectivity throughout the aquatic terrestrial transition zone (Junk, 2005). Episodic events, such as floods and droughts, appear to coincide with significant SAV loss on the UMRS. It has been hypothesized that nutrients play a role in SAV declines during drought conditions, in which high concentrations of P can occur in the water column stimulating algal growth, while very low concentrations of N can occur in the sediment pore water, negatively affecting SAV growth. Flood events create turbulent environments through scouring and sheer stress that can be difficult for rooted macrophytes. Also, movement of sediments during flood events has buried macrophyte beds. SAV has been suggested as a biological indicator of UMRS health because of its sensitivity to water quality impairments.

Moist soil and emergent vegetation are important vegetation communities for wildlife, and are primarily influenced by river hydrology. Due to their sensitivity to fluctuating water levels, moist-soil vegetation may act as an ecological indicator of optimal flood regime management. Despite their importance, few published articles have documented the presence, absence, or responses of these communities to ecological factors within the UMRS.

Future research efforts must continue to focus on understanding the ecological and anthropogenic impacts to all aquatic macrophyte communities within the landscape of one of the largest river systems in the world. Climate change, eutrophication,

and invasion by exotic species are among the greatest ecological threats to aquatic macrophytes. Long-term monitoring efforts can not only help us identify timing of changes within the UMRS, but may provide clues to early management options. Habitat restoration projects, drawdowns, and water management units have been effective programs for re-establishing submersed, emergent, and moist-soil vegetation. All efforts to restore aquatic macrophyte abundance and habitat on the UMRS will benefit from more hypothesis-driven research and adaptive management practices.

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