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Emerging reservoir delta-backwaters: biophysical dynamics and riparian biodiversity

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Abstract. Deltas and backwater-affected bottomlands are forming along tributary and mainstem confluences in reservoirs worldwide. Emergence of prograding deltas, along with related upstream hydrogeomorphic changes to river bottomlands in the backwater fluctuation zones of reservoirs, signals the development of new and dynamic riparian and wetland habitats. This study was conducted along the regulated Missouri River, USA, to examine delta-backwater formation and describe vegetation response to its development and dynamics. Our research focused specifically on the delta-backwater forming at the confluence of the White River tributary and Lake Francis Case reservoir. Objectives of the research were to: (1) describe and analyze the process of delta-backwater formation over space and time; (2) determine by field sampling and GIS mapping how vegetation has responded to development of the delta-backwater; and (3) compare the woody plant communities of the delta-backwater to those along free-flowing and regulated remnant river reaches. In response to base level changes caused by reservoir filling, the thalweg of the lower 31 km of the original White River channel and adjacent floodplain aggraded by up to 12 m between 1954 and 2011. The overall channel slope flattened from 0.70 to 0.29 m/km. Riparian *Populus–Salix* forests increased in area by nearly 50% during the post-dam period by colonizing new deltaic and floodplain deposits. Many of the native woody species found along natural and regulated river reaches were also found on the delta-backwater. Woody species sorted along a fluvial to delta gradient; wetland affiliated species (*Salix* spp., *Typha* spp.) dominated the delta-backwater near the reservoir while riparian species (*Populus, Fraxinus*) dominated in upstream portions of the delta-backwater. This habitat complex supports young stands of native riparian vegetation now in decline in remnant reaches protected from flooding.

Key words: dams; ecosystem services; flow regulation; Populus; *reservoir backwater; restoration; riparian;* Salix.

Introduction

The world's rivers are regulated by over 59,000 large dams (>15 m high; ICLD 2018). Flow regulation by dams has major ecological consequences for riverine ecosystems and biota. Dams transform rivers by fragmenting river networks (Jansson et al. 2000, Nilsson et al. 2005), replacing bottomlands with artificial reservoirs, disrupting natural patterns of sediment transport, and altering seasonal variation in stream flow (Poff et al. 1997). The global pace in new hydropower dam construction is rapidly increasing, with thousands of new dams currently proposed in developing economies (Zarfl et al. 2015, Winemiller et al. 2016).

Sediment that historically moved downstream and sustained coastal deltas is now accumulating in and upstream of reservoirs. Riparian and wetland ecosystems are forming on deltaic and related fluvial deposits that were non-existent along the free-flowing rivers of the past (Volke et al. 2015). The physical processes involved in delta formation are well understood from coastal delta research (Giosan and Bhattacharya 2005) with delta form and vegetation assemblages dictated by stream flow, sediment particle size, sediment depositional patterns, and the timing, frequency, and duration of inundation on newly deposited substrates (Johnson et al. 1985, White 1993). Reservoir deltas form in response to the same physical processes that produce river mouth deltas, but on different time scales. All river

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mouths are dynamic and subject to changes in base level, or the elevation at which a river enters still water. Tidal fluctuations affect coastal deltas and upstream river reaches on daily time scales, whereas sea level changes influence these systems over millennia. Reservoirs are superimposed on rivers, and base level changes affecting newly forming deltas and upstream river reaches fluctuate seasonally in response to reservoir management as well as over multi-year wet and dry cycles.

Considerable research effort has focused on understanding the physical and biotic processes that structure and maintain riverine and riparian ecosystems (Wolman and Leopold 1957, Junk et al. 1989, Gregory et al. 1991, Hupp and Osterkamp 1996, Poff et al. 1997) as well as the downstream effects of dams on riparian ecosystems (Johnson et al. 1976, Petts 1984, Friedman et al. 1998, Nilsson and Berggren 2000). Aside from work on development and succession of shoreline plant assemblages in the zone of fluctuation around reservoir margins (Nilsson and Keddy 1988, Nilsson et al. 1997, Merritt et al. 2010), comparatively little is known about the upstream effects of dams, especially in those dynamic zones where a river or stream enters a reservoir (Xu and Shi 1997, Liro 2019).

Deltas and associated backwater zones form in two locations in reservoirs: where tributaries enter reservoirs laterally and where the mainstem river enters the upstream end of the reservoir. We define a delta-backwater as a continuum of landforms where sediment accumulates due to the presence of a reservoir. To identify different hydrologic influences in delta-backwater environments, we distinguish shorter-term *flooding* related to fluvial processes from longer-term *inundation* related to reservoir fluctuations (Flick et al. 2012, Liro 2019). Both mainstem and tributary delta-backwaters comprise a complex that can be subdivided into two parts: a delta that progrades into the reservoir and a backwater that aggrades upstream into the former river bottomland. Reservoir levels set a new base level that represents the downstream end of the drainage network where fluvial processes end and delta formation begins (Leopold and Bull 1979). Fluctuations in reservoir backwaters shift base level and thus the locations of delta-backwater processes, which include sediment aggradation in upstream reaches (Holste 2013), alteration of channel form and process (Liro 2017), inundation of existing bottomland vegetation, and exposure of depositional surfaces for colonization by new vegetation during reservoir drawdown (Xu and Shi 1997). Liro (2019) presents a conceptual model of the effects of fluctuating reservoir backwaters on the abiotic and biotic components of fluvial systems and emphasizes that little work has been directed at understanding and quantifying the effects of these disturbances. He hypothesized that prolonged inundation and high rates of sediment deposition in fluctuating backwater zones may lead to less diverse plant assemblages than those along free-flowing rivers.

Similarly, Johnson (2002) and Volke et al. (2015) have inquired to what extent reservoir delta-backwaters may be able to replace some of the geomorphic processes, shallow aquatic environments, and early successional vegetation dynamics that have been lost because of river regulation. In regulated river systems, where the restoration of natural processes is not likely, delta-backwaters may recover some important ecological functions on a large spatial scale within a river regulation infrastructure designed primarily to support human economic, municipal, and recreational interests (Acreman et al. 2014).

The Missouri River of the north-central United States is an example of a highly regulated large river where ecosystems have been altered by decades of flow regulation, but little mitigation has occurred. Between 1937 and 1963, six large U.S. Army Corps of Engineers (USACE) dams and associated reservoirs were constructed along the mainstem Missouri River in Montana, North Dakota, South Dakota, and Nebraska. Numerous studies have been conducted to gauge the ecological effects of damming on the remnant sections of channel and floodplain below or between dams (Johnson et al. 1976, 2012, NRC 2002, 2011, Dixon et al. 2012, 2015, Scott et al. 2013). A major finding of these studies is that the cessation of flooding and channel movement has curtailed cottonwood (*Populus deltoides*) forest reproduction, while pre-dam forests are aging and senescing. Under current management, these forests are expected to lose much of their biodiversity-rich cottonwood component during this century (Dixon et al. 2012, Scott et al. 2013).

Prominent reservoir delta-backwaters have been forming at nine locations along the Missouri River, including where the free-flowing White River enters Lake Francis Case. Surprisingly, despite the worldwide abundance of dammed rivers, there is virtually no published research on delta-backwater ecosystems (Volke et al. 2015, Liro 2019). The dearth of research on these systems, yet their potential to contribute to the recovery of some of the ecological values of riparian and wetland ecosystems in regulated riverscapes, stimulated us to study the White River delta-backwater. Our study had three main objectives as follows: (1) describe and analyze the process of delta-backwater formation over space and time; (2) determine by field sampling and GIS mapping how vegetation has responded to development of the delta-backwater; and (3) compare the woody plant communities of the delta-backwater to those along free-flowing and regulated remnant river reaches.

Study Area

Missouri River basin

The Missouri is the longest river in the United States, originating in the Rocky Mountains near Three Forks, Montana and flowing 3,767 km to its confluence with the Mississippi River near St. Louis, Missouri (Fig. 1). The basin occupies 1,396,117 km^2, covering approximately one-sixth of the land area of the conterminous United States (NRC 2002, Galat et al. 2005). Historically, the middle and lower reaches of the Missouri were geomorphically diverse and dynamic, with a highly mobile sand-bed channel, braided and meandering channel morphologies, frequent overbank flows, unstable banks, high turbidity, and a massive sediment load (Jacobson et al. 2009). High flows typically began in April, fed by local snowmelt and rainfall, with a second larger flood peak occurring in June, fed by snowmelt in the Rocky Mountains and local rainfall (NRC 2002, 2011). A mosaic of vegetation types occurred along the middle reaches of the river, including riparian forests dominated by plains cottonwood (*Populus deltoides* ssp. *monilifera* [Aiton] Eckenw.), green ash (*Fraxinus pennsylvanica* Marsh.), box elder (*Acer negundo* L.), American elm (*Ulmus americana* L.), and peachleaf willow (*Salix amygdaloides* Andersson), with a greater number of tree species along the lower sections of the river (NRC 2002).

In 2011, the upper Missouri River basin experienced record runoff due to an above average snowpack in the Rocky Mountains in Montana combined with extreme spring rainfall events in the eastern Montana plains (USACE 2012). The flood produced record reservoir stages that required unprecedented flow releases, the volume of which constituted about 250% of normal runoff, based on the period of record from 1898–2009. Reservoir management dampened the flood peak but extended flood duration.

White River

The White River originates in the Pine Ridge region of northwestern Nebraska. It flows through the South Dakota Badlands en route to its confluence with Lake Francis Case, a mainstem impoundment on the Missouri River (Fig. 1). The length of the White River is 816 km with a drainage area of 25,650 km^2 (Galat et al. 2005). The Little White River is its largest tributary, originating in the Nebraska Sand Hills and supplying relatively stable flows to the lower White River. All other tributaries are small and intermittent. Land ownership in the basin is a mosaic of private, state, tribal, and federal land holdings.

The White River is one of the longest undammed, free-flowing rivers in the conterminous United States (Stanford and Ward 1979, Benke 1990). It was listed as one of 327 rivers in the United States critical for protecting biodiversity (Master et al. 1998). As modifications to the White River's hydrology, sediment regime, and floodplain have been relatively minor, it provided a suitable reference for riparian forests along free-flowing rivers in the region. Further, the free-flowing nature of the White River ensured that development of the associated delta-backwater was not influenced by major hydrologic modifications.

The White River basin has a semiarid continental climate. The mean annual temperature is 8.8°C, with mean monthly variation from −8°C in January to 24°C in July and August. Mean annual precipitation is 44 cm with nearly 70% occurring from April through August. The majority (85%) of precipitation falls as rain during summer convective thunderstorms (Galat et al. 2005).

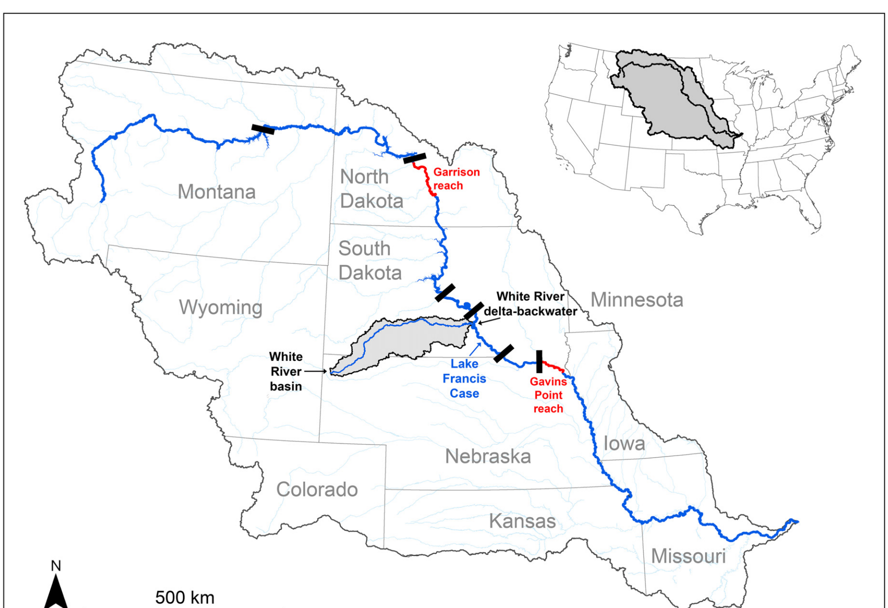

Fig. 1. Location of the White River basin within the Missouri River basin. Black bars locate the six major dams on the Missouri River.

The dominant riparian tree species along the lower White River is plains cottonwood (Cahlander-Mooers 2015). Green ash is the most common overstory associate, followed by peachleaf willow, box elder, and American elm. The nonnative Russian olive (*Elaeagnus angustifolia* L.) commonly occurs on the floodplain. Understory riparian shrubs and lianas include western snowberry (*Symphoricarpos occidentalis* Hook.), poison ivy (*Toxicodendron rydbergii* [Small ex Rydb.] Greene), chokecherry (*Prunus virginiana* L.), false indigo (*Amorpha fruticosa* L.), golden currant (*Ribes aureum* Pursh), Woods' rose (*Rosa woodsii* Lindl.), woodbine (*Parthenocissus vitacea* (Knerr) Hitchc.), riverbank grape (*Vitis riparia* Michx.), and sandbar willow (*Salix interior* Rowlee).

There are no major cities or towns alongside the White River; few occur in the basin. The largest towns are Chadron, Nebraska (population 5,767) and Winner, South Dakota (population 2,862). Population density across the basin is 1.3 people/km^2. Over 70% of the basin is in native grass or hay and 21% is in crops dominated by wheat, corn, sunflowers, sorghum, soybeans, and oats (Galat et al. 2005). Livestock grazing and selective cutting are the primary anthropogenic disturbances to riparian forests in the basin.

Most of the flow of the White River originates as precipitation and snowmelt in spring and early summer, with peaks in both March and May–June (USGS Oacoma Gage 06452000 near the mouth). The mean annual stream discharge at the Oacoma Gage is 16.6 m^3/s (1929–2013), ranging from a low of 4.6 m^3/s in 1974 to a high of 48.6 m^3/s in 1942. The record daily flow was around 1,470 m^3/s on 30 March 1952. The lowest flows occur during the winter months, when monthly flows average less than 4 m^3/s (Ferrick et al. 1995). Although the White River is unregulated, modest irrigation withdrawals and numerous low-head dams located on intermittent tributaries in the watershed may have minor impacts on the hydrograph. The hydrograph of record does not show a sharp decline in stream flow of the type typical of regulated rivers with mainstem dams (USGS Gage 06452000).

The White River is named for its white-gray color derived from naturally large loads of sands, clays, and volcanic ash (Galat et al. 2005). Mean annual suspended sediment concentration was 5,550 mg/L (1972–2013; USGS Gage 06452000). Likewise, the mean annual suspended sediment discharge was over 7.0 million Mg/yr and has ranged from about 1.7 million Mg/yr in 1985 to over 17.1 million Mg/yr in 1982. This sediment accumulates in the delta-backwater or is transported farther downstream and into the reservoir.

The slope of the White River ranges from 4.18 m/km in the uppermost 100 km to 0.58 m/km in the lowermost 120 km (USGS 2012). Sinuosity of the White River ranges from 2.16–2.48 (Ferrick et al. 1995).

Witness tree records from the 1890 and 1896 public land surveys near the mouth of the White River indicate that the pre-regulation floodplain was dominated by cottonwoods and willows, with a few scattered American elms. The 1894 Missouri River Commission map showed scattered riparian forests on the floodplain and numerous sandbars at the confluence (MRC 1895).

Lake Francis Case

The White River is the largest tributary to Lake Francis Case, a mainstem impoundment on the Missouri River in central South Dakota (Fig. 2). Lake Francis Case formed following closure of Fort Randall Dam (river kilometer [rkm] 1,416) in 1952. The primary functions of the dam are flood control, water storage, hydropower, and water supply (USACE 2006). The White River enters Lake Francis Case about 50 km downstream of the upper reservoir boundary and 122 km upstream of Fort Randall Dam. The reservoir has the second smallest storage capacity (6.7 km^3) of the six largest mainstem Missouri River reservoirs, with a surface area of ~384 km^2, length of 172 km, maximum depth of 43 m (USACE 2006), and an average annual vertical fluctuation of about 4 m (1989–2013; USGS Gage 06442996).

The high sediment load of the White River has accumulated at its confluence with Lake Francis Case forming a delta-backwater that has expanded during the post-regulation era (Fig. 2; USACE 2006). The river bottomland located downstream of the Highway 47 bridge (~29 rkm upstream of the mouth of the White River) was purchased by the federal government and placed into public (State) easements in the late 1990s when agriculture became difficult or impossible due to increased flooding, large debris deposition, and elevated water tables (USCFC 1987).

Study area

The study area was the lower 120 km of the White River and its floodplain (Fig. 3). The upstream limit of the study area was the western boundary of Lyman County, South Dakota. The confluence of the White River and Lake Francis Case, which fluctuates over time in response to reservoir management and stream flow (Fig. 4), formed the eastern, downstream limit. Backwater fluctuations between the minimum and maximum reservoir pool elevations within the bottomland of the White River create the delta-backwater, where there is an upstream to downstream continuum reflecting decreasing fluvial and increasing lacustrine processes.

Methods

Geomorphic cross sections

Geomorphic changes that occurred during the postdam era were identified using a time series of stream

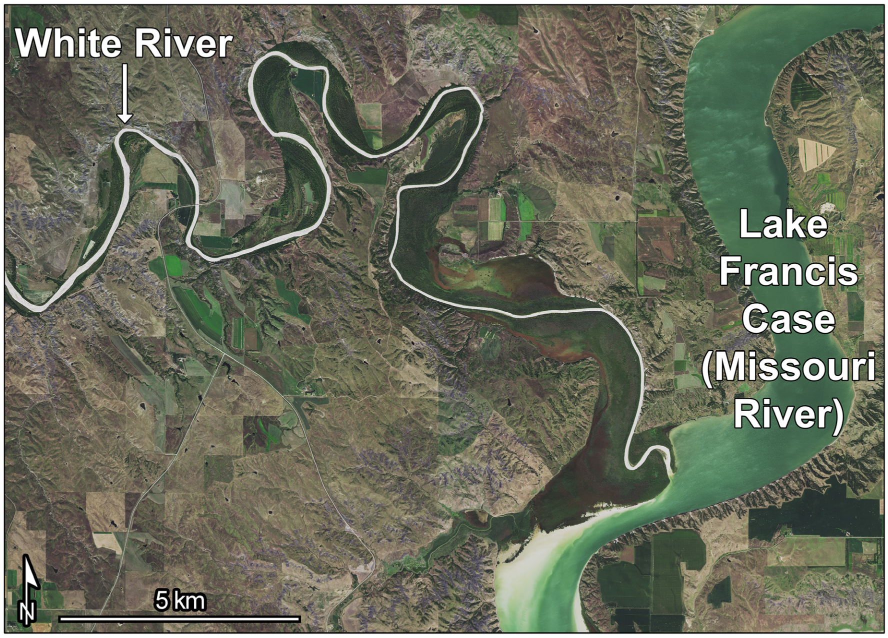

Fig. 2. Aerial photograph of the White River delta-backwater and surrounding landscape in South Dakota, USA. Source: U.S. Department of Agriculture, National Agriculture Imagery Program (2014).

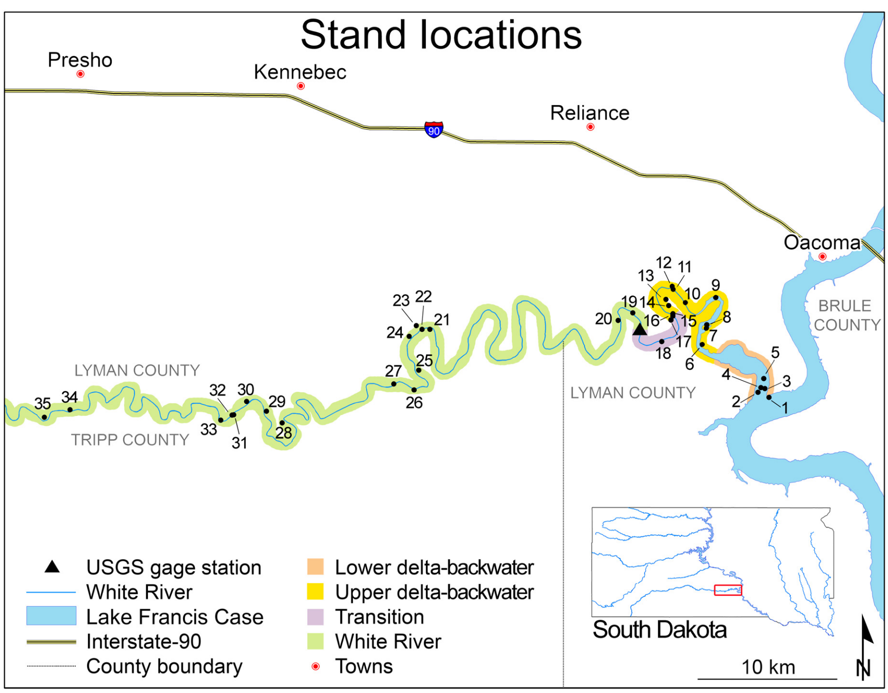

Fig. 3. The locations of all the sampled stands by assigned stand number along the lower 120 km of the White River in South Dakota, USA. The location of the enlarged map is indicated by the red rectangle on the inset map of South Dakota. The black triangle identifies the location of the USGS Oacoma Gage 06452000 on the highway 47 bridge.

cross sections. The USACE has resurveyed cross sections since 1953/1954 every few kilometers along the lower 42.3 rkm of the White River (distance is based on the channel length at the time of the original survey). The 1953/1954 cross-sectional surveys were completed just after closure of Fort Randall Dam but were considered representative of the pre-dam channel and floodplain environment.

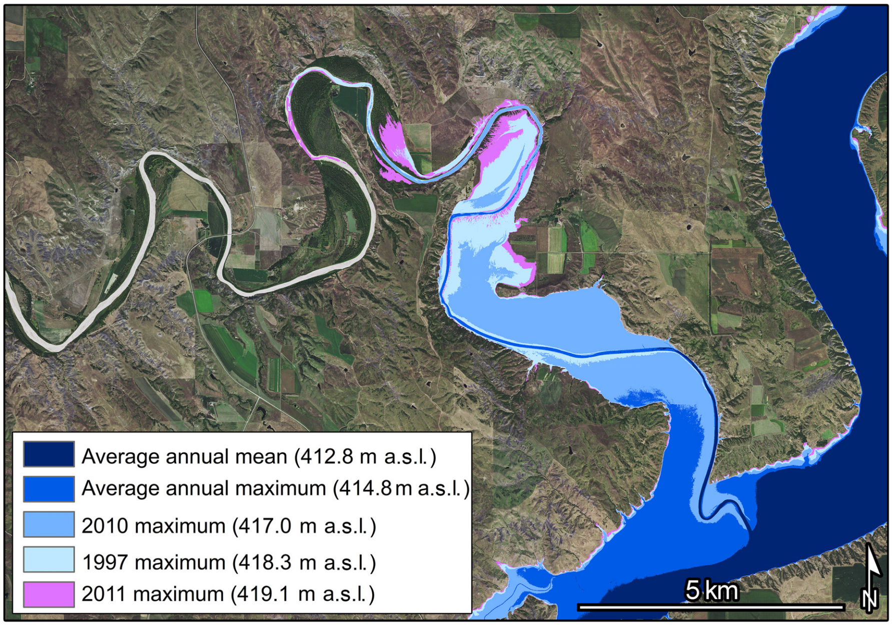

FIG. 4. Frequency of selected reservoir water surface elevations (WSEs) of Lake Francis Case (based on mean daily WSEs; 1989–2013), and related inundation of the lower White River valley. This figure was constructed from a digital elevation model (3-m resolution) along with data from USGS Gage 06442996 on Lake Francis Case. Image source: U.S. Department of Agriculture, National Agriculture Imagery Program (2014). Abbreviation is a.s.l., above sea level.

Five cross sections from the lower 31 km of the White River and one cross section from Lake Francis Case near the confluence were chosen to portray geomorphic change over time. Elevation along the cross sections was plotted to show changes in river channel and floodplain morphology among three measurement periods: 1953/1954–1973, 1973–1996, 1996–2011. The net change in thalweg elevation (minimum elevation) and the rate of change in thalweg elevation were calculated and compared numerically and graphically for each cross section at each measurement interval. The channel slopes of the lower 31 km (detectable geomorphic boundary) of the White River in 1954 and in 2011 were based on linear regression of thalweg elevations using SigmaPlot 12.0 (Systat Software, San Jose, California, USA) for a larger sample of cross sections (n = 9) within the study reach.

GIS mapping of vegetation change

Changes in the area and age classes of woody riparian vegetation within the lower 29 km (detectable vegetation boundary) of the White River during the post-dam era were determined using historical aerial photos and GIS mapping. The only pre-dam image available was for 1948. Post-dam aerial photos were for years 1983, 1991, 1998, 2004, 2010, and 2012.

Interpretation and digitizing of aerial photos were accomplished using "head's up" digitizing in ArcGIS 10.0 (ESRI, Redlands, California, USA). Land cover was broadly classified as either woody riparian vegetation (≥50% of canopy; hereafter referred to as "riparian woodland" or "woodland") or other features (e.g., herbaceous vegetation, sparse riparian woodland, agricultural fields, bare sediments, river channel, reservoir). This classification system provided a coarse estimate of riparian woodland area (≥0.1-ha patches) within the study area boundaries. Riparian woodland included cottonwood–willow forest, riparian shrubland, and seedlings of trees and shrubs. Classifications were improved by field reconnaissance (ground-truthing), which included sampling of riparian woodland composition and structure in selected stands and visual inspection by walking through the study reach. The area of riparian woodland was calculated for each time period and compared across years. Overlays of classified images from selected pairs of years (1948/2012, 1991/1998, 2010/2012) were produced to compare changes in the area and location of riparian woodland over the post-dam period and for intervals that included major floods on the Missouri River.

Two additional categories of riparian woodland were added to the 2012 classified image to assess flood damage and mortality caused by the 2011 Missouri River flood: dead riparian woodland and flood damaged riparian woodland. Dead woodland was assigned to patches of riparian woodland that were present in 2010 but no longer appeared as green woody vegetation in the 2012 image. Flood-damaged riparian woodland was defined as patches of woody vegetation that were present in both 2010 and 2012, but showed reduced live canopy cover (<50%) in 2012. The 2010 and 2012 classified images were overlaid to determine the location and areal extent of flood-related damage and mortality.

Riparian woodland age classes were delineated and mapped for three aerial photo dates: pre-dam (1948), post-dam midpoint (1983), and post-dam endpoint (2012) of the study period. On each image, the riparian woodland cover class was broadly divided into young, medium, and old age classes. The young age class was defined as woody seedlings and/or saplings and shrubland dominated by willows. The medium age class was defined as young forest typically composed of dense cottonwood trees of uniform size. The old age class was applied to later successional forest, typically with larger, more widely spaced cottonwood trees and a diverse understory of later successional woody plants.

Field vegetation sampling

The 120 rkm long study segment was divided into three sub-reaches to compare forest stand characteristics spanning the delta-backwater and related fluvial environments: (1) White River, (2) fluvial-delta-backwater transition, and (3) White River delta-backwater (Table 1, Fig. 3). Degree of reservoir influence and stand age (pre- or post-dam establishment) were used to delineate the three sub-reaches. For some analyses, the delta-backwater sub-reach was further subdivided into the lower and the upper delta-backwater to refine the gradient of reservoir effects on vegetation.

Cottonwood forest vegetation was sampled during the summers of 2011 and 2013. A total of 35 stands (17 stands from the White River, 2 stands from the transition sub-reach [only 2 stands fit the sampling criteria], and 16 stands from the White River delta-backwater) were sampled. Stands were selected according to the following criteria: (1) at least 20% of the canopy cover must be cottonwood (with the exception of one delta-backwater stand where cottonwood did not occur); (2) stands must occupy no more than one relatively uniformly flat alluvial surface; (3) stands must be at least 1.3 ha for tree stands and at least 0.6 ha for sapling stands; (4) vegetation structure should be relatively homogeneous; and (5) there should be no evidence of severe anthropogenic disturbance such as heavy cutting. Some stands fell into a tree category (stands in which the majority of cottonwoods were ≥10 cm dbh) and some fell into a sapling category (stands containing only saplings and shrubs <10 cm dbh and ≥1 m tall).

Table 1. Two methods of dividing the 120 rkm reach for different types of analysis.

Sub-reach	River km
Geomorphic boundary (cross sections)	
Delta-backwater deposits	0–31
Vegetation boundary (GIS mapping and field sampling)	
White River delta-backwater	0–29
Lower delta-backwater	0–9.5
Upper delta-backwater	9.5–24
Fluvial-delta-backwater transition	24–29
White River	29–120

Nearly all qualifying stands that occurred within the 120-km study reach were sampled. Stands were initially selected by using USDA National Agriculture Imagery Program (NAIP) orthophotography in ArcGIS 10.0 (ESRI). In 2011, stands were selected from 2010 NAIP orthophotography, and in 2013, stands were selected from 2012 NAIP orthophotography. The aerial imagery was inspected for patches (stands) of woody riparian vegetation with a uniform age class. When such a patch was found of adequate size, a polygon was drawn to define the sampling area. Some stands chosen from imagery were later rejected due to access refusal by landowners or if the stand did not meet the sampling criteria described above. The stands sampled captured the wide range of cottonwood forest heterogeneity along the lower White River and its delta-backwater.

Overstory trees.—The point-centered quarter method (Cottam and Curtis 1956) was used in most stands to sample trees with a diameter at breast height (dbh, 1.3 m above the ground surface) of ≥10 cm. This was the same method used by Johnson et al. (1976) and Dixon et al. (2010) in studies on the Missouri River. A stratified random sampling design was used to determine sampling points in each stand. The stand was first subdivided into two to eight equal-sized subunits, depending on stand area. A sampling transect running parallel to the subunit boundaries was located randomly within each subunit. The transects were in turn divided into 4–27 equal-sized subunits depending on stand area; a random number located the sampling point in each subunit. The number of sampling points per stand ranged from 20 to 40, depending on stand area.

At each point, the distance to the closest tree in each quadrant was recorded along with its species and dbh (measured to the nearest 0.1 cm). Distance was measured to the nearest 0.01 m using a Multi-Measure Combo PRO distance finder (SONIN, Inc., Charlotte, North Carolina, USA). For trees with multiple stems, the dbh of each stem was measured, combined, and averaged. Presence and species of a liana (woody vine) attached to the trunk of a sampled tree was recorded. The overstory in small stands 17 and 33 was sampled by a complete stand inventory to avoid sampling the same tree more than once.

Tree cores were collected using an increment borer to estimate cottonwood stand ages, stand age structure, and cottonwood and peachleaf willow growth rates. Cores were usually taken from trees at breast height to maintain consistency with diameter measurements. From 15 to 20 cores were taken in each stand from trees sampled on points or from randomly selected trees in stands with complete inventories. Because trees were buried to varying depths, especially in the delta-backwater and transition sub-reaches where there was more sedimentation, tree and stand ages probably were underestimated. Some aging inaccuracies also were expected due to indistinct rings produced by diffuse porous wood. Tree cores were aged by the Rocky Mountain Tree Ring Research Lab (Fort Collins, Colorado, USA).

Understory saplings.—The sapling vegetation layer included all woody saplings, shrubs, and lianas ≥1 m tall and <10 cm dbh. Sapling species were defined as small trees capable of attaining tree size (≥10 cm dbh). Shrub species were those that remain <10 cm dbh throughout their life span and are restricted to the seedling and sapling vegetation layers.

The sapling layer was sampled using Lindsey's line-strip method (Lindsey 1955). Methods to locate sample plots in stands followed the stratified method described for trees. Depending on stand area, 8–12 sample plots measuring 2 × 10 m were established in each stand. At each plot location, a measuring tape was stretched to a length of 10 m along the transect bearing. All qualifying stems rooted within 1 m of either side of the tape were counted and identified. The diameter of each stem was measured at ground level using a handcrafted measuring tool with notches of 0–2, 2–4, 4–6, 6–8, and 8–10 cm wide.

The percent cover of each qualifying species was estimated along the 10 m tape where it intercepted the vertical plane of the center transect line. Cover by sapling layer was totaled along the tape for each species. Species sometimes had overlapping coverage along the tape; thus, total percent sapling layer cover could exceed 100% on a single plot.

Understory seedlings.—Woody seedlings <1 m tall were sampled in 1 × 1 m subplots placed within the line-strip plots. Each 10 m long line-strip plot was divided into 1 m long segments. Two of these segments were selected randomly (one plot between 0–5 m, and one plot between 6–10 m) for a total of 16–24 plots per stand, depending on stand area. The quadrat was centered on the transect line in each of the selected segments. Within each quadrat, the number of stems per seedling species was counted, and the percent cover for each species was visually estimated to the nearest 5%. Species with trace occurrence were recorded as 1% cover. Total percent seedling cover could exceed 100% in a single quadrat.

Vegetation analysis

Measures of abundance.—Measures of abundance were calculated for each species in the overstory, sapling, and seedling layers of the 35 stands. Calculations for the overstory sampled using the point-centered quarter method followed the procedures of Curtis and McIntosh (1950) and Cottam and Curtis (1956). Importance value, which ranged from 0–300, was calculated as the sum of the relative frequency, relative density, and relative dominance of a species (Curtis and McIntosh 1951). Frequency could not be calculated for tree species in stands sampled by a complete inventory. Hence, tree species importance value for these stands was based on the sum of relative density and relative dominance with a maximum value of 200, and then scaled to a maximum value of 300 to allow for comparison with other stands.

Ordination.—Ordination was used to investigate the structural and compositional relationships of the vegetation among the delta-backwater, transition, and White River sub-reaches. All analyses were conducted in PRIMER 6.1 (Clarke and Gorley 2006). Compositional similarity among stands was computed using the Bray and Curtis (1957) index. Similarity matrices were constructed for all vegetation characteristics listed above. Nonmetric multidimensional scaling (NMDS) was used with the similarity scores to order all stands using 25 restarts and a minimum stress of 0.01. Two-dimensional NMDS configurations were produced for each vegetation characteristic.

Sub-reach similarity.—Vegetation community composition was compared between the White River delta-backwater (stands of post-dam origin located between rkm 0–24) and White River sub-reaches (stands above the zone of reservoir backwater influence upstream of rkm 29; Fig. 3) using two methods. Mean importance values for each species in a given sub-reach were calculated separately for each vegetation layer present in tree and sapling stands. Species were then ranked by mean importance values for each vegetation layer in each sub-reach. A Spearman's rank correlation coefficient (r_S; scale of −1 to 1) was calculated using Statistix 9.0 (Analytical Software, Tallahassee, Florida, USA) to determine the degree of association in species composition between sub-reaches. A similar analysis was conducted using the Bray-Curtis similarity index (scale of 0–100) using the resemblance function in PRIMER to statistically compare plant community composition between the two sub-reaches.

Delta-backwater -Missouri River vegetation comparisons.—Woody species presence on the White River delta-backwater was compared to that of two remnant reaches on the Missouri River floodplain (Garrison, North Dakota and Gavins Point, South Dakota and Nebraska; Fig. 1). Vegetation data for these reaches were from field studies conducted in 2007–2008 (Dixon et al. 2010, 2012). Only native woody species in stands <50 yr old (the maximum stand age on the delta-backwater downstream of the transition zone) sampled by similar methods and with geographic ranges common to all three sites were included in the analyses. Stand age for delta-backwater stands was based on tree ring analysis; stand age for the Missouri River reaches was based on analyses of a time-series of historical aerial photography supplemented by some tree ring data (Dixon et al. 2010, 2012). The small differences in the number of stands sampled across reaches (White River delta-backwater, n = 15; Garrison, n = 17; Gavins Point, n = 21) were judged not to have a significant effect on the comparisons.

Tree ring analysis

Tree ring measurements were used to: (1) determine the median age of cored cottonwoods in each stand; (2) construct frequency histograms to inspect cottonwood age structure in each stand; (3) determine mean annual cottonwood diameter growth rates (cm/yr); and (4) compare cottonwood and peachleaf willow growth rates (cm/yr) among the White River and White River delta-backwater sub-reaches. Mean growth rates were compared using the t test and Mann-Whitney test. A t test was used to test for significant differences between sub-reaches for datasets with a normal distribution. Alternatively, a Mann-Whitney test was used to test for significant differences between sub-reaches for datasets without a normal distribution. All statistical tests were performed at a significance level of $\alpha = 0.05$.

Results

Formation of the White River delta-backwater

The delta-backwater formed within the lower 31 rkm of the White River in response to both direct and indirect effects of the reservoir. The lowermost portions of the delta-backwater, representing a delta, formed in the shape of a lobe with a single thread channel that extended 2.3 rkm into Lake Francis Case and was frequently inundated by higher reservoir stages (Fig. 2; Appendix S1: Fig. S1). The delta-backwater also expanded upstream within the lower 28.7 rkm of the White River valley due to backwater effects associated with fluctuating reservoir stages. The downstream portions of this reach were periodically inundated by high reservoir stages (direct effects), while the upstream portions of this reach experienced increased overbank flooding (indirect effects) that resulted from decreases in the White River channel slope as the stream adjusted to a new base level. The record maximum reservoir stage (in 2011) corresponded to a pool boundary that extended ~24 rkm upstream of the pre-dam White-Missouri River confluence (Fig. 4).

Valley cross sections indicated that minor amounts of sediment deposition occurred above maximum reservoir stage and as far as 31 rkm upstream of the pre-dam White River–Missouri River confluence. This deposition, resulting from upstream propagating channel slope adjustments to reservoir backwater effects, can be considered a transition zone from purely fluvial to delta-backwater processes. No change in vegetation was noticeable or measurable above the 29 rkm boundary. Thus, the 29 rkm boundary was determined to be the upper limit of reservoir backwater influence for the vegetation component of this study (based on GIS mapping and field vegetation sampling data), whereas the 31 rkm boundary was determined to be the upper geomorphic boundary (based on cross section data; Table 1).

The lower White River and its confluence with Lake Francis Case experienced high rates of channel and floodplain aggradation and associated geomorphic change during the post-dam era. Increases in thalweg elevation ranged from 0.61 m (rkm 30.9) to 11.95 m (rkm 3.1; Table 2). Other post-dam changes to the channel and floodplain environment included: the width and depth of the active channel generally decreased; the floodplain aggraded to a similar degree as the thalweg; and at some cross sections, prominent natural levees formed adjacent to the active channel (Fig. 5). These changes represent a highly depositional environment with very little erosion or channel movement during the post-dam period.

Rates of aggradation for most cross sections were greatest during the first measurement interval following dam closure (1953/1954–1973), sharply declined during the second measurement interval (1973–1996), and moderately increased during the third measurement interval (1996–2011; Table 2). During the first and third measurement intervals, rates of thalweg aggradation were generally greatest at the most downstream cross sections and decreased in the upstream direction.

Sedimentation during the post-dam period created a "sediment wedge" that led to a flattening of the stream gradient across the delta-backwater (Fig. 6). In 1954 (2 yr post-dam), the mean stream gradient was 0.70 m/km. By 2011 (59 yr post-dam), the mean gradient had flattened to 0.29 m/km. This sediment wedge was thickest in the lowermost 13 rkm of the White River where the slope flattened to near 0.00 m/km.

Table 2. Change in thalweg elevation (m) and mean rate of change in thalweg elevation (m/yr) for each measurement interval at six cross sections from the lower White River and its confluence with the Missouri River (Lake Francis Case) in South Dakota, USA.

Cross section (rkm)	Change in thalweg elevation (m)				Mean rate of change in thalweg elevation (m/yr)		
	1953/1954–1973	1973–1996	1996–2011	Total	1953/1954–1973	1973–1996	1996–2011
Confluence	9.94	0.21	0.37	10.52	0.52	0.01	0.02
3.1	9.69	0.12	2.13	11.95	0.48	0.01	0.14
8.4	7.41	0.24	1.10	8.75	0.37	0.01	0.07
13.0	5.58	−0.06	0.33	5.85	0.28	0.00	0.02
23.2	1.04	0.70	0.52	2.26	0.05	0.03	0.03
30.9	−0.03	0.76	−0.12	0.61	0.00	0.03	−0.01

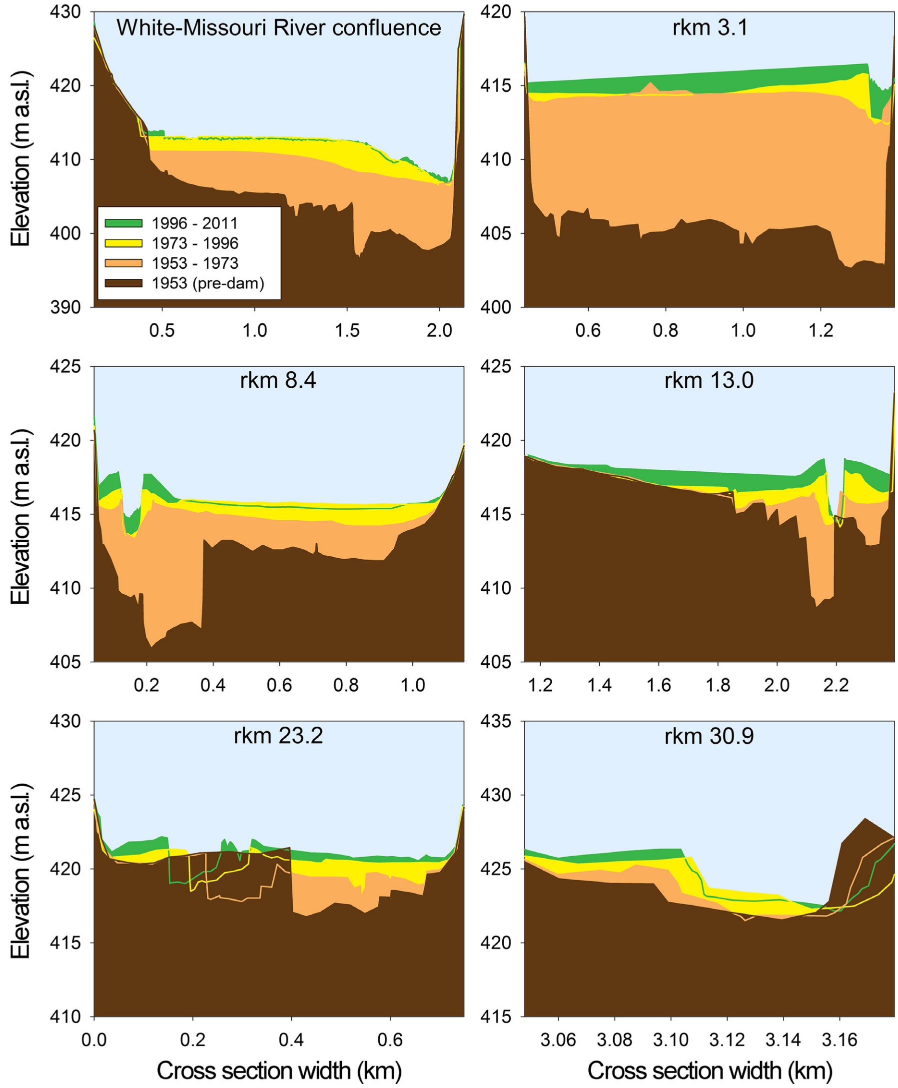

FIG. 5. Sedimentation history at six cross sections from the lower White River and its confluence with the Missouri River (Lake Francis Case) in South Dakota, USA. Vertical axes differ among graphs. The area under each curve is filled in to improve visual clarity. Abbreviations are a.s.l., above sea level; rkm, river kilometer.

Expansion of delta-backwater vegetation

GIS mapping of historic aerial photos indicated that riparian woodland area increased by 382 ha (49%) between 1948 (pre-dam) and 2012 (post-dam; Table 3, Fig. 7). Pre-dam (1948) woodland was dominated by the old age class (535 ha, 68%); woodland at the midpoint of the study period (1983) was dominated by the young age class (445 ha, 46%); and woodland at the end of the study period (2012) was dominated by the medium age class (539 ha, 46%).

Although there was a net increase in woodland area on the delta-backwater during the post-dam period, woodland area declined during years with floods on the Missouri River. Between 1991 and 1998, a period that included the 1997 Missouri River flood (the year of the second highest stage on record for Lake Francis Case), there was a loss of 101 ha of riparian woodland (Table 3). Woodland declined throughout the delta-backwater, but the greatest declines occurred between rkm 0–15 along the woodland edges closer to the valley walls. The interval 2004–2010 included the third highest reservoir stage on record (in 2010). About 22 ha of riparian woodland were eliminated by flooding, especially in the lower delta-backwater. During 2010–2012, which included the record high reservoir stage (in 2011), 45 ha of woodland died and 55 ha experienced flood damage concentrated between rkm 0–10. Much of the damaged woodland died by June 2013. The majority of woodland losses over the photographic record (1948–2012) were concentrated between rkm 0–10 where reservoir inundation was either permanent or was most

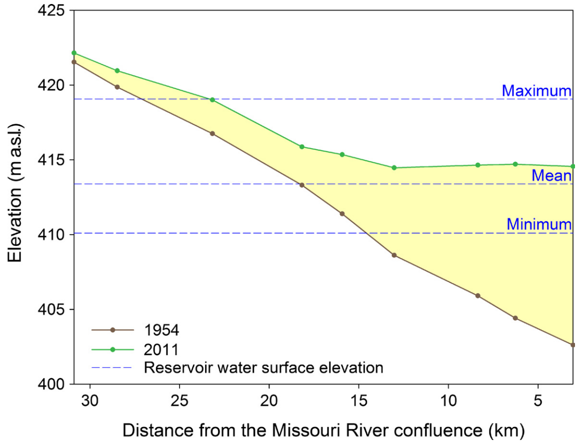

FIG. 6. Stream gradient of the lower 31 km of the White River in South Dakota, USA in 1954 and 2011, depicting the formation of a sediment wedge within the delta-backwater. The dotted blue lines depict minimum, mean, and maximum (2011) mean daily reservoir water surface elevations (1989–2014). The reservoir water surface elevations were derived from the USGS Gage 06442996 at Chamberlain, South Dakota, USA. Abbreviation is a.s.l., above sea level.

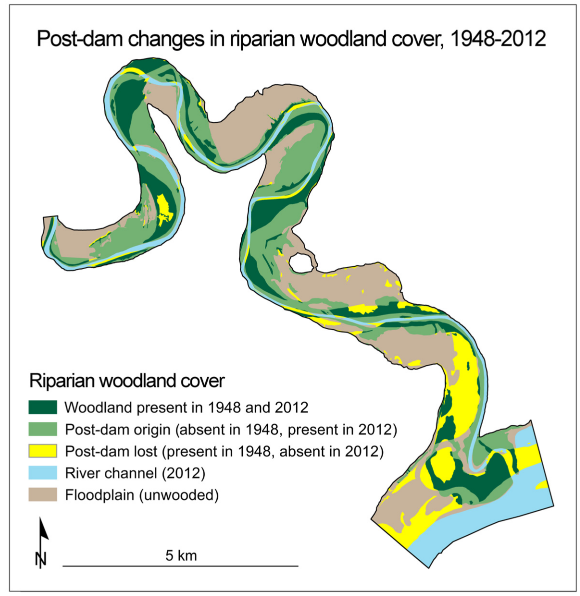

FIG. 7. GIS map of riparian woodland cover changes between 1948 (pre-dam) and 2012 (post-dam) from aerial photographs of the lower 29 km of the White River in South Dakota, USA.

TABLE 3. Total riparian woodland area (ha) by year and age class along the lower 29 km of the White River in South Dakota, USA.

	Riparian woodland area (ha)				
Year	Total	Young	Medium	Old	Partial mortality
1948	782	195	52	535	0
1983	968	445	335	188	0
1991	1,102				0
1998	1,001				0
2004	1,230				0
2010	1,209				0
2012	1,164	141	539	484	55

Note: Age classes were not determined for years 1991–2010.

frequent (Figs. 4 and 7). The smaller area of woodland lost upstream was caused by channel migration and clearing by landowners. Early in the formation of the delta-backwater, there was some minor channel movement that likely precluded the backwater influence. Since that time, there has been essentially no change in the channel alignment.

Vegetation comparisons among sub-reaches

Stand ages.—Tree ring data indicated that stand ages differed among the White River, transition, and delta-backwater sub-reaches (Fig. 8). Delta-backwater stands all were of post-dam origin (<60 yr old); the lower delta-backwater contained stands up to 14 yr old and the upper delta-backwater contained stands up to 48 yr old. Stands along the White River represented a wider range of ages (<10 to 134 yr old) that spanned both the pre- and post-dam periods. The two stands in the transition sub-reach (stands 17 and 18) were both of pre-dam origin (142 and 160 yr old, respectively). Seventy-five percent of stands on the delta-backwater were <20 yr old, vs. only 24% of stands along the White River.

Age structure in cottonwood stands generally followed a normal distribution across a narrow range of ages, consistent with the even-aged nature of cottonwood stands along unregulated rivers. Some stands on the delta-backwater and along the White River, however, contained multiple cohorts of tree-size cottonwoods. Two distinct cottonwood age cohorts (e.g., 10–15 yr old and 35–40 yr old) were present in four (25%) of the 16 delta-backwater stands (Appendix S1: Fig. S2) and in two (12%) of the 17 White River stands. In these mixed-age stands, the large majority of cottonwood trees were in the younger cohort. On the delta-backwater, mixed-age stands were the result of cottonwood recruitment that occurred within existing cottonwood stands ≥15 yr old undergoing repeated sedimentation. In contrast, mixed-age stands along the White River were formed by adjacent narrow bands of cottonwoods that established at different times.

Cottonwood and willow seedlings and saplings often occurred in the understory of tree stands on the delta-backwater and transition reaches, but not along the White River. Cottonwood and sandbar willow each occurred in the understory of 67% of tree stands on the delta-backwater, in stands up to 46 and 48 yr old, respectively. Likewise, peachleaf willow occurred in the understory of 33% of tree stands on the delta-backwater, and yellow willow (*Salix lutea* Nutt.) occurred in the

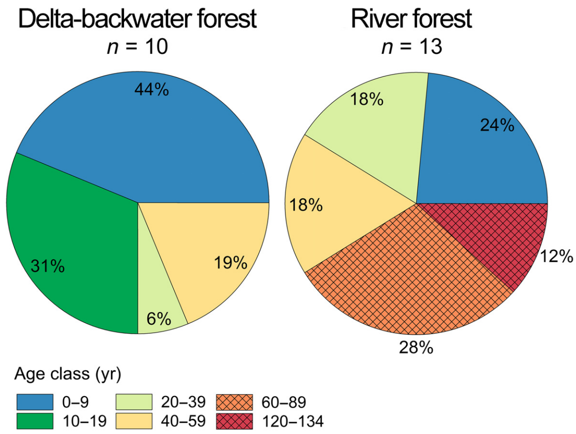

FIG. 8. Age class proportions of cottonwood stands on the White River delta-backwater and along the White River. Cross-hatching indicates stand age groups of pre-dam origin (≥60 yr old).

understory of 40% of tree stands on the delta-backwater, in stands up to 48 yr old. Cottonwood and willows also occurred in the understory of the two transition stands.

Cottonwood growth rates.—Cottonwood growth rates were greatest in the youngest age classes (Appendix S1: Fig. S3). For trees in a given age class, cottonwood growth rates were generally greatest on the lower delta-backwater, followed by the upper delta-backwater and then the White River. Cottonwood growth rates were significantly greater on the lower delta-backwater (2.117 ± 0.188 cm/yr) than along the White River (1.575 ± 0.133 cm/yr) for trees in the <10 yr age class ($t_{0.05(2),7} = 2.419$, $P = 0.046$), significantly greater on the lower delta-backwater (1.432 ± 0.144 cm/yr) than the upper delta-backwater (1.177 ± 0.041 cm/yr) for trees in the 10–19 yr age class ($U_{0.05(2),15,84} = 346.5$, $P = 0.006$), and significantly greater on the upper delta-backwater (1.094 ± 0.074 cm/yr) than along the White River (0.696 ± 0.027 cm/yr) for trees in the 30–39 yr age class ($U_{0.05(2),25,56} = 277.5$, $P < 0.001$). Conversely, the growth rate for peachleaf willow trees in the 10–19 yr age class was significantly lower on the delta-backwater (0.89 ± 0.06 cm/yr) than along the White River (1.51 ± 0.14 cm/yr; $t_{0.05(2),13} = 4.548$, $P < 0.001$).

Woody plant species diversity.—Twenty-three woody species were sampled in the study area. Cottonwood, peachleaf willow, and green ash were the dominant overstory species. Russian olive, native to Eurasia, occurred throughout the length of the study area, but only occurred as a dominant in the mid-story of a few White River stands. Honey locust (*Gleditsia triacanthos* L.), native to portions of the eastern United States, has been introduced as a windbreak tree to the study area and was present in small numbers along the White River. Eastern red-cedar (*Juniperus virginiana* L.), an upland species native to the region but often considered invasive on floodplains (Greene and Knox 2014), occurred in some stands along the White River. Three species of lianas were present, including riverbank grape, woodbine, and western white clematis (*Clematis ligusticifolia* Nutt.). Riverbank grape was by far the most common liana species, followed by woodbine. Overall, nonnative woody species were uncommon on the delta-backwater.

Woody plant diversity was much higher along the White River than on the delta-backwater (Fig. 9). Of the 23 species, 21 (91%) occurred along the White River, 14 (61%) occurred in the transition sub-reach, and 14 (61%) occurred on the delta-backwater. Nine species were found only along the White River, and several other species were more frequent along the White River than on the delta-backwater. For example, western snowberry was present in 82% of White River stands but only occurred in 27% of delta-backwater stands. Likewise, eastern red-cedar, poison ivy, golden currant, and fragrant sumac (*Rhus aromatica* Aiton) were present in stands along the White River but not on the delta-backwater. Chokecherry was present in stands along the White River and in one transition stand, but not in any delta-backwater stands. Willows were observed in more stands on the delta-backwater than along the White River. For example, sandbar willow was present in 80% of the stands on the delta-backwater compared to 24% of the stands along the White River; peachleaf willow was present in 67% of the stands on the delta-backwater compared to 41% of the stands along the White River; and yellow willow was present in 27% of the stands on the delta-backwater but was absent in the White River stands.

Age gradient analysis.—1. White River delta-backwater.—Arranging stands into a gradient of age exposed shifts in tree species diversity and composition through successional time. In general, tree species diversity was lowest in the youngest, early successional stands (Fig. 10). These stands were dominated almost exclusively by seedlings and saplings of cottonwood and peachleaf willow, both pioneer species. Willows as a group dominated the wettest sites along the lower delta-backwater, while cottonwood dominated the drier upper delta-backwater. Once these stands attained tree size (≥11 yr old), more tree species occupied the understory. The oldest forests on the delta-backwater were dominated by cottonwood in the overstory and green ash (especially) and Russian olive seedlings and saplings in the understory.

2. White River.—Patterns of species abundance along the age gradient were similar to those on the delta-backwater. Low tree species diversity and dominance by cottonwood seedlings and saplings typified the youngest stands (Fig. 10). Middle age stands were cottonwood dominated with green ash (especially) and Russian olive in the understory. American elm commonly occurred in the understory of the oldest stands, but due to Dutch elm disease, it was extremely rare in the overstory.

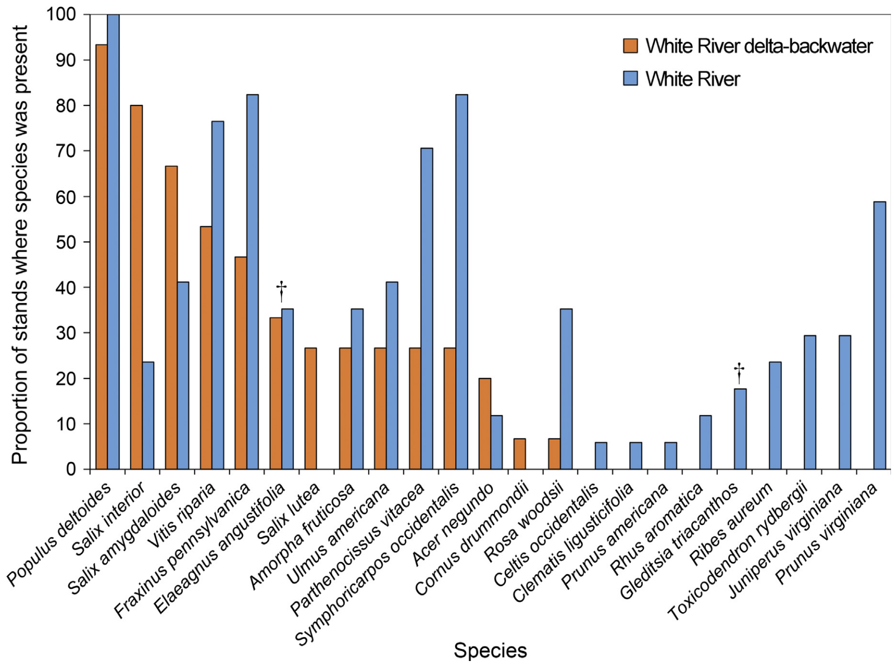

FIG. 9. Proportion of sampled stands on the White River delta-backwater and along the White River where each woody plant species occurred. †Nonnative species.

Compared to the delta-backwater, willow trees were a relatively minor component of stands along the White River (Fig. 10).

Longitudinal environmental gradient.—The ordination model visually exposed the vegetation similarities among the three sub-reaches in the study area. Stands aligned along the x-axis in accordance with their proportion of wetland affiliated species (facultative and facultative wetland; Fig. 11; USDA/NRCS 2015). The x-axis represents an environmental moisture gradient spanning the White River-White River delta-backwater, with relatively wet conditions in the lower delta-backwater and relatively dry conditions along the White River. Stands on the lower delta-backwater with the highest proportion of wetland affiliated species formed a group on the left side of the ordination, grading into a group of stands to the right located on the upper delta-backwater with a lower proportion of wetland affiliated species. Stands with intermediate proportions of wetland affiliates occurred in the transition reach in the middle of the gradient. The majority of White River stands formed a group on the right side of the ordination and contained the lowest proportions of wetland affiliated species of any sub-reach. Exceptions to this trend were two young pioneer stands from the White River that grouped with the lower delta-backwater stands on the left side of the ordination. Within sub-reaches, the White River and upper delta-backwater exhibited the greatest variability in vegetation composition among stands, as evidenced by more scatter in the ordination. The calculated two-dimensional stress value for the ordination of species presence was 0.12, which was favorable by being below the recommended upper limit of 0.15 (Clarke and Warwick 2001).

Similarity of White River delta-backwater and White River.—Woody vegetation on the White River delta-backwater and the White River was very similar in overstory and moderately similar in understory vegetation. The Bray-Curtis similarity score based on mean overstory importance values was 84.79. Likewise, the Spearman's rank correlation coefficient (r_S) based on mean species importance values in the overstory was 0.88 ($P = 0.01$), indicating high overstory similarity. The Bray-Curtis similarity scores for the sapling and seedling layers were lower, 46.98 and 48.13, respectively.

Similarity of the White River delta-backwater to Missouri River remnant reaches.—The White River delta-backwater shared many woody species with the Garrison and Gavins Point remnant reaches of the Missouri River. Of the native woody species present with geographic ranges common to all three sites, 11 occurred on the delta-backwater, 13 occurred along the Gavins Point reach, and 16 occurred along the Garrison reach (Fig. 12). Eleven of the 16 species that occurred along the Garrison reach and 10 of the 13 species that occurred along the Gavins Point reach also occurred on the delta-backwater. Ten species were common to all three sites, including cottonwood, green ash, peachleaf willow, sandbar willow, western snowberry, American elm, false indigo, woodbine, riverbank grape, and Woods' rose.

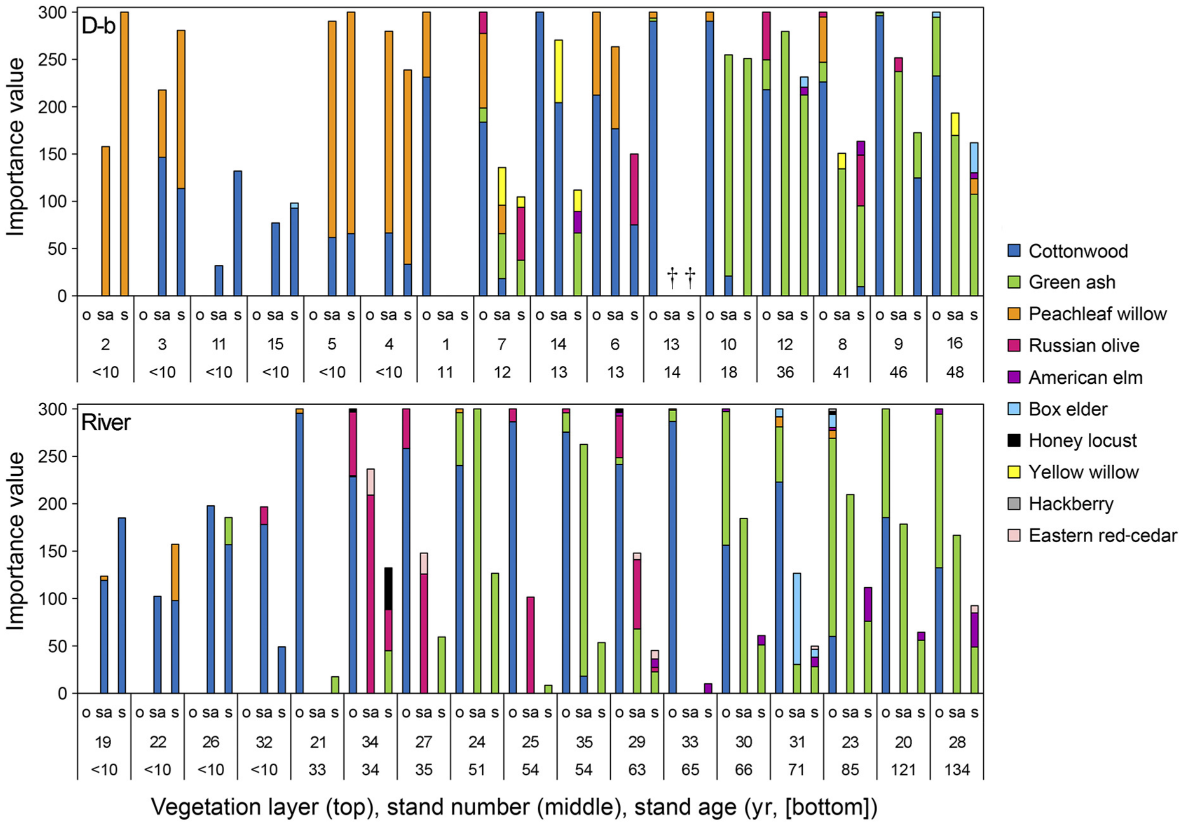

FIG. 10. Importance value for each tree species in the overstory (o), sapling layer (sa), and seedling layer (s; relative density + relative dominance + relative frequency; maximum = 300) in each stand on the White River delta-backwater (D-b; top panel) and along the White River (bottom panel) in South Dakota, USA. Stands are ordered from youngest to oldest at unequal intervals. †No applicable seedling or sapling layer data were collected in stand 13.

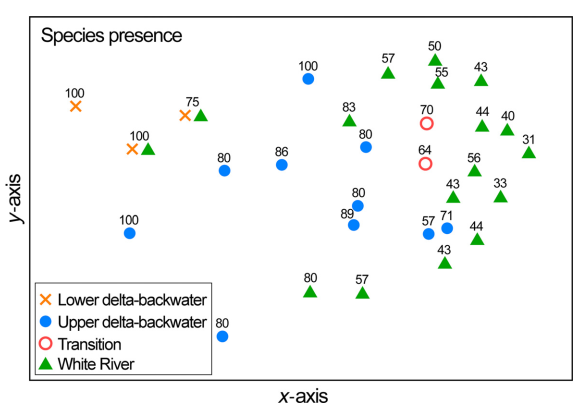

FIG. 11. A nonmetric multidimensional scaling stand ordination plot constructed from a matrix based on species presence in the seedling, sapling, and overstory layers. Two-dimensional stress = 0.12. Stands located near each other are very similar floristically, whereas stands far apart are more dissimilar. The percentage of species in each stand with either facultative or facultative wetland indicator status is labeled above each point (there were no obligate wetland species in the sample). Stand 13 from the upper delta-backwater was excluded from this analysis because of the absence of seedling and sapling layer data.

The White River delta-backwater had a higher proportion of wetland affiliated species, such as false indigo, riverbank grape, and yellow willow, than the Missouri River remnant reaches. Eighty percent of species on the delta-backwater were wetland affiliated, compared to only 56% and 54% of species along the Garrison and Gavins Point reaches, respectively. Conversely, a number of upland affiliated species, including American plum (*Prunus americana* Marshall) and American bittersweet (*Celastrus scandens* L.), occurred along the remnant reaches but not on the delta-backwater. Thus, compared to the remnant reaches, the delta-backwater was more suitable for wetland plants and less suitable for upland plants (Fig. 13).

DISCUSSION

Delta-backwater formation

The White River delta-backwater formed within 31 rkm of former river bottomland in response to construction of Lake Francis Case reservoir in 1952. As Lake Francis Case filled, the rising water inundated and eliminated former river and floodplain environments. Fluctuations in reservoir levels within the former river bottomland altered the base level of the stream along with the geomorphic processes that gave rise to the delta-backwater. Sediment transported by the White River accumulated in the drowned bottomlands and subaquatic delta deposits raised the elevation of the former riverbed and adjacent floodplain. Aggradation upstream in the backwater-affected bottomland formed a continuum of new geomorphic surfaces. The normal operating reservoir pool (Fig. 4) marked a transition from a lacustrine environment to a backwater-influenced, fluvial floodplain dominated by marsh near the reservoir, and woody riparian species farther upstream. Indirect effects of the reservoir backwaters created geomorphic changes 7 rkm upstream of the maximum pool elevation (Figs. 5 and 6), which represented another transition from backwater-influenced forested floodplain to the fluvial riparian forests of the White River. Newly deposited sediments, exposed during reservoir drawdown, became suitable for colonization by primarily native riparian plants. Increased surface roughness from vegetation helped capture sediment and further aggrade floodplain surfaces (Osterkamp and Hupp 2010). A similar pattern of channel and floodplain aggradation of fine sediments and establishment of herbaceous vegetation on newly exposed surfaces was reported in the fluctuating backwater zone of a reservoir along the Liaohe River, China (Xu and Shi 1997).

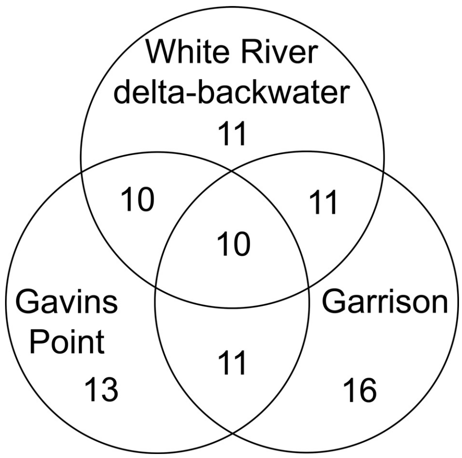

Fig. 12. Venn diagram comparing the number of woody plant species shared among the White River delta-backwater and two remnant reaches on the Missouri River floodplain (Garrison, North Dakota and Gavins Point, South Dakota and Nebraska, USA).

The vertical range accrued by the White River delta-backwater from its inception has been considerable; valley cross-sectional surveys of the White River showed that the bottomland aggraded from 0.6 to 12.0 m between 1954 and 2011 (Figs. 5 and 6). Sediment deposition was greatest in the lower 13 rkm of the delta-backwater where the channel slope was reduced to 0 m/km.

Fig. 13. Cottonwood forests in four divergent environments: lower delta-backwater frequently flooded, showing river channel and standing water on the floodplain behind well-developed natural levees; upper delta-backwater less frequently flooded but occasional understory burial with fine sediments; White River (active floodplain) short-term flooding and diverse, well-developed understory; Missouri River (protected floodplain) now rarely if ever flooded, xerification of the understory with nonnative Russian olive dominant in the mid-story.

As a result, upstream flow velocity slowed, and the width and depth of the active channel decreased, which increased the frequency of overbank flows delivering sediment, water, and coarse woody debris to the floodplain. Similarly, channel narrowing and change in channel planform, resulting from the accumulation of fine sediment, were reported for a braided, gravel bed river following a change in base level related to fluctuating reservoir backwaters in Poland (Liro 2017).

Sediment deposition was greatest adjacent to the active channel, forming natural levees with a higher elevation and drier conditions than the surrounding floodplain (Fig. 5; Adams et al. 2004). Levee formation along the margins of low gradient distributary channels is a widely reported process on coastal and inland deltas (Waldemarson Jensén 1979, Johnson et al. 1985, Kincheloe and Stehn 1991). With a reduced channel gradient and high sediment loads, channel narrowing and levee building were enhanced by the establishment of vegetation. Positive feedbacks between vegetation density and sediment deposition during channel narrowing have been observed in other settings (Friedman et al. 2015). Little lateral migration of the active channel occurred during the post-dam period (Bagnold 1966), particularly in the lower reaches of the delta-backwater where the channel slope was flattest. The formation of natural levees along the channel reduced the frequency of overbank flows that delivered water and sediment across the bottomland. When overbank flows overtopped the levees, or during high stages of the reservoir, standing water and fine sediment became trapped in flood basins between the levees and valley walls, increasing the duration of inundation on this portion of the delta-backwater.

The White River delta-backwater is one of nine prominent delta-backwater complexes currently forming in the upper Missouri River basin (Volke et al. 2015). Such complexes have been and are forming in tens of thousands of reservoirs worldwide that have been constructed over the past several decades in developed countries and more recently in developing countries (Lehner et al. 2011, Zarfl et al. 2015). These new and little-known environments are important elements of riverscapes on a global scale. Tributary delta-backwaters form where streams flow into the still water of reservoirs, often perpendicular to the long axis and into deeper portions of the reservoir. Likewise, mainstem delta-backwaters form where the trunk stream flows into the shallow, uppermost margins of the reservoir. Distal portions of the delta expand into the reservoir while the backwater-affected bottomland extends up the tributary or mainstem river valley. Because of differences in landscape position and stream gradient, the length of the delta-backwater often differs between the mainstem and tributaries. For example, the length of the White River tributary delta-backwater is ~31 rkm, while the mainstem Oahe Reservoir delta-backwater is over 100 rkm in length (Volke et al. 2015).

Basic geomorphic research on coastal delta formation (Giosan and Bhattacharya 2005) and studies of geomorphic response to base level changes (Leopold and Bull 1979), along with results from the White River delta-backwater and observations of other delta-backwaters in the upper Missouri River basin (Volke et al. 2015), suggest that the size, shape, growth rate, and vegetation communities of delta-backwaters are determined by multiple interacting factors. These factors include the sediment load and particle size of the contributing stream or river; the size, depth, and age of the reservoir; and the frequency and magnitude of reservoir level fluctuations, among others (Liro 2019). For example, the White River transports a high volume of fine-grained sediments (>19,000 Mg/d; USGS Gage 06452000) and has formed a backwater with a single thread channel and a prominent delta lobe that extends into Lake Francis Case reservoir. This reservoir can hold about 6.7 km^3 of water (USACE 2006) with an average annual vertical fluctuation of about 4 m (1989–2013; USGS Gage 06442996). Contrastingly, the Niobrara River, a nearby tributary to the Missouri (Fig. 1), transports mostly sand (about 4,000 Mg/d; USGS/USACE Gage 06465500) and has formed a braided channel delta-backwater at the shallow-water junction of the Missouri River and Lewis and Clark Lake above Gavins Point Dam (Coker et al. 2009, NRC 2011, Volke et al. 2015). Lewis and Clark Lake can store about 0.6 km^3 of water (USACE 2006) with an average annual vertical fluctuation of <1 m (USGS/USACE Gage 06466700). The White River delta-backwater currently supports approximately 50% woody vegetation cover, whereas the Niobrara River delta-backwater is dominated by herbaceous wetland vegetation (e.g., *Phragmites* spp. and cattails), although young riparian woodlands have developed in some locations (M. Dixon, *personal observation*). These two neighboring examples illustrate the range of variability in the abiotic factors that determine pattern and extent of delta-backwaters across river basins.

Vegetation response to delta-backwater formation

Progressive sediment deposition on the White River delta-backwater produced a flood-prone and sediment-rich environment with frequent opportunities for recruitment of early successional riparian species like cottonwood. The delta-backwater environment continuously produced new alluvial surfaces that provided suitable establishment sites for cottonwood and willow, which require bare moist soils for germination (Stromberg 1993, Scott et al. 1996, Mahoney and Rood 1998). Woody vegetation cover on the delta-backwater increased by 50% over the 60-yr post-dam period (Table 3, Fig. 7). All woody species found on the delta-backwater were native, with the exception of Russian olive, indicating that this novel environment supports riparian forests dominated by native species (Fig. 9). Vegetation successional patterns on the delta-backwater generally followed those along the free-flowing White

River with the establishment of secondary species like green ash in older stands (Fig. 10). However, whereas drought and flood-scour are common causes of seedling mortality along free-flowing river reaches (Mahoney and Rood 1998), survival of woody seedlings was likely enhanced by conditions across the developing delta-backwater, which featured enhanced deposition and higher groundwater levels (Liro 2019). Formation of delta-backwaters has the potential to reintroduce key processes such as flooding, fluvial disturbance, and sediment deposition, upon which riparian ecosystems depend (Scott et al. 1996, Naiman et al. 2005, Rood et al. 2007), but have been curtailed along regulated river reaches. However, these processes still differ in detail from those operating along free-flowing rivers, particularly with regard to the timing, magnitude, and duration of inundation from the reservoir.

Woody vegetation on the White River delta-backwater established predictably along disturbance and hydrologic gradients. Plant species favored by sub-irrigated or hypoxic soils over long time periods comprised a larger proportion of the flora in the downstream direction, where hydrology was dominated by fluctuation in reservoir stage (Fig. 11). The wettest portions of the delta-backwater near the reservoir supported emergent wetland vegetation, primarily cattails, peachleaf willow, and sandbar willow. Willows that co-occurred with cattails, however, often exhibited signs of flood stress, including production of adventitious roots and stunted growth (Timoney and Argus 2006). Riparian species adapted to flood recession and water table decline (i.e., drier soils) during the growing season were more abundant along the upstream longitudinal gradient, where hydrology was dominated by flows and sediment delivered from the White River rather than inundation from the reservoir. This pattern of occurrence for riparian species on less frequently inundated portions of the delta-backwater matches predictions of Bejarano et al. (2018) based on the exposure of riparian vegetation to frequent and rapid fluctuations in flow and water levels along streams subject to hydropeaking. Further, cottonwood grew faster on the sub-irrigated delta-backwater than along the White River, where growth may have been limited during low-flow periods or by seasonal flow recession (Appendix S1: Fig. S3). Nine non-wetland species were found only on sites along the White River; only two species were restricted to the delta-backwater. These findings suggest that conditions in the delta-backwater are generally more mesic but are nonetheless consistent with observations of riparian vegetation zonation on floodplains where plant species are distributed according to moisture tolerances (Hupp and Osterkamp 1985, Amlin and Rood 2001, Merigliano 2005). Compositional differences between the delta-backwater and White River sub-reaches may have been partially due to the absence of older stands on the delta-backwater.

Cottonwoods and willows showed distinct spatial patterns within the delta-backwater, reflecting known differences in inundation tolerance, although they often coexist (Noble 1979, Busch et al. 1992, Amlin and Rood 2001). Willows dominated the lower, wetter portions of the delta-backwater, while cottonwood dominated higher surfaces where soils were drier and flooding was of shorter duration. Spatial segregation between cottonwood and willow stands also was observed along the Duncan River–Kootenay Lake reservoir delta in British Columbia, Canada (Herbison and Rood 2015). Willows will likely remain a prominent feature of the downstream portions of the White River delta-backwater, while cottonwood establishment will be limited on lower delta-backwater surfaces that are frequently inundated by the reservoir and/or where groundwater levels remain high during the growing season.

Expansion of woody vegetation on the delta-backwater was curtailed at times by mortality from prolonged reservoir inundation. From 2% to 9% of the total woodland area on the delta-backwater was killed following high-water events in three sampling years between 1997 and 2011 (Table 3). During the record flood of 2011 (Dixon et al. 2015), vegetation on portions of the delta-backwater was flooded for over three months, far exceeding the typical pre-dam Missouri River flood duration of one to three weeks (NRC 2002). Multiple studies have documented cottonwood intolerance to season-long flooding (Amlin and Rood 2001, Nielsen et al. 2010). Although willows are more flood tolerant, many died when entirely or partially submerged for most of the growing season. These and other pioneering species re-established soon after reservoir levels returned to more normal levels, although reproduction was inhibited in places where flooding left behind standing dead and downed trees, and/or where recruitment was limited by nonnative herbaceous species. Cyclical increases and decreases in willow cover on the Peace-Athabasca delta, an inland freshwater delta in Alberta, Canada, were similarly related to flooding and drying of the delta coinciding with climate-related wet and dry cycles (Timoney and Argus 2006).

The extensive bare, nutrient-rich sediments of delta-backwaters exposed during low reservoir stages may initially favor weedy, nonnative species, depending on the timing and rate of drawdown (Stromberg 1997). Like rivers, delta-backwaters experience high rates of flood and human disturbance and linear connectivity that make them prone to the invasion and spread of nonnative species (Planty-Tabacchi et al. 1996, Richardson et al. 2007, Engel et al. 2014, Perkins et al. 2016). This has raised concerns about the role delta-backwaters may play in facilitating nonnative species invasions throughout entire river basins (Chen et al. 2016). However, weed invasion may be short lived; over time, some important native species may colonize weedy sites that are not reinundated (Engel et al. 2014).

An unexpected observation on the delta-backwater was the presence of cottonwood seedlings and saplings in established cottonwood stands. Throughout its range, cottonwood occurs principally in even-aged forests because seedlings fail to germinate or survive in the shade and litter of established stands (Braatne et al. 1996). In one-quarter of delta-backwater stands, younger cottonwood cohorts had recruited into the older overstory population (≥10 cm dbh; Appendix S1: Fig. S2). Frequent sedimentation and burial of understory vegetation and litter, canopy openings created by beaver, partial overstory mortality caused by flooding or historic clearing, and elevated groundwater levels adjacent to Lake Francis Case (Simons and Rorabaugh 1971) likely improved recruitment opportunities compared to free-flowing river conditions (Mahoney and Rood 1998). These observations suggest that pioneer cottonwood forests on the delta-backwater may be, to some degree, self-maintaining. Formation of uneven-aged stands of cottonwood has been reported under specific circumstances: extended cottonwood recruitment periods on a young island (Merigliano 1998), in a filling arroyo (Friedman et al. 2005), during the processes of channel narrowing (Friedman and Lee 2002) and channel abandonment (Stella et al. 2011), and under a partially flood-killed canopy (Yin 1998).

Spatial patterns of cottonwood establishment on the White River delta-backwater differed from those along free-flowing meandering rivers. Cottonwood forests on floodplains formed by a meandering river typically produce even-aged, arcuate bands on the inside of river meander loops (Everitt 1968, Johnson et al. 1976, Bradley and Smith 1986). These bands generally are youngest on point bars near the channel and progressively older with increasing distance away. On the White River delta-backwater, however, the natural stand age sequence was often reversed, with the oldest stands bordering the active channel and the youngest stands occurring on sites closer to the outer margins of the delta-backwater (Fig. 7). This pattern has two explanations: a fixed channel location and land use. The flattening of the stream gradient and the formation of levees reduced lateral movement of the single-thread channel (Bagnold 1966). This favored cottonwood reproduction on levees during early delta-backwater formation. As such, stands bordering the river channel were relatively protected from scour and persisted throughout the post-dam period. The raised natural levees also protected cottonwood stands from mortality caused by prolonged inundation. Levees in many natural deltas are typically the only sites dominated by woody species (Waldemarson Jensén 1979, Johnson et al. 1985).

Across the entire delta-backwater complex, the stable channel restricted point bar formation and the establishment of new stands along the channel, and instead, cottonwood seedling establishment was largely limited to recent sediment deposits in open areas on the floodplain (Fig. 7). The largest open patches that became colonized by cottonwood were former agricultural fields idled because of increased flood frequency, increased incidence of ice jamming due to the reduced stream gradient, and deposition of sediment and coarse woody debris. These areas often occurred farther from the channel and closer to the valley wall. This trend of new cottonwood forest establishment on the delta-backwater will likely continue until all open areas receiving sediment are forested.

Vegetation diversity comparisons

The White River delta-backwater shared many native woody species with the upstream reaches of the free-flowing White River and the Missouri River remnant reaches. All but two of the woody species that occurred on the delta-backwater also were present along the White River (Fig. 9). All woody species on the delta-backwater occurred along the Garrison reach, and the large majority (91%) of species that occurred on the delta-backwater occurred along the Gavins Point reach (Fig. 12). Russian olive was the only nonnative (Eurasian) woody species found on the delta-backwater. Despite the comparatively lower species richness on the delta-backwater, the large majority of native woody plants associated with riparian habitats were found there. Most tree species in the region are well-adapted to highly variable riparian environments (Van Bruggen 1985) and their propagules are well-dispersed by wind and water. The novel hydrology of the delta-backwater environment, featuring elevated groundwater and episodic reservoir inundation, was tolerated by most native woody species.

The delta-backwater supported a higher proportion of wetland affiliated species, while the White River and Missouri River remnant reaches supported a higher proportion of non-wetland species. This difference can be explained by consistently higher moisture levels on the delta-backwater, which favored plants that tolerate or require persistent moisture during the growing season (Fig. 13). Moreover, the high water table and variable inundation from fluctuating reservoir levels likely prohibited some upland species from establishing on the delta-backwater. The lower proportion of wetland affiliated species along the Missouri River remnant reaches may have been due in part to xerification of the remnant floodplain from lack of overbank flooding and channel degradation (Galat and Lipkin 2000). Compositional differences also may have been related to the relatively young stand age on the delta-backwater. The species best adapted to flooding and alluviation are early successional species that usually decline in abundance as stands age. As the delta-backwater landform ages, it may acquire more non-wetland and later successional species that are currently found along the White and Missouri Rivers.

Whether delta-backwaters will support native riparian diversity well into the future is important to determine. Restoration of the Missouri River's hydrologic and sediment regime has been delayed long enough that the chances of functional ecosystem restoration have been significantly reduced (Johnson et al. 2015). Despite small differences in composition and lower species richness, the natural composition of the Missouri River woody plant community is retained on the delta-backwater. Cottonwood and willow dominate both sites early in succession and the delta-backwater creates an expanding and suitable environment for early successional forests to establish and persist. In so doing, losses of cottonwood forests in remnant reaches are offset, but by an unknown proportion. The comparatively lower species diversity on the White River delta-backwater is consistent with Liro's (2019) hypothesis that these systems will be less diverse than natural riparian zones due to unnatural inundation cycles and high rates of deposition. Data from the White River delta-backwater are compelling enough to encourage ecologists to inventory other delta-backwaters and other critical components of riparian forests, particularly the herbaceous plant community, insect populations, and nesting avifauna. The term "novel" has been applied to newly established vegetation assemblages downstream of dams and to nascent delta-backwaters emerging in reservoirs (Stevens et al. 2001, Johnson 2002). The terms "historical," "hybrid," and "reconciled" have been recently used to describe an increasing diversity of ecosystems with mixtures of natural and human-influenced components (Moyle 2013, Hobbs et al. 2014). Whereas persistent, well-developed delta-backwaters are novel elements in a regulated river basin, the vegetation communities that develop on these features share key species occurring along free-flowing river reaches. Thus, the term hybrid (Hobbs et al. 2009) more correctly applies to delta-backwaters given that they possess both historical pre-dam and novel post-dam components.

Conclusions

1. The formation of Lake Francis Case reservoir in 1952 initiated major changes to the physical template of the lower White River and its bottomland, creating a 31 rkm long delta-backwater complex that was nonexistent in the pre-dam period. The delta-backwater was a highly depositional environment where the channel and floodplain aggraded by as much as 12 m during the post-dam period, creating a longitudinal continuum of fluvial and deltaic environments. Additional physical changes due to chronic sedimentation included flattening of the stream gradient, reduced channel capacity, formation of prominent natural levees adjacent to the active channel, and producing and exposing bare sediments throughout the delta-backwater. These geomorphic features and conditions provided the physical template for riparian forest establishment, although they differed from those along free-flowing rivers. Formation of the delta-backwater complex was controlled by the natural flow and sediment regimes of the White River and new base levels caused by filling of the reservoir and reservoir backwater fluctuations.
2. The cover of woody vegetation on the delta-backwater increased during the post-dam period. The current delta-backwater is best described as a "hybrid" ecosystem formed as a combination of older forests that established in the pre-dam period and younger forests that established under a novel hydrology in the post-dam period. Forest expansion has been slowed at times by chronic inundation during high reservoir stages that caused forest mortality.
3. Plant species were distributed along an environmental continuum running longitudinally from the White River above the delta-backwater to the lower lobe of the delta prograding into Lake Francis Case reservoir. This gradient ranges from drier, less flood-prone conditions along the White River that frequently supported facultative and non-wetland species, to wetter, sub-irrigated and frequently inundated conditions associated with the reservoir in the lower delta-backwater that favored wetland affiliated species, especially willows.
4. Post-dam forests on the delta-backwater were dominated by cottonwood and willow, the same dominants found on the White River floodplain upstream of the reservoir influence. Moreover, the new forests shared many of the same species with remnant reaches of the Missouri River floodplain. Although the physical processes controlling delta-backwater formation are novel to the river system, the delta-backwater forests are an analogue of those that formed historically in response to natural, pre-dam fluvial geomorphic processes.
5. There is surprisingly little information regarding the physical and ecological processes that shape the tens of thousands of reservoir delta-backwaters emerging in regulated rivers worldwide. Further study is needed to quantify the potential of delta-backwaters to contribute to riverine and riparian biodiversity and ecosystem services along regulated rivers.

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Supporting Information

Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecm.1363/full

Data Availability

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.6mn67g0