



Understanding Constraints on Submersed Vegetation Distribution in a Large, Floodplain River: the Role of Water Level Fluctuations, Water Clarity and River Geomorphology

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Abstract

Aquatic vegetation is a key component of large floodplain river ecosystems. In the Upper Mississippi River System (UMRS), there is a long-standing interest in restoring aquatic vegetation in areas where it has declined or disappeared. To better understand what constrains vegetation distribution in large river ecosystems and inform ongoing efforts to restore submersed aquatic vegetation (SAV), we delineated areas in ~1200 river km of the UMRS where the combined effects of water clarity, water level fluctuation, and bathymetry appeared suitable for establishment and persistence of SAV based on a 22-year dataset for total suspended solids (TSS), water surface elevation, and aquatic vegetation distribution. We found a large increase in suitable area downstream from a large natural riverine lake near the northern end of the UMRS (river km 1230) that functions as a sink for suspended material. Downstream from river km 895, there was much less suitable area due to decreased water clarity from tributary input of suspended material, changes in river geomorphology, and increased water level fluctuation. A hypothetical scenario of 75% reduction in TSS resulted in only minor increases in suitable area in the southern portion of the UMRS, indicating limitations by water level fluctuation and/or bathymetry (i.e., limited shallow area). These results improve our understanding of the structure and function of large river systems by illustrating how water clarity, fluctuations in water level, and river geomorphology interact to create complex spatial patterns in habitat suitability for aquatic species and may help to identify locations most and least likely to benefit from management and restoration efforts.

Keywords Submersed aquatic vegetation · Water surface elevation · Total suspended solids · River restoration · Upper Mississippi River system

Introduction

Aquatic vegetation plays a central role in large floodplain river ecosystems as it provides critical food and habitat for a diverse assemblage of biota (Caraco et al. 2006; Moore et al. 2010; Gurnell 2014). In addition, aquatic vegetation can affect geomorphology by altering current velocity and sediment resuspension, transport, and deposition (Barko et al. 1991; O'Hare

et al. 2010; Gurnell and Grabowski 2015). Due to its sensitivity to environmental conditions, aquatic vegetation is often used as a biological indicator of water quality impairments (Langrehr and Moore 2008; Grabas et al. 2012; Ciecierska and Kolada 2014).

The distribution and abundance of aquatic vegetation are affected by complex interactions between physical and biological drivers. Primary drivers limiting submersed aquatic vegetation (SAV) include light availability and water level fluctuation. Light availability, a function of depth and water clarity, can limit photosynthetic activity and therefore survival of SAV (Koch 2001; Kemp et al. 2004; Sass et al. 2017). The amount of light required for growth and survival varies by species; however, 1% of surface light is generally referred to as the minimum requirement for SAV and the compensation point for photosynthesis and respiration (Korschgen et al. 1997; Wetzel 2001). For example, Kreiling et al. (2007) found

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that light availability was the primary abiotic determinant of wild celery (*Vallisneria americana* Michx.) distribution and abundance. Submersed aquatic vegetation also requires sufficient depth to remain submersed (i.e., not dewatered by fluctuating water levels) throughout nearly all of the growing season. In many large river systems, SAV species richness is highest in floodplain lakes with small to moderate water level fluctuations (e.g., Rhine and Danube Rivers; Van Geest et al. 2005b; Ot'ahel'ova et al. 2007). Yin and Langrehr (2005) found that more than 80% of the variance in SAV prevalence in floodplain lakes was associated with water level fluctuation and water clarity.

Submersed aquatic vegetation provides critical habitat, food, and refuge for many organisms and also has a strong influence on water quality. Submersed aquatic vegetation improves water clarity by stabilizing substrates and reducing resuspension from wind and watercraft-generated waves, which further promotes the persistence and expansion of aquatic vegetation beds (Madsen et al. 2001; De Jager and Yin 2010). Density of SAV has been shown to be positively correlated with fish density, likely due to the rich invertebrate fauna that supports small forage fish as well as important nursery habitat and refuge from predators for young of the year fish (Holland and Huston 1984; Johnson and Jennings 1998; DeLain and Popp 2014). Submersed aquatic vegetation also represents an important food resource for migrating waterfowl (Korschgen and Green 1988; Stafford et al. 2007; Bouska et al. 2020).

Like other large river systems, the Upper Mississippi River System (UMRS) has been heavily managed (Fremling 2005) and has been degraded (Johnson and Hagerty 2008; McCain et al. 2018). The locks and dams constructed in the 1930s to enhance commercial navigation substantially altered the distribution and characteristics of aquatic environments, particularly in the Upper Impounded Reach where the modern river is characterized by large impounded areas and increased connectivity between river channels and floodplain lakes. These expanded off-channel areas and island complexes initially supported a diverse ecosystem with abundant aquatic vegetation. However, over time this diverse ecosystem began degrading, as island complexes eroded and sedimentation as well as sediment resuspension impaired habitat and water quality. There were substantial declines in aquatic vegetation beginning in the late 1980s (Rogers 1994; Fischer and Clafin 1995), but in some reaches of the river, there has been a subsequent recovery (Carhart and De Jager 2018; Bouska et al. 2020; Burdis et al. 2020). Nevertheless, aquatic vegetation remains scarce in many reaches of the UMRS today (Navigation Pools 1–3 and 14–26 and on the Illinois River; De Jager and Rohweder 2017; De Jager et al. 2018). In areas where aquatic vegetation has not returned, restoring aquatic vegetation remains a river restoration priority (Sparks 2010; USACE 2010; McCain et al. 2018; Bouska et al. 2020).

There is substantial spatial and temporal variation in water clarity and water level fluctuation within and among UMRS reaches (De Jager et al. 2018). In the lower reaches of the UMRS, magnitude and variation in river discharge have increased substantially from pre lock and dam conditions, likely reflecting changes in climate, watershed land use, levees, and river control structures (Sparks et al. 1998; Frans et al. 2013; De Jager et al. 2018). Floodplain levees are common in the lower UMRS and constrain the water storage capacity, causing larger water level fluctuations per unit discharge (Sparks et al. 1998; De Jager et al. 2018). Total suspended sediment concentrations also tend to be highest in the lower reaches of the UMRS (Houser et al. 2010). In the upper reaches, water level fluctuations are smaller because the floodplain is more connected, allowing increases in discharge to spread out over a larger area. The upper reach also benefits from a large natural riverine lake near the northern end of the UMRS (river km 1230) that functions as a sink for suspended material. Water clarity, sediment load, and discharge can be substantially affected by precipitation patterns and tributary input. Past and continued installation of drain tiles in these agriculture-dominated watersheds increases the speed and volume in which precipitation in the drainage basin is delivered to the river (Schottler et al. 2013).

Here we focus on the combined effects of water clarity, geomorphology (depth distribution), and water level fluctuations as these provide known constraints on where SAV can establish and grow. Specifically, we delineate areas in the UMRS where the combined effects of these conditions are not likely to limit establishment and persistence of SAV. In areas where these factors are unsuitable, vegetation is unlikely to establish; in areas where these factors are collectively suitable, other physical and biological factors such as current velocity, herbivory, and bioturbation can further limit SAV (Theiling et al. 2015; Wood et al. 2016; Sass et al. 2017). To improve our understanding of how changing river conditions may affect SAV distribution, changes in suitable area associated with hypothetical improvements in water clarity were assessed systemically. A better understanding of where these basic drivers limit SAV colonization and persistence will improve our understanding of the structure and function of large floodplain rivers and help identify locations most and least likely to benefit from management and restoration efforts.

Methods

Study Area

The UMRS, located in the USA, includes the Illinois River (i.e., Illinois Waterway; IWW) from Lake Michigan near Chicago to Grafton, Illinois, and the Upper Mississippi River (UMR) from Minneapolis, Minnesota, to the confluence

of the Ohio River (Fig. 1). This system is commonly divided into four river-floodplain reaches: Upper Impounded Reach (Navigation Pools 1–13), Lower Impounded Reach (Navigation Pools 14–26), Un-impounded Reach (“Open River”), and the Illinois River Reach (all Illinois River Navigation Pools; USACE, 2010). In general, the Upper Impounded Reach is characterized by relatively stable water levels and a substantial area of floodplain lakes that retain a connection to the main channel whereas extensive levees in the Lower Impounded Reach have isolated much of the main channel from backwaters and the floodplain. The Open River Reach (~82 river km) is characterized by the lack of dams, extensive channelization, low water clarity, and greater water

level fluctuation. The IWW follows a similar trend as the UMR, with the upper-most pools generally having more stable water levels and the lower pools containing more levees and greater water level fluctuation (Johnson and Hagerty 2008; De Jager et al. 2018).

Data

Water Surface Elevation

Daily water surface elevation (WSE) data for 22 years (1993–2014) were obtained for 121 gauges (Table S1) from [Rivergages.com](https://www.rivergages.com) (USACE 2019) or directly from the U.S. Army Corps of

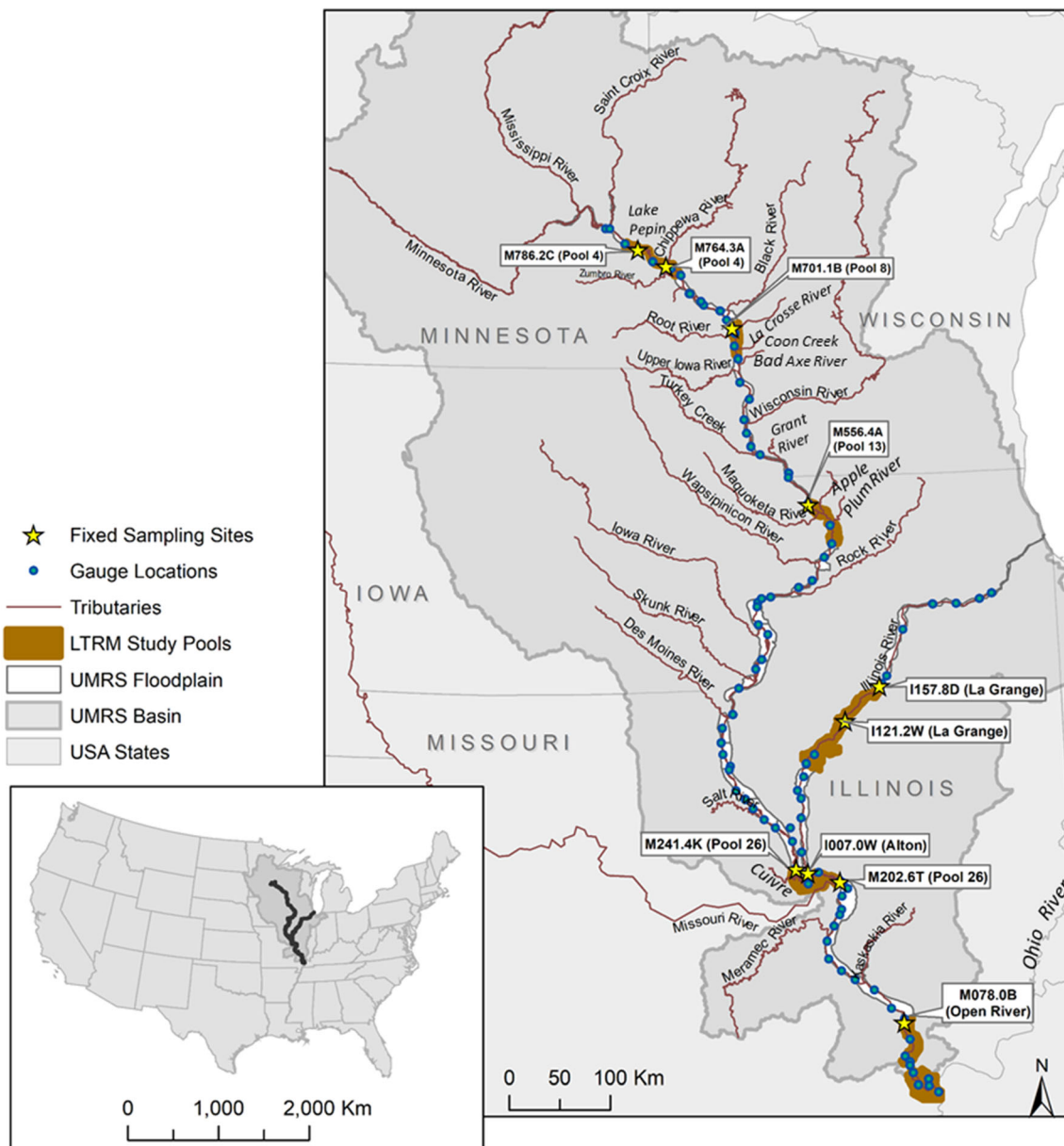


Fig. 1 Location of select main channel fixed sampling sites, gauges, and tributaries of the Upper Mississippi River System (UMRS), USA. Fixed-site sampling occurs within Long-Term Resource Monitoring (LTRM) study pools

Engineers District Water Management Centers. For the St. Paul District, surveys were conducted to determine the adjustment from the National Geodetic Vertical Datum (NGVD) of 1912 to North American Vertical Datum (NAVD) of 1988. For the Rock Island and St. Louis Districts, VERTCON (North American Vertical Datum Conversion) was used in the conversion of datasets from the NGVD of 1929 to NAVD of 1988 to coincide with the datum of the existing UMRS topobathy (UMRR LTRM, 2016). Water surface elevation statistics were summarized for each gauging station (typically 2–4 per pool) for the entire study period (R 2018: Stats package version 3.5). Linear interpolation (R 2018: ImputeTS package version 2.7) was used to estimate missing WSE data for periods shorter than 7 days.

Total Suspended Solids

Standardized research and monitoring are executed at six state-operated field stations (study pools; Fig. 1) as part of the U.S. Army Corps of Engineers' Upper Mississippi River Restoration (UMRR) Program, Long Term Resource Monitoring (LTRM) element (Johnson and Hagerty 2008).

Total suspended solids (TSS) concentration data from 10 UMRR LTRM fixed sampling sites in the UMRS navigation channel (1993–2014; Table 1, Fig. 1) were downloaded from the LTRM database (UMRR LTRM, 2018). Fixed-site sampling (FSS) was conducted biweekly (May–August) and monthly (September) at permanently designated locations (FSS occurred monthly in 2003). Additional information regarding collection methods and sampling design can be found in Soballe and Fischer (2004).

Aquatic Vegetation

Submersed aquatic vegetation data for Pools 4, 8, and 13 (1998–2014) were downloaded from the LTRM database (UMRR LTRM 2018). A minimum of 450 sites in each pool

were sampled annually (June–August) using a stratified random sampling (SRS) design and boat-based vertical rake sampling method. At each site, six subsites (0.3 m × 1.5 m) around the boat were sampled where a modified garden rake was pulled along the sediment surface and SAV caught in the rake teeth was examined for species identification and relative abundance. In addition, water depth at the time of sampling was recorded for each subsite. Submersed aquatic vegetation data (2015–2019) were used to assess model error. Additional information regarding collection methods, including the rake sampling technique, can be found in Yin et al. (2000).

Analyses and Calculations

Describing Aquatic Light Conditions across the UMRS

Suitable light conditions for SAV were estimated by assessing the relationship between the euphotic elevation (bed elevation of 1% surface light penetration) and the lowest bed elevations at which SAV was collected during annual vegetation surveys. Euphotic depth is determined by extinction coefficient which, in the UMRS is primarily determined by TSS. To describe light conditions at a daily time scale, across the entire UMRS, several assumptions and interpolations were necessary.

Daily estimates of TSS during the May–September growing season at each of the 10 fixed sampling sites were obtained using linear interpolation between sample dates (R 2018: ImputeTS package version 2.7). The longitudinal gradient in TSS was approximated by interpolation between each sampling site based on the locations of major tributary confluences, and the long-term average TSS contribution and discharge of those tributaries as reported in Wasley (2000). The magnitude of the change in TSS at each tributary confluence was approximated based on the discharge-corrected TSS contribution from that tributary as a proportion of the total TSS contribution from all major tributaries between those two sampling sites (Table S2; Example S1; Example S2). The change

Table 1 Main channel fixed sampling sites used to collect total suspended solids data in the Mississippi (UMR) and Illinois (IWW) Rivers (1993–2014)

Site	River	Location	River kilometer ^a	Northing	Easting	Dates Available	Description
M786.2C	UMR	Pool 4	1265	4,934,266	543,779	1993–2014	Above Lake Pepin
M764.3A	UMR	Pool 4	1230	4,917,826	571,635	1993–2014	Below Lake Pepin
M701.1B	UMR	Pool 8	1128	4,856,345	637,156	1993–2014	Upper Pool
M556.4A	UMR	Pool 13	895	4,681,070	712,780	1993–2014	LD12 Tail-Upper Pool
M241.4 K	UMR	Pool 26	388	4,319,647	700,637	1993–2014	LD25 Tail-Upper Pool
M202.6 T	UMR	Pool 26	326	4,307,283	744,053	1995–2014 ^b	Below IWW Confluence
M078.0B	UMR	Open River	126	4,167,464	807,933	1993–2014	Upper Open River Reach
I157.8D	IWW	La Grange	254	4,501,489	783,249	1993–2014	Upper Pool
I121.2 W	IWW	La Grange	195	4,466,765	749,108	1993–2014	Mid-pool
I007.0 W	IWW	Alton	11	4,315,756	712,523	1993–2014	Above UMR confluence

^a In the IWW, river km refers to the distance upstream from the confluence of the Mississippi River. In the UMR, river km refers to the distance upstream from the confluence of the Ohio River ^b TSS measurements from fixed site (M196.9Q; river km 317) were used to fill in missing data (1993–1994)

in TSS between any two sampling sites was distributed among intervening tributaries accordingly and incorporated into the calculations at the nearest gauge downstream from the tributary confluences. Due to the lack of any LTRM data upstream from Pool 4 of the Upper Mississippi River (UMR), TSS at all gauges in Pool 3 were estimated using values from the upper Pool 4 sampling site. The main determinant of TSS in this reach is inflow from the Minnesota River (Fig. 1), and because all of Pool 3 is downstream from that confluence, the extrapolation of Pool 4 TSS upriver is reasonable. There were no tributary inputs accounted for in the IWW by Wasley (2000) and therefore, longitudinal TSS changes were treated as occurring at the nearest gauge downstream from a sampling site. Due to the lack of TSS data in the upper IWW, TSS in the Dresden, Marseilles, Starved Rock, and Peoria Pools were estimated using values from the upper La Grange Pool sampling site (Fig. 1). Extrapolating TSS measurements upstream from a sampling site is not ideal; however, TSS concentrations in the upper IWW pools are likely similar to or lower than those at the La Grange Pool sampling site. We note that the resulting predicted suitable area in the IWW and Pool 3 are therefore conservative in extent.

Daily euphotic depth was estimated from the daily TSS values based on the relationship between long-term TSS and light extinction data at Lock and Dam 8 and 9 (Eq. 1; data from Wisconsin Department of Natural Resources) and transects located in Pools 8 and 13 ($r^2 = 0.75$, Fig. S1; Giblin et al. 2010). These TSS data spanned the range of TSS concentrations typically observed in the Lower Impounded Reach and Illinois River (UMRR LTRM 2018) and therefore, are assumed to be reasonable approximations of the relationship between euphotic depth and TSS throughout the UMRS.

$$\text{Depth}_{\text{kern2pt0fkern2pt1\%kern2ptlightkern2pt}(m)} = 6.0661 * \text{TSS}^{-0.45} \quad (1)$$

The daily riverbed elevation at the depth of 1% light penetration ($\text{RBE}_{1\%}$) was calculated by subtracting the daily euphotic depth from the daily water surface elevation at each gauge.

Determination of Suitable Conditions for SAV

Here we consider two primary constraints on aquatic vegetation suitability: light environment and water level fluctuation. Light and water level fluctuation conditions necessary for sustaining SAV were initially estimated in Pools 4, 8, and 13 where LTRM vegetation data are collected (hereafter referred to as reference areas). Sites where vegetation was detected and that were within 4.8 river km of the lower two gauges in each study pool were used in the analysis (see Table S1 for gauges used; Fig. S2). This was a large enough area to generate a

sufficient sample size, while also ensuring proximity to the gauges so that the water surface elevation measurements could be reasonably assumed to apply to the included sampling sites. Bed elevation at each site where SAV was detected was calculated by subtracting site depth from daily water surface elevation at the nearest gauge. As outlined above, there are several approximations required for generating these broad-scale estimates of SAV suitability. We used the central 95% of bed elevations where SAV was observed as a conservative estimate of the suitable range for SAV.

We estimated the light conditions suitable for supporting SAV by assessing growing season light conditions at bed elevations where SAV was detected (LTRM vegetation data spanning 1998–2014). Specifically, in the reference areas (Pools 4, 8, and 13) we compared the daily riverbed elevation at the depth of 1% light ($\text{RBE}_{1\%}$; May–September) and the lowest bed elevations where SAV was observed ($\text{RBE}_{\text{obsmin}}$; 1998–2014). There was a relationship between annual median $\text{RBE}_{1\%}$ and annual $\text{RBE}_{\text{obsmin}}$; the average difference between $\text{RBE}_{1\%}$ and $\text{RBE}_{\text{obsmin}}$ was 0.04 m ($N = 102$, $SD = 0.38$ m; Fig. S4). The data were approximately normally distributed with skewness of 0.02. Based on this relationship, we estimated the lower SAV bed elevation ($\text{RBE}_{\text{estmin}}$) at all UMRS gauges by subtracting 0.04 m from the annual median $\text{RBE}_{1\%}$ to reflect SAV detections in LTRM data. The $\text{RBE}_{\text{estmin}}$ for each year represents the bed elevation where at least 1% light reached approximately 75 days out of the 150-day growing season, although more than 1% light was often available (Fig. S3).

In addition to maximum depth constraints on SAV growth, we expect SAV to be limited by dewatering and minimum depth requirements. We analyzed the relationship between growing season WSE and the highest bed elevations where SAV was observed ($\text{RBE}_{\text{obsmax}}$, 1998–2014; Fig. S4) in reference areas. There was a relationship between 10th percentile of annual growing season WSE and $\text{RBE}_{\text{obsmax}}$; the average difference was 0.06 m ($N = 102$, $SD = 0.27$ m). The data were approximately normally distributed with skewness of -0.37 . Using this relationship, we estimated the upper SAV bed elevation ($\text{RBE}_{\text{estmax}}$) at all UMRS gauges by subtracting 0.06 m from the 10th percentile of annual growing season WSE. The 10th percentile, or 90% exceedance, represents low-water conditions and SAV at this elevation would experience some level of dewatering approximately 15 days out of the 150-day growing season.

Spatial Representation of Suitable Conditions

The upper and lower SAV boundary elevations ($\text{RBE}_{\text{estmax}}$ and $\text{RBE}_{\text{estmin}}$) at each gauge define the range of suitable conditions for SAV based on light availability and water level fluctuations, on an annual basis. Between each set of gauges, $\text{RBE}_{\text{estmax}}$ and $\text{RBE}_{\text{estmin}}$ were linearly interpolated by river mile (R 2018: ImputeTS package version 2.7). Elevation

ranges ≤ 0 are treated as zero and indicate that no elevations are suitable in those reaches. The geographic information system software package used for the spatial analysis in this project was ArcGIS version 10.6.1 (ESRI 2019).

A hydrologically enforced river mile polygon data layer (see Rogala 2019) was used to define the spatial extent of each UMRS river mile boundary. This data layer was developed by extending lines from each river mile marker perpendicular to the UMRS floodplain boundary and then extending upstream following the UMRS floodplain boundary to the next river mile. The polygon demarcated upstream from each river mile marker is given the river mile label assigned to the downstream river mile marker. Lateral hydrologic adjustments were then applied to this river mile polygon data layer to capture true water surface elevations of contiguous floodplain lakes. This was done to represent the hydrologic connectivity of these backwater areas more accurately within the floodplain as their connection point to the main channel may often fall within a different river mile polygon than the main body of the backwater area.

To produce a GIS layer of bed elevation within the aquatic areas of the UMRS, we first created a 10-m cell resolution bed elevation raster of the entire UMRS floodplain by averaging the depth values of the underlying 2-m cells from the existing topobathy layer (UMRR LTRM 2016). This bed elevation raster was then clipped to only include unveeved aquatic areas within the UMRS floodplain. Floodplain lakes that are isolated by levees generally have little water exchange with the main channel and therefore are minimally affected by water level fluctuations in the river. Leveed areas were identified using data accessed from the National Levee Database (USACE 2015). In cases where RBE_{estmax} was higher than the land-water boundary elevation defined by the extent of the spatial data layer “Water depth at the 75% exceedance discharge condition” (Rogala 2019), the maximum suitable area was limited to the aquatic extent of the data layer. Areas within the predicted SAV elevation range were identified spatially using the ArcGIS “Con” function and saved to a new data layer representing areas suitable for SAV.

Areas mapped as suitable or not suitable were determined as follows:

If bed elevation $>$ predicted upper elevation limit, then *not suitable* for SAV (dewatered); If bed elevation is within the predicted SAV elevation range, then *suitable* for SAV; If bed elevation $<$ predicted lower elevation limit, then *not suitable* for SAV (insufficient light availability).

There are uncertainties and necessary assumptions in our estimates of RBE_{estmax} and RBE_{estmin} . To assess the possible implications of the assumptions and uncertainties inherent in our estimates of suitable and unsuitable areas for SAV, four scenarios were mapped. These four scenarios assess the uncertainty in the lower SAV boundary elevation (RBE_{estmin}) and the sensitivity to the two main estimated model inputs: bed elevation and TSS.

The annual RBE_{estmax} at each gauge was paired with:

- 1) RBE_{estmin}
- 2) $RBE_{estmin} - 1 \text{ SD}$
- 3) $RBE_{estmin} + 1 \text{ SD}$
- 4) RBE_{estmin} when a 75% reduction in daily TSS was applied

Uncertainty in RBE_{estmin} was calculated as the magnitude of change in suitable area associated with a change in $RBE_{estmin} \pm 1 \text{ SD}$ (0.38 m; derived from the difference between median growing season $RBE_{1\%}$ and RBE_{obsmin}). The sensitivity to TSS concentrations was assessed in a subset of pools that span an informative gradient in geomorphology, water clarity, and magnitude of water level fluctuation (Pools 9, 16, 20, and 25; Table 2). We expanded the pilot analysis to estimate the area suitable for SAV under a system-wide, 75% reduction of daily TSS concentration. This allowed us to identify areas that show a relatively strong (or weak) response to TSS reduction and indicate which areas are likely to respond to improved land-use practices in the catchment or local river restoration actions that reduce TSS.

The uncertainties of RBE_{estmax} were not assessed because those estimates were already limited to include only the aquatic area at low water level as defined in Rogala (2019). We did not explore different water level fluctuation scenarios because restoration efforts that require manipulation of long-term water levels are difficult to implement due to navigation constraints and hydrologic limitations (Kenow et al. 2015).

The spatial analysis was run for all four scenarios, on an annual basis for each pool by river mile (1993–2014). The annual outputs developed for each river mile were subsequently merged into one systemic UMRS dataset for each scenario. These annual systemic UMRS datasets were then merged to create a dataset depicting the total number of years that each 10-m cell was predicted to be suitable for SAV for each scenario. A separate dataset was also developed depicting the percentage of total years ($n = 22$) for each cell that was predicted to be suitable for SAV for each scenario. These datasets are available for download from Rohweder (2020; <https://doi.org/10.5066/P9TWZXVZ>) and can be viewed spatially within the Upper Mississippi River System – Systemic Spatial Data Viewer (https://umesc.usgs.gov/management/dss/umrs_land_cover_viewer.html). A project summary is available at https://www.usgs.gov/centers/umesc/science/understanding-constraints-submersed-vegetation-distribution-a-large-floodplain?qt-science_center_objects=0#qt-science_center_objects.

Evidence suggests that multiple consecutive years of suitable light and depth conditions are needed for the establishment and persistence of SAV. Previous work in the northern reaches of the UMR determined that the TSS water quality standard must be attained in at least 50% of the growing

Table 2 Summary of total suspended solids (TSS) sensitivity analyses for Upper Mississippi River Pools 9, 16, 20, and 25. Median suitable area (ha) for SAV under a range of TSS scenarios (% change) compared to theestimated suitable area \pm 1 standard deviation (SD; \pm 0.38 m) of the estimated bed elevation of 1% light penetration

Pool	- 95%	- 90%	-75%	- 50%	- 1 SD	<i>Estimated suitable area</i>	+ 1 SD	+ 50%	+ 100%	+ 500%
9	9752	9493	8893	8362	8192	7627	5613	6552	5419	2808
16	2998	2036	1098	775	767	567	344	465	397	240
20	1204	705	345	205	225	101	15	64	43	3
25	1959	1282	607	296	349	96	0	31	10	0

seasons to support SAV growth (i.e., 5 growing seasons over 10 years; MPCA 2012). Therefore, we defined suitable areas for SAV as those with suitable light and depth conditions in >50% of years within the period of record.

To assess how well the predictions of suitable and unsuitable areas matched the observed distribution of vegetation in Pools 4, 8, and 13, we overlaid vegetation sampling locations (2015–2019, not included in analysis) on the predicted spatial coverages. Model error was reported for sites containing SAV in areas where the model determined conditions were unsuitable. Error may also occur in areas where the model determined conditions were suitable; however, SAV was not detected during sampling.

Results & Discussion

Spatial Assessment of Suitable Elevation Range, Euphotic Depth, and Water Level Fluctuation

In general, the median bed elevation range suitable for SAV decreased from upstream to downstream in both the UMR and IWW (Fig. 2). The largest change occurred within Pool 4; upstream from Lake Pepin (Pool 3 and the upper section of Pool 4), median suitable elevation ranges were between 0.5 and 1.0 m, while downstream from Lake Pepin, median suitable elevation ranges were near 2.0 m and subsequently decreased downstream (Fig. 2; Fig. S5). Lake Pepin is a natural delta lake located within Pool 4 that is approximately 34 river km in length (Fig. 1). Lake Pepin acted as a major sediment sink that removed approximately 78% of suspended sediment that entered the lake. As a result, water clarity downstream from Lake Pepin is significantly greater than upstream of the lake (Houser et al. 2010; Burdis et al. 2020); median euphotic depth was ~1.0 m upstream from the lake compared to almost 2.0 m downstream from the lake. These results are similar to the estimations reported in Lund (2019).

The rate of decrease in median euphotic depth downstream from Lake Pepin was consistently low until the confluence of the relatively turbid Wisconsin River in Pool 10, where it declined by ~0.24 m (Fig. 2). Tributaries in the Lower Impounded Reach contributed substantial suspended material

into the UMR (Wasley 2000; Kreiling and Houser 2016; Robertson and Saad 2019). The Iowa River (Pool 18), Skunk River (Pool 19), and Des Moines River (Pool 20) tributaries reduced the euphotic depth by approximately 0.10 m each. The shallowest euphotic depths (0.65 m) occurred downstream from Pool 26 at the confluence of the Missouri River, where a 0.30-m decrease in euphotic depth was observed. Due to the non-linear relationship between TSS and euphotic depth, increases in TSS above ~60 mg/l have minimal effects on light penetration and euphotic depth (Fig. S1).

Many reaches that had shallow euphotic depths also experienced large water level fluctuations (e.g., Pools 21–26 and OR; Fig. 2A). For example, in Pools 21–26, median water level fluctuation during the growing season was ~5.0 m and ~3.0 m at the tailwater and pool gauges, respectively (Fig. S6). The Open River Reach experienced fluctuations greater than 7.0 m during the growing season. With water level fluctuations of that magnitude, no area was both submersed throughout the growing season and receiving sufficient light required for the growth and survival of submersed plants.

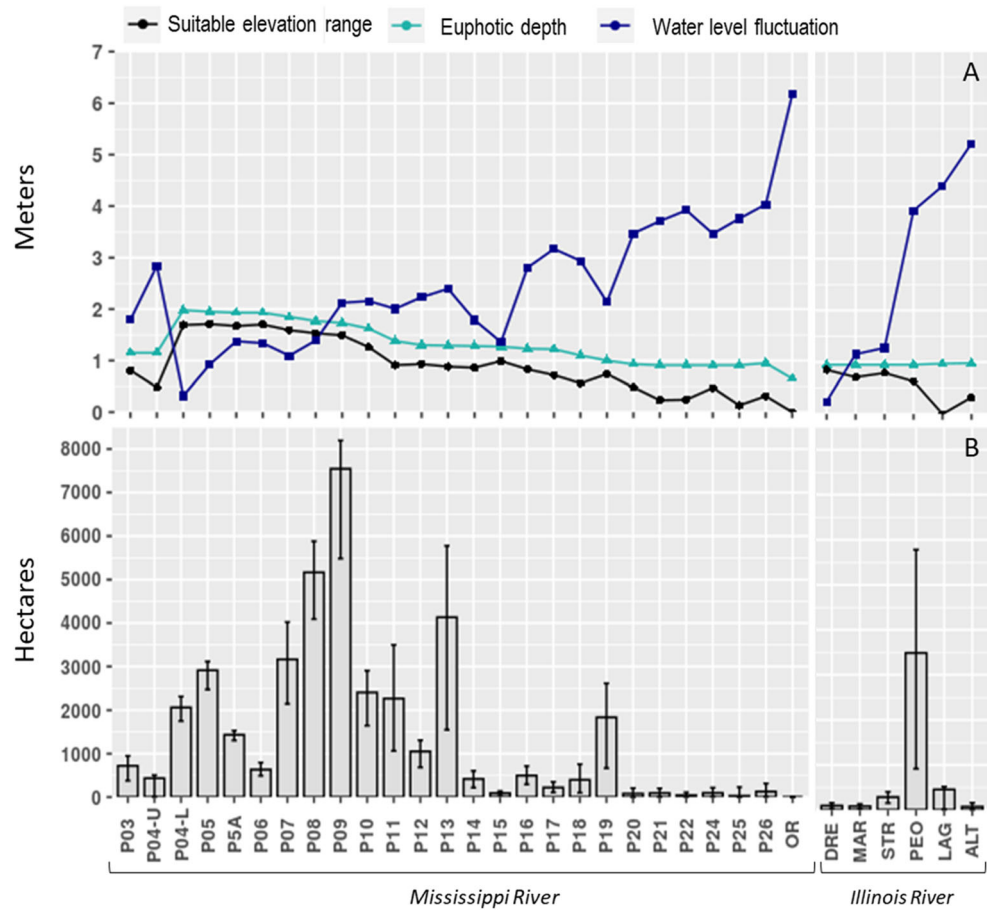
Distribution of Suitable Conditions for SAV

Pool size, bathymetry, and water level fluctuation interact with euphotic depth to determine the suitable area for SAV.

The Upper Impounded Reach contained the largest proportion of suitable area for SAV, corresponding to its relatively low water level fluctuations, deep euphotic depth, and abundant shallow area compared to downstream reaches (Fig. 2). In addition, this reach contained the largest proportion of connected floodplain lakes, which provide optimal off-channel areas for SAV to establish and grow (Fig. 3A). The estimated suitable area varied substantially with changes in suitable bed elevation, especially in the Upper Impounded Reach. Most pools in the Upper Impounded Reach are characterized by large shallow aquatic areas, and therefore the standard deviation in bed elevation (\pm 0.38 m) for this reach corresponds to a larger variation in predicted area (e.g., 565–2014 ha in Pool 9; Table 2; Fig. 2B).

The total suitable area was substantially less in the Lower Impounded Reach, as was the area of connected floodplain lakes and shallow area (< 2.0 m; Figs. 3 and 4). For many pools in the

Fig. 2 (A) Pool-scale euphotic depth, water level fluctuation, and the resulting suitable elevation range and (B) area suitable for submersed aquatic vegetation (SAV) \pm 1 SD (\pm 0.38 m of the estimated bed elevation of 1% light penetration). Positive suitable elevation ranges (A) correspond to the spatial extent that is suitable for SAV (i.e., suitable light and depth conditions $>$ 50% of years, 1993–2014). Elevation ranges \leq 0 (OR = -2.1, LAG = 0) are treated as zero and indicate that no elevations are suitable in those reaches. All values are reported as medians during the May–September growing season. Water level fluctuation refers to the maximum fluctuation during the growing season (median of tailwater and pool gauges combined; 1993–2014). By convention, Upper Mississippi River pools are numbered (except Open River Reach = OR) and Illinois River pools are abbreviated as follows: Dresden (DRE), Marseilles (MAR), Starved Rock (STR), Peoria (PEO), La Grange (LAG), and Alton (ALT)



Lower Impounded Reach, there was little area suitable for SAV based on the criteria developed here (i.e., conditions are suitable $>$ 50% of years; Fig. 2). This reflects the much shallower euphotic depth, greater water level fluctuations, and scarcity of shallow areas in these downstream pools. For some years in Pools 20–26, La Grange, and Alton and all years in the Open River Reach, the combined effects of water clarity, water depth, and water level fluctuation conditions were such that our results indicate a complete absence of suitable area for SAV. The standard deviation in bed elevation (\pm 0.38 m) for these reaches corresponds to a relatively small change in suitable area (e.g., 96–253 ha in Pool 20; Table 2; Fig. 2B).

Due to the interactions between pool size, bathymetry, and water clarity, larger suitable elevation ranges do not always equate to increased suitable area for SAV. For example, the median elevation range suitable for SAV in Pool 15 was nearly 1.0 m; however, the area suitable for SAV was only 91 ha (Figs. 2B and 3C). Pool 15 is a very small pool spanning only 16 river km with a total aquatic area of \sim 1400 ha. Of that, the area less than 2.0-m deep was only \sim 318 ha ($<$ 25% of total area; Fig. 4). Therefore, the small predicted suitable area was due to the pool not having substantial shallow area ($<$ 2.0 m), which was approximately the maximum depth of observed SAV in the UMRS. Conversely, Pool 19 had substantial aquatic area less

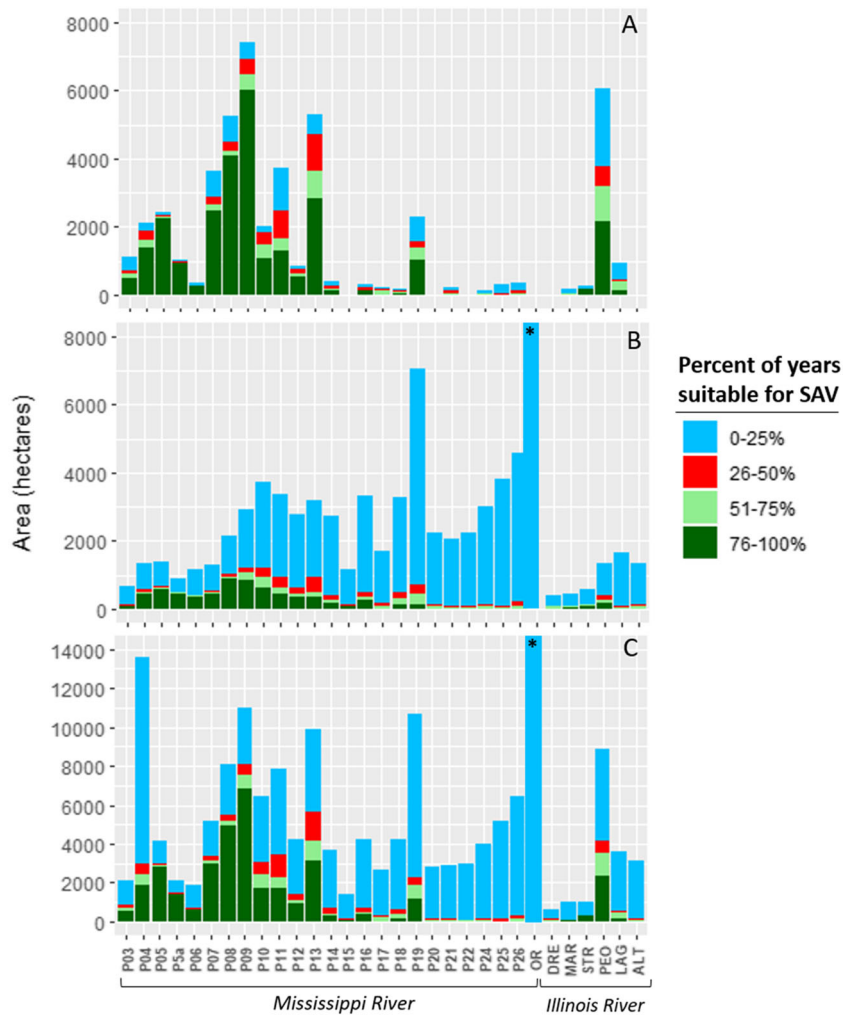
than 2.0 m deep ($>$ 40% of total area or \sim 4000 ha; Fig. 4). Even though the median elevation range suitable for SAV (0.74 m) was smaller for Pool 19 than Pool 15, the total area suitable for Pool 19 was over 1800 ha (Fig. 2).

Similar to Pool 19, the Peoria Pool in the IWW contains substantial area less than 2.0 m in depth ($>$ 75% of total area or \sim 7000 ha) and had a median suitable elevation range of 0.63 m yielding over 3400 ha of suitable area (Fig. 2). Sass et al. (2017) found that SAV in the IWW was largely limited to Dresden and Starved Rock Pools with no aquatic vegetation found in Peoria Pool. Sass et al. (2017) hypothesized that in addition to water level fluctuation and clarity, herbivory (carp and turtles), seed bank viability, sedimentation, and water quality (potentially chemical pollution) may limit SAV growth and establishment in these navigation pools. Our results indicate that water clarity and water level fluctuation were not limiting in much of the Peoria Pool and that other factors such as those described above likely contribute to the absence of vegetation in this area.

Sensitivity to Simulated Changes in TSS

The simulated 50% increase in TSS along the downstream gradient (Pools 9, 16, 20, and 25) resulted in decreased

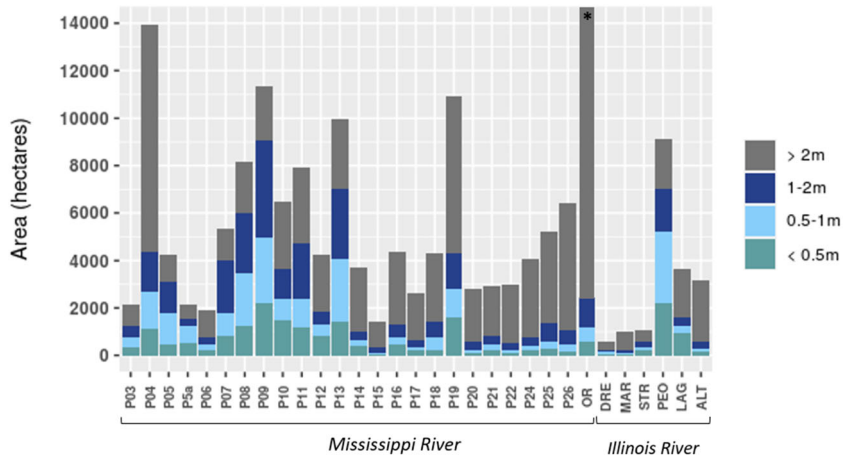
Fig. 3 Area suitable (by percent of years category) for submersed aquatic vegetation (SAV) within aquatic area types: (A) contiguous floodplain lake, (B) channel, and (C) pool-wide. The height of each histogram bar represents the total aquatic area evaluated. Channel includes main channel border, side channel, and tertiary channel combined. Estimated suitable areas for SAV are defined as those with sufficient light and depth conditions in >50% years during the period of record. By convention, Upper Mississippi River pools are numbered (Open River Reach = OR) and Illinois River pools are abbreviated as follows: Dresden (DRE), Marseilles (MAR), Starved Rock (STR), Peoria (PEO), La Grange (LAG), and Alton (ALT). Note the scale of the y-axis differs among panels. *The maximum area in the Open River Reach (OR) extends to 20,415 ha in panels B and C



suitable area in all pilot pools (Table 2); Pool 9 exhibited the largest decrease in estimated suitable area. This is likely due to the larger proportion of shallow area (and associated low bed slope within that area) characteristic of the Upper Impounded Reach and indicates that small changes in euphotic depth cause a large change in suitable area. The *simulated* 75%

reduction in TSS increased the predicted suitable area for SAV in all pools (except Open River) and fits the UMRS in terms of what may be attainable from a management perspective (Fig. 5). A decline of that magnitude has previously been observed in some of the upper reaches of the UMRS (e.g., Pool 81,993–2007; UMRR LTRM 2018). Furthermore, a

Fig. 4 Pool-wide area (hectares) by depth class. By convention, Upper Mississippi River pools are numbered (except Open River Reach = OR) and Illinois River pools are abbreviated as follows: Dresden (DRE), Marseilles (MAR), Starved Rock (STR), Peoria (PEO), La Grange (LAG), and Alton (ALT). *The maximum area in the Open River Reach (OR) extends to 20,415 ha



75% reduction of TSS in the lower reaches would create water clarity conditions that are similar to the upper reaches (e.g., Pool 25 median TSS ~60 mg/l reduced to 15 mg/l). Model results were relatively insensitive to TSS reduction in the Upper Impounded Reach because TSS is already relatively low in these areas.

River restoration and management actions can be used to modify bed elevation (e.g., via dredging or island construction), and catchment land-use practices can be modified to reduce TSS (e.g., increased acreage with cover crops; Dabney et al. 2001). The sensitivity analysis provides insights into the possible consequences of such actions. Under a system-wide, 75% reduction of daily TSS concentration, the overall area suitable for SAV would increase by approximately 54% (Fig. 5). There were reaches (e.g., Open River) and areas within pools (e.g., tailwaters of Pool 26) that were relatively insensitive to increased light penetration resulting from a 75% TSS reduction, indicating limitations by water level fluctuation or bathymetry (i.e., depth and slope). Even with a 75% reduction in TSS, many pools in the Lower Impounded Reach had only minor increases in suitable area for SAV (median 330 ha; Fig. 5). In pools with relatively steep bathymetry and a small proportion of shallow area (e.g., Pools 14–18, Pools 20–Open River, and the Dresden-Starved Rock reaches; Fig. 4), little additional suitable area accrues with substantial decreases in TSS. In pools where water level fluctuations are very large (e.g., Pools 20–Open River and the La Grange–Alton reaches; Fig. 2), there is little or no area deep enough to remain submersed through the growing season (i.e., not dewatered) and shallow enough to receive adequate light to support SAV, even with substantial decreases in TSS (Fig. 5).

Assessing Model Error

The model error (15.3%; 897/5858 sites) associated with unvegetated sites in “suitable” areas is difficult to assess because it is impossible to separate possible over-inclusivity of the model regarding the actual response of SAV to light intensity from other plausible explanations for vegetation not growing in areas suitable by light and water level fluctuation criteria. For example, some SAV species may require >1% surface light for seedling survival and tuber production (e.g., wild celery; Kimber et al. 1995); however, we intentionally erred on the side of inclusivity in this model. In addition, other factors such as current velocity, substrate, wind fetch, and herbivory may further limit SAV in these areas (e.g., Madsen et al. 2001; Sass et al. 2017). While there are several plausible reasons for SAV to be absent in areas where light and water level fluctuation are suitable, SAV growing in “unsuitable” areas is a clear indication of shortcomings of the model. The incidence of this was low, with only 8.67% (507/5858) of sites containing SAV reported in areas where the model stated conditions were unsuitable >50% of years. Many of these errors occurred as isolated instances on the edges of highly suitable areas or steep slopes (i.e., channel borders). Error may also be due to the assumptions and approximations used to develop our model, boat drift during sampling, GPS accuracy, and changes in bathymetry.

Evaluating Suitable Habitat for SAV at Multiple Scales

UMRS reaches were grouped into four general classes based on the combined effects of water clarity (median growing season TSS), bathymetry, and water level fluctuation

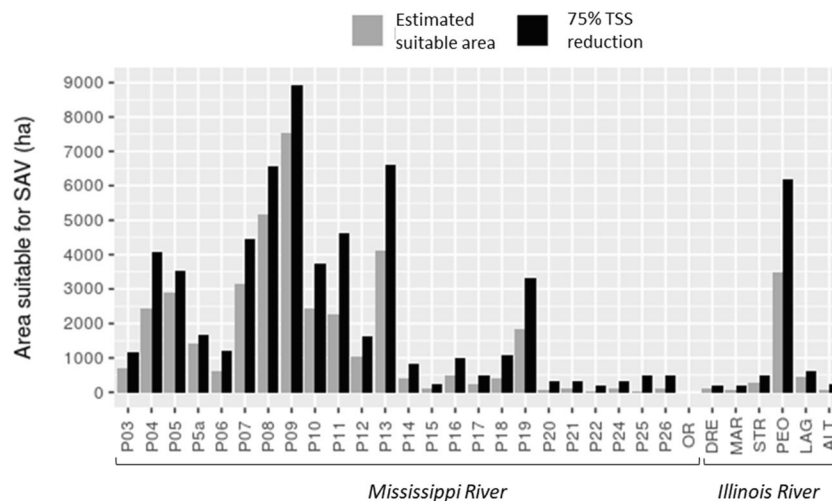


Fig. 5 Area suitable (hectares) for submersed aquatic vegetation (SAV), by pool. Grey bars represent the estimated area suitable for SAV. Black bars represent the area suitable for SAV when a 75% reduction in TSS is applied. Suitability refers to the area with suitable light and depth conditions >50% of years (1993–2014). By convention, Mississippi River

pools are numbered (except Open River Reach = OR) and Illinois River pools are abbreviated as follows: Dresden (DRE), Marseilles (MAR), Starved Rock (STR), Peoria (PEO), La Grange (LAG), and Alton (ALT)

(Table 3; Figs. 2 and 4; Fig. S6). In general, the northern portion of the UMRS contains reaches with low TSS, low water level fluctuations, and abundant shallow areas. Because median TSS is already low (12–19 mg/l) during the growing season, these areas are relatively insensitive to further reductions in TSS, and there is very limited potential to increase available area suitable for SAV. Reaches with moderate TSS and water level fluctuations and abundant shallow areas are relatively sensitive to changes in TSS and show a strong increase in area suitable for SAV in the 75% TSS reduction scenario (Fig. 5). However, many pools in the Lower Impounded Reach have relatively little shallow water area and therefore response to 75% TSS reduction is relatively small. Floodplain lake area is also limiting in the southern reaches of the UMRS; Pool 9 in the Upper Impounded Reach contains more floodplain lake area than Pools 14- OR and all of the Illinois River, combined (Fig. 3A). Moderate to high TSS and large water level fluctuations may further limit suitable area for SAV. Plausible changes in TSS will not affect the abundance of suitable area for SAV in these reaches.

In addition to these classes, higher resolution information by river km within pools identify smaller areas where suitable area for aquatic vegetation is the most sensitive to changes in TSS. For example, upper and lower Pool 4 illustrate an interesting contrast in sensitivity to TSS changes (Fig. 6). The 75% TSS reduction scenario resulted in an additional 1635 ha of suitable area in upper Pool 4; however, there were minimal changes in suitable area below Lake Pepin as much of this area was already suitable. Areas that are “near suitable” (26–50% of years) may become suitable with increased light availability and represent areas where restoration efforts may be more likely to succeed.

Conclusions

The majority of today’s large floodplain rivers are regulated for navigation, water diversion, and extraction (Dynesius and Nilsson 1994; Van Geest et al. 2005a). Many of these rivers have been described as degraded and in need of ecosystem

management (Sparks 1995; Buijse et al. 2002; Zhao et al. 2005). The UMRS, like many large rivers, is facing challenges due to changes in land use, more frequent and longer duration flooding, and loss of depth due to sedimentation (Johnson and Hagerly 2008; Bouska et al. 2018; Rogala et al. 2020). Because the resources available to manage and restore rivers are limited, the ability to provide systemic assessments of ecosystem conditions to effectively target restoration efforts is essential. Our results provide river managers the ability to evaluate suitable habitat by river kilometer and therefore, may focus their efforts on specific areas of interest.

The distribution and abundance of aquatic vegetation is affected by complex interactions of physical and biological drivers (Van Geest et al. 2003; Van Geest et al. 2005a; Van Geest et al. 2005b; Lacoul and Freedman 2006; Schneider et al. 2015). Many large rivers lack sufficient data to assess long-term trends in aquatic vegetation and therefore, the effects of environmental and spatial gradients in structuring communities cannot be assessed (Alahuhta et al. 2021). Furthermore, few studies have documented the effects of changing river conditions due to modified hydrological regimes, land use, and climate.

The model presented here requires only water level and water clarity information to predict suitable area for SAV and therefore is widely applicable to other river systems. This method is particularly useful for river managers with limited resources for long-term monitoring and those seeking guidance on proposed restoration projects. This work builds on the results of other large floodplain river studies that show associations between macrophytes and water clarity (Danube River; Coops et al. 1999) and water level fluctuation (Lower Rhine River; Coops and Van Geest 2003; Van Geest et al. 2005b). The results presented here improve our understanding of the factors determining the distribution of SAV in floodplain river ecosystems and provide insights into how changing river conditions (e.g., TSS) may affect SAV growth and establishment.

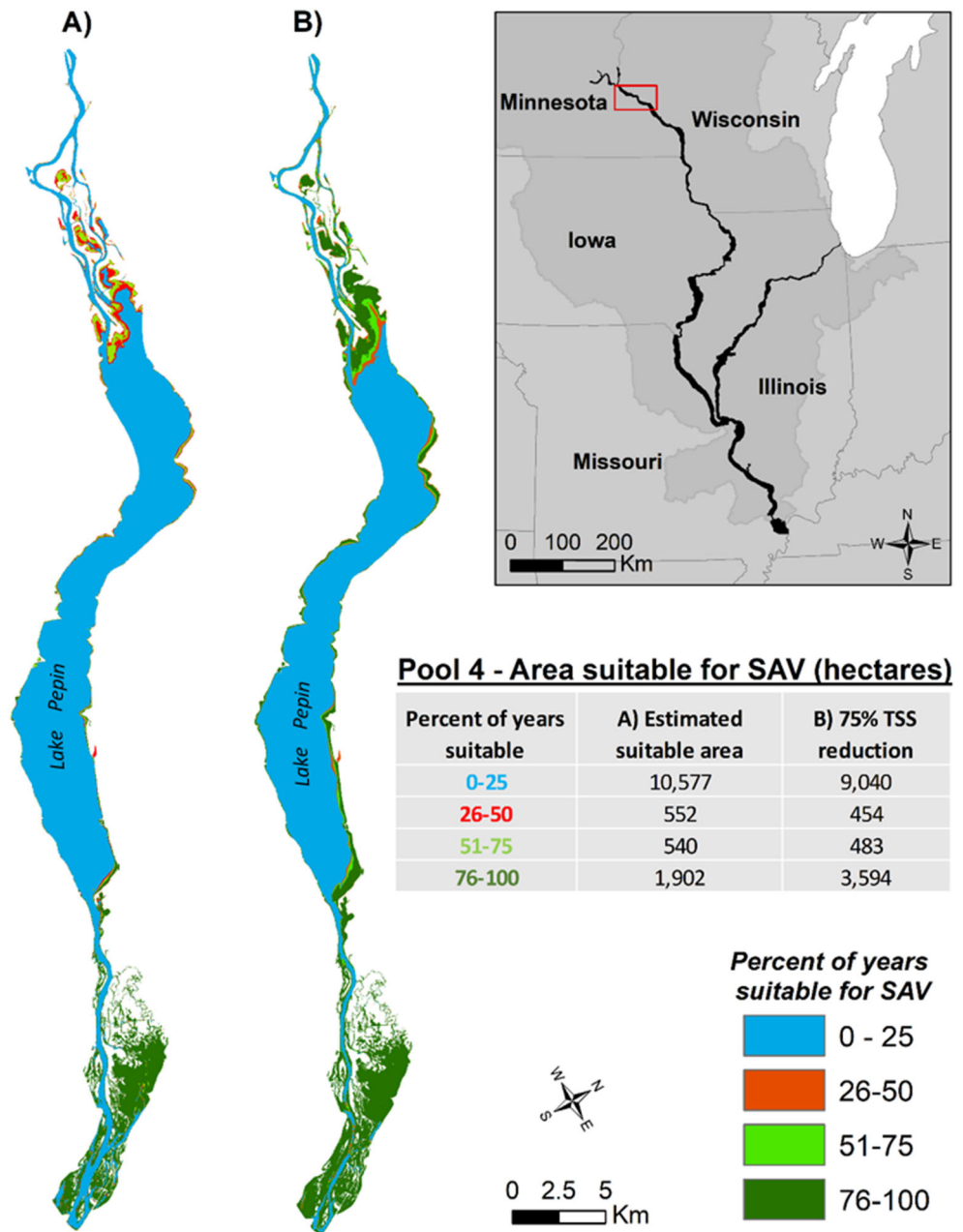
Here we demonstrate how water clarity, river geomorphology, and water level fluctuations interact to contribute to the distribution of areas suitable for submersed aquatic vegetation. We intentionally focused on a subset of suitability

Table 3 General classes of Upper Mississippi River System pools based on the combined effects of water clarity (median of growing season total suspended solids; TSS), bathymetry, and water level fluctuation (median of maximum fluctuation at tailwater and pool

gauges combined; 1993–2014). TSS indices defined as low (< 30 mg/l), moderate (30–60 mg/l), high (> 60 mg/l). Shallow area defined as <2 m. Water level fluctuation indices defined as low (< 2 m), moderate (2–4 m), high (> 4 m)

Pool	Median TSS	Water level fluctuation	Shallow area
Lower 4, 5–10	low	low	abundant
3, Upper 4, 11–13, 19, PEO	moderate	moderate	abundant
14–18, 20–26, DRE, MAR, STR	moderate	moderate	scarce
OR, LAG, ALT	moderate-high	high	scarce

Fig. 6 (A) Estimated area suitable (hectares) for submersed aquatic vegetation (SAV) compared to (B) area suitable under a 75% TSS reduction scenario for Pool 4, Upper Mississippi River. Suitability refers to the area with suitable light and depth conditions >50% of years (1993–2014, green on map). Note minor changes in Lake Pepin and lower Pool 4, and more response in upper Pool 4 (additional 1635 ha of suitable area)



conditions—those related to light and potential for dewatering—because these are known physical limitations on aquatic vegetation and any areas unsuitable because of these criteria are areas where establishment and growth are very unlikely. In the context of river restoration and management, these are areas where actions to establish vegetation are unlikely to succeed. Areas that meet the suitable criteria, but do not currently support vegetation, need to be further assessed regarding other limiting factors including current velocity, herbivory, and bioturbation. These are areas where management actions to re-establish vegetation may succeed if other limiting factors can be addressed. Although the presence of aquatic vegetation promotes feedbacks to maintain

existing communities (Madsen et al. 2001; De Jager and Yin 2010), further analyses incorporating other physical and biological drivers, beyond those related to light and potential for dewatering, will be critical for predicting species composition and abundance of aquatic vegetation in the future.

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Availability of Data and Material The datasets generated and analyzed here are available at <https://doi.org/10.5066/P9TWZ XVZ> and https://umesc.usgs.gov/ltrm/projects/aquatic_veg_constraints.html.

Author Contributions All authors contributed to the study conception and design. Data acquisition was performed by AC, JK, JJR and JTR and data analysis was performed by AC and JJR. The original draft was written by AC and JK and DD and JH reviewed and edited subsequent versions of the manuscript.

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Code Availability The R-code generated and analyzed is available upon request from the corresponding author.

Declarations

Ethics Approval Not applicable.

Consent to Participate Not applicable.

Consent for Publication Not applicable.

Conflict of Interest The authors have no conflicts of interest to declare that are relevant to the content of this manuscript.

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