THE ECOLOGICAL SIGNIFICANCE OF EMERGING RESERVOIR DELTAS: EVIDENCE FROM THE WHITE RIVER DELTA IN SOUTH DAKOTA

BY

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This dissertation is approved as a creditable and independent investigation by a candidate for the Doctor of Philosophy in Biological Sciences degree and is acceptable for meeting the requirements for this degree. Acceptance of this does not imply that the conclusions reached by the candidates are necessarily the conclusions of the major department.

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ABBREVIATIONS

Abbreviation	Term
cm	centimeter
dbh	diameter at breast height (1.3 m above ground surface)
FAC	facultative species (wetland indicator status)
FACU	facultative upland species (wetland indicator status)
FACW	facultative wetland species (wetland indicator status)
ha	hectare
IV	importance value
km	kilometer
l	liter
m	meter
masl	meters above sea level
mg	milligram
mm	millimeter
NAIP	National Agriculture Imagery Program
NMDS	nonmetric multidimensional scaling
NRCS	Natural Resource Conservation Service
NWS	National Weather Service
OBL	obligate wetland species (wetland indicator status)
RIV	relative importance value
rkm	river kilometer
r_s	Spearman's rank correlation coefficient
s	second
TMDL	Total Maximum Daily Load
UPL	upland species (wetland indicator status)
USACE	United States Army Corps of Engineers
USDA	United States Department of Agriculture
USGS	United States Geological Survey
WSE	water surface elevation

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ABSTRACT

THE ECOLOGICAL SIGNIFICANCE OF EMERGING RESERVOIR DELTAS: EVIDENCE FROM THE WHITE RIVER DELTA IN SOUTH DAKOTA

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This research examined the *Populus* communities that have established on the novel reservoir delta forming at the confluence of the White River and Fort Randall Reservoir (Lake Francis Case), a mainstem impoundment on the Missouri River in South Dakota. The research included: investigation of post-dam channel and floodplain morphodynamics based on repeat cross section surveys; GIS mapping of time, space, and age dynamics of post-dam riparian woodland cover using historical aerial imagery; and a field study of woody plant characteristics in 35 cottonwood stands along a 120 km reach of the lower White River and its delta.

Cross sectional surveys for the lower White River showed that the thalweg aggraded by as much as 12 m between 1954 (2 years post-dam) and 2011. Sediments accumulated in the form of a broad wedge that currently occupies the last 31 km of the White River valley. The mean slope of this reach decreased from 0.70 m/km in 1954 to 0.29 m/km in 2011.

Riparian woodland cover on the expanding delta increased by nearly 50 percent from pre-dam (1948) to present (2012). Age structure also changed, from domination by older woodland in the pre-dam period to younger woodland in the post-dam period. Woodland established on young alluvial surfaces near the reservoir and farther upstream on abandoned agricultural land undergoing increased flooding and sedimentation.

Field inventories in 2011 and 2013 determined that cottonwood forest stands were similar in woody plant structure and composition to natural stands along the White and Missouri Rivers. Plant species were arranged along an environmental moisture gradient spanning the length of the river-delta continuum; wetland affiliated species comprised a larger proportion of the flora in the downstream direction and non-wetland species comprised a larger proportion of the flora in the upstream direction.

Pioneer forest establishment on reservoir deltas offers new opportunities to counterbalance losses of high biodiversity riparian ecosystems along the Missouri and other regulated rivers. Further study is needed to determine the contribution of reservoir deltas to biodiversity along regulated rivers, and how active and passive restoration could improve the establishment and survival of cottonwood forests over the long-term.

INTRODUCTION

Importance of riparian ecosystems

Natural riparian ecosystems are among the most ecologically diverse and productive habitats on earth (Naiman et al. 2005). Although they occupy only a small percentage of the total land area, riparian habitats provide important habitat for many species, and are vital to maintaining regional biodiversity (Gregory et al. 1991, Naiman et al. 1993, Patten 1998, Sabo et al. 2005). Studies of riparian vascular plants in the Pacific Northwest of the United States (Pollock et al. 1998), the Amazonian basin (Junk 1989), southern France (Planty-Tabacchi et al. 1996), Sweden (Nilsson 1992, Nilsson and Svedmark 2002), and southern California (Rundel and Sturmer 1998) report unusually high levels of biodiversity. For example, Nilsson and Svedmark (2002) found that the riparian corridor along the main channel of the Vindel River in Sweden includes 60 percent of the vascular plant species in the entire river basin. Rundel and Sturmer (1998) report that in the Santa Monica Mountains in southern California, less than one percent of the total land area is riparian, but approximately 20 percent of the native vascular plants use riparian areas as their primary habitat. Studies of riparian faunal diversity in Namibia (Robertson et al. 1998), New South Wales, Australia (Shelly 2000), and the Rocky Mountains in Colorado (Finch and Ruggiero 1993) found greater species diversity than in adjacent non-riparian areas. Hoover and Wills (1984) found that cottonwood riparian woodlands in Colorado supported the greatest diversity of birds, amphibians, and reptiles of any forest type in the region. Riparian areas in the Rocky Mountain Region also supported more endemic and listed vulnerable species than the surrounding upland forests (Finch 1992). Liknes et al. (1994) and Rumble and Gobeille (2005) found that

riparian woodlands along the Missouri River in South Dakota were uniquely important to avian species diversity. High concentrations of biodiversity in riparian areas have made these habitats conservation hot spots.

River systems and their riparian zones function as important natural corridors for the movement of organisms and materials through landscapes (Forman and Godron 1986, Forman et al. 2003, Hilty et al. 2006). Riparian corridors are important for migrating animals, such as neotropical birds (Farley et al. 1994, Gentry et al. 2006), and for dispersal of plant propagules (Gregory et al. 1991). Movements of species facilitate floral and faunal mixing on a broad scale, thus enhancing regional biodiversity. Riparian ecosystems also function as refuges during periods of widespread environmental shifts, such as periods of prolonged drought, thereby conserving regional biodiversity over the long-term (Naiman et al. 2005).

In addition to supporting high levels of biodiversity, riparian systems provide numerous other ecological services. Riparian forests exert strong controls on stream microclimate, including light and temperature regimes, which regulate many biological processes and ecosystem functions. For example, the primary productivity of aquatic plants, organism behavior, and water temperature are strongly linked to the amount of solar radiation reaching a stream. Water temperature influences the distribution, metabolism, phenology, and behavior of stream organisms (Blann et al. 2002, Naiman et al. 2005, Cross et al. 2013). In many regions, riparian forests contribute substantial amounts of particulate and dissolved organic matter to stream ecosystems, which provide the base for stream food webs (Fisher and Likens 1973, Gurtz et al. 1988, Webster and Meyer 1997, Allan et al. 2003, Baxter et al. 2005). Along with functioning as a nutrient

source to streams, riparian zones also serve as buffers against nutrient and sediment pollution from upland runoff, and thus are critical to protecting water quality in many regions (Karr and Schlosser 1978, Lowrance et al. 1984, Peterjohn and Correll 1984). Inputs of woody debris from riparian forests to streams influence channel morphology, sediment routing (Gregory et al. 1991), and instream habitat (Anderson and Sedell 1979). Riparian systems are also regionally and globally important for biogeochemical cycling, as they regulate fluxes and elemental transformations of nutrients between uplands, rivers, and the atmosphere (Naiman and Décamps 1997). Due to their diverse functions, riparian zones play a central ecological role in many landscapes.

The diversity of species and ecological processes in riparian ecosystems is sustained by a dynamic natural disturbance regime. Natural streamflow variability and fluvial action (erosion, transport, and deposition) impart considerable spatial and temporal heterogeneity to the biophysical components of the system. The resulting mosaic of diverse habitats within the riparian environment allows a wide variety of species to persist side by side (Poff et al. 1997). For example, along the Rio Grande River in the southwestern United States, avian species richness correlated positively with habitat heterogeneity and was maximized by the simultaneous availability of vegetation of different age and size classes (Farley et al. 1994). A dynamic disturbance regime is necessary to maintain a diversity of habitat types in riparian systems.

Major threats to riparian ecosystems

Although riparian ecosystems have long been recognized for their high levels of biodiversity and important ecosystem functions, they are among the most threatened landscapes worldwide (Tockner and Stanford 2002). Because of their rich resources,

riparian ecosystems belong to the environments most disturbed by humans and with the longest history of human disturbance (Nilsson and Svedmark 2002). Human-mediated land use change, including urbanization and conversion to agriculture, has destroyed large areas of riparian habitat all over the world (Tockner and Stanford 2002). It is estimated that 70 percent of the native riparian forests in the coterminous United States have been converted into other uses (Turner et al. 1998). Remaining riparian ecosystems are further threatened by flow regulation, bank stabilization, channelization, pollution (Nilsson and Svedmark 2002), grazing (Kauffman and Krueger 1984, Auble and Scott 1998, Belsky et al. 1999, Scott et al. 2003), invasive species (Howe and Knopf 1991, Pearce and Smith 2001, Stromberg et al. 2007), timber harvesting (DeBano and Schmidt 1989), climate change (Perry et al. 2012), groundwater depletion (Kranjcec et al. 1998, Scott et al. 1999), and fire (Busch and Smith 1995, Smith et al. 2009). For example, only two percent (~10,000 km) of the 5.2 million km of streams in the United States have sufficiently high quality features to qualify for federal protection (Benke 1990). Consequently, biodiversity in freshwater and riparian ecosystems has declined more than in terrestrial ecosystems (Tockner and Stanford 2002). Nearly half of all animals listed as federally endangered in the United States are freshwater species (Stein 2001).

Dams are a common threat to riparian ecosystems worldwide. An estimated two-thirds of the fresh water flowing to the world's oceans is obstructed by more than 45,000 large dams (>15 m in height) and more than 800,000 small dams (Petts 1984, McCully 1996, WCD 2000). Dams fragment over half of the world's large rivers (rivers with a virgin mean annual discharge of $\geq$350 m^3/s,); the 21 largest river systems in the world are all strongly or moderately regulated by dams (Nilsson et al. 2005). In the United States,

all large rivers have been structurally regulated; some of the greatest hydrologic changes (i.e., the highest ratios of reservoir storage capacity to annual runoff) occur in the Great Plains region (Dynesius and Nilsson 1994, Graf 1999, Graf 2006). The multiple effects of dams have changed riparian conditions dramatically worldwide (Jansson et al. 2000a, Nilsson and Berggren 2000).

The major impacts of dams on river and riparian systems are fragmentation (Jansson et al. 2000b), inundation, flow manipulation (Nilsson and Berggren 2000), and disruption to sediment transport (Florsheim et al. 2008). Fragmentation by dams disrupts the migration and dispersal of organisms and reduces the transfer of genes through landscapes (Werth et al. 2014). Inundation by reservoirs permanently destroys riparian and terrestrial habitats and creates less favorable conditions for lotic biota. Flow regulation by dams disrupts the downstream hydrologic regime and generally results in reduced peak flows, reduced flood frequency, increased low flows, and an overall decrease in annual hydrograph variability. Sediment becomes trapped behind dams (Graf et al. 2010, Kondolf et al. 2014, Juracek 2015), leading to alterations in downstream geomorphic processes (Graf 2006, Constantine et al. 2014). For example, clear water releases from dams can erode and degrade the receiving channel, reducing the frequency of overbank flows and disconnecting the channel from its floodplain (Poff et al. 1997, Nilsson and Berggren 2000). Stabilized flow and water levels reduce the recruitment, growth, and cover of flood-dependent plants, and decrease plant diversity because of fragmentation and fewer natural disturbances (Bradley and Smith 1986, Rood et al. 1995, Nilsson et al. 1997, Beauchamp et al. 2007). Hydrologic alterations also may lead to vegetation community shifts toward species that are less flood tolerant (Johnson et al.

1976) and may facilitate invasion by exotic plants (Stromberg et al. 2007, Greet et al. 2013).

The Missouri River floodplain forest ecosystem

The Missouri River is the longest river in the United States, stretching 3,767 km across an expansive drainage basin that encompasses parts of 10 states and two Canadian provinces and represents approximately one-sixth of the land area of the continental United States (NRC 2002a). Historically the river was known for its turbid waters, variable flow regime, highly mobile channel, massive floods, and extensive floodplain. During the last century, public desires to control floods, irrigate the Great Plains, improve navigation, and generate electricity initiated major modifications to the Missouri River (Galat and Lipkin 2000). Between 1937 and 1963, six large U.S. Army Corps of Engineers dams and associated reservoirs were constructed along the mainstem Missouri River in Montana, North Dakota, and South Dakota/Nebraska. Collectively, these dams can store up to 90.5 km^3 of water, which is more capacity than any other river system in the United States (USACE 2006). System impoundment, flow regulation, and other basin developments have had considerable impacts on the Missouri River and its floodplain ecosystem (Galat and Lipkin 2000).

The pre-regulation Missouri River and floodplain

The pre-regulation Missouri was characterized by a combination of meandering and braided river channel morphologies in wide, alluvial valley settings, large meander loops, backwaters, and shallow wetlands. The river also produced natural levees, oxbow lakes, islands, sand bars, sand dunes, and forests. The channel itself was scattered with abundant woody debris that was mobile during floods. The width of the main channel

was highly variable, ranging from 300 m to 3,000 m during normal flow periods, and from 7,600 m to 10,600 m during high flow events (NRC 2002a, 2011).

The journals of Lewis and Clark Expedition (1804-1806) describe the dynamic Missouri River of the past (Coues 1893):

> *"I observe a great alteration in the Current course and appearance of this pt. of the Missouri. in places where there was Sand bars in the fall 1804 at this time the main current passes, and where the current then passed it is now a Sand bar. Sand bars which were then naked are now covered with willow several feet high. the enterance [sic] of some of the Rivers & creeks changed owing to the mud thrown into them, and a layor [sic] of mud over some of the bottoms of 8 inches thick."*
>
> –Captain William Clark, August 20, 1806

These observations depict a highly dynamic river channel that continuously shaped and was shaped by its broad floodplain.

The historical hydrograph of the Missouri River in middle and lower reaches was characterized by spring and summer rises that typically occurred in April and June, respectively. The spring rise was caused by snowmelt on the plains and local rainfall; the summer rise was caused by snowmelt in the Rocky Mountains and rainfall at lower elevations. During the spring and summer rises, the channel and floodplain would undergo rapid physical changes. As flows increased, the riverbed would degrade, the channel would migrate, the main channel and floodplain habitats would be connected by overbank flows, and riparian vegetation would be eroded and washed into the channel.

As flood water receded, the riverbed would refill with sediment, and fresh substrates would be deposited for colonization by plants and animals (NRC 2002a).

The pre-regulation Missouri River contained diverse forest communities along its length. Floodplain forests along the geologically constrained reaches of the upper Missouri River (modern day Montana) were strongly dominated by plains cottonwood (*Populus deltoides* ssp. *monilifera* (Aiton) Eckenw.) and typically occurred in small, scattered patches along the narrow and relatively immobile channel (Coues 1893). Recent studies of vegetation along this reach (Scott et al. 2003, Scott et al. 2013) indicate that more continuous stands of cottonwood and willow (*Salix* L. spp.) formed on channel margins and bars in wider, less constrained river reaches. Box elder (*Acer negundo* L.), green ash (*Fraxinus pennsylvanica* Marsh.) and peachleaf willow (*Salix amygdaloides* Andersson) occurred as uncommon associates. Understory riparian shrubs included western snowberry (*Symphoricarpos occidentalis* Hook.), Woods' rose (*Rosa woodsii* Lindl.), silver sagebrush (*Artemisia cana* Pursh), and chokecherry (*Prunus virginiana* L.) (Scott et al. 2013). Yellow willow (*Salix lutea* Nutt.) and sandbar willow (*Salix interior* Rowlee) were common on active alluvial surfaces. Pioneer forests succeeded to shrub-steppe vegetation in many locations along the upper Missouri (Scott et al. 2003). Riparian plant species diversity along the upper Missouri River was and continues to be comparatively lower than along the downstream reaches, because many eastern affiliated species that are present in the Dakotas drop out in the comparatively drier, western portions of the basin (NRC 2002a).

Floodplain forests along the middle portions of the Missouri River (modern day North Dakota and South Dakota) were likewise dominated by plains cottonwood.

Common associates were green ash, box elder, and American elm (*Ulmus americana* L.). Subdominant trees included peachleaf willow and bur oak (*Quercus macrocarpa* Michx.). Common understory riparian shrubs and woody vines (lianas) included sandbar willow, redosier dogwood (*Cornus sericea* L.), roughleaf dogwood (*Cornus drummondii* C.A. Mey), western snowberry, chokecherry, juneberry (*Amelanchier alnifolia* (Nutt.) Nutt. ex M. Roem.) woodbine (*Parthenocissus vitacea* (Knerr) Hitchc.), and riverbank grape (*Vitis riparia* Michx.) (NRC 2002a).

Along the lower Missouri River, cottonwood and willow were the dominant species on recently exposed sandbars, as they were throughout the length of the river. Later successional tree species were more diverse than in upstream reaches of the river. For example, box elder, silver maple (*Acer saccharinum* L.), red mulberry (*Morus rubra* L.), and several elms (*Ulmus* L. spp.) replaced cottonwood and willow and formed an intermediate successional stage. The mature forest included several species of oaks (*Quercus* L. spp.), hickories (*Carya* Nutt. spp.), black walnut (*Juglans nigra* L.), American basswood (*Tilia americana* L.), hackberry (*Celtis* L. spp.), and sycamore (*Platanus occidentalis* L.) (Bragg and Tatschl 1977, NRC 2002a).

The middle Missouri River's floodplain forests formed a successional series of ecological communities. The youngest forests were dominated by cottonwood and willow that formed on new alluvial surfaces at low elevations. The older forests were dominated by green ash, box elder, and elm on relatively high floodplain surfaces. Channel movement during floods initiated the successional process by eroding existing forests of all ages while creating new alluvial deposits suitable for colonization by cottonwood and willow (Johnson et al. 1976).

Recent alluvial deposits and exposed sandbars are optimal habitat for cottonwood and willow seedlings, both of which require moist unvegetated soil for germination (Moss 1938, Wilson 1970, Noble 1979). Peak seed dispersal of cottonwood and willow occurs from June to July, coinciding with the historical recession of flood waters and exposure of fresh alluvium (Fenner et al. 1985). Of all the floodplain tree species, cottonwood and willow are uniquely adapted to germinate under the difficult conditions of low soil fertility, variable soil moisture, and high solar radiation found on exposed sandbars (Braatne et al. 1996). As a pioneer species, cottonwood cannot, however, reproduce successfully in its own forests (Johnson et al. 1976). Therefore, periodic channel movement along with erosion, transport, and deposition of sediments are necessary to recruit new populations of cottonwood and willow and to maintain a diverse mosaic of forest ages on the floodplain (Johnson 1992, Stella and Battles 2010, Stella et al. 2011).

Cottonwood forests in the Great Plains region are biodiversity "hot spots" that support a large number of species. Many avian species, such as the Bald Eagle (*Haliaeetus leucocephalus* L.), use cottonwood forests for nesting and overwintering habitat. Liknes et al. (1994) found over 50 species of songbirds along the middle Missouri River, approximately 50 percent of which were neotropical migrants. Dean (1999) found 39 species of neotropical migrants utilizing Missouri River cottonwood forests as stopover habitat. Cottonwood forests also support high levels of plant diversity. Keammerer et al. (1975) recorded 220 species of vascular plants growing in cottonwood forests along an already highly regulated remnant river section in North Dakota.

Floodplain forest decline

Extensive areas of floodplain forest along the Missouri River and its tributaries have been lost or degraded due to river regulation and other anthropogenic disturbances. Large areas of forests were cleared to provide fuel for steamboats during the nineteenth century (Lass 2005, Lass 2008), and more recently for agriculture and urbanization. In the Dakotas, the majority of floodplain forests (~70 percent) was destroyed under reservoirs when the big dams were built during the twentieth century (Volke et al. 2015). Remnant cottonwood forests, which are mostly confined to gaps (remnant reaches) between reservoirs, have broadly failed to reproduce in the flood-protected post-dam environment, and are now approaching the end of their lifespan. Some cottonwood recruitment occurred in remnant reaches during the first couple of decades following dam closure, possibly due to post-dam channel adjustment, but rates of recruitment have been low during the last ~30 years. Consequently, these forests have been referred to as the "living dead". Under current river management, these forests are expected to lose much of their biodiversity-rich cottonwood component during this century (Dixon et al. 2012, Johnson et al. 2012).

Major ecological changes in riparian vegetation have occurred in remnant reaches along the middle Missouri River in response to flow regulation. The first study to investigate these changes was conducted in 1969 and 1970 along a 166 km-long remnant floodplain reach of the heavily regulated Missouri River between Garrison Dam and Oahe Reservoir in North Dakota (Johnson et al. 1976). This research detected major changes in several ecological processes after dam construction, including poor prospects for seedling recruitment of cottonwood and peachleaf willow, low survivorship of box

elder and American elm reproduction, and a decline in the radial growth of most tree species. Johnson et al. (1976) predicted that the long-term effect of these changes would alter future forest composition, diversity, and productivity.

A forty year remeasurement of this reach (Johnson et al. 2012) confirmed many of the predictions laid out in the 1976 study; however, many changes were not anticipated. For example, cottonwood forest health declined as predicted due to greatly reduced seedling recruitment, as did the abundance of box elder, one of the trees that normally replaced cottonwood and willow in succession. Changes over the 40 year period that were unexpected included: the formation of deltas where sediment has been deposited at mainstem/reservoir and tributary/reservoir junctions (Volke et al. 2015); the apparent inability of a large unplanned flood to move the river channel significantly in 2011 (Dixon et al. 2015); the appearance of Dutch Elm disease shortly after the Johnson et al. (1976) study that subsequently decimated American elm trees, one of the dominant species on the floodplain historically; and rapid expansion of exotic herbaceous plants such as smooth brome (*Bromus inermis* Leyss.), reed canary grass (*Phalaris arundinacea* L.), and Canada thistle (*Cirsium arvense* (L.) Scop.). Without major restoration efforts, the collective effects of these changes and the continued effects of river regulation forecast a bleak future for the Missouri River cottonwood forest ecosystem (Johnson et al. 2014).

The emergence of novel reservoir deltas

The Missouri River of the past was known as the “Big Muddy” as it transported a large volume of sediment annually (NRC 2011). Historically the river delivered over 270 million metric tons of sediment per year to its confluence with the Mississippi River near

St. Louis, Missouri (Jacobson et al. 2009). The high turbidity and dynamic sediment regime of the historical Missouri River, including erosion, transport, and deposition processes, created a diversity of habitats that were important in shaping the life history traits that allowed native riverine species to survive and reproduce in such a dynamic environment. Today the sediment regime of the river has been dramatically altered by dams and flow regulation, and the volume of sediment delivered to the mouth of the Missouri has been reduced to less than one-third of its former volume (Meade and Moody 2009). Consequently, many native plant and animal species that evolved in a highly turbid environment are in decline (NRC 2011).

As the reservoir system has aged, sediment that historically moved downstream has become trapped behind dams (NRC 2011). This sediment has noticeably accumulated in the form of deltas where the mainstem river connects with the upper end of reservoirs and where tributaries enter reservoirs (Johnson 2002, Coker et al. 2009, Skalak et al. 2013). When, at these junctions, flowing water transporting bed and wash load sediment meets the relatively still reservoir water, much of this sediment accumulates on both submerged and emergent portions of the rivers entering the reservoir. Over time, these sediment deposits expand in area and sometimes aggrade above the normal operating reservoir level, forming a novel delta that did not exist in the free-flowing river of the past. These reservoir deltas are neither distinctly lotic nor lentic, as they are influenced both by the flow regime of the contributing stream and by the management of the receiving reservoir. Evidence suggests that most of these deltas support young native woody riparian vegetation that is largely failing to establish elsewhere along the Missouri River (Volke et al. 2015).

With continued sediment supply and related channel and floodplain aggradation, mainstem and tributary deltas will continue to expand up and down gradient. Because of progressive sediment accumulation, reservoir fluctuations, and the often less-regulated contributing streams, reservoir deltas represent some of the more hydrologically dynamic and geomorphically active environments remaining in the regulated Missouri River. These highly dynamic environments may offer opportunities to replace or restore some of the geomorphic processes, shallow aquatic environments, and early successional vegetation dynamics that have been lost because of river regulation. Despite their potential ecological significance as shallow water and subirrigated environments, these nascent deltas have gone largely unstudied. No published studies have investigated the vegetation dynamics on reservoir deltas or their potential contribution to riparian forest diversity along regulated rivers (Volke et al. 2015).

The White River delta

The White River is the largest tributary to Fort Randall Reservoir (Lake Francis Case), a mainstem impoundment on the Missouri River in central South Dakota (Figure 1). The White River is unregulated; its sediment load has accumulated at the confluence of the White River and Fort Randall Reservoir, forming a novel delta that has expanded during the post-regulation era (Figure 2; USACE 2006) The delta is forming in two locations: the lower end of the delta extends into the deeper portions of Fort Randall Reservoir and the upper end of the delta extends up the lower White River valley where high reservoir stages periodically inundate the floodplain and cause sedimentation well upstream of the normal reservoir boundary. New cottonwood forests have established on the expanding surfaces of the White River delta during the post-dam era.

Study objectives

This study examined the characteristics of cottonwood stands along a 120 km reach of the lower White River and its delta, and the channel and floodplain morphodynamics that permitted these stands to establish and expand on the delta during the post-dam period. The primary objectives of this study were to: (1) Quantify and assess post-dam changes to channel and floodplain morphology along the lower White River; (2) Quantify the current and historical riparian woodland age-area distribution on the delta; (3) Characterize the woody plant structure and composition of cottonwood stands (seedlings, saplings, and trees) along the lower White River and on its delta; (4) Determine whether delta stands were similar to natural stands along the White River and the Missouri River; (5) Compare stand characteristics along the longitudinal gradient spanning the delta and riverine environments; and (6) Consider how reservoir deltas could contribute to recovery of riparian forests along the Missouri and other regulated rivers.

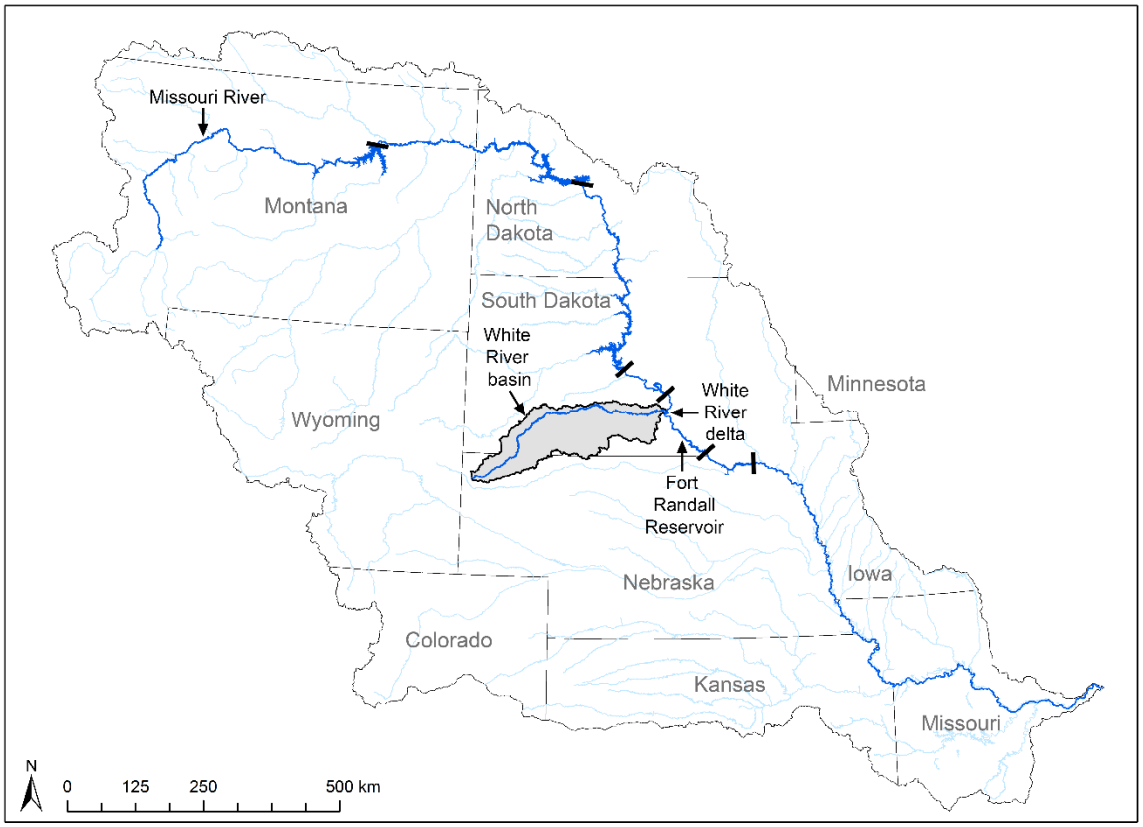

Figure 1. Location of the White River basin within the Missouri River basin. The locations of the six large mainstem Missouri River dams are shown with black bars.

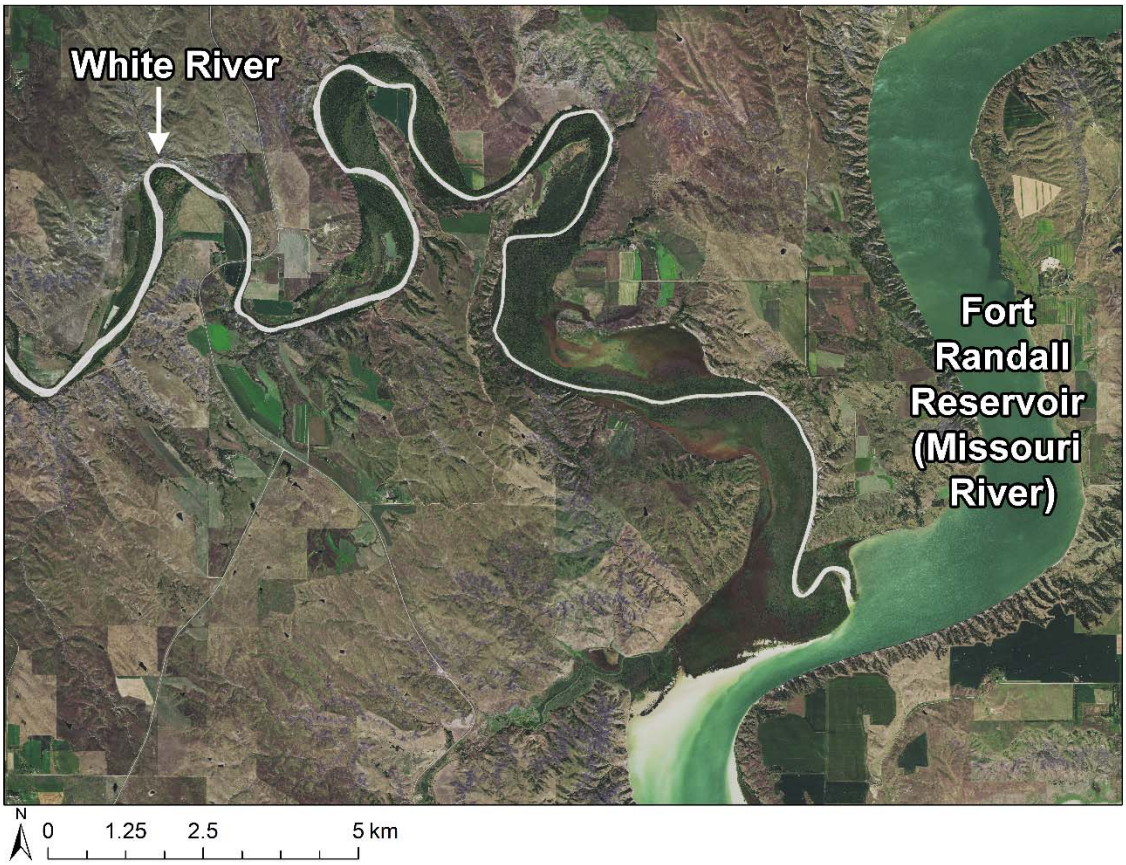

Figure 2. Aerial photograph of the White River delta and surrounding landscape in South Dakota. Source: U.S. Department of Agriculture, National Agriculture Imagery Program (2014).

METHODS

Description of the study area and broader region

The White River originates in the Pine Ridge region of northwestern Nebraska and flows northeasterly into the South Dakota Badlands where it assumes an easterly course through south-central South Dakota towards its confluence with Fort Randall Reservoir, a mainstem impoundment on the Missouri River (Figure 1). Sources estimate the length of the White River to be from 816 km to over 1,100 km and the drainage area of the basin to be from 25,563 km^2 to 26,418 km^2 (SDDRM 1975, Ferrick et al. 1995, Fryda 2001, Galat et al. 2005, USGS 2012). The largest tributary is the Little White River, which originates in the Nebraska Sand Hills and supplies 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 (South Dakota Department of Game, Fish, and Parks), tribal (Pine Ridge and Rosebud Indian Reservations), and federal (National Park Service, U.S. Forest Service, and U.S. Fish and Wildlife Service) land holdings (Galat et al. 2005).

The White River is one of the longest undammed, free-flowing rivers in the coterminous United States (Stanford and Ward 1979, Benke 1990) and was listed as one of 327 rivers in the United States critical for protecting biodiversity (Master et al. 1998). This riverine system is particularly important for regional biodiversity, as it provides habitat for aquatic and riparian organisms that have declined following river regulation in the Missouri River basin (Fryda 2001). Further, the natural hydrologic regime of the White River supports floodplain forest successional processes and related ecosystem functions that have been diminished by dams or diversions on most other rivers.

Physical environment

The semi-arid continental climate of the White River basin is characterized by hot summers and cold winters, with pronounced diurnal and seasonal extremes in temperature (Hogan 1995, Galat et al. 2005). At the Kennebec climate station, which is located near the eastern edge of the basin, mean annual temperature was 9.1 ºC (1893-2013). Temperature ranged from an average minimum of -14.4 ºC in January to an average maximum of 32.6 ºC in July. Mean annual precipitation was 45 cm with nearly 70 percent occurring from April through August. The driest months were December, January, and February when an average of about 3.5 cm were received as snow (HPRCC 2013). The majority (85 percent) of precipitation fell as rain during summer convective thunderstorms, therefore the location, frequency, and intensity of precipitation within the basin was highly variable within and between years (SDDRM 1975, Galat et al. 2005).

The White River basin is located in the unglaciated Pierre Hills and Southern Plateau physiographic regions (Johnson et al. 1995) in the Missouri River Plateau section of the Northwestern Great Plains ecoregion (Bryce et al. 1998). The western portion of the basin occupies the Southern Plateau region, which is characterized by highlands of benches and buttes underlain by Tertiary sandstones and mudstones. Soils are primarily loams and silt loams (Johnson et al. 1995). This region contains the White River Badlands, a highly dissected landscape of eroded walls and escarpments, isolated tablelands, and buttes formed by the erosion of Oligocene Brule and Chadron claystone formations (Bryce et al. 1998). The eastern portion of the basin occupies the Pierre Hills region which is characterized by an erosional landscape of rounded hills and ridges. Soils

in this region are predominantly clays derived from Cretaceous Pierre Shale (Johnson et al. 1995).

Present vegetation

The upland portions of the basin are dominated by short and midgrasses including buffalograss (*Bouteloua dactyloides* (Nutt.) Columbus), western wheatgrass (*Pascopyrum smithii* (Rydb.) Barkworth & D.R. Dewey), and blue grama (*Bouteloua gracilis* (Kunth) Lag. ex Griffiths) (Weaver and Albertson 1956). Smooth brome, a cool-season exotic grass, is widespread in the eastern portion of the basin where it is often cultivated as hay or pasture (SDDRM 1975).

Reconnaissance during this study identified the following general vegetation patterns for the river corridor which are similar to those of Van Bruggen (1985) and Bryce (1998). The dominant riparian tree species along the lower White River is plains cottonwood. Green ash is the most common overstory associate, followed by peachleaf willow, box elder, and American elm. The non-native Russian olive (*Elaeagnus angustifolia* L.) commonly occurs on the floodplain (Appendix Figures 1 and 2). Understory riparian shrubs and lianas include western snowberry, poison ivy (*Toxicodendron rydbergii* (Small ex Rydb.) Greene), chokecherry, false indigo (*Amorpha fruticosa* L.), golden currant (*Ribes aureum* Pursh), Woods' rose, woodbine, and riverbank grape (Appendix Figures 3 and 4), whereas sandbar willow is common on recent alluvial deposits.

Land use

There are no major cities or towns adjacent to the White River; few occur in the basin. The largest towns are Chadron, Nebraska (pop. 5,787) and Winner, South Dakota

(pop. 2,853). Population density ranges from 0.3 to 3.0 people per km^2. Over 70 percent of the basin is in native grass or hay, and 21 percent is in row crops dominated by wheat, but some are planted with corn, sunflowers, sorghum, oats, and soybeans (Galat et al. 2005). Livestock grazing and selective cutting are the primary anthropogenic disturbances to riparian forests in the basin (Appendix Figure 5).

River hydrology, chemistry, and geomorphology

Most of the White River's flow occurs in response to precipitation and snowmelt in spring and early summer, with peaks in both March and May-June (Figure 3). At the USGS Oacoma gaging station near the mouth (06452000), streamflow varies considerably between seasons (especially spring and summer) and years. The lowest flows throughout the basin occur during the winter months, when monthly flows average less than 4 m^3/s (Ferrick et al. 1995). The mean annual stream discharge at the Oacoma station is 16.6 m^3/s (1929-2012), ranging from 4.6 m^3/s in 1974 to 48.6 m^3/s in 1942. The greatest stream flow on record was 1,469.6 m^3/s which occurred on March 30, 1952 (Figure 4).

The White River is named for its white-gray color, derived from naturally large loads of sands, clays, and volcanic ash from the middle and lower segments of the basin (Galat et al. 2005). In their journals, Lewis and Clark remarked on the river's color: "[…] we proceeded, and soon passed the entrance of White River, the water of which is at this time nearly the color of milk" (Coues 1893). Sergeant Patrick Gass, a member of the Lewis and Clark expedition, also noted, "We […] passed White River on the south side. The Missouri here is very full of sand bars and shoals, and we find difficulty in getting along" (MacGregor 1997). Due to its large suspended sediment load, the White River is

listed as an impaired water body, as it fails to meet certain designated uses (i.e., limited contact recreation). It is excluded, however, from the Federal Total Maximum Daily Load (TMDL) limits because the majority of sediments are derived from natural sources (SDDENR 2012). At the Oacoma gaging station, mean annual suspended sediment concentration was 5,584 mg/l (1972-2012). Likewise, the mean annual suspended sediment discharge was 7,171,965 metric tons/year, and has ranged from 1,696,009 metric tons/year in 1985 to 17,152,142 metric tons/year in 1982. This sediment accumulates in the delta or is transported farther into Fort Randall Reservoir and beyond.

The gradient 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 (Figure 5), although there is inconsistency in gradient estimates among sources (Ferrick et al. 1995, Galat et al. 2005, USGS 2012). The gradient values reported above were derived from the USGS StreamStats Program (USGS 2012). The White River meanders across its floodplain; sinuosity scores range from 2.16-2.48 (Ferrick et al. 1995).

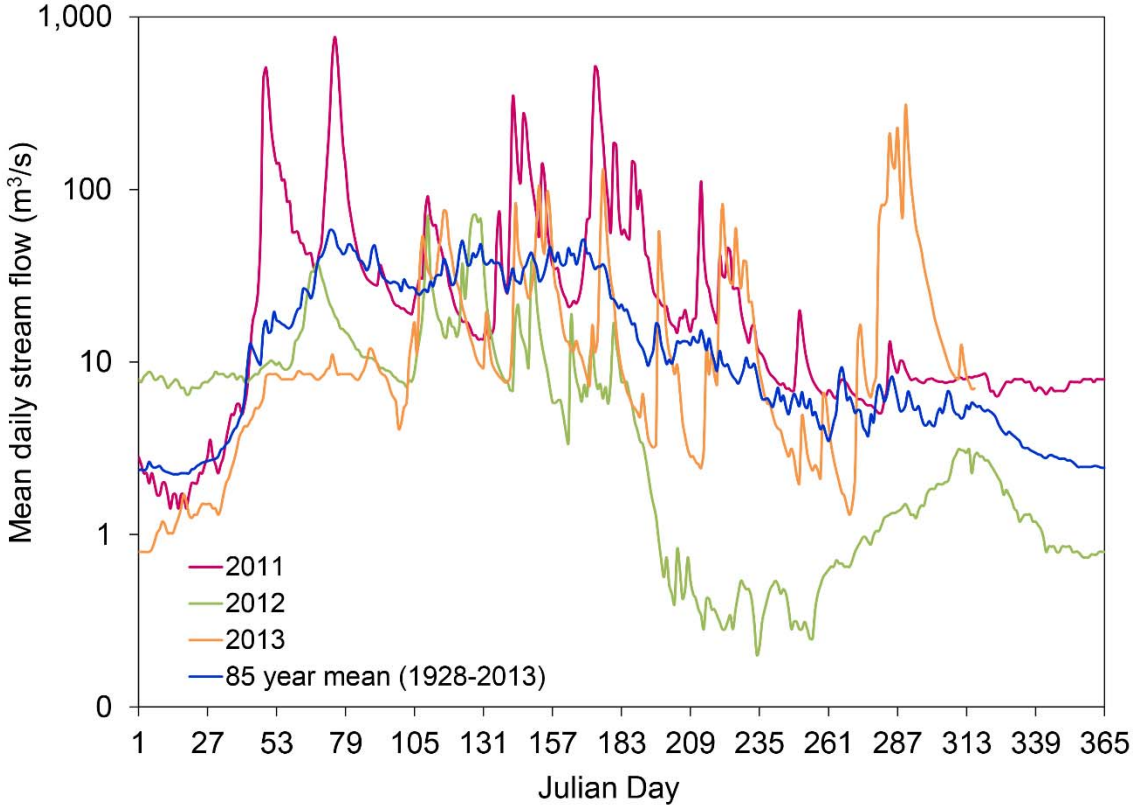

Figure 3. Hydrograph of the lower White River in 2011, 2012, 2013, and the 85 year mean (1928-2013). A base-10 log scale is used for the *y*-axis. The 2013 curve is truncated due to no available data. Source: USGS Oacoma gaging station 06452000.

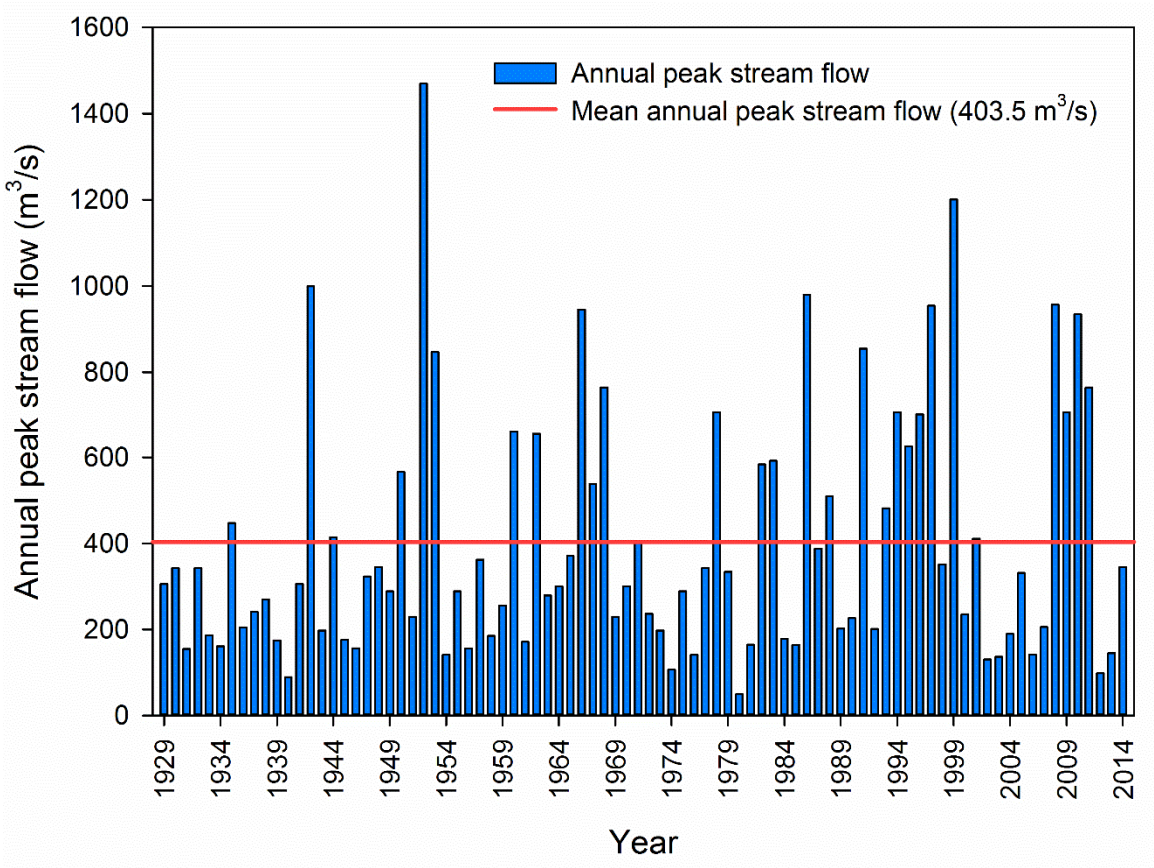

Figure 4. Annual peak streamflow (m^3/s) of the lower White River for the period of record (1929-2014). Source: USGS Oacoma gaging station 06452000.

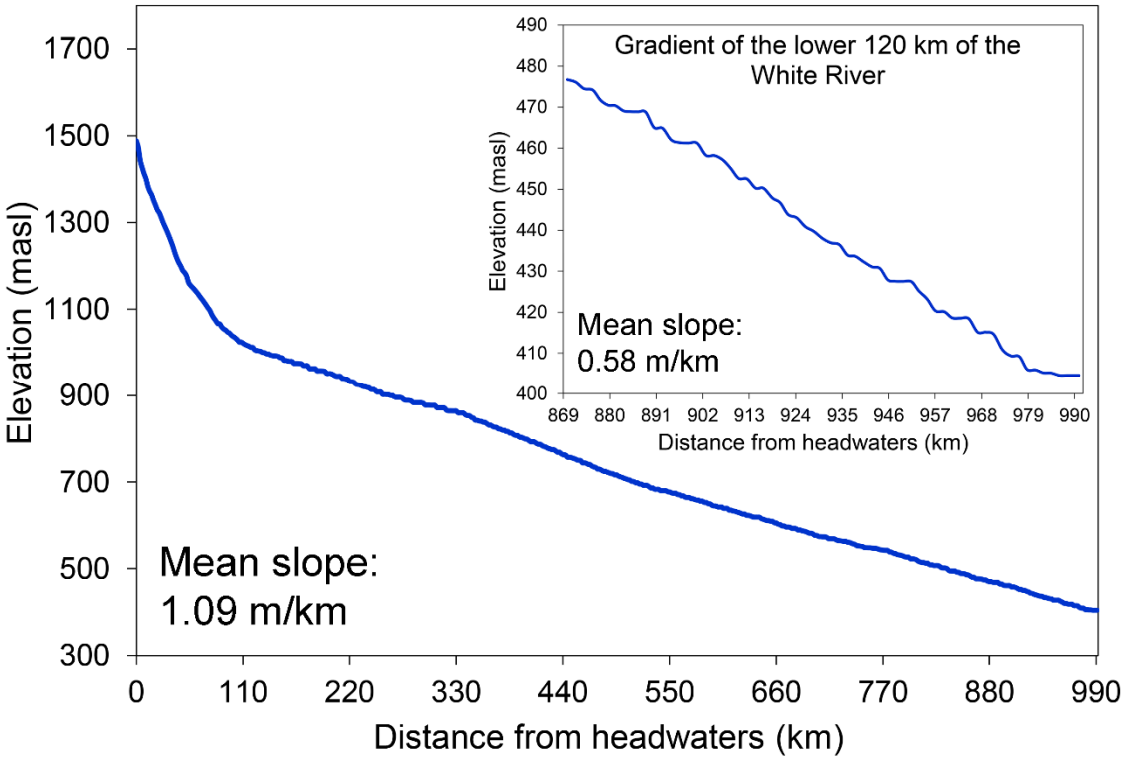

Figure 5. The stream gradient of the White River from headwaters to mouth. The inset shows the gradient of the lowermost 120 km of the White River, which was the focus of this study. Elevation units are in meters above sea level (masl). Source: USGS StreamStats Program.

Pre-settlement characteristics of the lower White River

On September 15, 1804, the Corps of Discovery expedition led by Lewis and Clark reached the confluence of the White and Missouri Rivers. The explorers made the following observations near the mouth of the White River (Coues 1893):

> *We passed, at an early hour, the creek near last night's camp; and at two miles' distance reached the mouth of the White river, coming from the south. We ascended a short distance, and sent a sergeant [Gass] and another man to examine it higher up. This river has a bed of about 300 yards, though the water is confined to 150; in the mouth are a sand-island and several sand-bars. The current is regular and swift, with sand-bars projecting from the points. It differs very much from the Platte and Quicurre [sic], in throwing out comparatively little sand, but its general character is like that of the Missouri. This resemblance was confirmed by the sergeant, who ascended about twelve miles; at which distance it was about the same width as near the mouth, and the course, which was generally west, had been interrupted by islands and sand-bars. The timber consisted chiefly of elms; he saw pine-burrs [sic – pine cones], and sticks of birch were seen floating down the river; he also met with goats, such as we have heretofore seen, great quantities of buffalo, near which were wolves, some deer, and villages of barking squirrels.*

At the confluence of White River with the Missouri is an excellent position for a town, the land rising by three gradual ascents, and the neighborhood furnishing more timber than is usual in this country.

After his 19 km expedition up the White River, Sergeant Patrick Gass recorded the following observations in his journal (MacGregor 1997):

Passed White river on the south side; one of the men and myself went up it to examine the country, and encamped about twelve miles from the mouth, where it is 150 yards broad. We found good bottoms on this creek but timber scarce, and none upon the hills. The current and colour of the water are much like those of the Missouri.

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, with a few scattered American elms. The survey notes also indicate that the confluence of the White and Missouri Rivers was dominated by willows. The 1894 Missouri River Commission map depicting the confluence of the White and Missouri Rivers shows scattered riparian forests on the floodplain and abundant sandbars within the Missouri River channel (Figure 6).

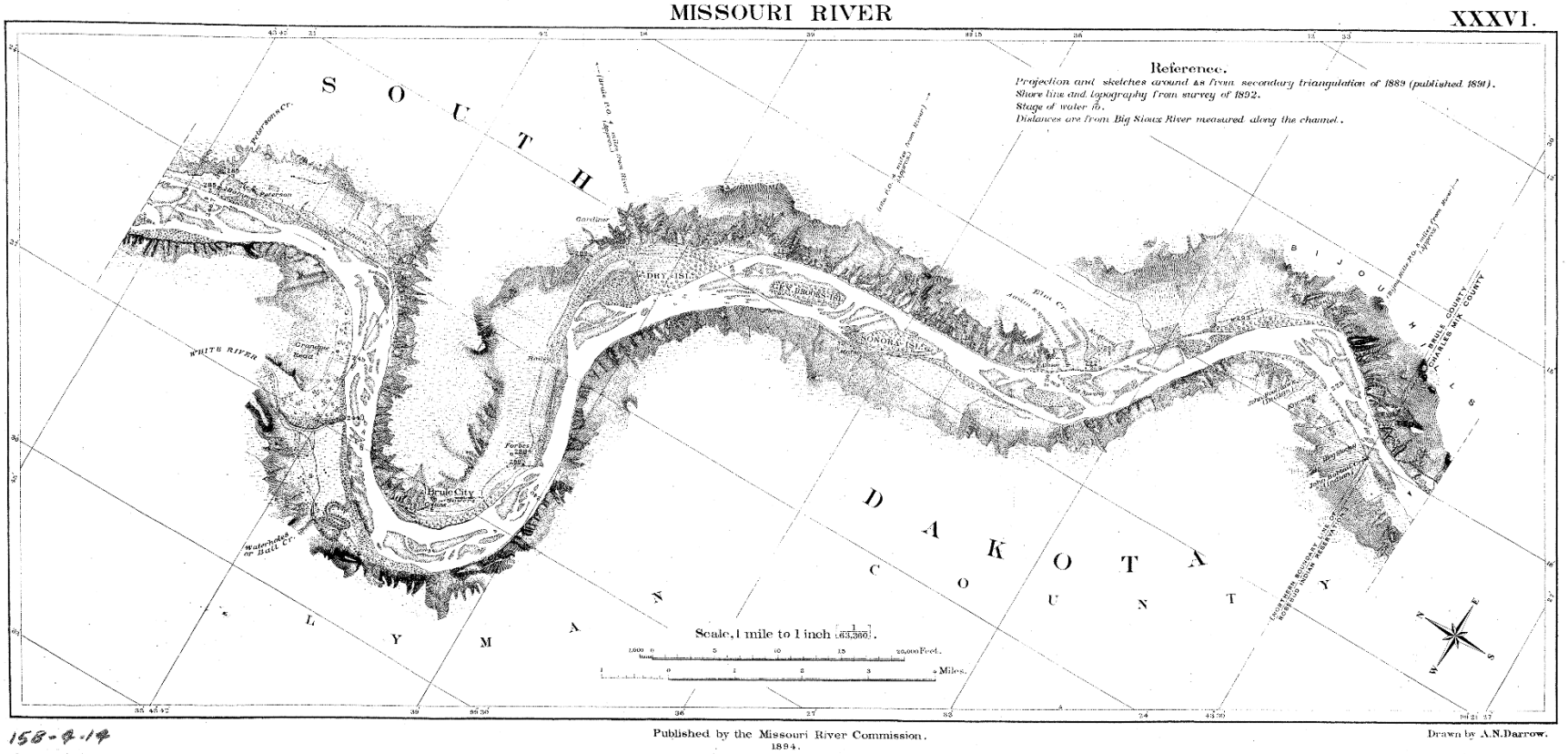

Figure 6. The 1894 Missouri River Commission map depicting the confluence of the White and Missouri Rivers, with riparian forests scattered on the floodplain and abundant sandbars within the Missouri River channel.

Fort Randall Reservoir

Fort Randall Reservoir is a mainstem impoundment on the Missouri River in south-central South Dakota. The reservoir formed in 1953 following closure of Fort Randall Dam (river kilometer [rkm] 1,416) in 1952. With a surface area of 384 km^2 and a length of 172 km, it is the fourth largest of the six mainstem Missouri River reservoirs (USACE 2006). The primary functions of the reservoir (USACE 2006) are to:

> *(1) capture plains snowmelt and localized rainfall runoffs in the drainage area from Big Bend Dam to Fort Randall Dam that are then metered out at controlled release rates to meet System requirements, while reducing flood damages in the Fort Randall reach, where several areas have homes and cabins in close proximity to the river; (2) to serve as a primary storage location, along with Oahe [Reservoir], for water accumulated in the System when System releases are reduced due to major downstream flood control regulation, thus helping to alleviate large pool increases in the very small Gavins Point project; (3) to provide a location to store the water necessary to provide increased winter energy to the basin by allowing an annual fall drawdown of the reservoir to occur with a winter reservoir refilling that is unique to Fort Randall; and (4) to provide the extra water needed to meet all of the System's Congressionally authorized project purposes, particularly navigation and downstream water supply, that draft storage during low-water years.*

The White River, the largest tributary to Fort Randall Reservoir, enters the reservoir about 16 km downstream of Chamberlain, South Dakota at Missouri River km

1,537. In 1991, the Corps observed that the White River delta was having a damming effect that created different reservoir elevations upstream and downstream of the delta. The upper reservoir elevation has been as much as 1.8 m higher than that for the reservoir downstream from the delta (USACE 2006).

The USGS gaging station near Chamberlain (06442996) records the water surface elevation (WSE) of the upper reservoir pool of Fort Randall Reservoir (Figure 7). The mean daily WSE for the period of record (1989-2013) was 412.67 masl, and has ranged from 409.68 masl on November 29, 1992 to 419.08 masl on July 8, 2011. Prior to 2011, the greatest mean daily WSE on record was 418.25 m on May 6, 1997, followed by 417.03 m on June 24, 2010.

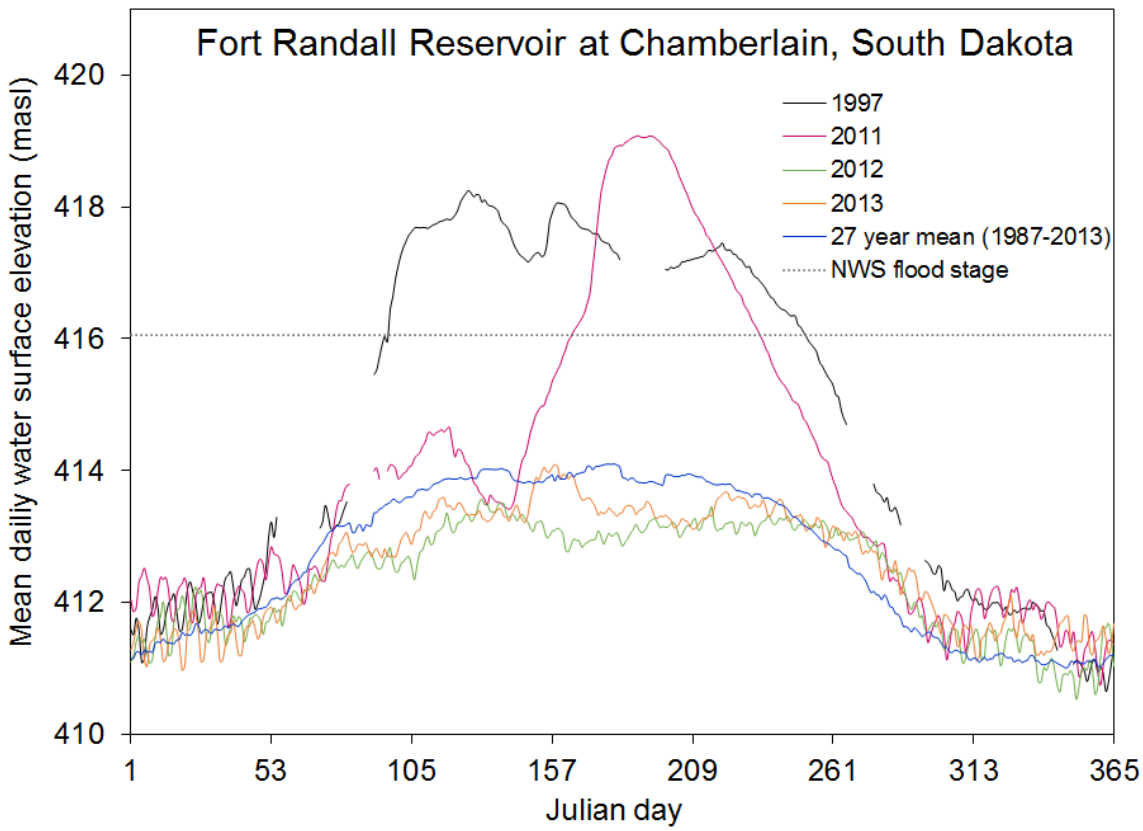

Figure 7. Mean daily water surface elevation of Fort Randall Reservoir at Chamberlain, South Dakota in 1997, 2011, 2012, 2013, and the 27 year mean (1987-2013). The National Weather Service (NWS) flood stage is indicated by the dotted grey line. Line breaks indicate no available data. Source: USGS gaging station 06442996.

Specific location of the study area

The study area was a 120 km reach of the lower White River and its floodplain in South Dakota (Figure 8). The western limit of the study area extended to the western boundary of Lyman County which provided a similar number of cottonwood stands sampled in other comparable studies (e.g., Johnson et. al 1976) and could be sampled within the duration of this study. The confluence of the White River and Fort Randall Reservoir formed the eastern limit of the study area. The western extent of Fort Randall Reservoir at its confluence with the White River fluctuates between seasons and between years, depending on reservoir management and precipitation. These fluctuating reservoir levels regularly inundate large portions of, and influence stream flow in, the lowermost ~29 rkm of the White River and its floodplain (Figure 9). In recent decades, a delta uncharacteristic of free-flowing rivers has formed and expanded within this ~29 rkm zone of reservoir influence (Figure 2). New riparian forests have established on this delta, which are affected by both river flow and reservoir management.

The 29 rkm long delta has formed in two main locations. The lower end of the delta extends 2.3 rkm into the deeper portions of Fort Randall Reservoir and is frequently inundated by higher reservoir stages (Figures 2 and 10, Appendix Figures 6 and 7). The delta also has formed within the lower portion of the White River valley, and extends from the normal reservoir margin 26.7 rkm upstream to the Highway 47 bridge. The upper portions of the delta are occasionally inundated by high reservoir stages and/or related backup flow (Figure 9).

To compare forest stand characteristics along the longitudinal gradient spanning the delta and riverine environments, the 120 km study reach was divided into three main

subreaches: (1) White River delta; (2) river-delta transition; and (3) White River. Stands of post-dam origin that were located within the lowermost 24 rkm of the White River were assigned to the White River delta subreach, reservoir-affected stands of pre-dam origin (>60 years old) that were located between rkm 24 and rkm 29 were assigned to the transition subreach, and stands located upstream of rkm 29 were assigned to the White River subreach (Figure 8). For some analyses, the delta subreach was subdivided into the lower delta and the upper delta to further examine the gradient of reservoir effects on vegetation. The lower delta extended from rkm 0-9.5 within the zone of relatively frequent reservoir inundation. The upper delta extended from rkm 9.5-24 within the zone of reservoir influence, but upstream of the zone of frequent reservoir inundation. Five stands were located on the lower delta and 11 stands were located on the upper delta. Two stands were located in the transition subreach and 17 stands were located in the White River subreach.

Minor amounts of sediment deposition (delta expansion) have occurred as far as 31 rkm upstream of the White River-Missouri River confluence, extending 2 rkm upstream of the boundary used to define the upper limit of reservoir influence for the vegetation component of this study. Field reconnaissance and vegetation data indicated, however, that the reservoir had minimal influence on the vegetation between rkm 29 and 31 compared to the hydrologic and sediment regimes of the White River. Therefore, the 29 rkm boundary was used for the vegetation component of this study, and the 31 rkm boundary was used for the geomorphic component of this study.

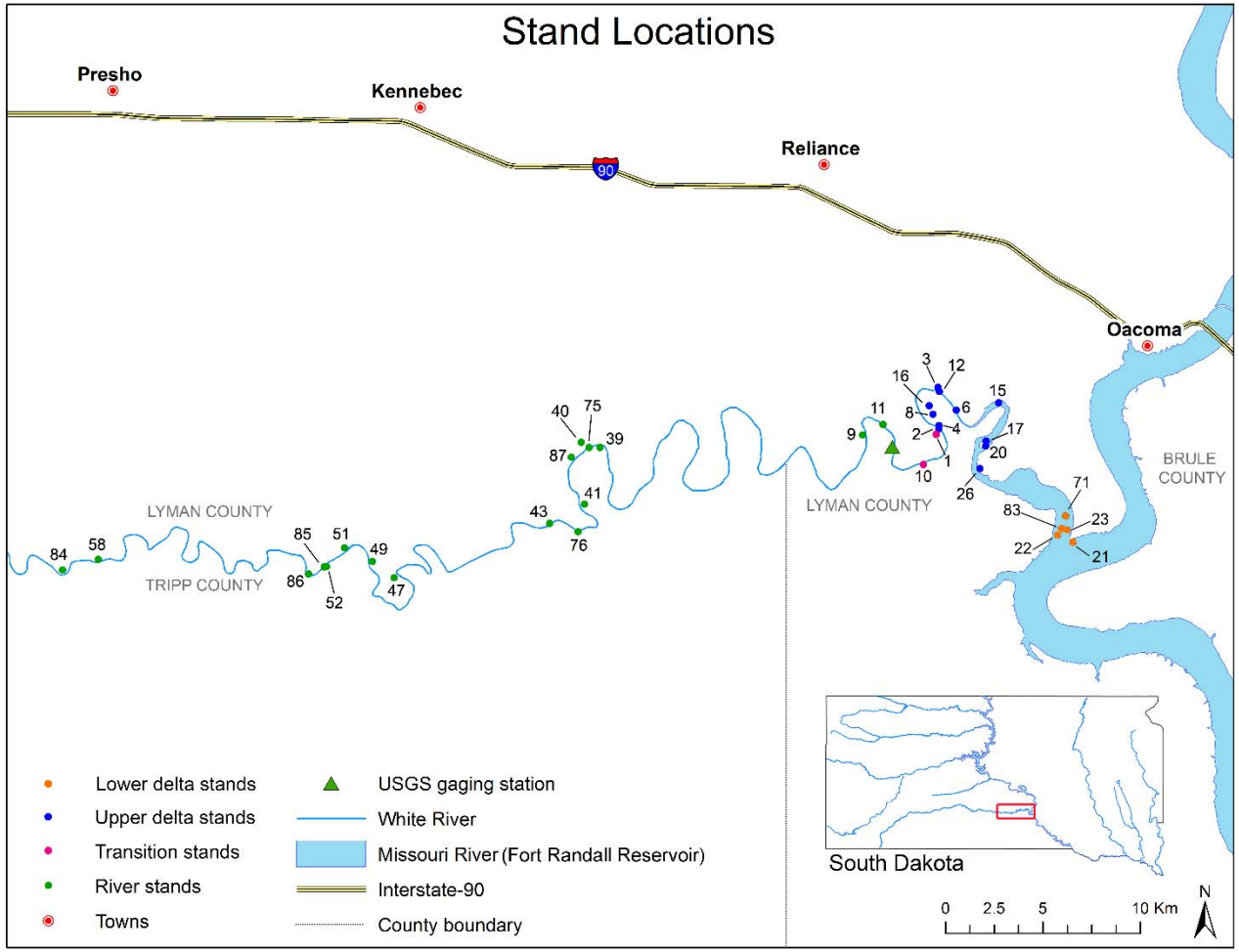

Figure 8. The locations of all the sampled stands by assigned stand number along the lower 120 km of the White River and its delta in South Dakota. The location of the enlarged map is indicated by the red rectangle on the inset map of South Dakota.

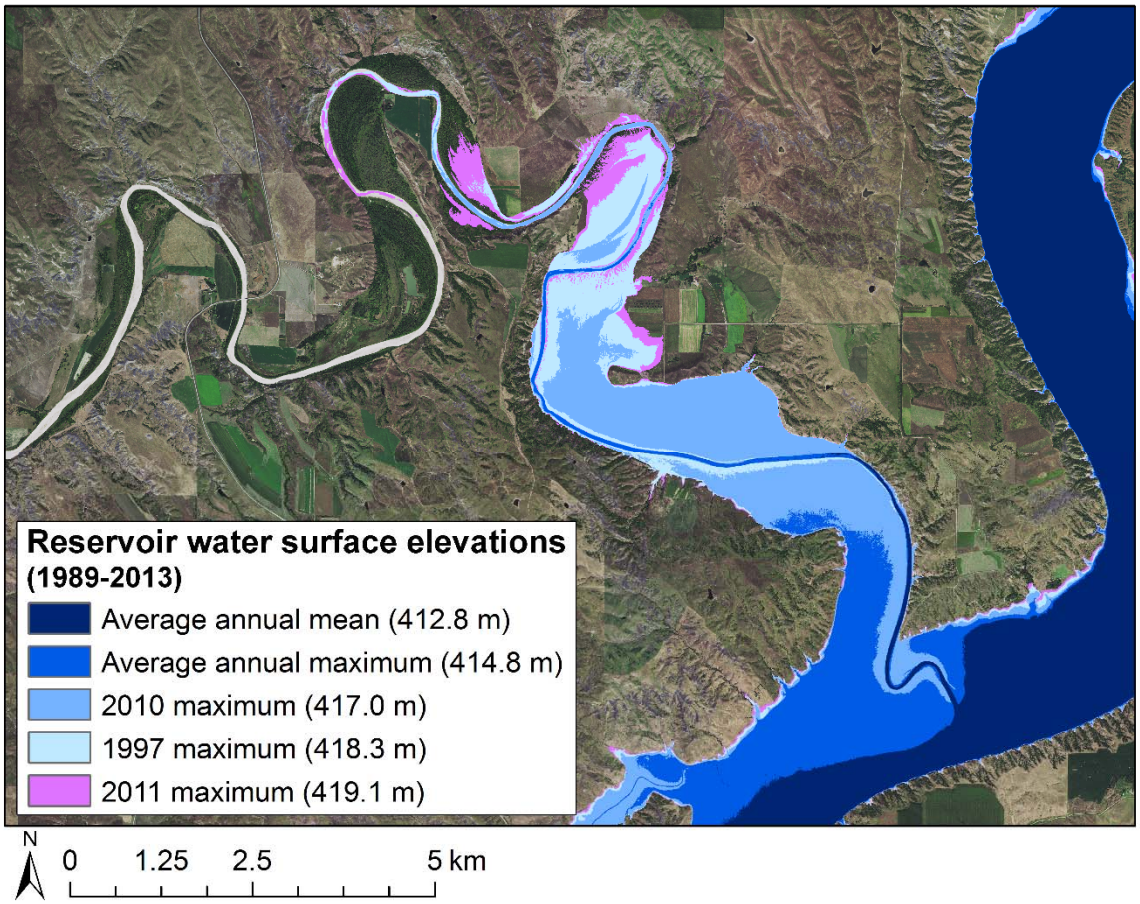

Figure 9. Frequency of selected reservoir water surface elevations (WSEs) of Fort Randall Reservoir (based on mean daily WSEs; 1989-2013), and related inundation of the White River delta. This figure was constructed from a digital elevation model (3 m) along with USGS data from gaging station 06442996 on Fort Randall Reservoir. Image source: U.S. Department of Agriculture, National Agriculture Imagery Program (2014).

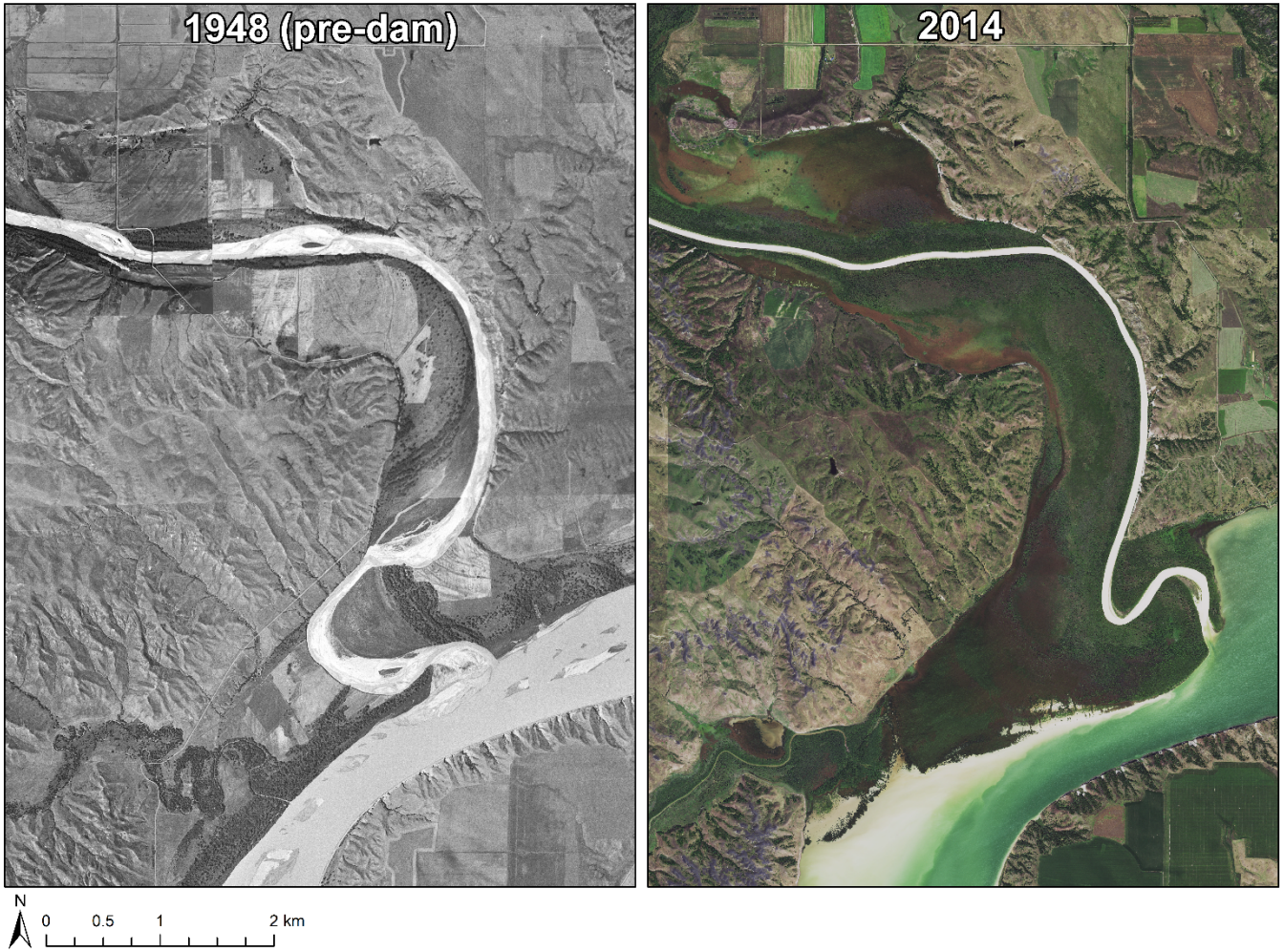

Figure 10. Aerial photographs of the confluence of the White and Missouri Rivers during the pre-dam (1948) and post-dam (2014) periods. Note the novel delta lobe that extends into Fort Randall Reservoir in the post-dam image. The smaller tributary to the southwest is Bull Creek. Sources: U.S. Department of Agriculture (left panel), and USDA National Agriculture Imagery Program (right panel).

Cross sections

Historical stream cross sections were used to investigate geomorphic changes that occurred during the post-dam era along the lower White River and along the Missouri River (Fort Randall Reservoir). The U.S. Army Corps of Engineers resurveyed cross sections since 1954 every few kilometers downstream of rkm 42.3 on the White River and near the White River-Missouri River confluence since 1953 at Missouri River km 1608.4. The 1953/1954 cross section surveys were completed one to two years following dam closure and were considered representative of the pre-dam channel and floodplain environment for this investigation.

Five cross sections from the lower 31 km of the White River and one cross section from Fort Randall Reservoir near the confluence were used to construct graphs illustrating geomorphic change over time. Cross section width was plotted against elevation using SigmaPlot 12.0 to identify changes in river channel and floodplain morphology between measurement periods spanning 1953/1954-1973, 1973-1996, and 1996-2011. The net change in thalweg elevation (minimum elevation) and the rate of change in thalweg elevation for each cross section at each measurement interval were calculated and compared graphically. The gradient of the lower 31 km of the White River in 1954 (2 years post-dam) and in 2011 (59 years post-dam) was constructed from thalweg elevations from a larger sample of cross sections ($n = 9$) within the study reach. The mean gradient of the lower White River in 1953 and in 2011 was determined by calculating the slope of a linear regression line running through the thalweg elevation at all nine cross sections using SigmaPlot 12.0.

Mapping changes in area of woody riparian vegetation over time

Changes in the area and age classes of woody riparian vegetation within the lower White River during the post-dam era were quantified using historical aerial photos and GIS-based mapping. The only pre-dam image available was from 1948, taken four years prior to complete closure of Fort Randall Dam in 1952. Post-dam aerial photos were for years 1983, 1991, 1998, 2004, 2010, and 2012. Imagery from 1948-1998 was obtained from the USDA Aerial Photography Field Office (http://www.apfo.usda.gov/); imagery from 2004-2012 was obtained from the USDA NRCS Geospatial Data Gateway (http://datagateway.nrcs.usda.gov/) (Table 1).

Aerial photos older than 2004 lacked geospatial information, hence these were geo-rectified using ArcGIS 10.0 with the 2010 NAIP orthophotography as a base map. At least three points linking features common to both images (e.g., road intersections, buildings) were selected as control points to reference the historical image to the base map. The default projection for the NAIP orthophotography was NAD 1983 UTM Zone 14N, which was utilized for all other images and subsequent shapefiles.

Table 1. Description of historical aerial photos used in this study.

Date(s)	Source	Description	Scale	Pixel Resolution
1948	United States Department of Agriculture (USDA)	black-and-white	1:20,000	0.5-0.6 m
1983	National High Altitude Photography (NHAP)	color-infrared	1:60,000	1.3 m
1991, 1998	National Aerial Photography Program (NAPP)	black-and-white	1:40,000	0.5 m
2004	National Agriculture Imagery Program (NAIP)	county mosaic orthophotography, natural color	1:40,000	1 m
2010, 2012	National Agriculture Imagery Program (NAIP)	county mosaic orthophotography, natural color	n/a	1 m

The study area was a 29 km reach of the lower White River and its floodplain which included both the White River delta and the river-delta transition subreaches, as previously defined. The lateral boundary was determined from a digital elevation model (3 m pixel size) contour that marked the transition from the low relief of the valley floor to the steep valley wall. Adjustments were made to align this boundary with the 2010 NAIP orthophotography to exclude non-floodplain features such as intersecting upland watersheds from the study area. The study area included a total of 2,699 ha of river bottomland and reservoir.

Interpretation and digitizing of aerial photos were done on a computer screen using "head's up" digitizing in ArcGIS 10.0. Land cover was broadly classified as either woody riparian vegetation (≥50 percent of canopy; hereafter referred to as "riparian woodland" or "woodland") or features other than woody riparian vegetation (e.g., herbaceous vegetation, agricultural fields, bare sediments, river channel, reservoir). This classification system provided a coarse estimate of riparian woodland area (0.1 ha patches or greater) within the study area boundaries. Riparian woodland included patches of woody riparian plants of any height and diameter, such as 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 between years. Overlays of classified images from selected pairs of years (1948/2012, 1991/1998, and 2010/2012) were produced to compare changes in the area and location of riparian woodland over time.

To assess flood damage and mortality associated with the 2011 Missouri River flood, the highest water level on record for Fort Randall Reservoir, two additional categories of riparian woodland were added to the 2012 classified image: complete mortality of riparian woodland and flood damaged riparian woodland. Complete mortality 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 percent) in 2012. Dead canopy cover was visually estimated from both the proportion of leafless trees and the presence of bare soil or woody debris within the 2010 woodland polygon. 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 from three aerial photos representing the 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 vegetation less than tree size (<10 cm diameter at breast height [dbh]; 1.3 m above ground surface), including sandbars colonized by woody seedlings and/or saplings and shrubland typically dominated by willows. The medium age class was defined as young forest (trees ~10-20 cm dbh and ~10-25 years old) 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 (>25 years old). The area of riparian woodland age classes was

compared numerically and graphically between years. To detect any longitudinal pattern related to riparian woodland age classes, the study reach was evenly divided into six, 4.8-km long segments. The percent of riparian woodland area in the young, medium, and old age classes was then calculated for each segment.

Field sampling of vegetation

Cottonwood stands from a broad range of size (and presumably age) classes were sampled along the 120 km study reach. Stands were divided into two main size categories. These included a tree size category (stands in which the majority of cottonwood trees were ≥10 cm dbh) and a sapling size category (stands containing only saplings, shrubs, and lianas <10 cm dbh and ≥1 m tall). The study reach was divided into three subreaches for vegetation sampling: (1) White River delta (subdivided into upper and lower delta for some analyses as previously described); (2) river-delta transition; and (3) White River. Much of the text and many of the tables and figures that follow were organized by stand size (tree or sapling) and subreach (delta, transition, or river).

Cottonwood forest vegetation was sampled during the summers of 2011 and 2013. A total of 35 stands (16 stands from the White River delta, 17 stands from the White River, and 2 stands from the transition subreach) was sampled according to the following criteria: (1) at least 20 percent of the canopy cover must be cottonwood (with the exception of one delta 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 size stands and at least 0.6 ha for sapling size stands; (4) vegetation structure should be relatively homogeneous; and (5) there should be no evidence of severe anthropogenic disturbance such as heavy cutting or overgrazing by livestock. Stand

selection criteria were similar to those of Johnson et al. (1976) and Dixon et al. (2010) and were based on the requirements of the sampling methods and the White River environment (i.e., relatively small stand size). Of the 35 stands, 13 stands were sampled in 2011 (stands assigned a number $\leq$17) and 22 stands were sampled in 2013 (stands assigned a number >17). Stand numbers do not necessarily correspond to the sampling order.

Stands were initially selected by using USDA National Agriculture Imagery Program (NAIP) orthophotography in ArcGIS 10.0. 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 texture and minimal gaps in the canopy. When such a patch was found of adequate size, the patch area was measured and a polygon was drawn within the patch to define the sampling area. Polygons were usually drawn as rectangles, although other polygon shapes were used where appropriate. Each polygon was assigned a unique stand number and saved within a shapefile.

All qualifying stands that were located within the 120 km study reach were selected for potential sampling. Some stands were later eliminated due to difficulty with access or because permission was not granted by the landowner. When a stand was first visited in the field, inspections were made to ensure that the stand met the sampling criteria. If the stand did not meet one or more of the criteria, it was not sampled.

There were only a few cases in which a stand was rejected based on field observations, mostly in the delta subreach where vegetation and environmental conditions were highly heterogeneous. Because the delta was primarily an aggrading

system, with very little erosion or channel meandering, there were no distinct floodplain channel shelves or terraces (Hupp and Osterkamp 1996), especially in the lower portion of the delta. Thus, a patch of vegetation that appeared to be of uniform elevation and structure on the aerial photo could have actually contained a mixture of these elements when viewed on the ground. Likewise, stands along the White River and its delta tended to be small (<6 ha) and occurred in close proximity to other stand types, especially in the delta subreach. When viewed on an aerial photo, small, adjacent stands sometimes appeared as a single stand of similar age and origin, especially if the stands had aged and grown together. When observed in the field, however, it was obvious that the previously defined stand boundary actually contained two or more stands of different age and structure. For example, in one predetermined stand, the vegetation transitioned from a mature cottonwood overstory with young green ash in the midstory to a middle age cottonwood overstory with no green ash in the midstory, within a distance of 50 m.

Stand delineations containing mixed vegetation types were not sampled in this study for three reasons. First, they did not meet the condition of uniform structure required by the conventional forest sampling methods used in this and in other comparable studies (Johnson et al. 1976, Dixon et al. 2010). Second, accurate delineations of these dissimilar stands would have resulted in small stands that fell well below the area requirements of the sampling methods. Third, including mixed stands would have limited the usefulness of comparisons between stands and between the White River delta, transition, and White River subreaches.

Stands with evidence of severe anthropogenic disturbance were not sampled because they may have contained an impoverished flora and/or exhibited a structure that

was not representative of a natural stand. Similarly, the flora of a disturbed stand may not have been representative of a particular successional stage, limiting the usefulness of comparisons among stands along the age gradient. Despite these exclusions, stand selection criteria employed captured a wide range of cottonwood forest heterogeneity along the lower White River and its delta.

Vegetation sampling – overstory

For most tree size stands, the point centered quarter method (Cottam and Curtis 1956) was used to sample trees with a diameter at breast height (dbh, [1.3 m above the ground surface]) of ≥10 cm. This is the same plotless distance method used by Johnson et al. (1976) and Dixon et al. (2010) to survey cottonwood forests along the Missouri River. A stratified random sampling design was used to locate sampling points in each stand. The stand was first subdivided into several strata, producing a stand subdivided into 2-8 equal sized subunits. Within each subunit a transect parallel to those in other subunits was located laterally within each subunit by obtaining a random value using the RANDBETWEEN function in MS-Excel. This function was programmed to generate a random distance to locate the transect starting point on the border of each subunit. The transects were in turn divided longitudinally into 4-27 equal sized subunits, and a randomly located point was obtained along the transect for each subunit by following the same methods as above. When the distances between transects and points were converted to paces, the stratified random sampling design was ready for field use.

The number of sampling points per stand ranged from 20-40, depending on stand size. For stands <6 ha, the sampling density was at least 6.5 points per ha, and for stands ≥6 ha, sampling density was always 40 points per stand (≤6.7 points per ha). This

sampling density is consistent with that used by Johnson et al. (1976) and Dixon et al. (2010).

Each sampling point was the center of four, 90 degree quadrants, with the predetermined transect line giving orientation. At each point, the closest live tree to the point in each quadrant was sampled. The species and dbh of each tree was recorded (measured to the nearest 0.1 cm). The distance from the point to each tree was measured to the nearest 0.01 m using a Sonin® Multi-Measure Combo PRO distance finder. For trees with multiple stems, the dbh of each stem was measured and a single diameter was calculated based on the combined basal area of all stems. Distance for multi-stemmed trees was measured from a point at the center of the stem cluster. Additionally, a record was made if a liana (woody vine) was attached to the trunk of a sampled tree.

The overstory in stands 1 and 86, where stand size was small and tree density was low, was sampled by a complete stand inventory (i.e., all trees within the stand boundaries were measured) rather than by a sample obtained from the point centered quarter method. This was done to avoid sampling the same tree more than once.

Tree cores were collected in each stand using a 3-threaded 5.15 mm Suunto® or Haglöf® increment borer. When possible, cores were taken from trees at breast height to maintain consistency with diameter measurements. Because many trees were buried to varying depths, especially in the delta and transition subreaches where there was more sedimentation, this method of tree coring may have underestimated stand age or differentially affected ages among the trees in the stand.

In 2011, the four trees occurring at five randomly selected overstory sampling points were cored, regardless of species, for a total of 20 cores per stand. In 2013, all four

trees were similarly cored at overstory sampling points, but these points were selected according to a stratified random sampling design. Specifically, each stand was evenly divided into subsets of 4-8 points, and one point from each subset was randomly selected for coring all four trees. Additional cottonwood trees were cored between the predetermined sampling points to ensure that at least 15 cottonwood trees from a wide range of size classes were cored in each stand. In stand 1, which was sampled by a complete stand inventory in 2011, trees were randomly selected for coring. In stand 86, which was sampled by a complete stand inventory in 2013, one out of every six consecutive trees was randomly selected for coring. Tree cores were stored in plastic straws, labeled according to stand, species, and dbh, and sent to the Rocky Mountain Tree Ring Research Lab (Fort Collins, Colorado) for analysis.

Vegetation sampling – sapling layer

The sapling layer included woody plants of all life forms (saplings, shrubs, and lianas) ≥1 m tall and <10 cm dbh. Sapling species were defined as small trees that can eventually attain tree size (>10 cm dbh) and enter the overstory. Shrub species were defined as those that remain <10 cm dbh throughout their lifespan and are restricted to the seedling and sapling layers. Lianas were defined as woody vines <10 cm dbh.

The sapling layer was sampled using Lindsey's line-strip method (Lindsey 1955). Transects and plots were established according to a stratified random design. The stand was first subdivided into several strata, producing a stand subdivided into 3-12 equal sized subunits. Within each subunit a transect running perpendicular to the channel was located laterally within each subunit by obtaining a random value using the RANDBETWEEN function in MS-Excel. This function was programmed to generate a

random distance to locate the transect within each subunit. The transects were in turn divided longitudinally into 2-8 equal sized subunits, and a randomly located point was obtained along the transect for each subunit by following the same methods as above. When the distances between transects and points were converted to paces, the stratified random sampling design was ready for field use. Depending on stand size, 8-12 sampling plots measuring 2 m by 10 m were established in each stand. For stands <6 ha, minimum sampling density was 2 plots per ha, and for stands ≥6 ha, sampling density was 12 plots per stand. This sampling density is consistent with methods used by Dixon et al. (2010).

At each plot location, a measuring tape was stretched to a length of 10 m along the transect bearing. All sapling layer stems rooted within 1 m of either side of the tape were counted and identified to species. The diameter of each stem was measured at ground level to the nearest 2 cm using a handcrafted measuring tool (Figure 11). In cases where the stem diameter was ≥10 cm at ground level, but was <10 cm at 1 m above ground level, the stem was counted in the sapling layer in the 8-10 cm size class.

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 species was totaled along the tape for each species. Percent cover was estimated whether stems were rooted in or out of the plot. Species were allowed to have overlapping coverage for the same length of tape; thus, total percent sapling layer cover could exceed 100 percent for a single plot.

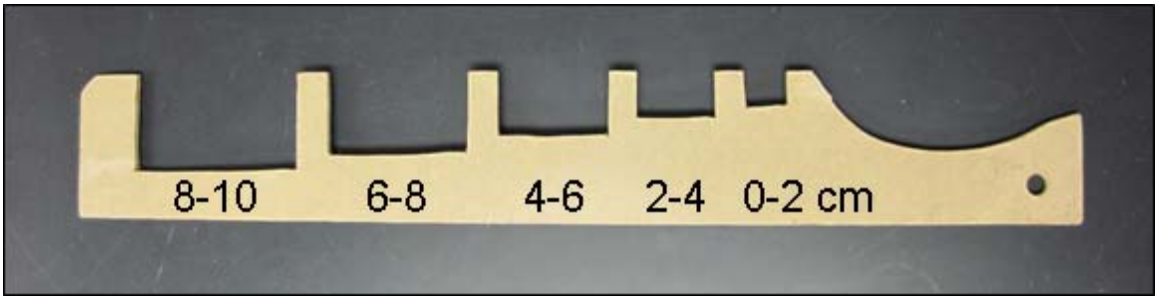

Figure 11. The handcrafted tool used to quickly measure the diameter class of woody stems occurring in the sapling layer.

Vegetation sapling – seedling layer

Woody seedlings <1 m tall were sampled in 1 m by 1 m subplots placed within the line-strip plots used for sapling layer sampling. Each 10 m long line-strip plot was divided into 1 m long segments. Two of these segments were then selected in stratified random fashion (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 size. 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 five percent. Species with trace occurrence were recorded as one percent cover. Percent cover was estimated separately for each species, with no adjustments made for overlap with other seedling species. Thus, total percent seedling cover could exceed 100 percent in a single quadrat. In each stand, the seedling layer was sampled first, followed by the sapling layer and then the overstory layer, to avoid trampling the shorter vegetation prior to sampling.

Voucher specimens for each recorded species were collected, pressed and deposited in the C. A. Taylor Herbarium of South Dakota State University in Brookings. Oral permission was granted for plant collecting on all private and public lands.

Vegetation data summarization and analysis

Frequency, relative frequency, dominance, relative dominance, density, relative density, importance value (IV), and relative importance value (RIV) were calculated for each species in the overstory, sapling layer, and seedling layer of the 35 stands. These statistics were summarized in tabular and graphic form and compared among stands and between the White River delta, transition, and White River subreaches.

Overstory

Calculations for the overstory sampled using the point centered quarter method largely followed the procedures of Curtis and McIntosh (1950) and Cottam and Curtis (1956). The equations used to calculate each vegetation characteristic were:

- Species frequency (percent):

$$\frac{\text{Total number of points at which a given species occurred}}{\text{Total number of points sampled per stand (20 to 40)}} \times 100$$

- Stand density (trees/ha):

$$\frac{10{,}000}{\text{mean distance}^2},$$

  where mean distance (m) was equal to the average of all point to tree distances in a stand.

- Species density (trees/ha by species):

$$\frac{\text{Number of trees sampled of a given species}}{\text{Total number of trees sampled in a stand (80 to 160)}} \times \text{stand density}$$

- Stand dominance (basal area [m²/ha]):

$$\text{Mean basal area per tree} \times \text{stand density}$$

- Species dominance (basal area [m²/ha] by species):

$$\text{Stand dominance} \times \frac{\text{Total basal area of a given species}}{\text{Total basal area of all trees sampled in a stand}}$$

- Liana species frequency (percent):

$$\frac{\text{Number of sampled trees where a given liana species was attached to the trunk}}{\text{Total number of trees sampled in each stand (80 to 160)}} \times 100$$

- Relative frequency:

$$\frac{\text{Total number of points at which a given species occurred}}{\text{Total number of occurrences of all species}} \times 100$$

- Relative density:

$$\frac{\text{Species density}}{\text{Stand density}} \times 100$$

- Relative dominance:

$$\frac{\text{Species dominance}}{\text{Stand dominance}} \times 100$$

- Species importance value:

$$\text{Relative frequency} + \text{Relative density} + \text{Relative dominance},$$

which ranged from 0 to 300 (Curtis and McIntosh 1951).

- Relative importance value:

$$\frac{\text{Species importance value}}{300} \times 100$$

Frequency could not be calculated for tree species in stands sampled by a complete inventory (stands 1 and 86). 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. This same importance value calculation (relative dominance + relative density; maximum = 200) was performed for stands sampled using the point centered quarter method to allow for comparison among all stands.

Overstory size structure was graphed by grouping trees into 5 cm size classes. Graphs were compared to detect structural and successional differences among stands and between the subreaches.

Sapling layer

- Species frequency (percent):

$$\frac{\text{Number of plots in which a given species occurred}}{\text{Total number of plots within the stand (8 to 12)}} \times 100$$

- Species density (saplings/ha by species):

$$\frac{\text{Total number of saplings of a given species}}{\text{Total area sampled per stand (160 to 240 m}^2\text{)}} \times 10{,}000$$

- Species density by size class (saplings/ha by species and size):

$$\frac{\text{Total number of saplings of a given species in a given size class}}{\text{Total area sampled per stand (160 to 240 m}^2\text{)}} \times 10{,}000$$

- Species dominance (percent cover by species):

$$\frac{\text{Total number of meters of line cover by a given species}}{\text{Total transect length per stand (80 to 120 m)}} \times 100$$

- Relative frequency:

$$\frac{\text{Total number of plots in which a given species occurred}}{\text{Total number of occurrences of all species}} \times 100$$

- Relative density:

$$\frac{\text{Species density}}{\text{Total density of all species}} \times 100$$

- Relative dominance:

$$\frac{\text{Species dominance}}{\text{Total cover of all species}} \times 100$$

Importance value and relative importance value were calculated by the same procedures as above.

Seedling layer

- Species frequency (percent)

$$\frac{\text{Total number of quadrats in which a given species occurred}}{\text{Total number of quadrats per stand (16 to 24)}} \times 100$$

- Species density (seedlings/ha by species)

$$\frac{\text{Total number of seedlings of a given species}}{\text{Total area of all the quadrats per stand (16 to 24 m}^2\text{)}} \times 10{,}000$$

- Species dominance (percent cover by species)

$$\frac{\text{Total percent cover of a given species}}{\text{Total number of quadrats per stand (16 to 24)}} \times 100$$

- Relative frequency (percent):

$$\frac{\text{Total number of quadrats in which a given species occurred}}{\text{Total number of occurrences of all species}} \times 100$$

- Relative density:

$$\frac{\text{Species density}}{\text{Total density of all species}} \times 100$$

- Relative dominance:

$$\frac{\text{Species dominance}}{\text{Total cover of all species}} \times 100$$

Importance value and relative importance value were calculated by the same procedures as above.

Ordination analysis

Ordination was used to investigate the structural and compositional relationships of the vegetation on the delta, transition, and White River subreaches. All analyses were

conducted in PRIMER version 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 (species presence, frequency, relative frequency, density, relative density, dominance, relative dominance, importance value, and relative importance value), with species as columns and stands as rows. 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.

The two-dimensional stress, a measure of the distortion between the similarity rankings in the ordination plot (i.e., the relationship between the similarity in stand composition and the closeness in ordination space), was calculated for each ordination. Stress indicates how faithfully the high-dimensional relationships among the samples are represented in the two-dimensional ordination plots (Clarke and Gorley 2006). Stress <0.1 corresponds to a good ordination with no real prospect of a misleading interpretation; stress <0.2 still gives a potentially useful two-dimensional picture, though for values at the upper end of this range too much reliance should not be placed on the details of the plot (Clarke and Warwick 2001).

Similarity of the White River delta to the White River

Vegetation community composition was compared between the White River delta and White River subreaches using two methods. First, mean importance values for each species in a given subreach were calculated separately for the overstory, sapling layer, and seedling layer of both tree size and sapling size stands (e.g., for seedlings in tree size stands on the delta). Species were then ranked by mean importance values for each

category. This dataset was used to compute a Spearman's rank correlation coefficient (r_s; scale of -1 to 1) using Statistix 9.0 software to determine to what degree the species rankings were correlated across subreaches. Likewise, a Bray-Curtis similarity score (scale of 0 to 100) was computed using the resemblance function in PRIMER version 6.1. To compare the degree of community similarity *between* subreaches to the degree of community similarity *within* a given subreach, mean stand to stand Bray-Curtis similarity scores were computed for each subreach using the resemblance function in PRIMER.

For selected species, importance value, frequency, and density also were compared between the White River delta and White River subreaches. For example, the density of peachleaf willow trees in occupied stands on the delta was compared to stands along the White River. A *t*-test was used to test for significant differences between the delta and White River for datasets with a normal distribution. Alternatively, a Mann-Whitney test was used to test for significant differences between the delta and White River for datasets without a normal distribution. These analyses only included stands that were occupied by the species of interest. All statistical tests were performed at a significance level of $\alpha = 0.05$.

Similarity of the White River delta to Missouri River remnant reaches

The diversity of native woody plants (species richness) in cottonwood stands was compared between the White River delta and two remnant reaches of the Missouri River (Garrison and Gavins Point reaches). Cottonwood stand diversity data for the Missouri River were used from previous studies of the Garrison reach (rkm 2,237-2,069.6) in North Dakota (Keammerer 1972, Johnson et al. 1976) and the Gavins Point reach (rkm 1,305.3-1,211.8) in South Dakota and Nebraska (Dixon et al. 2010, Dixon et al. 2012).

Only native species sampled by similar methods and with ranges common to both sites were included in the analyses.

Comparisons of woody species richness were made between stands of similar age on the delta and along the Missouri River. In the Garrison reach, stand age was indirectly determined by mean cottonwood diameter (Johnson et al. 1976). This same approach was used for stands on the White River delta, and stands were assigned to one of two diameter classes common to both sites (14.4-20.6 cm and 32.0-43.2 cm). Because cottonwood growth rates may have differed between the delta and the Garrison reach, the two diameter classes may not represent equivalent age classes, but they do represent similar structure of trees. Sapling layer data were not available for the Garrison reach, so species on the White River delta that only occurred in the sapling layer were removed from this particular analysis. The total number of woody species in the seedling and overstory layers per stand were then compared within each stand age class between the White River delta and the Garrison reach using *t*-tests. There were very small differences in the number of stands sampled across sites which may have had a small effect on species richness comparisons.

Stands in the Gavins Point reach were aged by analysis of historical aerial photography and were assigned to one of the following five age classes (Dixon et al. 2010, Dixon et al. 2012): <10 years, 10-24 years, 25-49 years, 50-114 years, and >114 years. Tree size stands on the White River delta were similarly classified based on tree ring data. Sapling size stands on the White River delta were assigned to the <10 year age class. The total number of woody species in the seedling, sapling and overstory layers per stand was then compared between the White River delta and the Gavins Point reach.

Two-sample *t*-tests were used to test for significant differences in species richness between stands of similar age across the two sites. There was a large difference in the number of stands sampled across sites in the 25-49 year age class; thus, species richness was not compared between the White River delta and the Gavins Point reach for this age class.

Tree ring analysis

Tree cores were aged by the Rocky Mountain Tree Ring Research Laboratory. The main uses for tree ring measurements were to: (1) determine stand age based on the median age of cored cottonwoods in each stand; (2) investigate cottonwood age structure within each stand from frequency histograms; (3) determine mean annual cottonwood growth rates (cm/year); (4) compare cottonwood and peachleaf willow growth rates (cm/year) between pairs of the following subreaches: lower delta, upper delta, and White River (*t*-tests were used to compare data sets with a normal distribution and Mann-Whitney tests were used to compare data sets without a normal distribution); (5) conduct regression analysis to (a) determine the relationship between cottonwood age and size, and (b) determine whether the relationship (slope) between cottonwood age and size was significantly different between the delta and White River by performing a *t*-test.

There was a small sample of cores from species other than cottonwood; thus, data from these species were mainly used to supplement analyses of stand age structure and successional patterns. In stand 10, which contained only a small number of large cottonwood trees, no cottonwood trees were randomly picked for coring. Hence, stand age was estimated by extrapolating from known ages of the largest cottonwood trees in

other stands where the center of the trees could be reached by the available increment borers.

Stand ages, age structure, and growth rates were compared among stands and subreaches with a variety of graphical methods. For example, bar graphs were constructed to compare tree species density by stand and subreach. Although stands in each subreach were not selected by a strictly random sample, and thus did not include the full range of cottonwood forest ages present in the study reach, they were broadly representative of the age class distributions in each subreach. Nearly all cottonwood stands within the 120 km study reach that were accessible and met the requirements of the sampling methods were included in this study.

RESULTS

Formation of the White River delta

The lower White River and its confluence with Fort Randall Reservoir experienced high rates of channel and floodplain aggradation and associated geomorphic change during the post-dam era. Total increases in thalweg elevation over the study period ranged from 0.61 m at rkm 30.9 to 11.95 m at rkm 3.1 (Figures 12, 13, and 14). In addition to increases in thalweg elevation, post-dam changes to the channel and floodplain environment included: the active channel generally narrowed; the floodplain aggraded to a similar degree as the thalweg; and at some cross sections, prominent natural levees formed adjacent to the active channel (Figure 13). These changes reflect a highly depositional environment where there has been very little erosion or channel movement during the post-dam period (Appendix Figure 8).

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) (Figure 15). Between 1953/1954 and 1973, rates of thalweg aggradation were greatest at the most downstream cross sections and declined in the upstream direction. Conversely, rates of thalweg aggradation between 1973 and 1996 were greatest at the two most upstream cross sections. Between 1996 and 2011, thalweg aggradation rates were generally greatest at the most downstream cross sections and decreased in the upstream direction.

Sedimentation during the post-dam period led to a flattening of the stream gradient within the delta, creating a “sediment wedge” within the lower 31 km of the

White River (Figure 16). In 1954 (2 years post-dam), the mean stream gradient was 0.70 m/km. By 2011 (59 years post-dam), the mean gradient had declined to 0.29 m/km. This sediment wedge was thickest in the lowermost 13 rkm of the White River where the gradient approached 0.00 m/km.

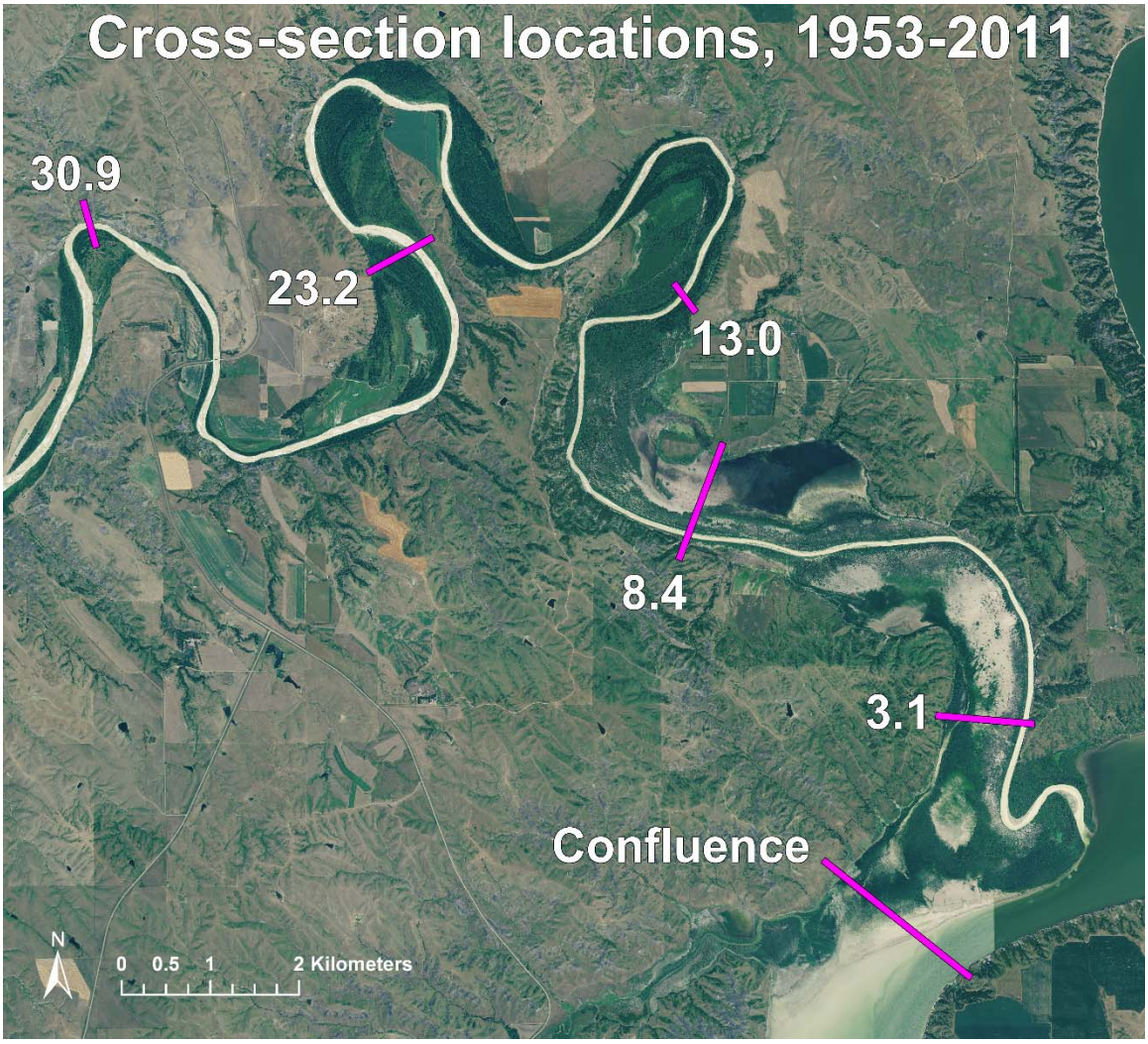

Figure 12. Locations of six selected cross sections (magenta) and corresponding rkm (white text; distance upstream of the confluence) along the lower White River and its confluence with the Missouri River (Fort Randall Reservoir) in South Dakota. Image source: U.S. Department of Agriculture, National Agriculture Imagery Program (2012).

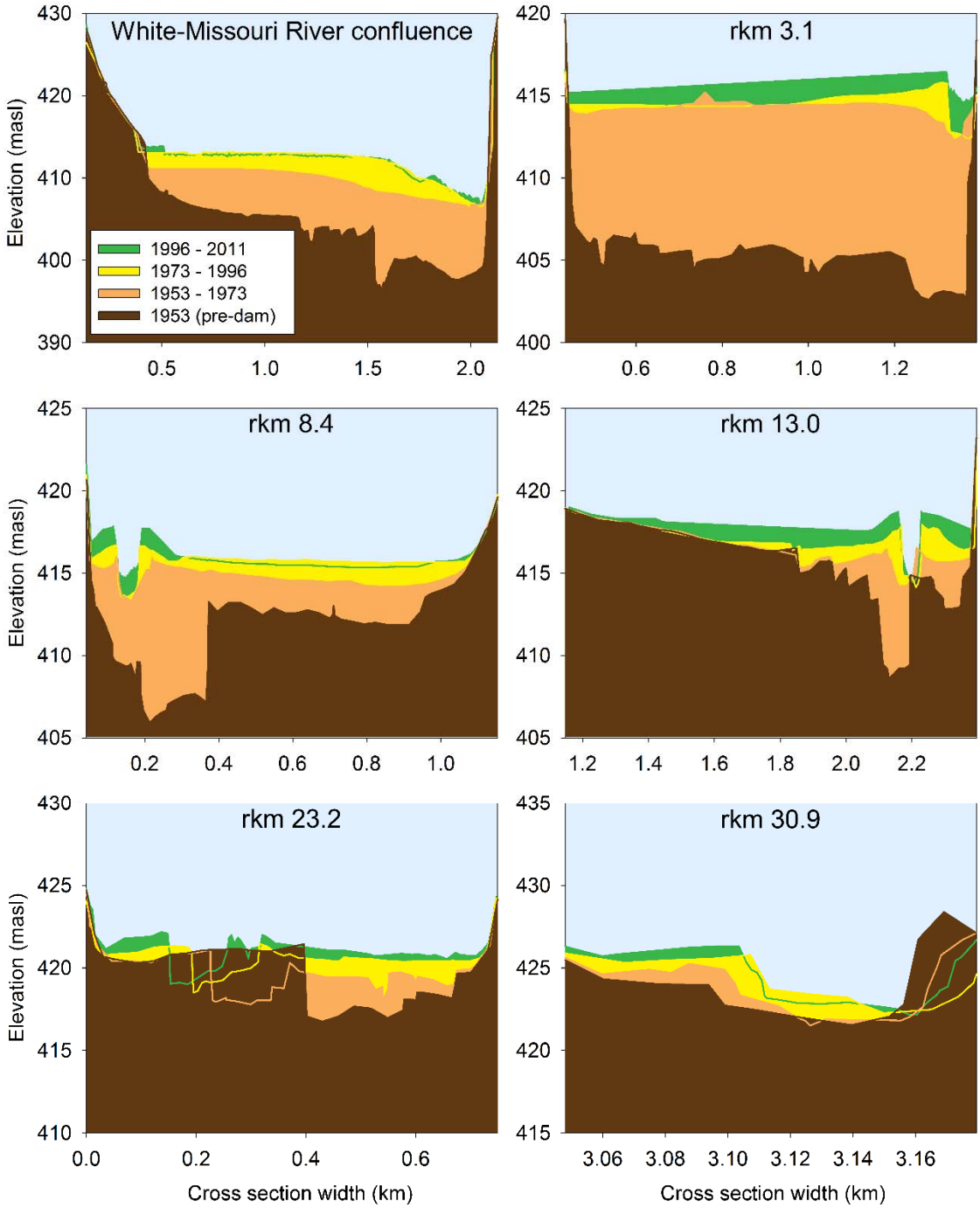

Figure 13. Sedimentation history at six cross sections from the lower White River and its confluence with the Missouri River (Fort Randall Reservoir) in South Dakota. The ordinate is scaled in equal units for each of the graphs from the White River. The area under each curve is filled in to improve visual clarity.

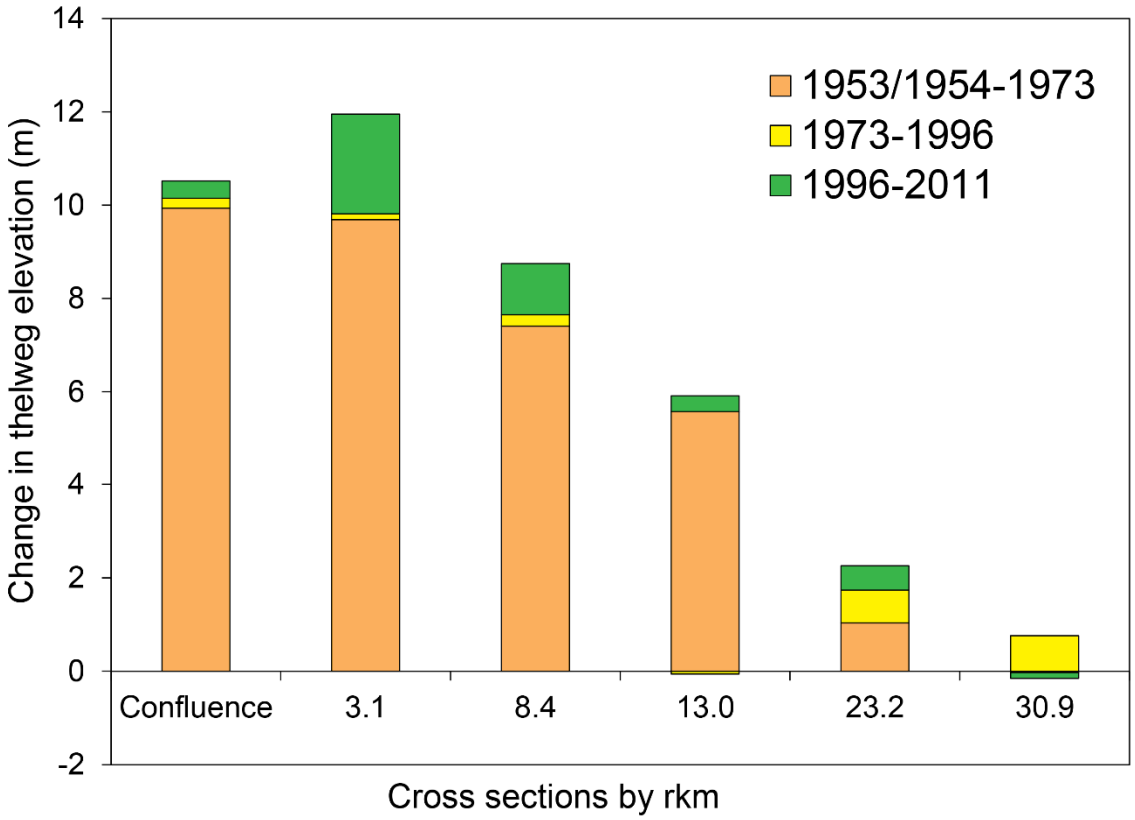

Figure 14. Change in thalweg elevation (m) at six cross sections from the lower White River and its confluence with the Missouri River (Fort Randall Reservoir) in South Dakota.

Figure 15. Mean rate of change in thalweg elevation (m/year) for each measurement interval at six cross sections along the lower White River and its confluence with the Missouri River (Fort Randall Reservoir) in South Dakota.

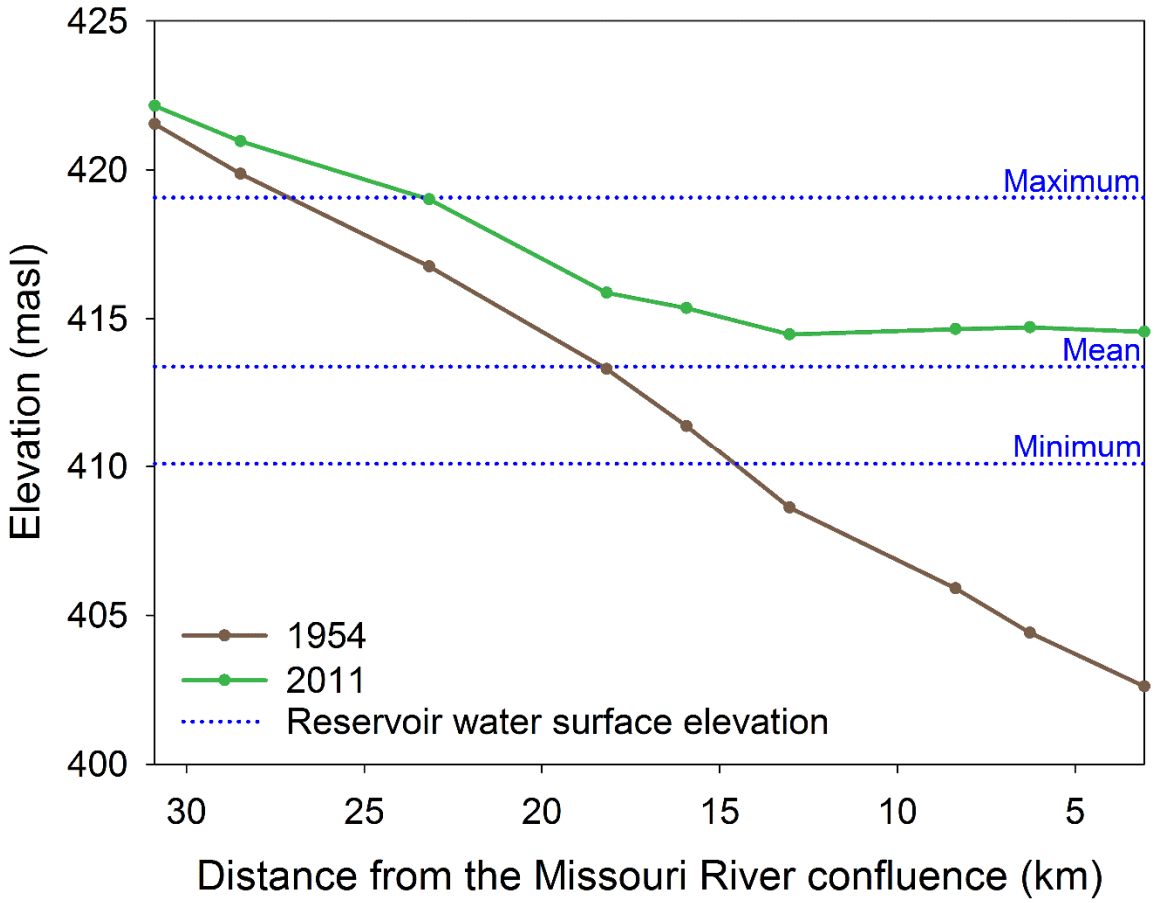

Figure 16. Stream gradient of the lower 31 km of the White River in South Dakota in 1954 and 2011, depicting the formation of a sediment wedge within the delta subreach. The dotted blue lines depict minimum, mean, and maximum (2011) mean daily reservoir water surface elevations (1989-2014). The reservoir water surface elevations were derived from the USGS gaging station 06442996 at Chamberlain, South Dakota.

Temporal changes in riparian woodland area

The area of riparian woodland generally increased during the post-dam period (Figure 17). Riparian woodland area was 782 ha in 1948, four years prior to complete closure of Fort Randall Dam. By 1983, riparian woodland area had expanded to 968 ha. Riparian woodland area peaked at 1,230 ha in 2004, and declined to 1,164 ha in 2012. This represents a net increase in woodland area of 381 ha (49 percent) during the post-dam period. Riparian woodland expansion occurred not only near the confluence of the White and Missouri Rivers, but also throughout most of the study reach (Figure 18). Pre-dam woodland was mostly concentrated in narrow bands near the active channel, but during the post-dam era, woodland expanded landward.

Although total riparian woodland area increased between 1948 and 2012, riparian woodland area declined during intervals spanning flood years on the Missouri River. Between 1991 and 1998, an interval that included the 1997 Missouri River flood (the second greatest annual maximum stage on record for Fort Randall Reservoir), there was a net loss of 101 ha of riparian woodland (Figure 17). Visual inspection of the 1991-1998 overlay (Figure 19) showed that riparian woodland declined throughout the longitudinal range of the study reach, but the greatest declines occurred between rkm 0-15 along the woodland edge opposite the active channel. Between 2004 and 2010, an interval that included the high water year of 2010 (the third greatest annual maximum stage on record for Fort Randall Reservoir), there was a net loss of 22 ha of riparian woodland, most of which was concentrated in the lower delta. A similar woodland mortality pattern was observed following the record 2011 Missouri River flood (Figure 20, Appendix Figure 9). Between 2010 and 2012, 45 ha of riparian woodland experienced complete mortality and

55 ha of riparian woodland experienced flood damage, most of which was concentrated between rkm 0-15. Field reconnaissance in 2013 indicated that much of the flood damaged woodland present in 2012 likely transitioned to a state of complete mortality by June 2013 (Appendix Figures 10, 11, and 12).

The majority of woodland losses during the study period were concentrated between rkm 0-10 where reservoir inundation was either permanent or was most variable and extreme (Figure 9). Losses also occurred farther upstream by different means where there was channel migration or woodland clearing by private landowners (Figure 18).

Age class proportions of the riparian woodland changed markedly during the post-dam era (Figure 21). Pre-dam (1948) woodland was dominated by the old age class (535 ha, 68 percent), woodland at the midpoint of the study period (1983) was dominated by the young age class (445 ha, 46 percent), and woodland at the end of the study period (2012) was dominated by the medium age class (539 ha, 46 percent). The medium age class was the least common at the pre-dam (1948) measurement (7 percent), but was the most common in 2012 (46 percent).

The longitudinal distribution of riparian woodland age classes throughout the study reach changed considerably during the post-dam era (Figure 22). Prior to damming (1948), the old age class dominated (49-88 percent) all 4.8 km long sub-segments of the reach, without any distinct longitudinal pattern. However, at the midpoint of the study period (1983), the young woodland became dominant in the lowermost sub-segments, but dominance gradually transitioned to the medium and old age classes in the upstream direction. At the end of the study period (2012), the medium age class dominated the lower half of the reach, but the old age class dominated the upper half of the reach.

Young woodland was most common between rkm 0-4.8 mostly within the margins of the mean annual maximum reservoir pool boundary and between rkm 24-28.8, in recently abandoned fields (Appendix Figure 13).

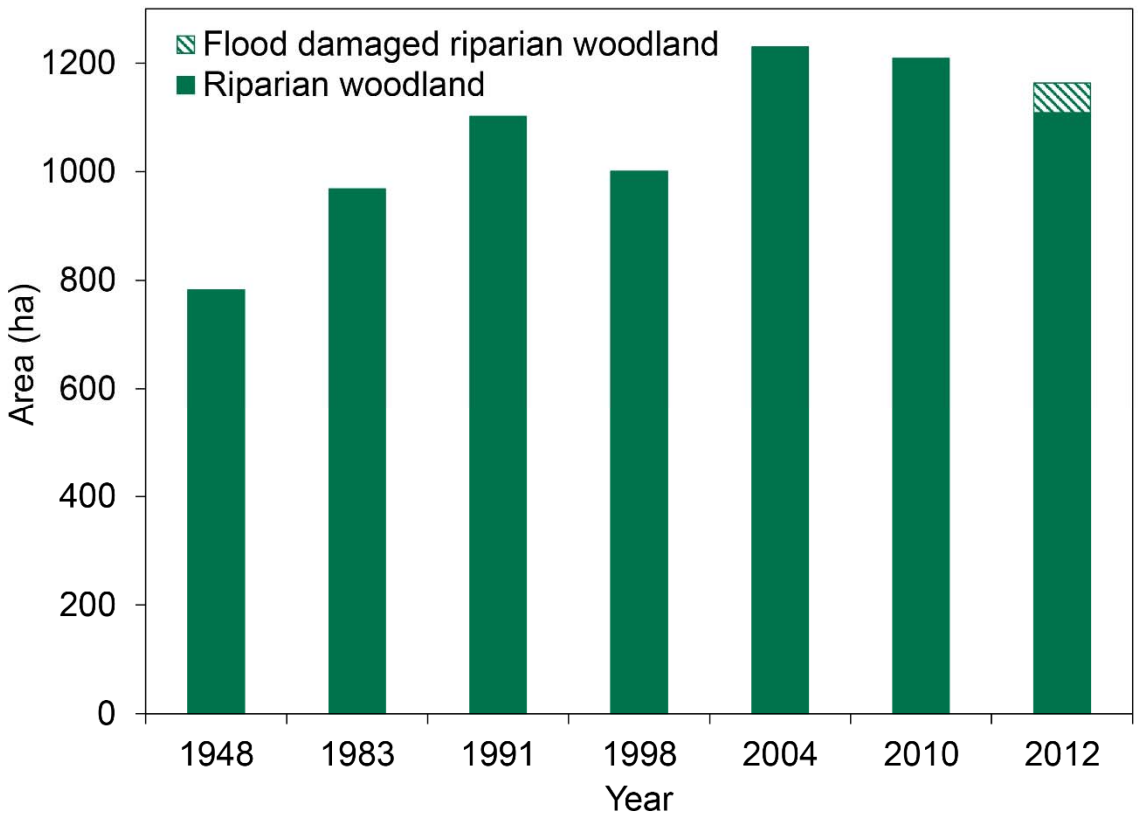

Figure 17. Total riparian woodland area (ha) by year along the lower 29 km of the White River in South Dakota.

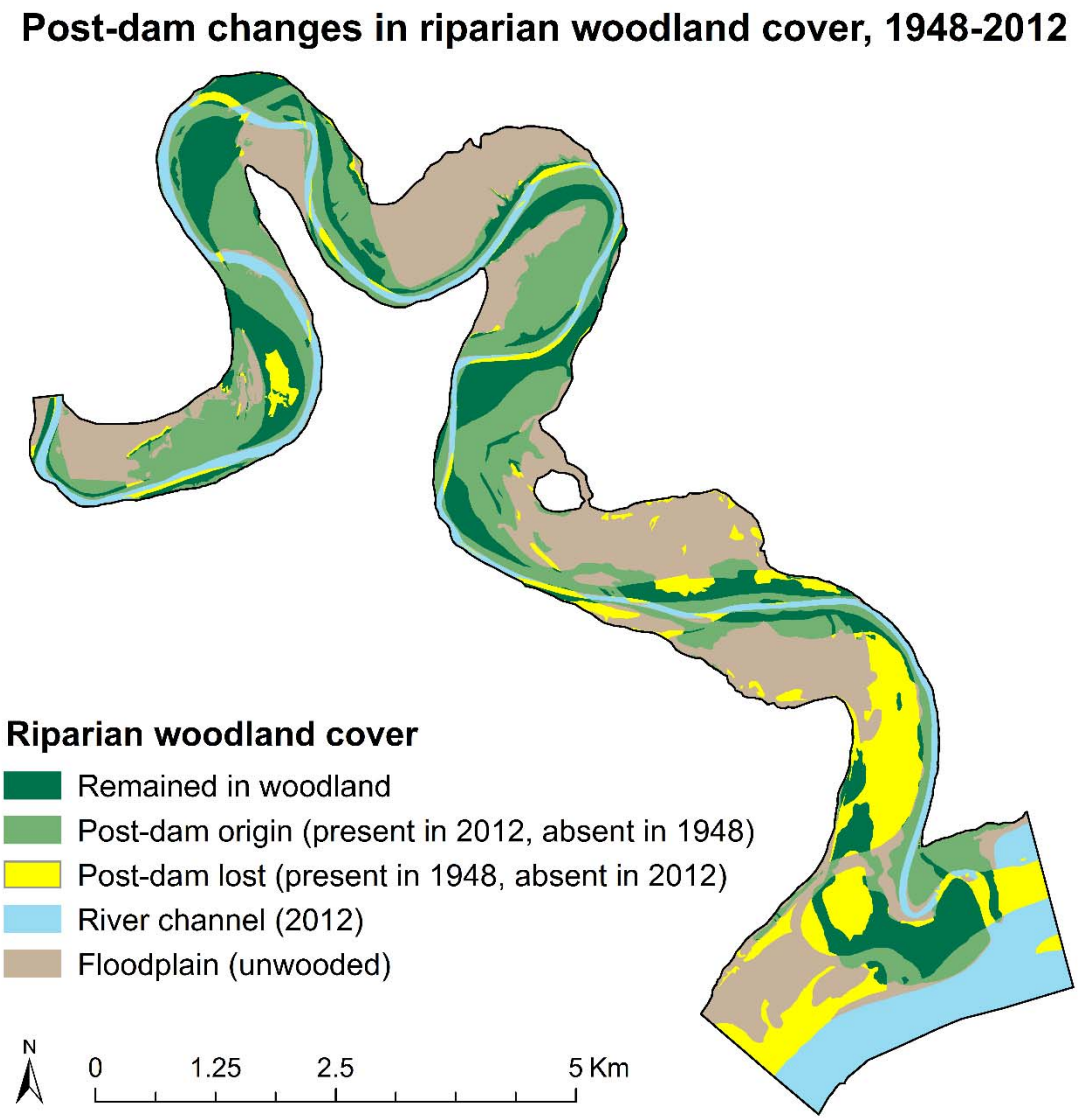

Figure 18. GIS map of riparian woodland cover changes between 1948 (pre-dam) and 2012 (post-dam) from aerial photographs of the lower 29 km of the White River in South Dakota.

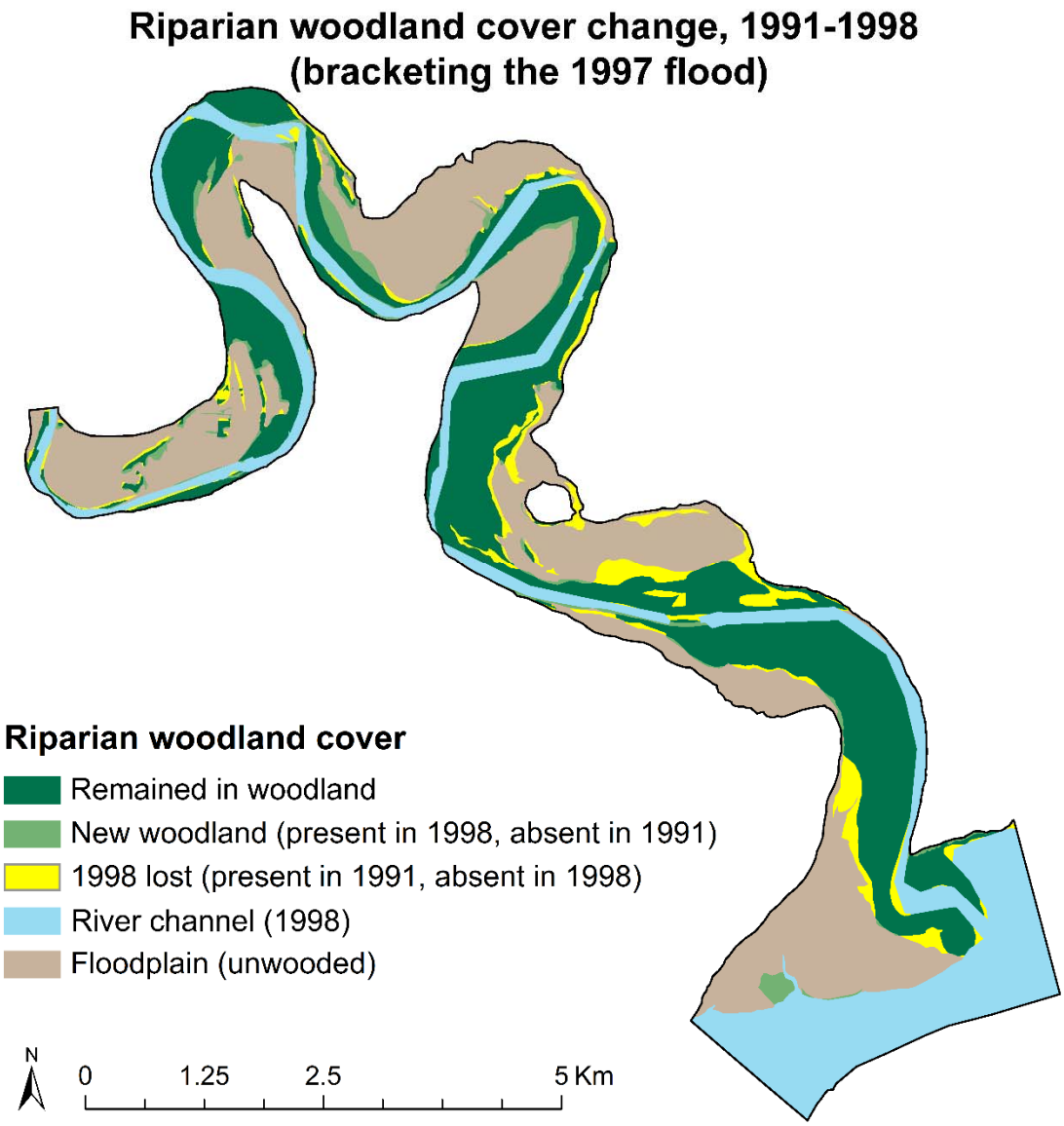

Figure 19. GIS map of riparian woodland cover changes between 1991 and 1998 from aerial photographs of the lower 29 km of the White River in South Dakota.

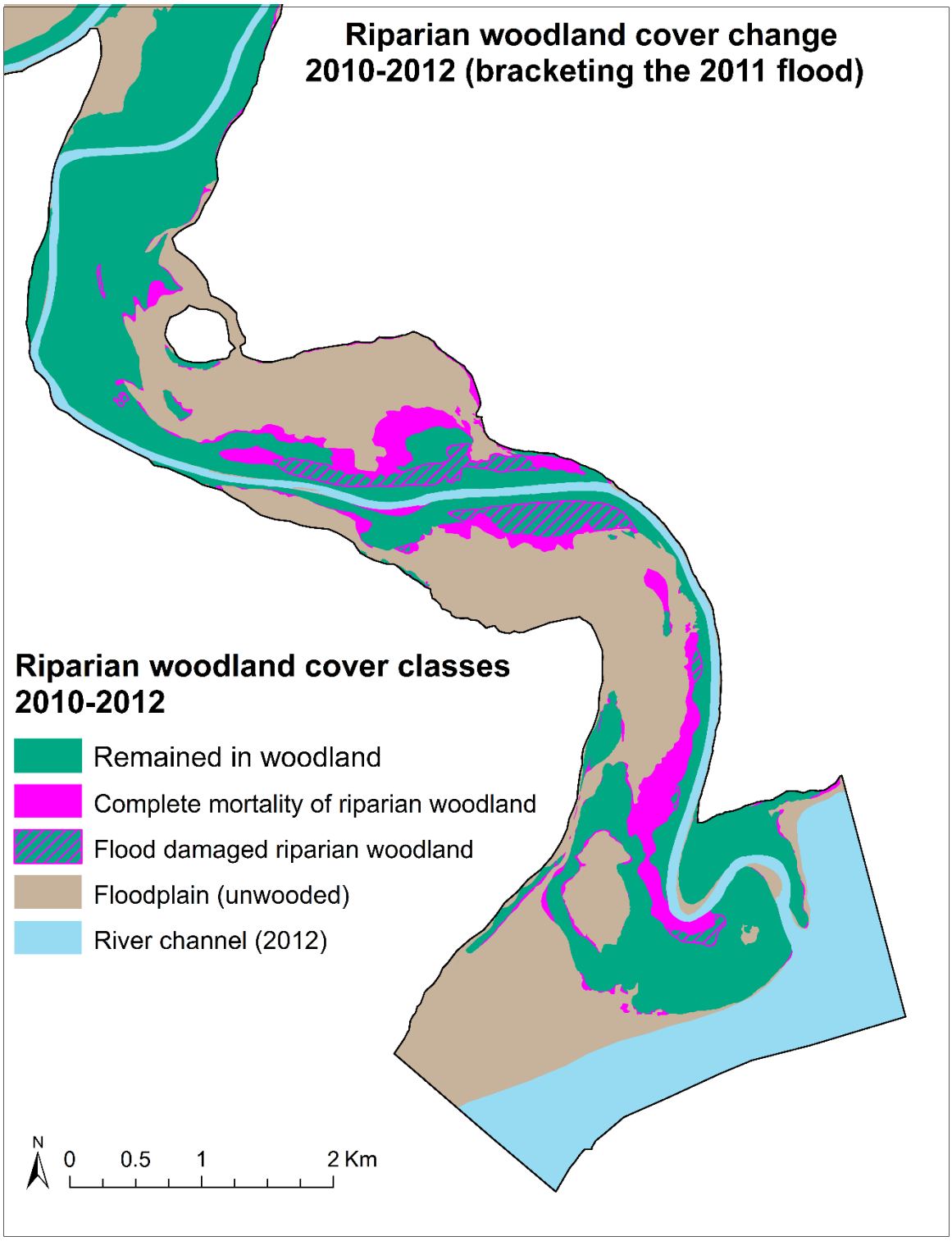

Figure 20. GIS map of riparian woodland cover changes between 2010 and 2012 from aerial photographs of the lower White River delta in South Dakota.

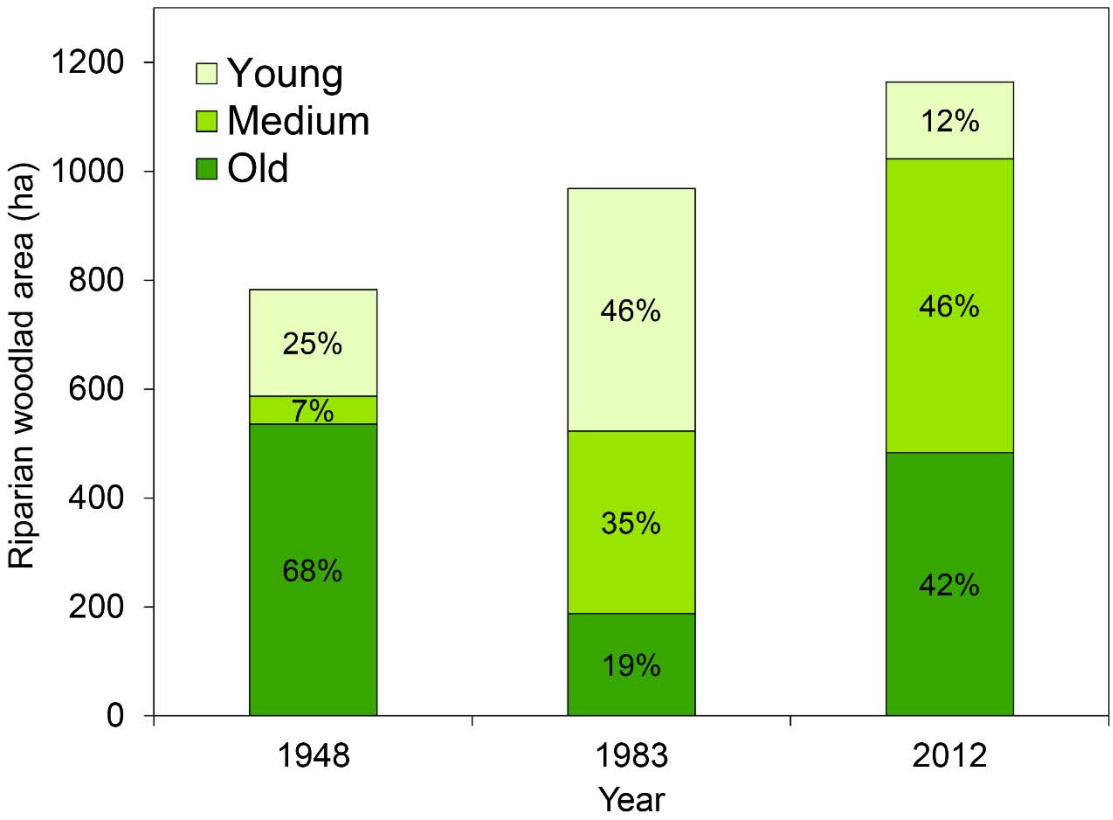

Figure 21. Total riparian woodland area (ha) by age class and year along the lower 29 km of the White River in South Dakota.

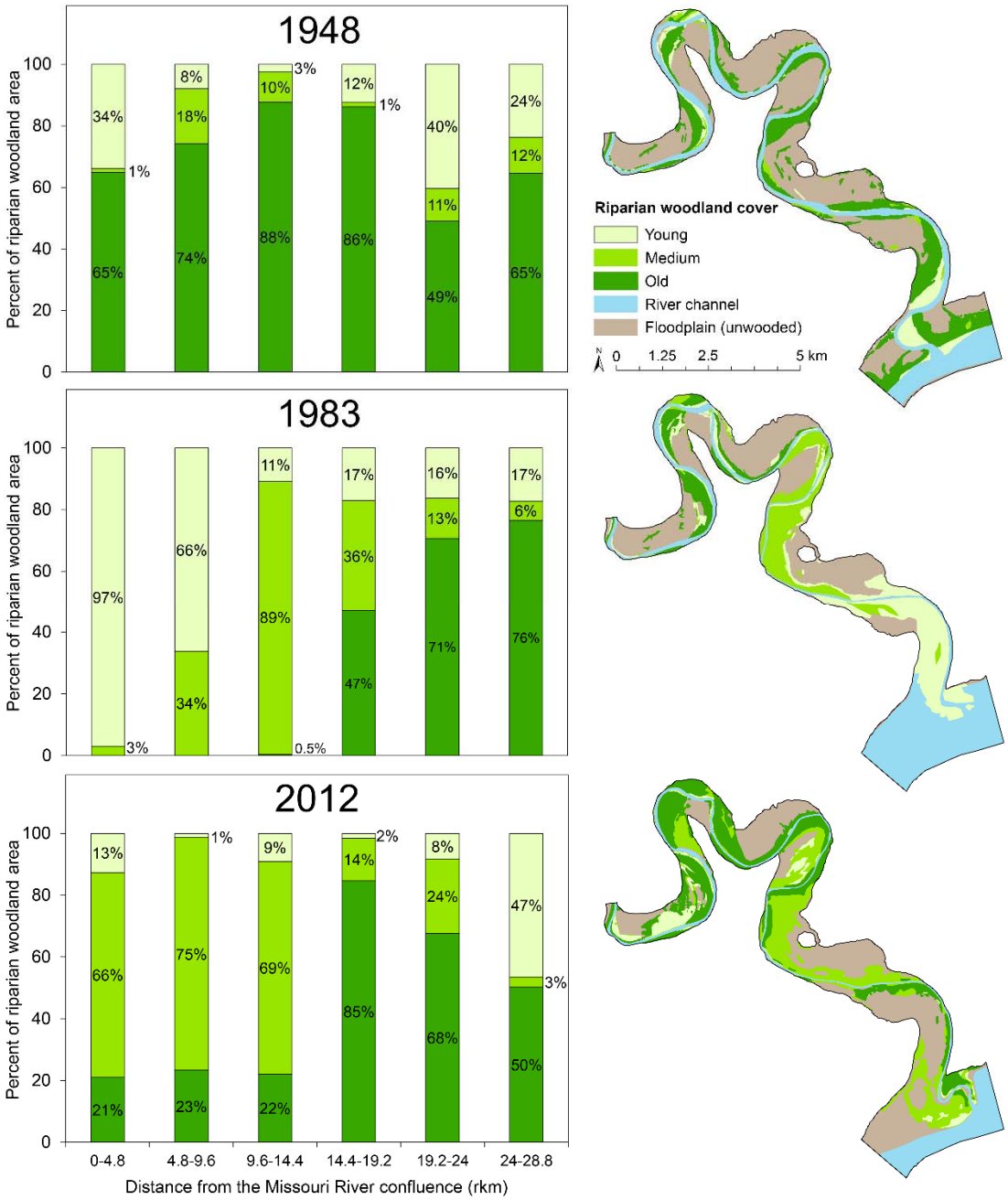

Figure 22. Distribution of young, medium, and old age classes of riparian woodland along the lower 29 km of the White River in South Dakota in 1948, 1983, and 2012. The stacked bar graphs (left) display the proportion of each age class within 4.8-km long segments of the study reach for each measurement period. The maps (right) display the location of riparian woodland age classes for each measurement period. River-kilometers are based on the 2012 channel and do not necessarily coincide with U.S. Army Corps of Engineers numbers.

Stand characteristics

Stand ages

Age classes of sampled stands were not equally represented across the White River, transition, and delta subreaches (Table 2, Figure 23). Delta stands were all of post-dam origin (<60 years old) whereas stands along the White River represented a wider range of ages (<8 to 134 years old) that spanned both the pre- and post-dam periods. The two stands in the transition subreach (stands 1 and 10) were both of pre-dam origin (142 and 160 years old, respectively). Forty-four percent of stands on the delta were in the 0-9 year age class, compared to only 24 percent of stands along the White River. Stands in the 10-19 year age class made up 31 percent of the stands on the delta, but were entirely absent from the White River. Thus, 75 percent of stands on the delta were <20 years old, versus only 24 percent of stands along the White River. Stands of pre-dam origin (≥60 years old) made up 40 percent of the stands sampled along the White River.

Cottonwood age structure generally followed a normal distribution across a narrow range of ages in most stands (Figure 24). This pattern is consistent with the even-aged nature of cottonwood stands along natural rivers, indicating that cottonwood reproduction within stands ceases shortly after the initial establishment period. Some stands on the delta and along the White River, however, contained multiple cohorts of tree size (≥10 cm dbh) cottonwoods. Two distinct cottonwood age groups were present in four (25 percent) of the 16 delta stands (Figure 25) and in two (12 percent) of the 17 White River stands (Figure 26). In these mixed-age stands, the large majority of cottonwood trees occupied the younger of the two age groups. The temporal spacing between the oldest and youngest trees in mixed-age stands ranged from 16-37 years on

the delta (mean = 26.5 years) and from 32-36 years along the White River (mean = 34 years).

Table 2. Cottonwood age characteristics and growth rates (cm/year) in tree size stands along the White River and its delta in South Dakota. The dashes indicate no applicable data.

		Cottonwood age (years)				
Stand	n	Minimum	Median	Maximum	Range	Average mean cottonwood growth rate (cm/year)
White River delta						
2	13	37	48	52	15	0.9
3	17	22	36	46	24	1.0
6	20	17	18	33	16	0.9
8	24	10	13	16	6	1.3
15	18	42	46	49	7	0.7
16	18	9	14	15	6	1.3
17	13	35	41	45	10	1.2
20	16	9	12	36	27	1.6
21	19	8	11	45	37	1.7
26	16	10	13	36	26	1.0
Transition						
1	2	135	142	148	13	0.6
10	0	–	160*	–	–	–
White River						
9	3	107	121	134	27	0.6
39	20	21	33	52	31	0.6
40	11	83	85	115	32	0.8
41	16	37	54	58	21	0.6
43	15	30	35	39	9	0.8
47	7	132	134	142	10	0.5
49	15	53	63	75	22	0.8
51	13	56	66	74	18	0.8
52	8	41	71	76	35	0.6
58	15	29	34	44	15	0.8
84	15	51	54	58	7	0.6
86	9	57	65	93	36	0.7
87	14	45	51	64	19	0.7

*No cottonwood trees were cored in stand 10. Therefore, median stand age was estimated by extrapolating from known ages of the largest cottonwood trees in other stands where the center of the trees could be reached by the available increment borers.

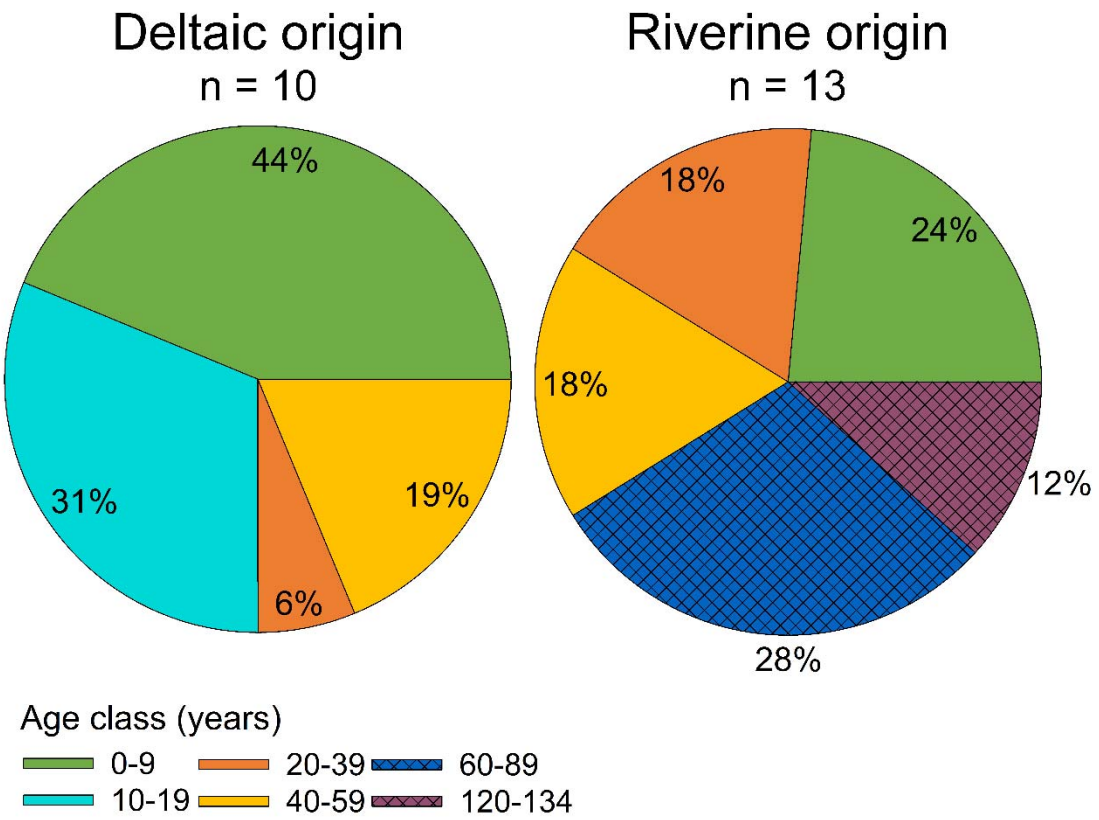

Figure 23. Age class proportions of cottonwood stands of deltaic origin (stands on the White River delta) and of riverine origin (stands along the White River). Cross-hatching indicates stand age groups of pre-dam origin (≥60 years old).

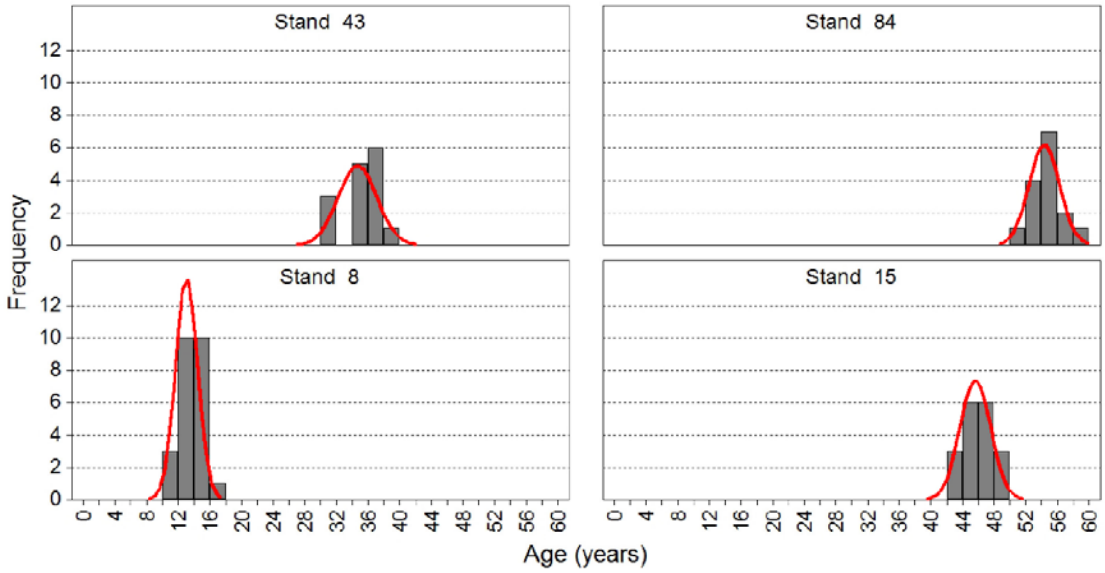

Figure 24. Cottonwood age frequency histograms for two stands along the White River (stands 43 and 84) and for two stands on the White River delta (stands 8 and 15) in South Dakota. The normal curve is shown as a red line.

Inspection of historical aerial photos showed that the processes that produced mixed-age stands on the delta were different than those that produced mixed-age stands along the White River. On the delta, mixed-age stands were the result of cottonwood recruitment that occurred within existing cottonwood stands ≥15 years old. At some locations, cottonwood recruitment within stands coincided with abandonment of agricultural fields (Figure 27). Along the White River, however, distinct age groups were likely the result of past channel movement and the periodic establishment of parallel bands (cohorts) of cottonwoods on new alluvial surfaces adjacent to the active channel or in abandoned channels (Figure 28). As two or more of these bands grew and developed over multiple years or decades, they merged into a single stand that contained more than one age group.

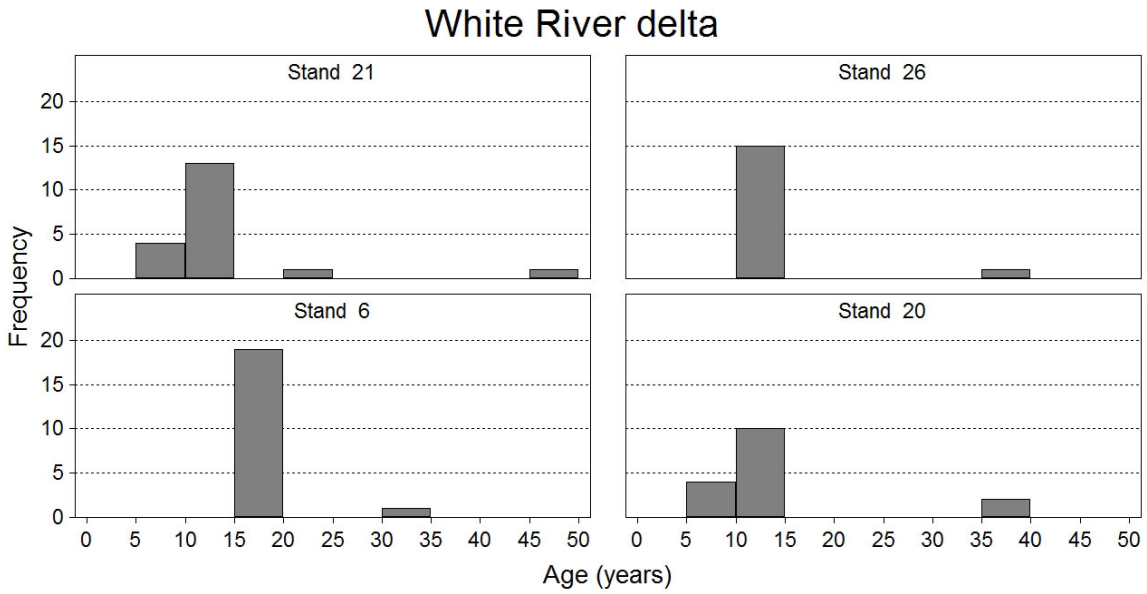

Figure 25. Age frequency histograms for cottonwood trees in the four mixed-age stands on the White River delta in South Dakota.

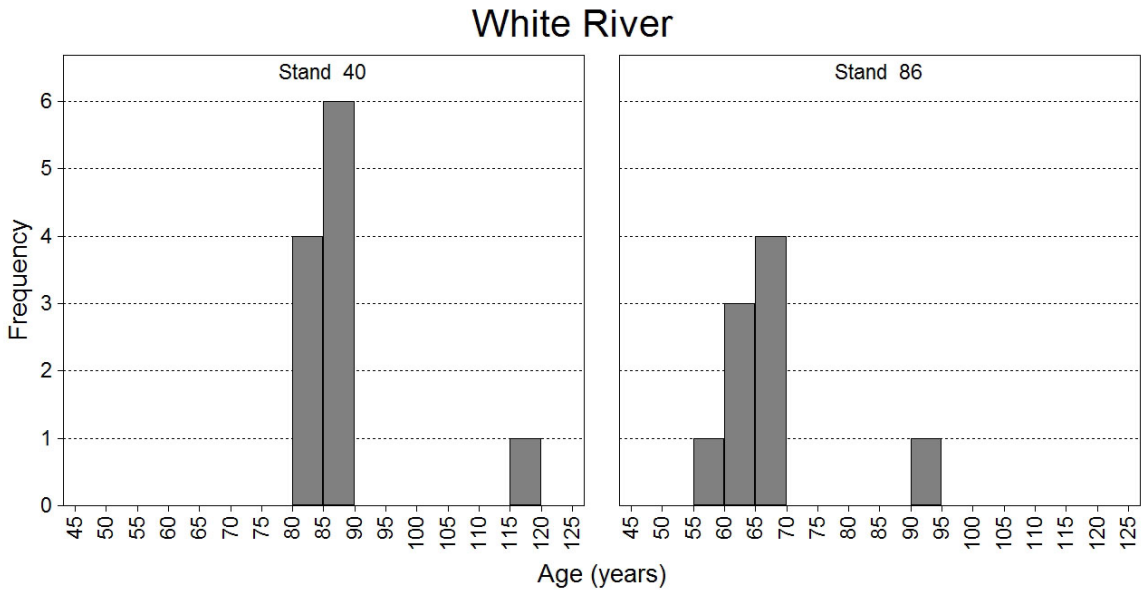

Figure 26. Age frequency histograms for cottonwood trees in the two mixed-age stands along the White River in South Dakota.

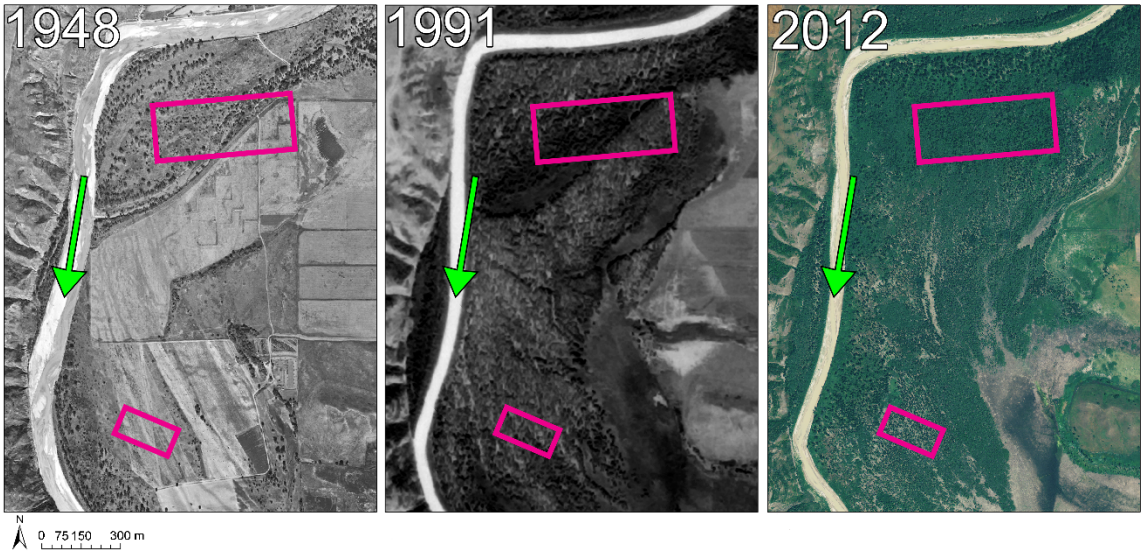

Figure 27. Time-series aerial photography showing a 64 year history of two mixed-age stands (stand 20 [north] and stand 26 [south]) on the White River delta in South Dakota. Stand boundaries are drawn in magenta. The green arrows indicate the direction of stream flow. Image sources: U.S. Department of Agriculture (1948), National Aerial Photography Program (1991), and USDA National Agriculture Imagery Program (2012).

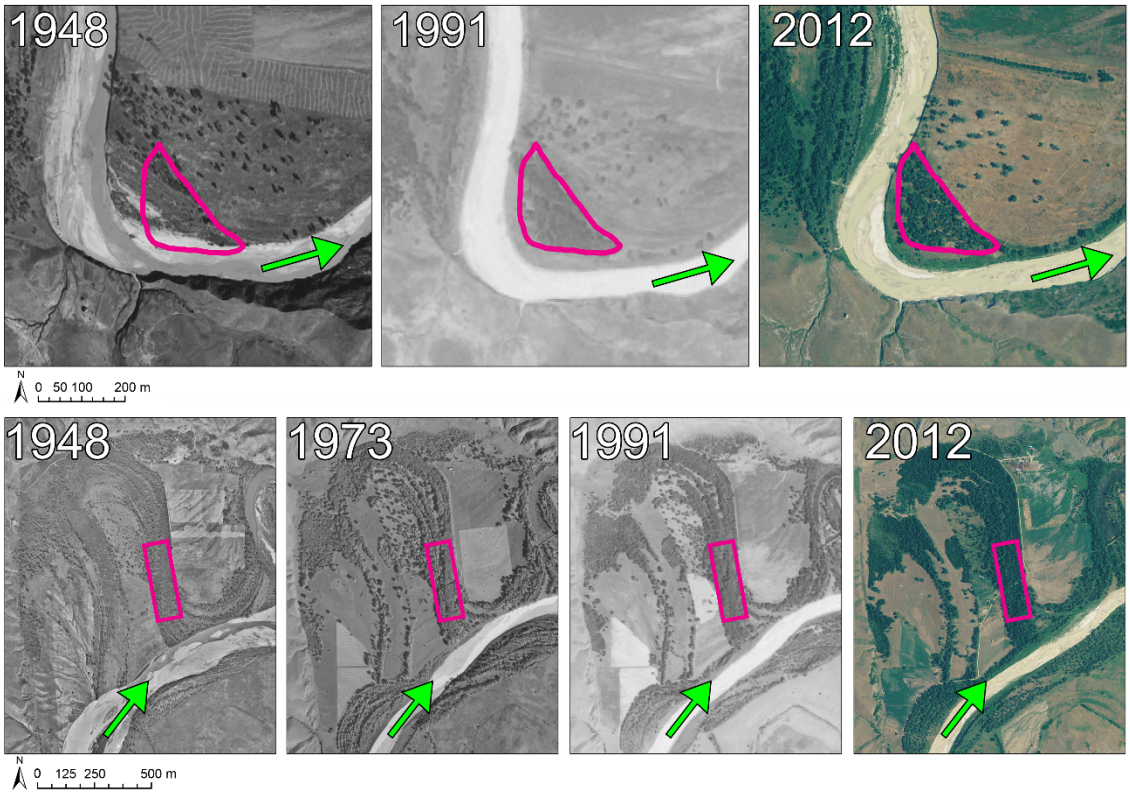

Figure 28. Time-series aerial photography showing a 64 year history of two mixed-age stands along the White River in South Dakota. Top panel: stand 86; bottom panel: stand 40. Stand boundaries are drawn in magenta. The green arrows indicate the direction of stream flow. Image sources: U.S. Department of Agriculture (1948), U.S. Geological Survey (1973), National Aerial Photography Program (1991), and USDA National Agriculture Imagery Program (2012).

Cottonwood growth rates

The age-growth relationship was examined for cottonwoods ≤52 years old (the maximum age of cored cottonwood trees on the delta) in the delta and White River subreaches. This enabled comparison of growth rates across a similar range of cottonwood ages in the two subreaches. Cottonwood age and diameter were positively correlated; however, there was considerable variation in this relationship, which tended to increase with age (Figure 29). The average cottonwood growth rate based on the slope of the linear regression line was 0.68 cm/year on the delta and 0.56 cm/year along the White River. The difference between the slopes of the regression lines for the delta and the White River was not statistically significant ($t_{0.05(2),236} = 1.31$, $P = 0.19$).

Cottonwood growth rates on the delta and along the White River were greatest in the youngest age classes and generally decreased with age (Figure 30). For trees in a given age class, cottonwood growth rates were generally greatest on the lower delta, followed by the upper delta and then the White River. Cottonwood growth rates were significantly greater on the lower delta than along the White River for trees in the <10 year age class ($t_{0.05(2),7} = 2.419$, $P = 0.046$), significantly greater on the lower delta than the upper delta for trees in the 10-19 year age class ($U_{0.05(2),15,84} = 346.5$, $P = 0.006$), and significantly greater on the upper delta than along the White River for trees in the 30-39 year 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 year age class was significantly lower on the delta (0.89 ± 0.06 cm/year) than along the White River (1.51 ± 0.14 cm/year; $t_{0.05(2),13} = 4.548$, $P < 0.001$).

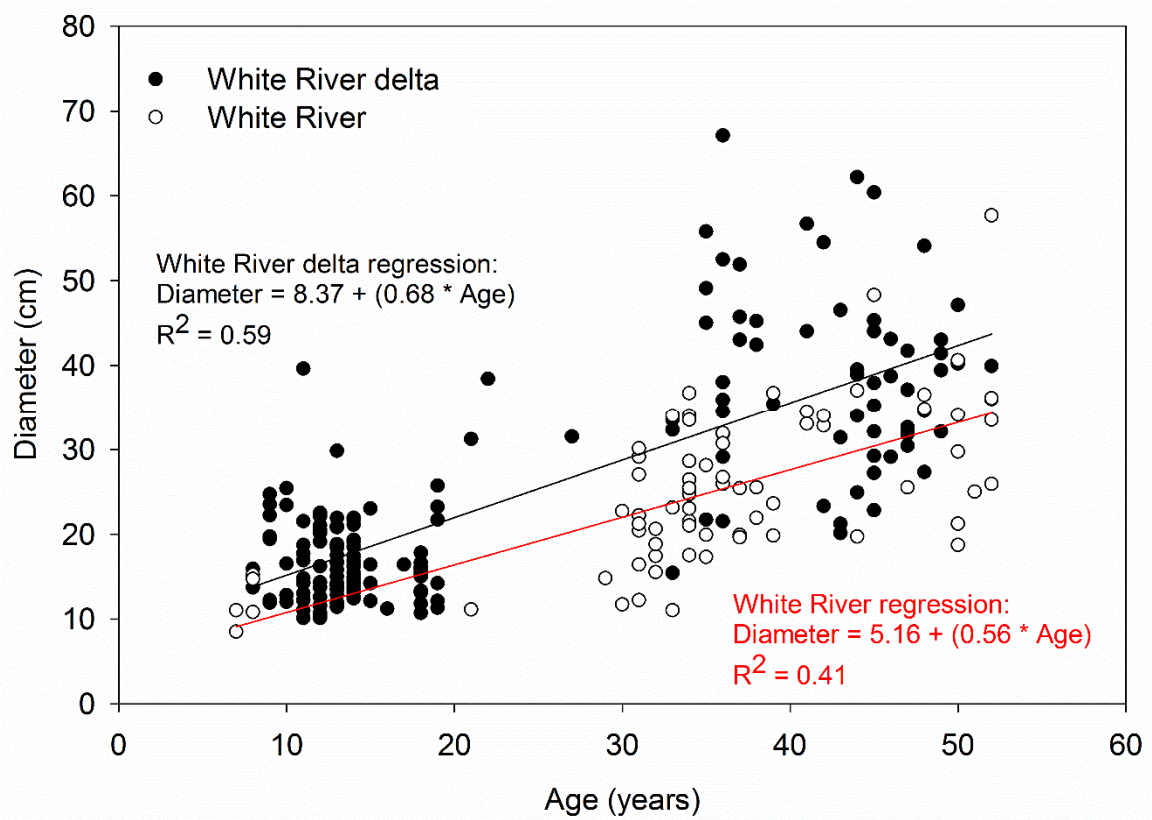

Figure 29. Cottonwood diameter (cm) versus age (years) for trees ≤52 years old along the White River and its delta in South Dakota.

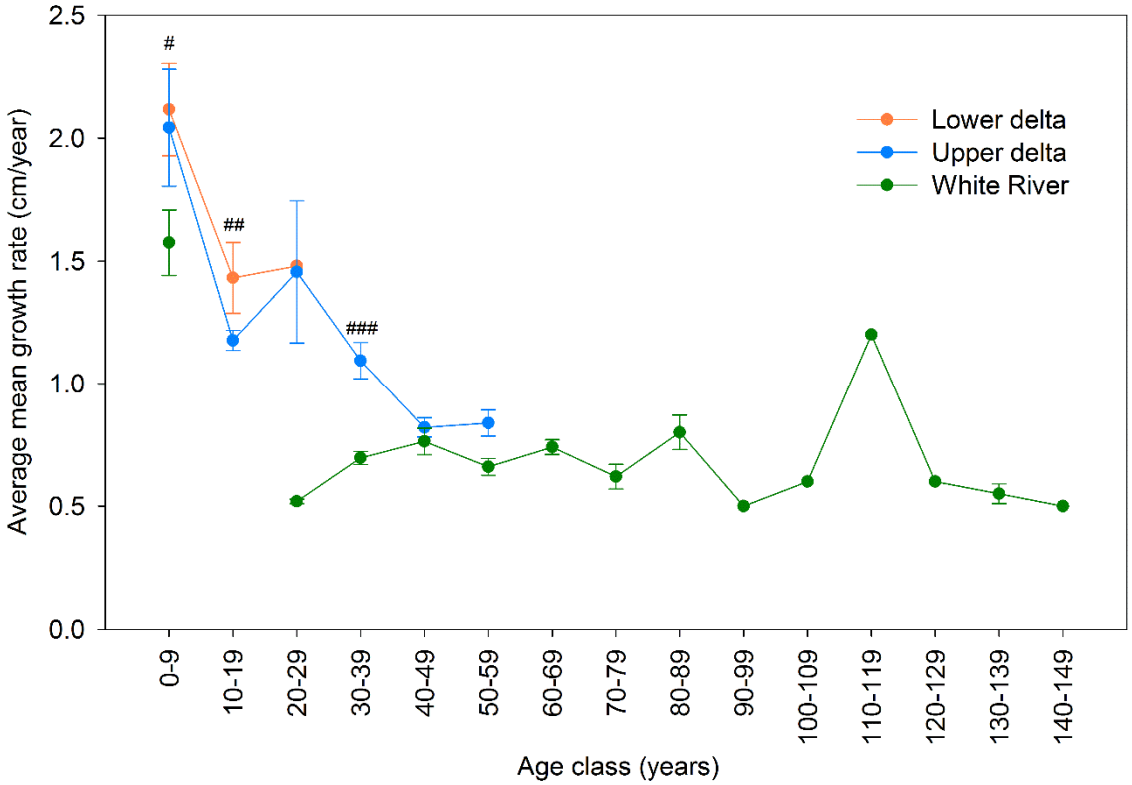

Figure 30. Average mean growth rates (cm/year) of cottonwoods occurring on the lower and upper White River delta and along the White River in South Dakota plotted along the age class gradient. Error bars represent standard error. #Cottonwood growth rates on the lower delta were significantly greater than along the White River ($t_{0.05(2),7} = 2.419$, $P = 0.046$). ##Cottonwood growth rates on the lower delta were significantly greater than on the upper delta ($U_{0.05(2),15,84} = 346.5$, $P = 0.006$). ###Cottonwood growth rates on the upper delta were significantly greater than along the White River ($U_{0.05(2),25,56} = 277.5$, $P < 0.001$).

Vegetation composition

Twenty-three woody species occurred in the sample from the 35 stands in the study area (Tables 3 and 4). Of these 23 species, nine (39 percent) occurred in the overstory, 16 (70 percent) occurred in the sapling layer, and 21 (91 percent) occurred in the seedling layer. Three species (13 percent) occurred as lianas, two of which also occurred in the seedling and sapling layers. Eleven species (48 percent) were found only in the seedling and/or sapling layers, although individuals of some of these species could reach tree size (≥10 cm dbh) if given enough time. Of the 23 species, 21 (91 percent) occurred along the White River, 14 (61 percent) occurred on the White River delta, and 14 (61 percent) occurred in the transition subreach.

Two introduced species were among the 23 species in the sample (Table 4). Russian olive, a species that is native to Eurasia, occurred throughout the length of the study area. Honey locust (*Gleditsia triacanthos* L.), which is native to portions of the eastern United States, has been introduced 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, also occurred in some stands along the White River. The remaining 20 species were native to the region.

Based on species importance values, cottonwood was the dominant overstory species across the delta, transition, and White River subreaches. Peachleaf willow was the second leading overstory dominant on the delta, whereas green ash was the second leading overstory dominant in the transition and White River subreaches (Table 5).

Table 3. Characteristics of the 35 stands sampled along the lower White River and its delta in South Dakota. Layers are abbreviated as: (s) seedling layer, (sa) sapling layer, (o) overstory. For stands <10 cm dbh, age was estimated as <10 years old based on evidence from cottonwood increment cores. Units for elevation are in meters above sea level (masl). Water surface elevation is abbreviated as WSE.

Stand number	Year sampled	UTM coordinates (NAD83 Zone 14N)	Stand size (ha)	Layer(s) sampled	Median cottonwood age (years)	Mean cottonwood diameter (cm)
White River delta						
Lower delta						
21	2013	464354 4839230	3.6	s, sa, o	11	20.6
22	2013	463568 4839583	6.7	s, sa	<10	<10
23	2013	464064 4839849	3.4	s, sa	<10-14*	<10
71	2013	463992 4840563	8.4	s, sa	<10	<10
83	2013	463774 4839921	1.9	s, sa	<10	<10
Upper delta						
2	2011	457461 4845036	3.5	s, sa, o	48	41.7
3	2011	457430 4847167	4.3	s, sa, o	36	32.0
4	2011	457477 4845203	0.6	s, sa	<10	<10
6	2011	458367 4846001	1.9	s, sa, o	18	16.3
8	2011	457168 4845778	2.3	s, sa, o	13	16.5
12	2011	457489 4846949	0.7	s, sa	<10	<10
15	2011	460540 4846374	2.9	s, sa, o	46	33.3
16	2011	456980 4846231	3.7	o	14	16.7
17	2011	459899 4844409	6.8	s, sa, o	41	43.2
20	2013	459871 4844159	10.5	s, sa, o	12	20.5
26	2013	459582 4842996	2.5	s, sa, o	13	14.4

Transition						
1	2011	457338 4844751	4.9	s, sa, o	142	86.5
10	2011	456680 4843207	3.3	s, sa, o	160**	134.9
White River						
9	2011	453552 4844719	3.7	s, sa, o	121	65.0
11	2011	454608 4845262	0.9	s, sa	<10	<10
39	2013	440072 4844083	4.0	s, sa, o	33	26.7
40	2013	439090 4844348	6.9	s, sa, o	85	81.5
41	2013	439272 4841164	4.0	s, sa, o	54	31.7
43	2013	437486 4840192	2.7	s, sa, o	35	26.2
47	2013	429489 4837394	2.8	s, sa, o	134	76.8
49	2013	428372 4838224	3.6	s, sa, o	63	41.5
51	2013	426941 4838922	4.8	s, sa, o	66	58.0
52	2013	426012 4837975	1.5	s, sa, o	71	51.8
58	2013	414293 4838339	4.1	s, sa, o	34	26.4
75	2013	439510 4844087	1.1	s, sa	<10	<10
76	2013	438941 4839748	1.2	s, sa	<10	<10
84	2013	412386 4837749	4.0	s, sa, o	54	35.9
85	2013	425902 4837958	0.7	s, sa	8	<10
86	2013	425096 4837586	1.3	s, sa, o	65	45.1
87	2013	438590 4843572	3.6	s, sa, o	51	43.1

*Stand 23 was a sapling size, <10 year old stand that occurred within a standing dead (2011 flood-killed) 14 year old overstory stand.
**No cottonwood trees were cored in stand 10. Therefore, median stand age was estimated by extrapolating from known ages of the largest cottonwood trees in other stands where the center of the trees could be reached by the available increment borers.

Table 4. List of woody species sampled in the 35 stands along the lower 120 km of the White River and its delta in South Dakota and corresponding vegetation layer(s) and subreach(es) where each species occurred. Layers are abbreviated as: s = seedling layer, sa = sapling layer, o = overstory, and l = liana. Subreaches are abbreviated as: d = White River delta, t = transition, and r = White River.

Scientific name	Common name	Layer(s) where present	Subreach(es) where present
Acer negundo L.	box elder	s, sa, o	d, t, r
Amorpha fruticosa L.	false indigo	s, sa	d, t, r
Celtis occidentalis L.	Hackberry	o	r
Clematis ligusticifolia Nutt.	western white clematis	l	r
Cornus drummondii C.A. Mey	roughleaf dogwood	s	d
Elaeagnus angustifolia L.	Russian olive	s, sa, o	d, t, r
Fraxinus pennsylvanica Marsh.	green ash	s, sa, o	d, t, r
Gleditsia triacanthos L.	honey locust	s, o	r
Juniperus virginiana L.	eastern red-cedar	s, sa	r
Parthenocissus vitacea (Knerr) Hitchc.	Virginia creeper	s, sa, l	d, t, r
Populus deltoides ssp. *monilifera* (Aiton) Eckenw.	plains cottonwood	s, sa, o	d, t, r
Prunus americana Marshall	American plum	s, sa	r
Prunus virginiana L.	chokecherry	s, sa	t, r
Rhus aromatica Aiton	fragrant sumac	s, sa	r
Ribes aureum Pursh	golden currant	s, sa	r
Rosa woodsii Lindl.	Woods' rose	s	d, t, r
Salix amygdaloides Andersson	peachleaf willow	s, sa, o	d, t, r
Salix interior Rowlee	sandbar willow	s, sa	d, r
Salix lutea Nutt.	yellow willow	s, sa, o	d, t
Symphoricarpos occidentalis Hook.	western snowberry	s, sa	d, t, r
Toxicodendron rydbergii (Small ex Rydb.) Greene	poison ivy	s	r
Ulmus americana L.	American elm	s, o	d, t, r

Vitis riparia Michx.	riverbank grape	s, sa, l	d, t, r

Green ash was the dominant species in the sapling layer of tree size stands across the delta, transition, and White River subreaches. Sandbar willow, riverbank grape, and Russian olive were the second leading dominants in the sapling layer in the delta, transition, and White River subreaches, respectively (Table 6).

In the seedling layer of tree size stands, green ash was dominant on the delta, whereas western snowberry was dominant in the transition and White River subreaches. Sandbar willow, green ash, and riverbank grape were the second leading dominants in the delta, transition, and White River subreaches, respectively (Table 7).

In the sapling layer of sapling size stands, sandbar willow was the dominant species on the delta, followed by peachleaf willow. In contrast, cottonwood was the dominant species along the White River, followed closely by sandbar willow (Table 6).

In the seedling layer of sapling size stands, peachleaf willow was the dominant species on the delta, followed by cottonwood. Along the White River, cottonwood was the dominant species, followed by sandbar willow (Table 7).

Table 5. Summary values for all overstory species occurring in the 25 tree size stands along the study reach. Importance value is the sum of the relative value of density and dominance; maximum = 200.

Species	Presence (%)	Mean density (trees/ha)	Mean basal area (m²/ha)	Mean importance value
White River delta				
Box elder	10	0.4	0.01	0.2
Cottonwood	100	279.5	13.82	172.2
Green ash	60	9.9	0.14	5.6
Peachleaf willow	60	13.3	0.39	15.9
Russian olive	40	10.9	0.55	6.0
Total		314.0	14.91	200.0
Transition				
American elm	100	16.5	1.35	11.2
Box elder	100	18.5	0.25	6.0
Cottonwood	100	15.4	15.18	96.4
Green ash	100	147.8	7.29	83.8
Peachleaf willow	50	4.6	0.05	1.4
Russian olive	50	0.2	<0.01	0.5
Yellow willow*	50	2.3	0.03	0.7
Total		205.3	24.16	200.0
White River				
American elm	31	0.9	0.05	0.4
Box elder	15	1.9	0.07	0.7
Cottonwood	100	163.4	23.14	157.2
Green ash	77	85.2	2.45	34.8
Hackberry	8	0.2	0.01	0.1
Honey locust	23	0.6	0.01	0.3
Peachleaf willow	38	1.5	0.20	1.1
Russian olive	38	12.6	0.25	5.4
Total		266.3	26.19	200.0

*Yellow willow rarely attained tree size.

Table 6. Summary values for all sapling layer species occurring in 34* stands along the study reach. Importance value is the sum of the relative values of frequency, density and dominance; maximum = 300.

Species	Presence (%)	Mean density (saplings/ha)	Mean importance value
White River delta			
Sapling size stands			
Cottonwood	83	2476.4	63.9
Peachleaf willow	67	9204.2	111.8
Sandbar willow	100	4472.9	124.3
Total		16153.5	300.0
Tree size stands			
Cottonwood	44	85.6	46.7
False indigo	22	18.5	5.2
Green ash	67	833.3	122.5
Peachleaf willow	22	23.1	13.0
Riverbank grape	56	46.3	21.0
Russian olive	11	4.6	1.6
Sandbar willow	67	2946.8	73.9
Yellow willow	44	64.8	16.2
Total		4023.1	300.0
Transition			
Tree size stands			
Box elder	50	41.7	8.9
Chokecherry	50	354.2	25.4
Green ash	100	791.7	203.6
Riverbank grape	50	187.5	42.7
Woodbine	50	41.7	4.4
Yellow willow	50	83.3	15.1
Total		1500.0	300.0
White River			
Sapling size stands			
Cottonwood	100	8659.7	149.3

False indigo	25	83.3	2.9
Peachleaf willow	25	55.6	1.1
Russian olive	25	62.5	4.6
Sandbar willow	100	14409.7	142.0
Total		23270.8	300.0
Tree size stands**			
American plum	8	4.8	5.6
Box elder	8	86.5	8.0
Chokecherry	38	139.7	38.7
Cottonwood***	8	0.0	1.5
Eastern red-cedar	23	19.2	4.7
False indigo	23	68.9	13.6
Fragrant sumac	8	57.7	3.1
Golden currant	15	24.0	1.9
Green ash	62	393.9	115.2
Riverbank grape	62	218.3	39.5
Russian olive	31	72.1	42.5
Western snowberry	23	336.5	25.8
Total		1421.8	300.0

*The seedling and sapling layers of stand 16 were not sampled; thus, only 34 stands were included in this analysis.
**Stand 39 was excluded from the total importance value calculation because no woody plants occurred in the sapling layer plots.
***Percent cover of cottonwood saplings was recorded in one stand; however, no cottonwood sapling stems were rooted in any sampling plots, hence, the calculated density of cottonwood saplings was zero.

Table 7. Summary values for all seedling species occurring in 34* stands along the study reach. Importance value is the sum of the relative values of frequency, density and dominance; maximum = 300.

Species	Presence (%)	Mean density (seedlings/ha)	Mean importance value
White River delta			
Sapling size stands			
Box elder	17	69.4	0.9
Cottonwood	83	28069.4	72.8
False indigo	17	69.4	2.4
Peachleaf willow	67	7291.7	151.2
Sandbar willow	67	21770.8	66.4
Woods' rose	17	277.8	6.3
Total		57548.6	300.0
Tree size stands			
American elm	44	277.8	5.7
Box elder	22	740.7	4.7
Cottonwood	33	34884.3	23.3
False indigo	22	138.9	6.1
Green ash	78	35138.9	89.8
Peachleaf willow	11	138.9	1.8
Riverbank grape	89	4976.9	47.1
Roughleaf dogwood	11	46.3	2.5
Russian olive	33	1504.6	20.5
Sandbar willow	56	10518.3	57.9
Western snowberry	44	2156.1	25.8
Woodbine	44	787.0	11.0
Yellow willow	22	92.6	3.7
Total		91401.3	300.0
Transition			
Tree size stands			
American elm	100	2500.0	17.9
Box elder	50	208.3	8.6
Chokecherry	50	5208.3	37.8

Cottonwood	50	416.7	3.7
False indigo	50	4166.7	25.1
Green ash	100	17083.3	53.5
Peachleaf willow	100	3333.3	10.5
Riverbank grape	100	4166.7	36.8
Western snowberry	100	34166.7	61.0
Woodbine	50	5208.3	27.4
Woods' rose	50	1875.0	12.0
Yellow willow	50	833.3	5.7
Total		79166.7	300.0

White River

Sapling size stands

Chokecherry	25	156.3	6.7
Cottonwood	100	19531.3	122.2
False indigo	25	156.3	17.1
Green ash	25	156.3	7.2
Peachleaf willow	25	1406.3	14.8
Riverbank grape	25	156.3	6.7
Sandbar willow	100	16354.2	109.0
Western snowberry	25	208.3	2.5
Woodbine	50	312.5	13.9
Total		38437.5	300.0

Tree size stands

American elm	54	1472.0	9.1
American plum	8	817.3	3.8
Box elder	8	96.2	0.6
Chokecherry	62	3439.1	14.1
Eastern red-cedar	23	144.2	1.5
False indigo	23	304.5	4.9
Fragrant sumac	15	1105.8	4.0
Golden currant	31	240.4	3.0
Green ash	92	15048.1	45.6
Honey locust	8	48.1	3.4
Poison ivy	39	3121.8	15.9
Riverbank grape	85	11344.2	48.1
Russian olive	15	576.9	3.7

Western snowberry	100	35006.4	94.3
Woodbine	77	12557.7	37.1
Woods' rose	46	1762.8	11.0
Total		87085.5	300.0

*The seedling and sapling layers of stand 16 were not sampled; hence, only 34 stands were included in this analysis.

Successional and age gradient analysis

White River delta

Stands on the delta exhibited considerable variation in overstory structure across the age gradient. Tree density was highly variable and did not exhibit any strong patterns related to stand age. Density was lowest (<100 trees/ha) among 11 year old and 41 year old stands and was greatest (833 trees/ha) in an 18 year old stand (Figure 31). Basal area generally increased with stand age, although there was some variability in this trend (Figure 32). Basal area was lowest (3.79 m^2/ha) in an 11 year old stand and was greatest (41.24 m^2/ha) in a 46 year old stand.

Strong trends were observed in sapling layer (saplings, shrubs, and lianas <10 cm dbh and $\geq$1 m tall) structure across the age gradient. These trends were similar among the delta and White River subreaches, so are introduced here together. Sapling layer densities were maximum in the youngest stands that contained no tree size individuals and declined with increasing stand age (Figures 33 and 34). The resultant curve for sapling layer density along the stand age gradient was nearly identical to an inverse J-shaped curve (negative exponential). Most stands were dominated by sapling size individuals in the smallest size class (<2 cm diameter); the proportion of sapling size individuals in larger size classes generally increased with stand age.

Three stands from the delta were selected from the age gradient to illustrate changes that occurred in overstory population structure with increasing stand age (Figure 35). In the youngest of these stands (stand 8), cottonwood density was greatest in the smallest size classes and the population curve approximated an inverse J-shaped curve

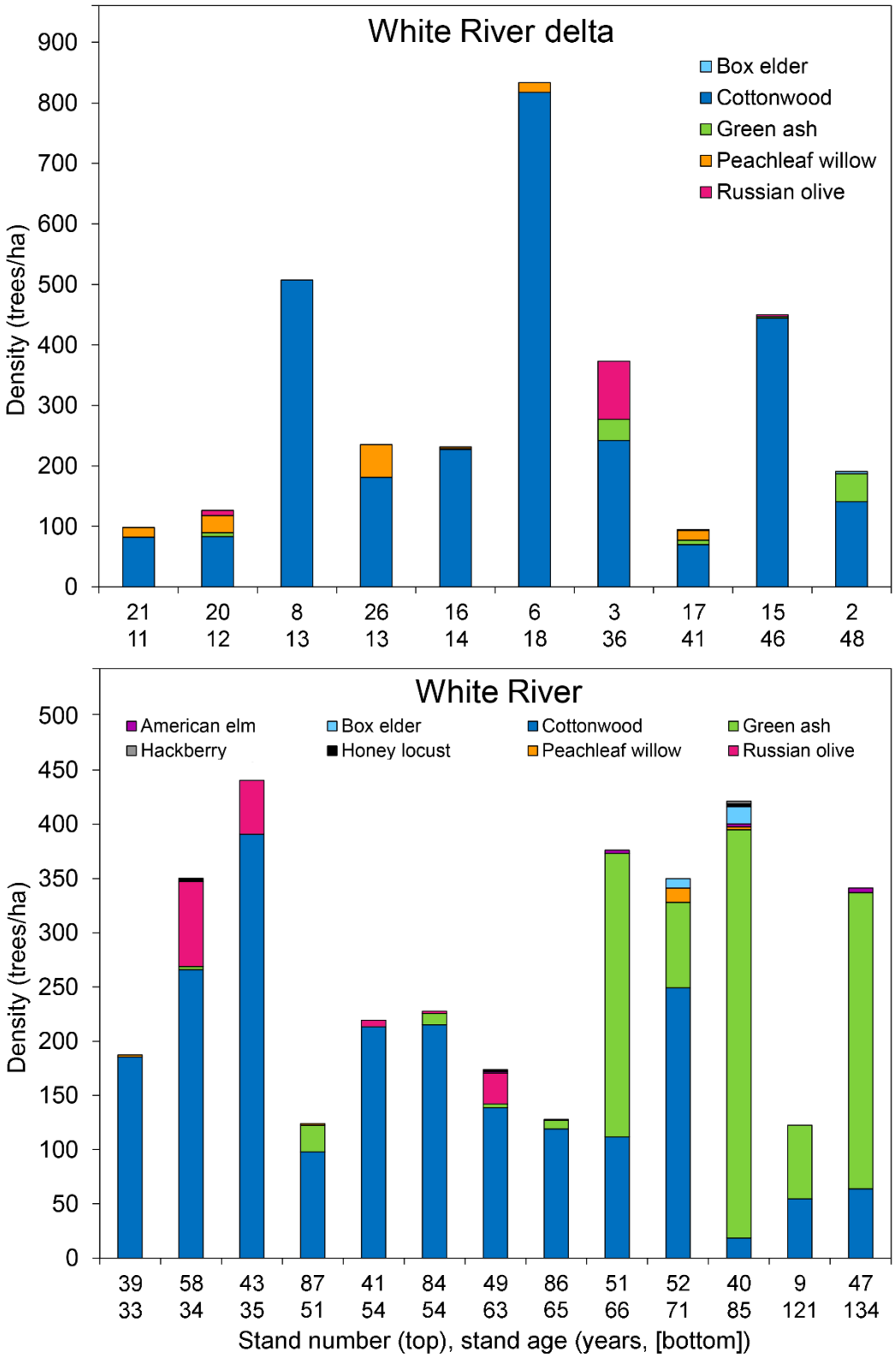

Figure 31. Density (trees/ha) of each tree species occurring on the White River delta (top panel) and along the White River (bottom panel) in South Dakota. Stands are ordered from youngest to oldest at unequal intervals.

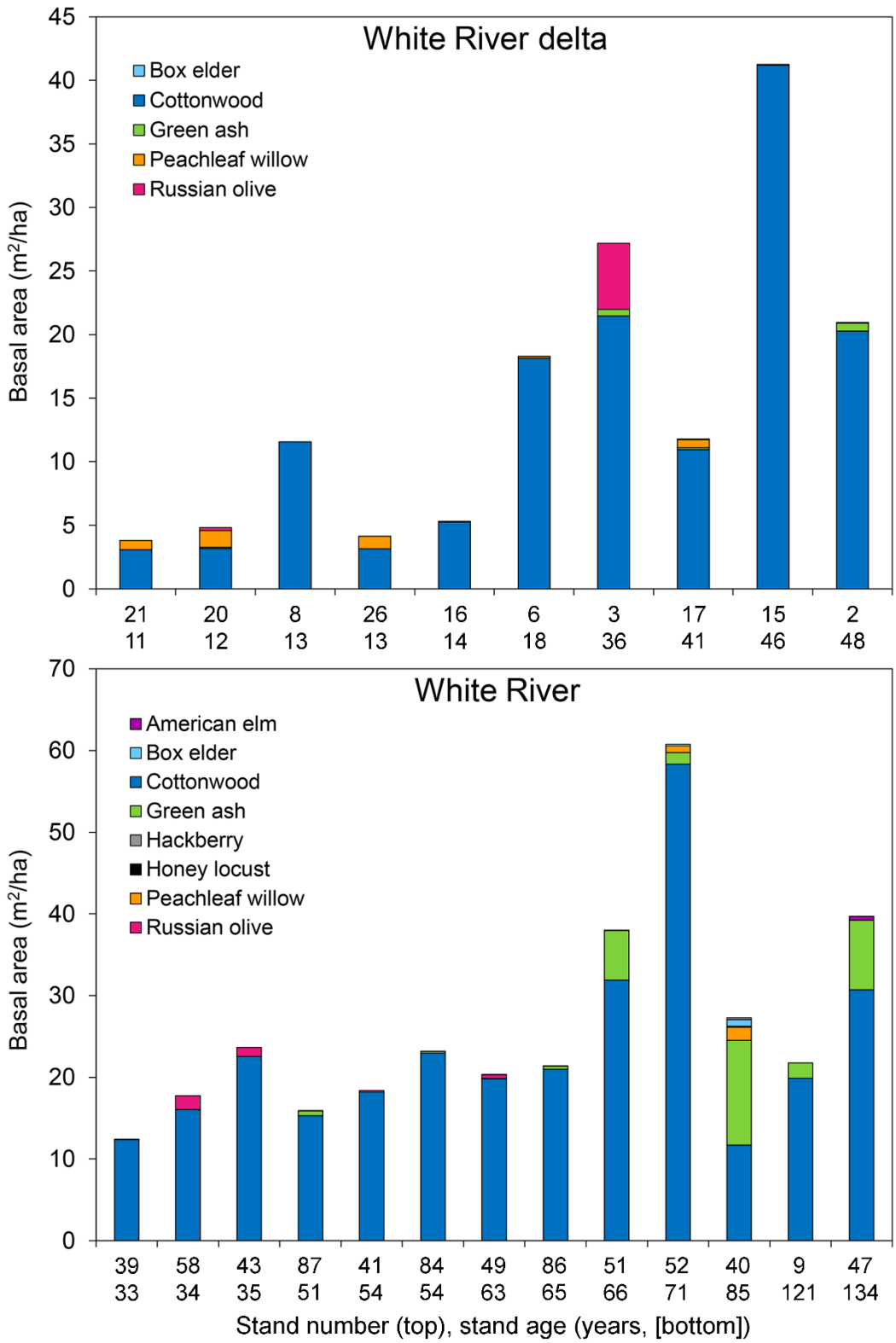

Figure 32. Basal area (m^2/ha) of each tree species occurring on the White River delta (top panel) and along the White River (bottom panel) in South Dakota. Stands are ordered from youngest to oldest at unequal intervals.

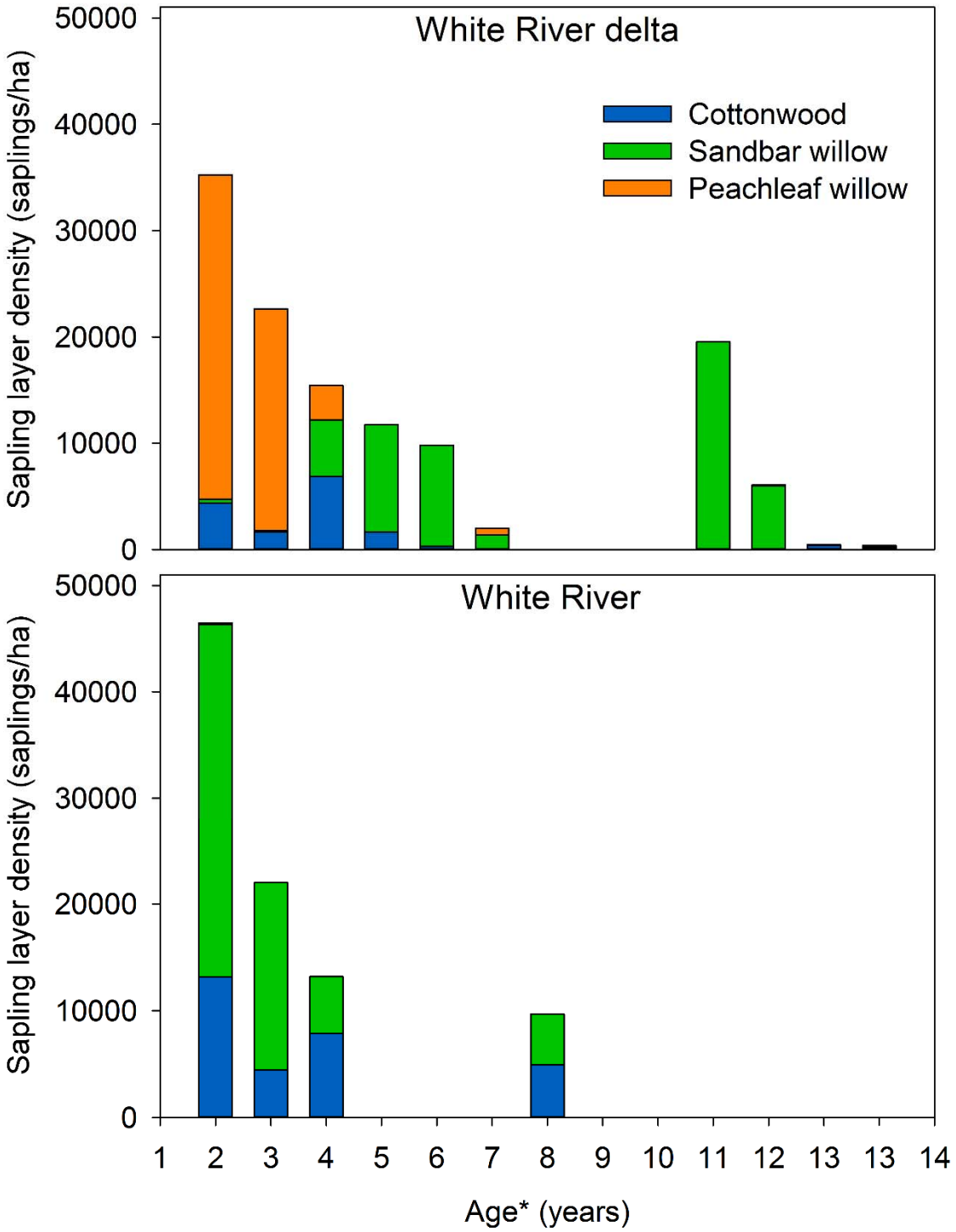

Figure 33. Density (saplings/ha) of cottonwood, sandbar willow, and peachleaf willow in the sapling layer of stands <14 years old on the White River delta (top panel) and along the White River (bottom panel) in South Dakota. *On the delta, age was estimated for stands <10 years old, and along the White River, age was estimated for stands <8 years old.

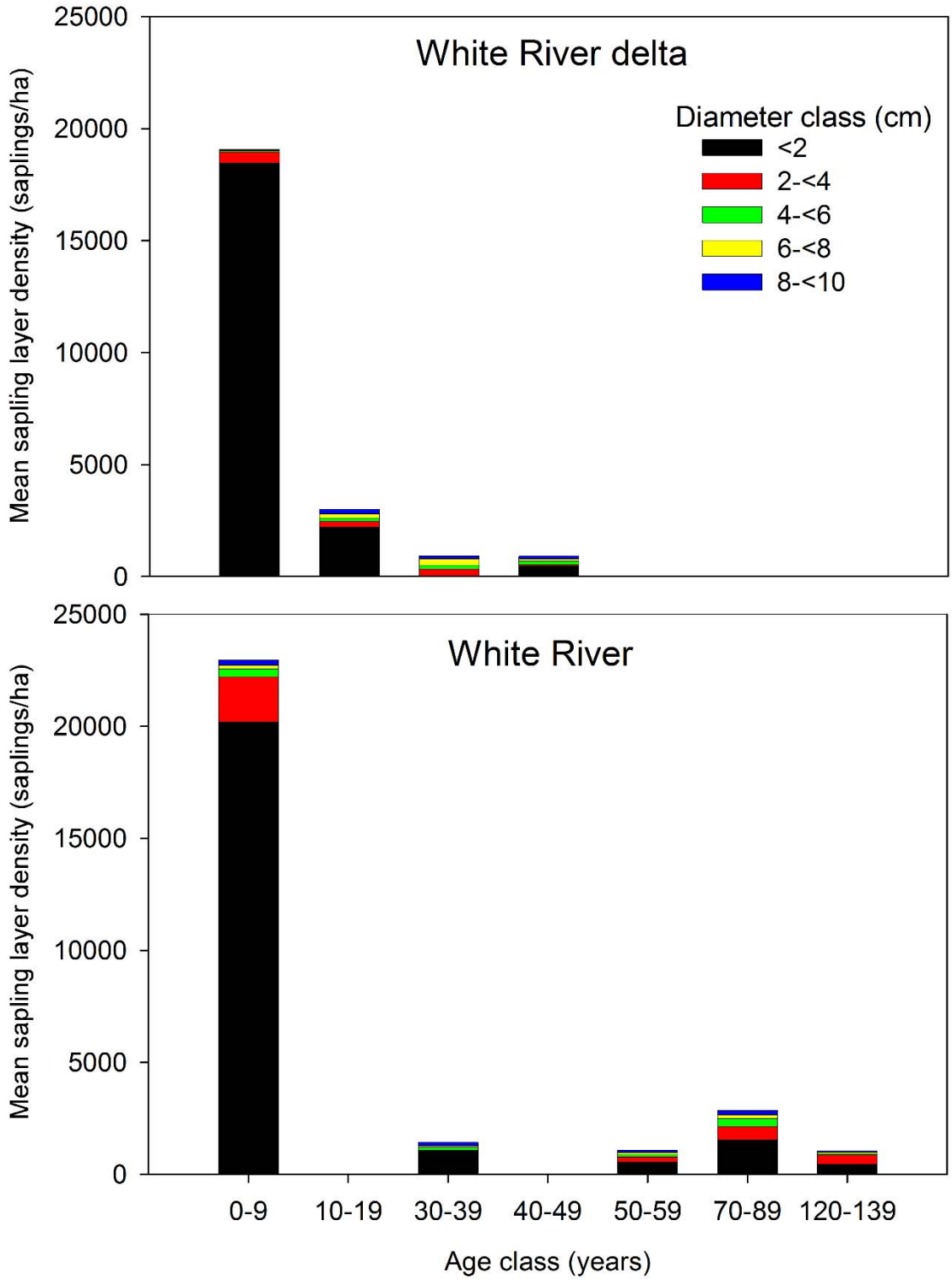

Figure 34. Mean sapling layer density (saplings/ha) according to size and age classes in stands on the White River delta (top panel) and along the White River (bottom panel) in South Dakota.

(negative exponential). All trees in this young stand were cottonwood. In stand 3, a middle age stand, there was a decrease in cottonwood density in the smallest size classes; the resultant population curve for cottonwood approached a normal distribution. Green ash occurred in the smallest size classes and Russian olive occurred in all but the largest three size classes occupied by cottonwood. In stand 2, the oldest of the three stands, the peak of the cottonwood curve decreased and also moved three size classes to the right. Green ash density was greatest in the smallest size classes and the population curve approximated an inverse J-shaped curve similar to that of the cottonwood population in the youngest stand. Box elder occurred at low densities in the smallest size classes. No cottonwood trees <19.9 cm dbh occurred in this stand. These structural curves illustrate the pioneer, even-aged nature of cottonwood forests and the general pattern of succession by other species.

Tree species importance value patterns on the delta further illustrated compositional changes across the stand age gradient. In general, tree species diversity was lowest in the youngest, early successional stands and was greatest in stands ≥12 years old (Figure 36). The youngest stands were dominated almost exclusively by seedlings and saplings of cottonwood and peachleaf willow, both pioneer species. Cottonwood and peachleaf willow attained tree size in stands ≥11 years old, marking a transitional stage whereby cottonwood was dominant in the overstory and an increasing number of tree species occupied the understory. Cottonwood was also sometimes a dominant tree species in the understory of these young, transitional forests. The oldest forests on the delta were characterized by cottonwood dominance in the overstory and high dominance of green ash saplings and seedlings in the understory.

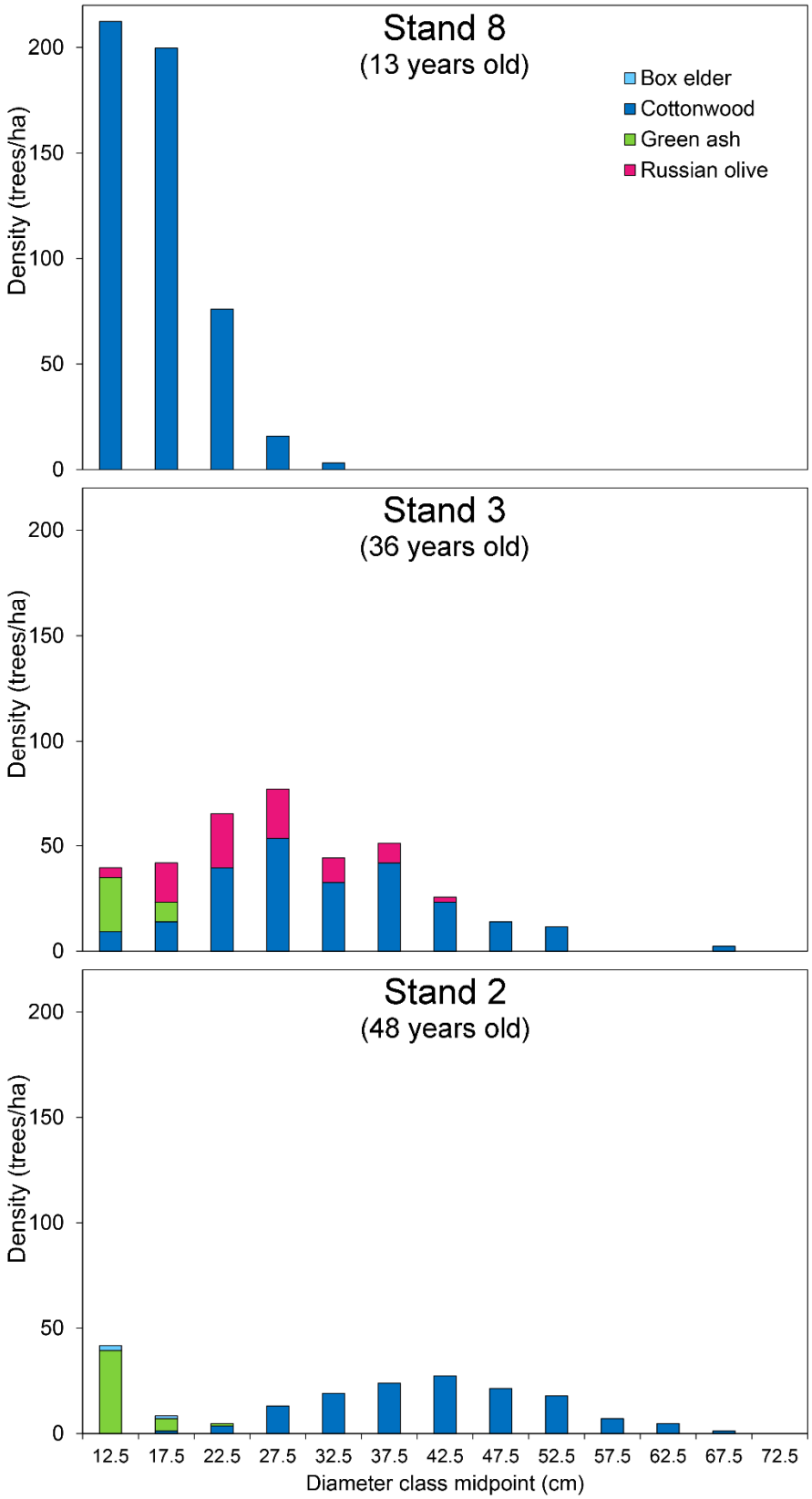

Figure 35. Mean density (trees/ha) per size class for tree species occurring in three stands (stands 8, 3, and 2) on the White River delta in South Dakota.

Peachleaf willow exhibited much greater importance values on the delta than along the White River, especially in the youngest, sapling size stands where it was often more dominant than cottonwood (Figure 36, Appendix Figure 14). Yellow willow only attained tree size in the transition subreach, but commonly occurred in the seedling and sapling layers of middle age and older stands on the delta.

Green ash was the most dominant species in the understory of older stands on the delta, far exceeding the importance values of other later successional species, including American elm and box elder (Figure 36). Green ash will thus likely become a strong component of the overstory in the future. This same pattern was observed on the White River, to be discussed further in the next section.

Russian olive was the only non-native tree species that occurred on the delta. It appeared in the successional sequence at the same time as green ash (in stands $\geq$12 years old), and was a minor to moderate component of the understory and overstory in some tree size stands.

The frequency of liana species attached to the trunks of sampled trees was lowest in the youngest stands and generally increased with stand age on the delta and along the White River (Figure 37). Because the pattern of liana frequency was similar, both subreaches are introduced here together. Riverbank grape was by far the most frequent liana species in both subreaches, ranging from 0.0 to 18.8 percent frequency on the delta, and from 0.0 to 55.0 percent frequency along the White River. Woodbine was the second leading dominant liana species, ranging from 0.0 to 4.4 percent frequency on the delta, and from 0.0 to 14.5 percent frequency along the White River. Western white clematis (*Clematis ligusticifolia* Nutt.) occurred infrequently in one stand along the White River.

The overall greater frequency of liana species along the White River compared to the delta is likely due to the greater proportion of older stands along the river.

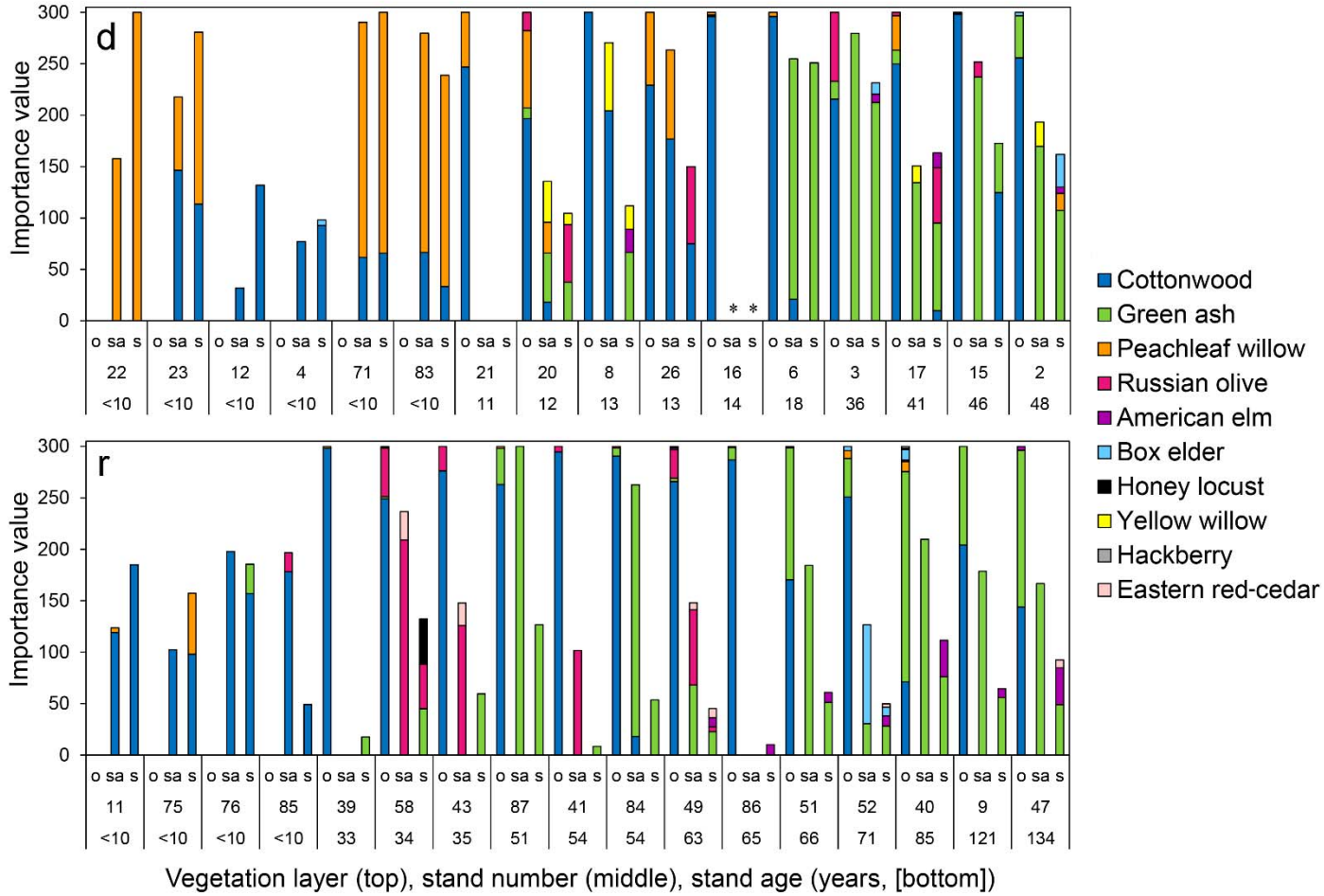

Figure 36. Importance value for each tree species in the overstory (o) (relative density + relative dominance; scaled to a maximum of 300), sapling layer (sa), and seedling layer (s) (relative density + relative dominance + relative frequency; maximum = 300) in each stand on the White River delta (panel d) and along the White River (panel r) in South Dakota. Stands are ordered from youngest to oldest at unequal intervals. *No applicable seedling or sapling layer data was collected in stand 16.

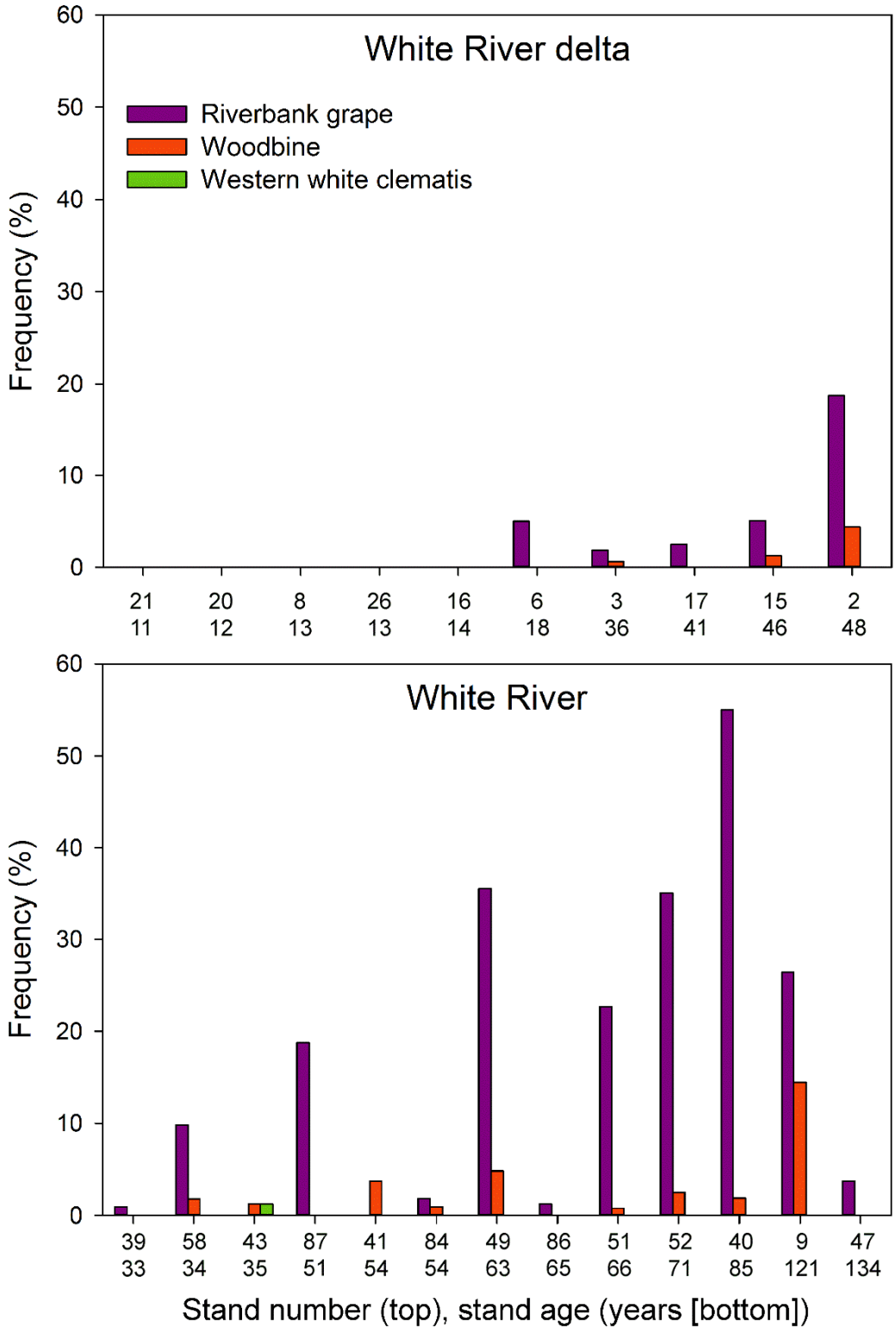

Figure 37. Frequency (percent) of each liana species (riverbank grape, woodbine, and western white clematis) attached to the trunks of sampled trees on the White River delta (top panel) and along the White River (bottom panel) in South Dakota. Stands are ordered from youngest to oldest at unequal intervals.

White River

Stands along the White River also exhibited considerable variation in overstory structure across the stand age gradient. Tree density was generally greatest in the youngest and oldest stands, but did not otherwise exhibit a strong pattern related to stand age (Figure 31). Stand basal area was lowest in the youngest stands and generally increased with stand age. Maximum basal area (60.74 m^2/ha) occurred in a 71 year old stand (Figure 32).

Three stands from the White River were selected from the age gradient to illustrate changes that occurred in population structure with increasing stand age (Figure 38). In the youngest of the three stands (stand 39), cottonwood density was greatest in the four smallest size classes and the shape of the population curve approximated a normal distribution that was strongly skewed to the right. All trees in this young stand were cottonwood, with the exception of one peachleaf willow tree that occurred in the smallest size class. In stand 52, a middle age stand, maximum density was lower and the peak of the cottonwood curve was four size classes to the right of the peak in stand 39. Cottonwood was absent from the smallest size classes but covered a wide range of larger size classes; the shape of the cottonwood population curve approximated a normal distribution that was somewhat skewed to the right. Green ash and box elder filled the smallest size classes; peachleaf willow occurred at low densities in two of the three the smallest size classes occupied by cottonwood. In the oldest of the three stands (stand 47), overall cottonwood density was low and the shape of the population curve was broad and flat. The cottonwood trees were large and covered a wide range of size classes. Green ash filled the smallest size classes where cottonwood was absent.

Tree species importance value patterns in stands along the White River also revealed compositional changes across the age gradient. The youngest, early successional stands had low tree species diversity and were dominated by cottonwood seedlings and saplings (Figure 36, Appendix Figure 15). Middle age stands occupied the transitional portion of the successional sequence in which cottonwood was dominant in the overstory and green ash and Russian olive were the dominant tree species in the understory. The overstory of the oldest stands was dominated by cottonwood and green ash, with very low dominance by other species. Green ash was by far the most dominant tree species in the understory of the oldest stands. American elm, although present in low numbers, was ubiquitous in the understory of the oldest stands along the White River.

Compared to the delta, willow trees were a relatively minor component of the understory and overstory of stands along the White River (Figure 36). Peachleaf willow occurred in the seedling and sapling layers of some sapling size stands, but rarely occurred in the overstory of older stands. Yellow willow did not occur in any stands along the White River.

Green ash was often the most dominant species in the understory of middle age stands, and was common in both the seedling and sapling layers (Figure 36). In older stands, green ash always occurred in the overstory, and was by far the most dominant species in the understory. Importance values for green ash sometimes exceeded those of cottonwood in the oldest stands.

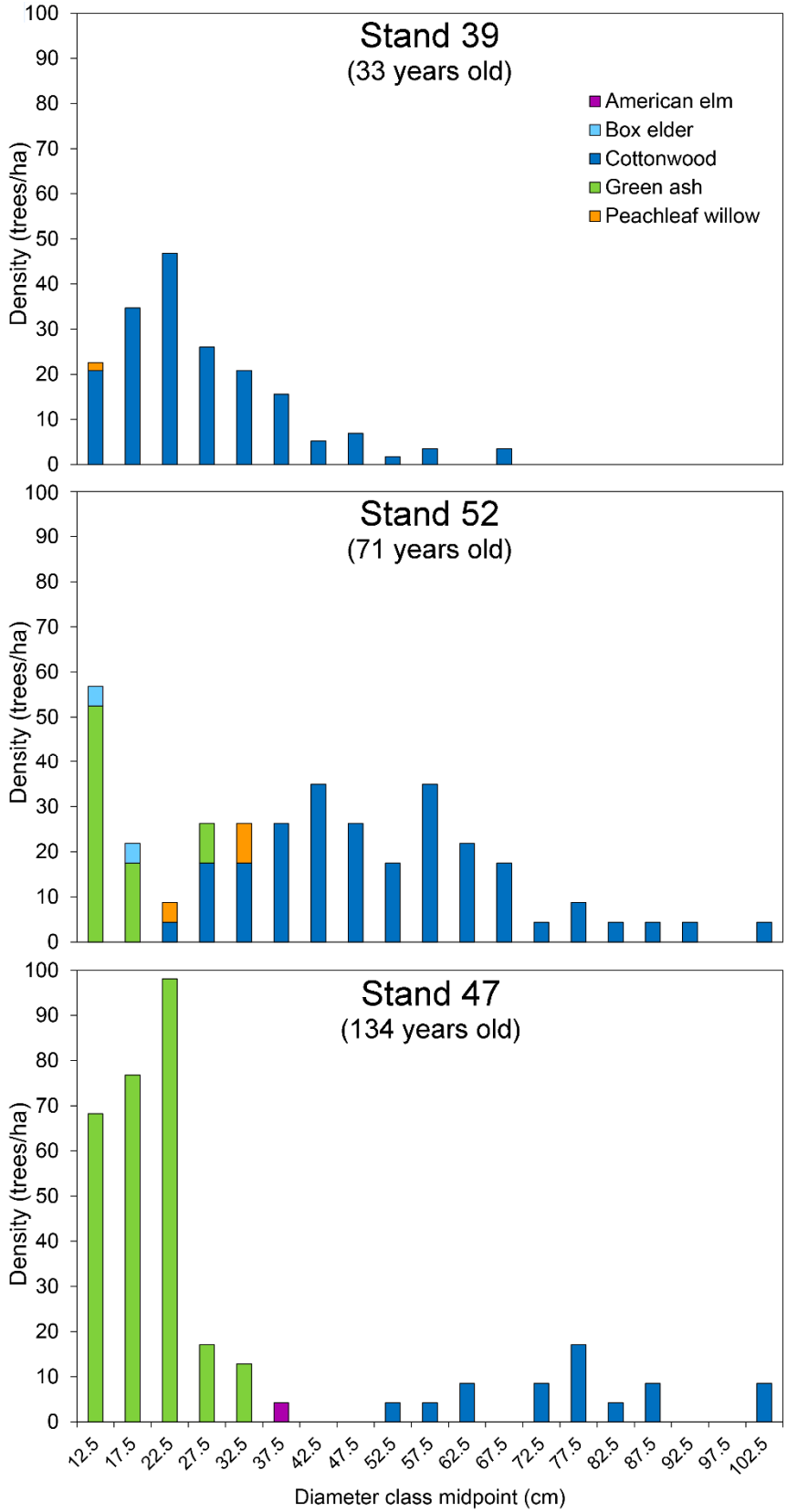

Figure 38. Mean density (trees/ha) per size class for tree species occurring in three stands (stands 39, 52, and 47) along the White River.

As on the delta, Russian olive was the only non-native tree species to occupy stands along the White River, although honey locust, a species native to the eastern United States but introduced to the White River basin, and eastern red-cedar, an upland species, occurred in some stands along this subreach (Figure 36). Similar to the delta, Russian olive entered the successional sequence at around the same time as green ash. Russian olive often dominated the understory of middle age stands, where it also sometimes occurred in the overstory. Importance values for Russian olive declined with stand age; it did not occur in the oldest stands.

Of the eight tree species occurring in the White River and delta subreaches, only cottonwood and peachleaf willow germinate and persist on freshly deposited alluvial surfaces, such as point bars on the inside of river curves. Cottonwood and peachleaf willow can thus be considered pioneer species that rarely reproduce in stands in which they are overstory dominants (there were some exceptions to this trend to be introduced in the next section). Rather, their seeds germinate almost exclusively on fully exposed alluvium recently deposited by the river. The six other overstory species have the capacity to germinate and establish under the cottonwood canopy, and given sufficient time, will eventually replace the cottonwood-willow overstory. Given the strong dominance of green ash in the understory and overstory of the oldest stands, it will eventually become the dominant species in later successional stands, persisting until eroded by the river or otherwise disturbed (Johnson et al. 1976).

Pioneer species recruitment within tree size stands

The four pioneer species (cottonwood, peachleaf willow, sandbar willow, and yellow willow) each occurred in the understory (seedling and sapling layers) of some tree

size stands (>10 years old) in the delta and transition subreaches, but were absent or extremely rare in the understory of tree size stands along the White River. Cottonwood and sandbar willow each occurred in the understory of 67 percent of tree size stands on the delta, in stands up to 46 and 48 years old, respectively (Table 8, Appendix Figures 16 and 17). Likewise, peachleaf willow occurred in the understory of 33 percent of tree size stands on the delta, and yellow willow occurred in the understory of 40 percent of tree size stands on the delta, in stands up to 48 years old. Cottonwood and yellow willow each occurred in the understory of one of the two transition stands and peachleaf willow occurred in the understory of both transition stands. No pioneer species were found in the understory of tree size stands along the White River, with the exception of trace cottonwood sapling cover in the understory of one 54 year old stand. Mean densities of pioneer species generally decreased with stand age, although there were exceptions to this trend.

Table 8. Mean seedling and sapling layer density (stems/ha) for cottonwood, peachleaf willow, sandbar willow, and yellow willow by subreach and stand age class. The dashes indicate that there were no applicable data because stands of a given age class were extremely rare or nonexistent in a given subreach.

	Mean density (stems/ha)					
Age class (years)	White River delta		Transition		White River	
	seedling	sapling	seedling	sapling	seedling	sapling
Cottonwood						
0-9	28069	2476	–	–	19531	7604
10-19	125	154	–	–	–	–
30-39	0	0	–	–	0	0
40-49	104444*	0	–	–	–	–
50-59	–	–	–	–	0	0**
60-69	–	–	–	–	–	–
70-79	–	–	–	–	0	0
80-89	–	–	–	–	0	0
130-139	–	–	–	–	0	0
140-149	–	–	0	0	0	0
160-169	–	–	833	0	0	0
Peachleaf willow						
0-9	7292	9204	–	–	1406	42
10-19	0	42	–	–	–	–
30-39	0	0	–	–	0	0
40-49	417	0	–	–	–	–
50-59	–	–	–	–	0	0
60-69	–	–	–	–	–	–
70-79	–	–	–	–	0	0
80-89	–	–	–	–	0	0
130-139	–	–	–	–	0	0
140-149	–	–	6250	0	0	0
160-169	–	–	417	0	0	0
Sandbar willow						
0-9	21771	4473	–	–	16354	15198
10-19	11683	5121	–	–	–	–
30-39	0	0	–	–	0	0
40-49	12083	306	–	–	–	–
50-59	–	–	–	–	0	0
60-69	–	–	–	–	–	–

70-79	–	–	–	–	0	0
80-89	–	–	–	–	0	0
130-139	–	–	–	–	0	0
140-149	–	–	0	0	0	0
160-169	–	–	0	0	0	0
Yellow willow						
0-9	0	0	–	–	0	0
10-19	417	250	–	–	–	–
30-39	0	0	–	–	0	0
40-49	0	42	–	–	–	–
50-59	–	–	–	–	0	0
60-69	–	–	–	–	–	–
70-79	–	–	–	–	0	0
80-89	–	–	–	–	0	0
130-139	–	–	–	–	0	0
140-149	–	–	0	0	0	0
160-169	–	–	1667	167	0	0

*Dominated by one stand (stand 15).
**Cover of cottonwood saplings was detected in one 54 year old tree size stand (stand 84) along the White River, but no stems were rooted in any sampling plots; hence, the density of cottonwood saplings in this stand was calculated as zero.

Compositional differences between subreaches

Although woody plant species composition on the delta was very similar to that along the White River, some species, particularly willows, were observed in a greater proportion of stands on the delta than along the White River. For example, sandbar willow was present in 80 percent of the stands on the delta compared to 24 percent of the stands along the White River; peachleaf willow was present in 67 percent of the stands on the delta compared to 41 percent of the stands along the White River; and yellow willow was present in 27 percent of the stands on the delta but was not observed in any stands along the White River (Figure 39).

Conversely, numerous species were more common along the White River than on the delta. For example, western snowberry was present in 82 percent of White River stands but only occurred in 27 percent of delta stands (Figure 39). 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. Chokecherry was present in stands along the White River and in one stand in the transition subreach, but did not occur in any delta stands.

In addition to occupying a greater proportion of stands on the delta, peachleaf willow was also more abundant where it occurred in the overstory on the delta compared to stands along the White River. In occupied stands, peachleaf willow frequency in the delta overstory (median = 50 percent) was significantly greater than along the White River (median = 16 percent; $U_{0.05(2),4,5} = 1.0$, $P = 0.032$). Likewise, peachleaf willow density in the delta overstory (median = 3.9 trees/ha) was significantly greater than along the White River (median = 1.7 trees/ha; $U_{0.05(2),5,6} = 1.0$, $P = 0.009$).

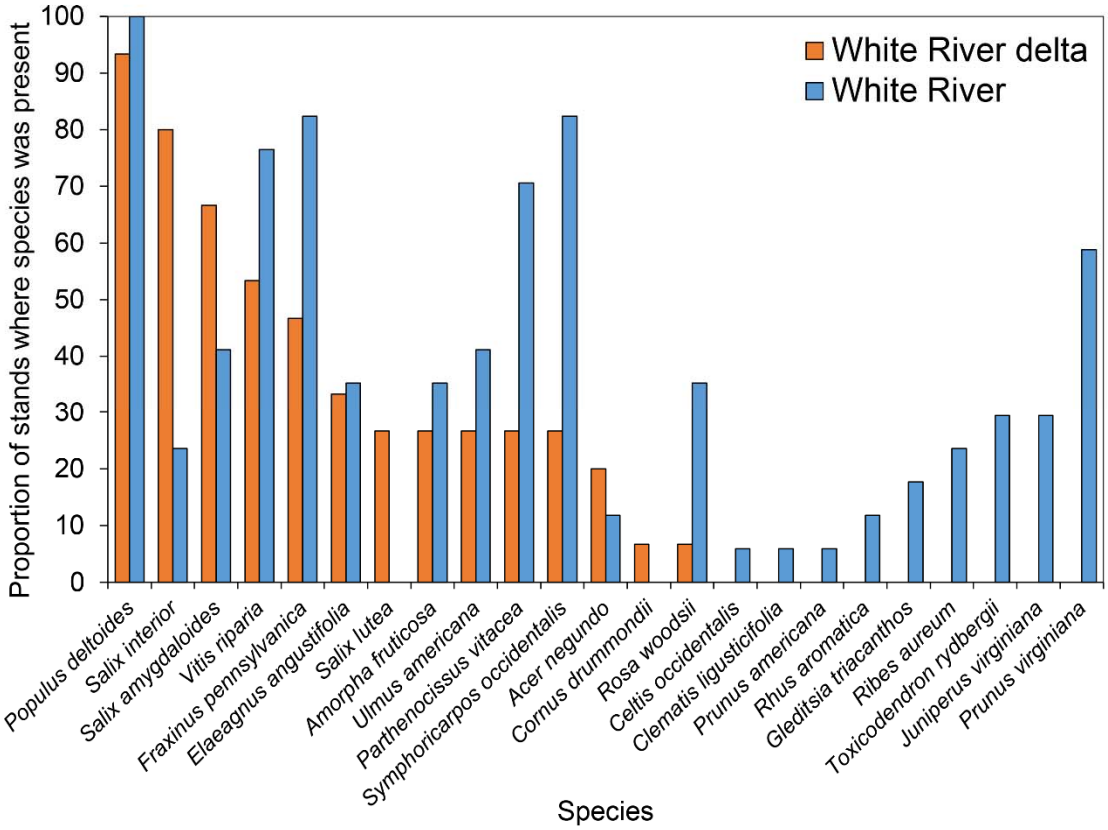

Figure 39. Proportion of sampled stands on the White River delta (orange) and along the White River (blue) where each species occurred.

Longitudinal gradient analysis

The structural and compositional relationships along the longitudinal gradient were best displayed by ordination models. In the ordination of species presence (all vegetation layers), stands were sorted along the *x*-axis according to their position along the longitudinal gradient and the proportion of wetland affiliated species (facultative and facultative wetland) in a given stand (Figure 40). Stands on the lower delta with a high proportion of wetland affiliated species (75-100 percent) formed a group on the left side of the ordination, grading into a group of stands located on the upper delta with a lower proportion of wetland affiliated species (80-89 percent). The two stands in the transition subreach were composed of 64-70 percent wetland affiliated species, and grouped together to form a loose boundary between the group of upper delta stands and the group of White River stands. 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 subreach (31-57 percent). This pattern indicates that the *x*-axis represents an environmental moisture gradient spanning the White River-White River delta continuum, with relatively wet conditions in the lower delta and relatively dry conditions along the White River. There were two cases in which White River stands overlapped with lower delta stands on the left side of the ordination. This overlap occurred for stands <10 years old dominated by cottonwood and willow. In these cases, close similarity in stand age and composition produced continuity in the ordination, indicating that only a few species were able to initiate riparian forest succession within the study area. Within subreaches, the White River and upper delta exhibited the greatest differences among stands, as evidenced by the greater spread of stands, whereas the lower delta exhibited the smallest

differences among stands. The calculated two-dimensional stress for the ordination of species presence was 0.12, which falls below the recommended upper limit of 0.15 (Clarke and Warwick 2001).

The ordinational model based on seedling percent cover further revealed a longitudinal gradient in stand composition (Figure 41). The *x*-axis represents the environmental moisture gradient spanning the White River and its delta, with relatively wet, lower delta stands on the left side of the ordination and relatively dry, White River stands on the right side of the ordination. Similar to the ordination of species presence, the longitudinal stratification of stands was partially disrupted by the influence of an age gradient. Stands of similar age, especially the youngest stands, grouped together, regardless of subreach. The *y*-axis loosely corresponds to the percent cover of green ash, with increasing green ash cover from top to bottom. The two-dimensional stress calculated for the ordination of seedling percent cover was 0.13.

The ordinational model based on tree species importance values (maximum = 200) revealed the compositional gradient existing among the tree size stands (Figure 42). Stands with high cottonwood importance values formed a compact v-shaped group near the bottom left corner of the ordination which graded along the *y*-axis into a group of stands dominated by cottonwood and peachleaf willow. Stands with high green ash importance values formed an isolated linear group that ran parallel to the *x*-axis on the right side of the ordination. The two-dimensional stress calculated for this ordination was 0.05.

The major compositional groupings based on tree importance values were generally consistent with subreach groupings along the longitudinal gradient. The

cottonwood and peachleaf willow dominated group included stands located in the lower delta and upper delta subreaches (Figure 42). The cottonwood dominated group included stands located in the upper delta and White River subreaches. The oldest stands located in the transition and White River subreaches formed the group of stands with high green ash importance values. The age gradient runs from approximately left to right, with decreasing cottonwood importance values. The *y*-axis represents the longitudinal moisture gradient, with increasing peachleaf willow importance values from bottom to top.

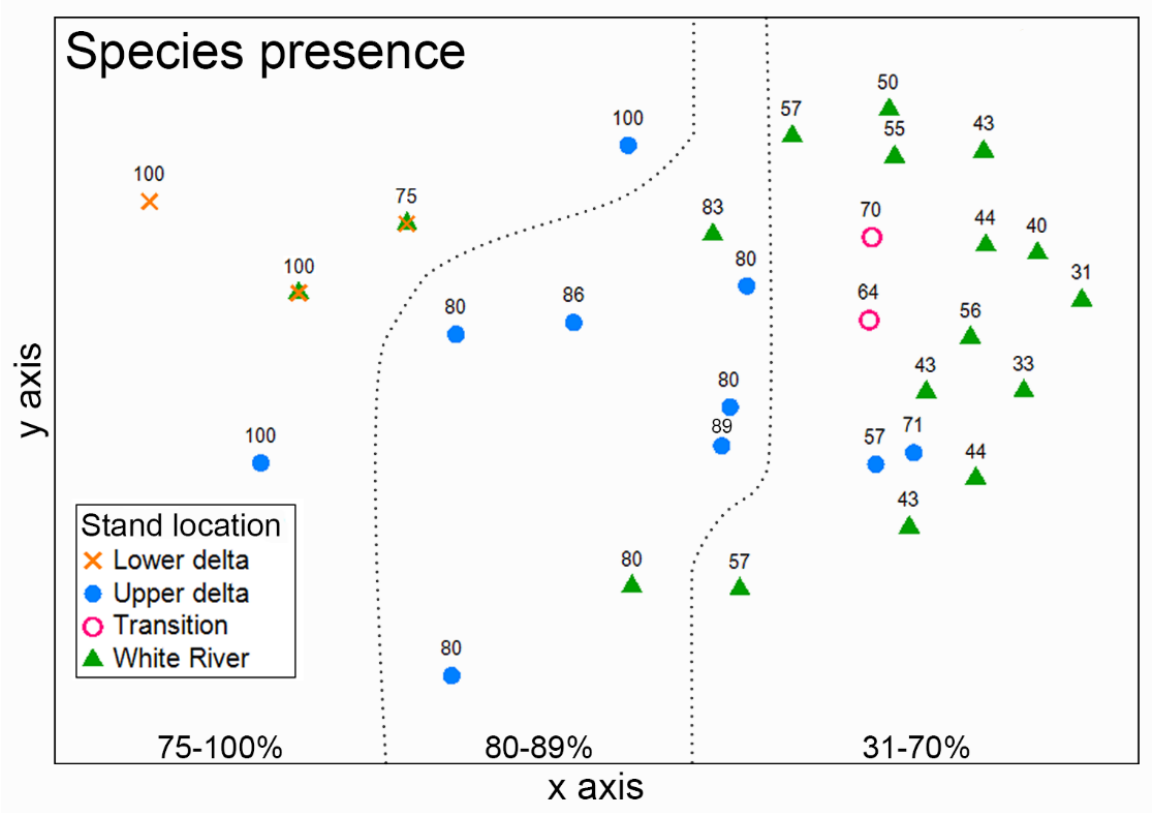

Figure 40. A nonmetric multidimensional scaling stand ordination plot constructed from a matrix based on species presence in the seedling, sapling, and overstory layers. Two-dimensional stress = 0.12. Stands located near each other are very similar floristically, whereas stands far apart are more dissimilar. The percentage of species in each stand with either facultative (FAC) or facultative wetland (FACW) indicator status is labeled above each point (there were no obligate wetland [OBL] species in the sample). The plot is subdivided into three groups based on the proportion of wetland affiliated species in each stand; the ranges of wetland affiliated species percentages for each group are given along the *x*-axis. Stand 16 from the upper delta was excluded from this analysis because of the absence of seedling and sapling layer data.

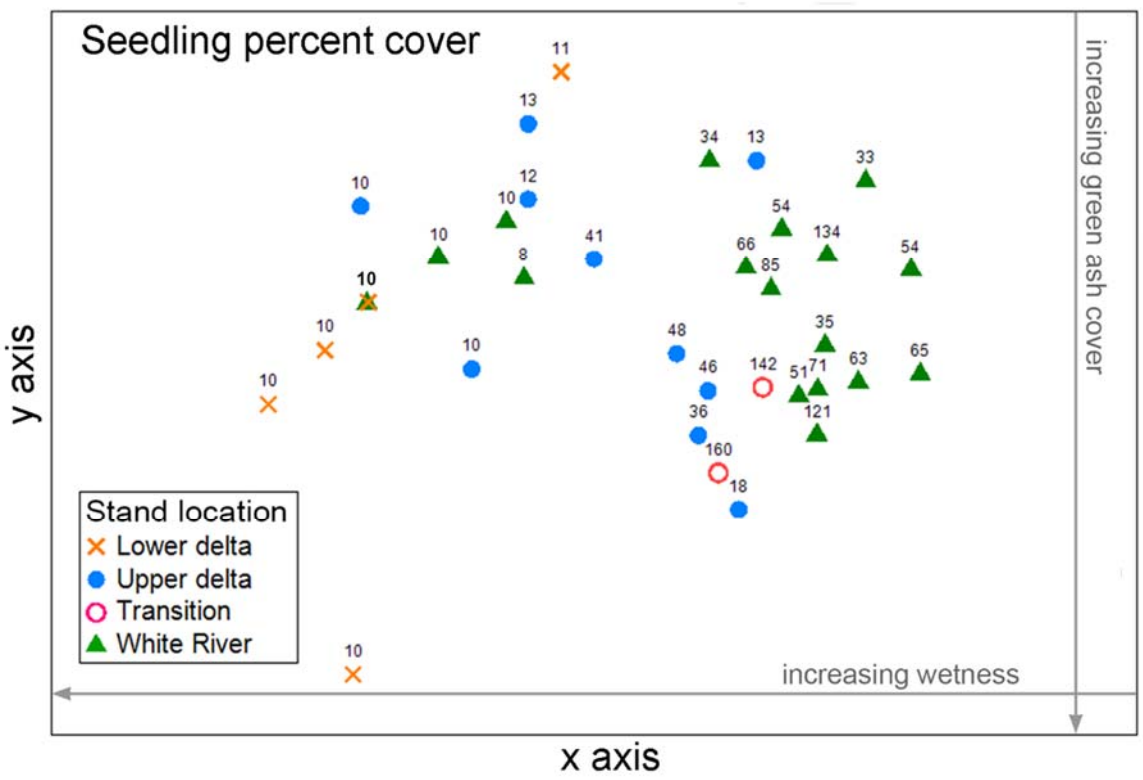

Figure 41. A nonmetric multidimensional scaling stand ordination plot constructed from a matrix based on seedling percent cover. Two-dimensional stress = 0.13. Stand age (years) is labeled above each point, with stands <10 years old labeled as 10. Stands plotted close together are very similar, whereas stands plotted far apart are more dissimilar. Stand 16 from the upper delta was excluded from this analysis because of the absence of seedling and sapling layer data.

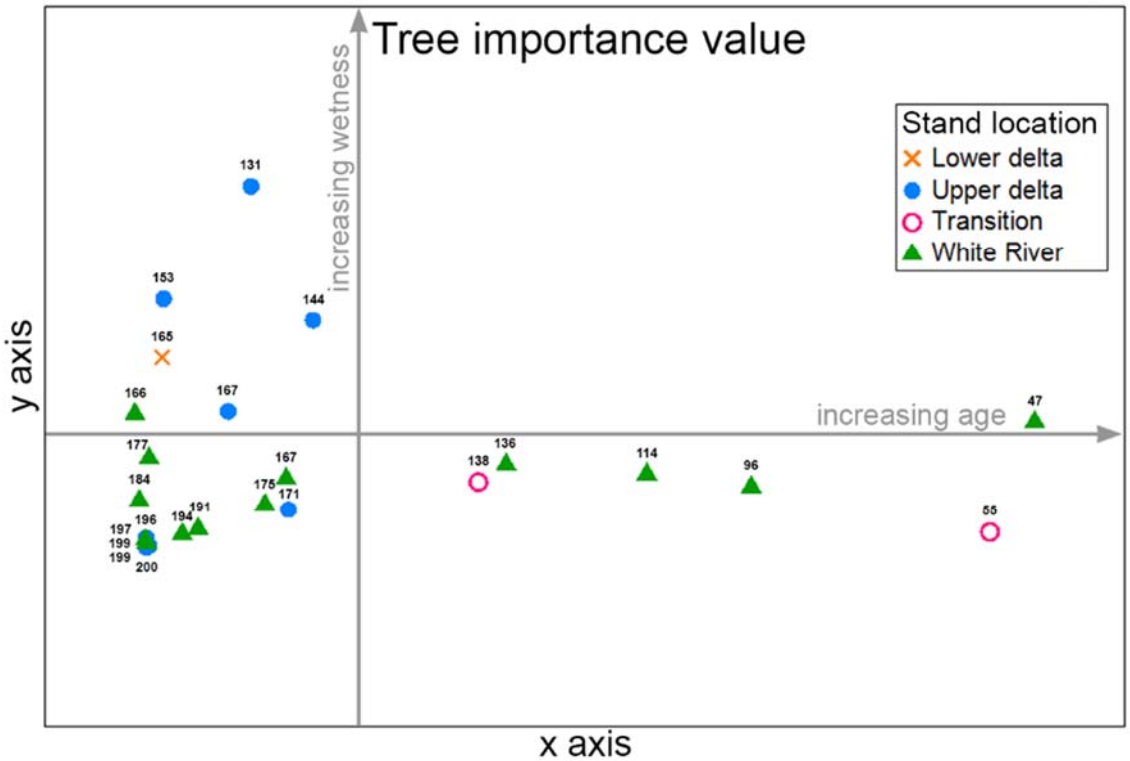

Figure 42. A nonmetric multidimensional scaling stand ordination plot constructed from a matrix based on tree species importance values. Two-dimensional stress = 0.05. Cottonwood importance value (relative density + relative dominance; maximum = 200) is labeled above each point.

Similarity of the White River delta to the White River

There was a high degree of similarity between the overstory vegetation and a moderate degree of similarity between the understory vegetation occurring in tree size stands on the White River delta and along the White River. The Bray-Curtis similarity score based on mean overstory importance values was 84.79, indicating high similarity between the delta and White River (Table 9). This value exceeded the mean stand to stand Bray-Curtis similarity scores calculated separately for the White River delta (81.86) and for the White River (71.81). 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 that the overstory vegetation was very similar. The Bray-Curtis similarity scores for the sapling and seedling layers were 46.98 and 48.13, respectively, indicating greater dissimilarity in understory vegetation between the delta and the White River.

The density of pioneer seedlings and saplings (cottonwood, peachleaf willow, and sandbar willow) in <10 year old stands was similar between the delta and river subreaches (Figure 43). Yellow willow, which is also a pioneer species, did not occur in any stands <10 years old on the delta or along the White River. The differences in seedling and sapling densities were not significantly different between subreaches. The lack of a significant difference in the density of pioneer seedlings in young stands between the river and delta subreaches supports the conclusion that the early successional plant communities are highly similar along the White River-White River delta continuum. The lack of statistical significance could also be partially due to the small sample size and the relatively low statistical power (<0.50) of these tests.

Table 9. Similarity scores for the vegetation communities occurring on the White River delta and along the White River in South Dakota. The left side of the table contains vegetation community similarity scores *between* the delta and river subreaches, and the right side of the table contains stand to stand vegetation community similarity scores *within* individual subreaches.

Stand size and vegetation layer	White River delta versus White River: Spearman's rank correlation coefficient (r_s)		Bray-Curtis similarity score	Stand to stand Bray-Curtis similarity score by subreach: White River delta			White River		
	r_s	*P*		min	mean	max	min	mean	max
Tree size stands									
Trees*	0.88	0.01	84.79	65.52	81.86	99.51	23.66	71.81	98.28
Sapling layer	-0.09	0.75	46.98	0.00	28.79	87.83	0.00	24.58	91.60
Seedlings	0.15	0.52	48.13	0.00	37.08	87.19	12.99	47.15	87.87
Sapling size stands									
Sapling layer	-0.15	0.78	60.43	13.90	47.76	94.88	64.26	76.55	92.90
Seedlings	0.49	0.13	52.13	0.00	46.81	80.87	50.39	60.77	80.91

*The overstory vegetation on the White River delta and along the White River was very similar.

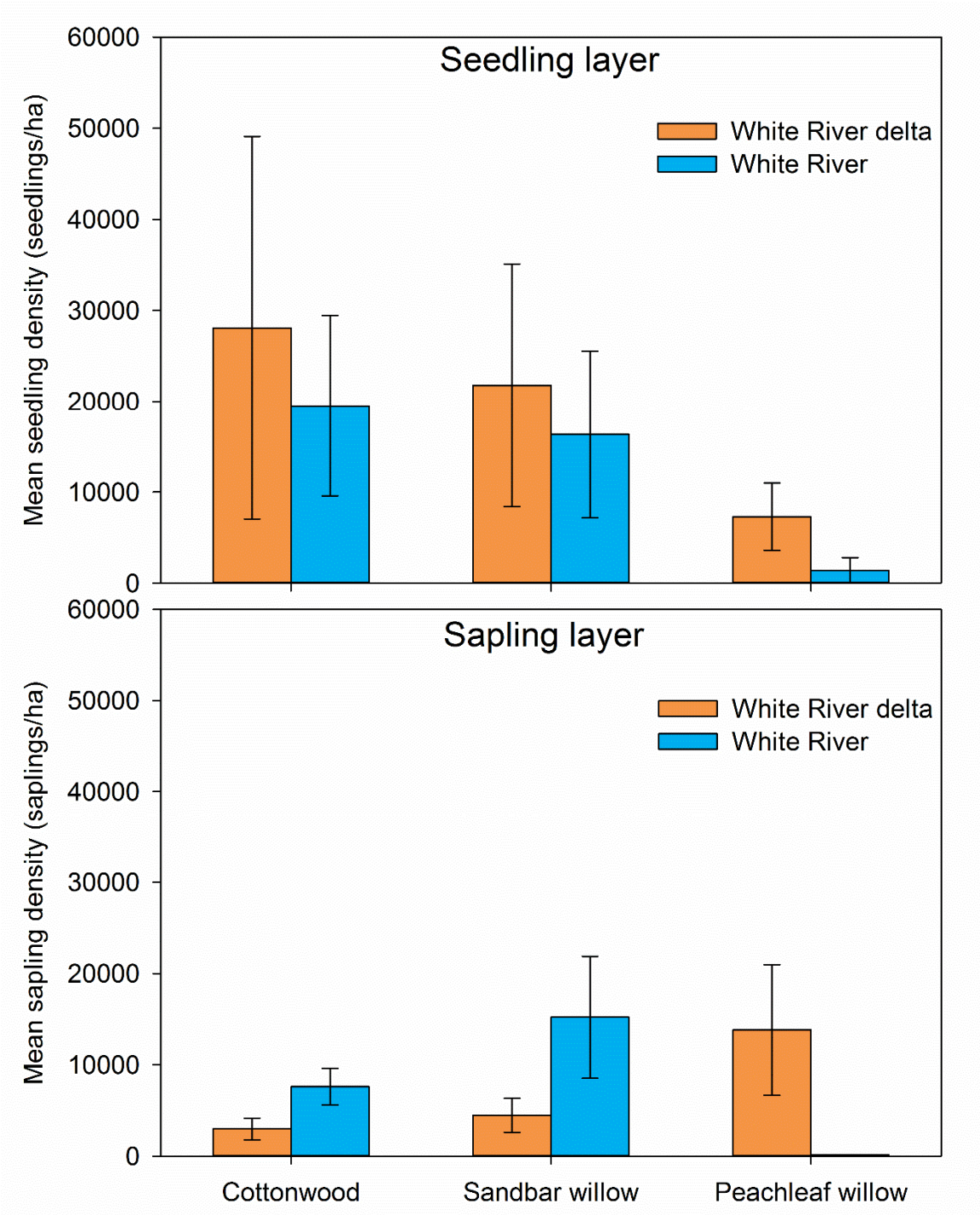

Figure 43. Mean seedling and sapling layer density (stems/ha) of three pioneer species in sapling size stands <10 years old on the White River delta and along the White River in South Dakota. Error bars represent standard error. The differences in seedling and sapling densities were not significantly different between the delta and the White River.

Similarity of the White River delta to Missouri River remnant reaches

Woody species richness in the seedling and overstory layers on the White River delta equaled or exceeded that along the Garrison reach of the Missouri River (Keammerer et al. 1975, Johnson et al. 1976), depending on stand age. In the younger size class (14.4-20.6 cm dbh), woody species richness was similar between the delta and Garrison reach, averaging around five species per stand at each site (Table 10). In the older size class (32.0-43.2 cm dbh), however, mean species richness on the delta (8.5 species per stand) was significantly greater than along the Garrison reach (4.8 species per stand; $t_{0.05(2),7} = 2.631$, $P = 0.034$).

Species assemblages on the White River delta and the Garrison reach were moderately similar. Five species (35 percent of the total) were common to both sites, all of which were tree species. Twenty-five percent of species in the younger stands (green ash, cottonwood, and peachleaf willow) and 42 percent of species in the older stands (American elm, box elder, cottonwood, green ash, and peachleaf willow) were common to both sites (Table 11).

Delta stands had a higher proportion of wetland affiliated species (facultative and facultative wetland; USDA/NRCS 2015), such as false indigo, riverbank grape, and yellow willow, than stands along the Garrison reach. In the younger age class, 89 percent of species on the delta were wetland species, compared to 67 percent of species along the Garrison reach. In the older age class, 80 percent of species on the delta were wetland species, compared to 71 percent of species along the Garrison reach (Table 11).

Table 10. Comparisons of woody species richness between the White River delta and the Garrison and Gavins Point reaches of the Missouri River. *P*-values were derived from a two-tailed *t*-test. Results for the 25-49 year age class (White River delta versus Gavins Point reach) are not shown because of greatly different sample sizes across sites. The dashes indicate no applicable data.

	Number of woody species per stand												
	White River delta				Garrison reach[1]				Gavins Point reach[2]				
Size class (cm)	min	mean	max	n	min	mean	max	n	min	mean	max	n	*P*
14.4-20.6	3	5.2	8	6	3	4.6	6	5	–	–	–	–	0.810
32.0-43.2*	7	8.5	10	4	3	4.8	6	5	–	–	–	–	0.034
Age class (years)													
<10**	2	3	5	6	–	–	–	–	3	5.2	8	6	0.038
10-24	3	4.8	8	6	–	–	–	–	2	6.5	9	6	0.244

[1]Sources: Keammerer et al. (1975) and Johnson et al. (1976).
[2]Source: Dixon et al. (2010).
*Species richness was significantly greater on the White River delta than along the Garrison reach for stands in the 32.0-43.2 cm size class ($t_{0.05(2),7} = 2.631$, $P = 0.034$).
**Species richness was significantly greater on the Gavins Point reach than on the White River delta for stands <10 years old ($t_{0.05(2),10} = 2.381$, $P = 0.038$).

Table 11. Species presence by size class on the White River delta in South Dakota and the Garrison reach of the Missouri River in North Dakota. A "1" indicates species presence and a "0" indicates species absence.

Species	Wetland indicator status*	White River delta	Missouri River (Garrison reach)**
14.4-20.6 cm dbh			
Acer negundo L.	FAC	0	1
Amorpha fruticosa L.	FACW	1	0
Clematis ligusticifolia Nutt.	FACU	0	1
Fraxinus pennsylvanica Marsh.	FAC	1	1
Populus deltoides ssp. *monilifera* (Aiton) Eckenw.	FAC	1	1
Salix amygdaloides Andersson	FACW	1	1
Salix interior Rowlee	FACW	1	0
Salix lutea Nutt.	FACW	1	0
Shepherdia argentea (Pursh) Nutt.	UPL	0	1
Symphoricarpos occidentalis Hook.	UPL	1	0
Ulmus americana L.	FAC	1	0
Vitis riparia Michx.	FAC	1	0
32.0-43.2 cm dbh			
Acer negundo L.	FAC	1	1
Amorpha fruticosa L.	FACW	1	0
Clematis ligusticifolia Nutt.	FACU	0	1
Fraxinus pennsylvanica Marsh.	FAC	1	1
Parthenocissus vitacea (Knerr) Hitchc.	FACU	1	0
Populus deltoides ssp. *monilifera* (Aiton) Eckenw.	FAC	1	1
Quercus macrocarpa Michx.	FACU	0	1
Salix amygdaloides Andersson	FACW	1	1
Salix interior Rowlee	FACW	1	0
Symphoricarpos occidentalis Hook.	UPL	1	0
Ulmus americana L.	FAC	1	1
Vitis riparia Michx.	FAC	1	0

*FAC = facultative; FACW = facultative wetland; FACU = facultative upland; UPL = upland. FACW and FAC species were considered "wetland affiliated" species in this study. Source: USDA, NRCS PLANTS Database.
**Sources: Keammerer et al. (1975) and Johnson et al. (1976).

Woody species richness in the seedling, sapling, and overstory layers of stands on the White River delta was lower than or equal to that along the Gavins Point reach of the Missouri River, depending on stand age. In stands <10 years old, mean species richness along the Gavins Point reach (5.2 species per stand) was significantly greater than on the White River delta (3 species per stand; $t_{0.05(2),10} = 2.381$, $P = 0.038$; Table 10). In stands 10-24 years old, however, species richness was statistically indistinguishable between the delta and the Gavins Point reach.

Although most (75 percent) of the species that occurred on the White River delta were also present along the Gavins Point reach, there were compositional differences between the two sites. Thirty-three percent of species in the youngest age class (<10 years old) and 56 percent of species in the 10-24 year old age class were common to both sites (Table 12).

Delta stands contained a higher proportion of wetland affiliated species (facultative and facultative wetland; USDA/NRCS 2015) than the Gavins Point reach, except in the <10 year old age class where the proportion of wetland affiliated species at each site was similar. In stands <10 years old, 83 percent of species on the delta were wetland affiliated species and 90 percent of species along the Gavins Point reach were wetland affiliated species. In the 10-24 year age class, 90 percent of species on the delta were wetland affiliated species, compared to 60 percent of species along the Gavins Point reach. Conversely, a higher proportion of upland species, including American plum (*Prunus americana* Marshall), eastern red-cedar, and American bittersweet (*Celastrus scandens* L.), occurred along the Gavins Point reach than on the delta (Table 12).

Table 12. Species presence by age class on the White River delta in South Dakota and the Gavins Point reach of the Missouri River in South Dakota and Nebraska. A "1" indicates species presence and a "0" indicates species absence.

Species	Wetland indicator status*	White River delta	Missouri River (Gavins Point reach)**
<10 years old			
Acer negundo L.	FAC	1	0
Amorpha fruticosa L.	FACW	1	1
Cornus drummondii C.A. Mey	FAC	0	1
Fraxinus pennsylvanica Marsh.	FAC	0	1
Juniperus virginiana L.	UPL	0	1
Populus deltoides ssp. *monilifera* (Aiton) Eckenw.	FAC	1	1
Rosa woodsii Lindl.	FACU	1	0
Salix amygdaloides Andersson	FACW	1	1
Salix interior Rowlee	FACW	1	1
Salix lutea Nutt.	FACW	0	1
Ulmus americana L.	FAC	0	1
Vitis riparia Michx.	FAC	0	1
10-24 years old			
Amorpha fruticosa L.	FACW	1	1
Celastrus scandens L.	UPL	0	1
Celtis occidentalis L.	FACU	0	1
Cornus drummondii C.A. Mey	FAC	1	1
Fraxinus pennsylvanica Marsh.	FAC	1	1
Gleditsia triacanthos L.	FACU	0	1
Juniperus virginiana L.	UPL	0	1
Parthenocissus vitacea (Knerr) Hitchc.	FACU	0	1
Populus deltoides ssp. *monilifera* (Aiton) Eckenw.	FAC	1	1
Prunus americana Marshall	UPL	0	1
Salix amygdaloides Andersson	FACW	1	1
Salix interior Rowlee	FACW	1	1
Salix lutea Nutt.	FACW	1	1
Symphoricarpos occidentalis Hook.	UPL	1	0
Ulmus americana L.	FAC	1	1
Vitis riparia Michx.	FAC	1	1

*FAC = facultative; FACW = facultative wetland; FACU = facultative upland; UPL = upland. FACW and FAC species were considered “wetland affiliated” species in this study. Source: USDA, NRCS PLANTS Database.
**Source: Dixon et al. (2010)

DISCUSSION

Delta favorability to cottonwood recruitment

The system of six large dams on the upper Missouri River has dramatically altered the flow and sediment dynamics that historically sustained the cottonwood forest ecosystem. Dams have cut peak flows, reducing channel migration (Shields et al. 2000) and formation of flood-deposited sandbars that enable recruitment of cottonwood and other pioneering species to initiate forest succession (NRC 2002a). In addition to changes in flow regime, reaches downstream of dams suffer from sediment deficits and channel incision due to sediment trapping by the upstream reservoir (NRC 2011). The hydrogeomorphic changes imposed by the dams have severely limited opportunities for pioneer seedling establishment on the post-dam river; new recruitment is confined primarily to near channel environments that are highly vulnerable to erosion (Dixon et al. 2012, Johnson et al. 2012). Consequently, cottonwood forests in remnant reaches of the Missouri River are now dominated by older trees that established prior to dam construction (Dixon et al. 2010, Dixon et al. 2012, Volke et al. 2015). Without major restoration efforts, the Missouri River cottonwood forest ecosystem will continue to decline (Johnson 1992, Johnson et al. 2012). A key question of this research was whether recent emergence of deltas associated with reservoirs could lead to cottonwood forest replenishment.

As the Missouri River reservoir system has aged, sediment that historically would have been transported downstream has become short-stopped behind dams (Meade and Moody 2009, NRC 2011). Clear water releases below the dams have eroded sediment from portions of the riverbed and banks. Some of this sediment has accumulated in the

form of deltas where the mainstem river contacts the upper end of reservoirs and where tributaries enter reservoirs (Johnson 2002, Coker et al. 2009, Skalak et al. 2013, Volke et al. 2015). These deltas are novel habitats that were not present in the former river system and are built and shaped by river flow and sediment regimes and reservoir level fluctuations. The delta forming at the confluence of the White River and Fort Randall Reservoir on the Missouri River in South Dakota is one such delta where cottonwood forest has expanded during the post-regulation era.

The lowermost portions of the historical White River and its floodplain were destroyed when Fort Randall Reservoir was initially filled in 1953. The current delta formed in the new lower section of the river. The delta has expanded in both directions over time, up the White River valley and farther downstream into the reservoir. This expansion continued upstream of the maximum reservoir pool boundary as the channel slope flattened and flooding increased, often due to ice jams.

The hydrogeomorphic conditions on the post-dam White River delta often have been favorable for cottonwood establishment. Over time, the abundant sediments from the White River have accumulated in the form of a broad wedge that now occupies the last 31 km of the White River valley. Formation of the sediment wedge created new areas of freshly deposited alluvium that provided an ideal seed bed for cottonwood when exposed during the seed dispersal period. At the same time, sedimentation flattened the stream gradient and reduced the flow capacity of the active channel, increasing the frequency of overbank flows that delivered new sediments to the floodplain. These physical changes reflect a sediment-rich environment where there has been continual and dynamic formation of new potential cottonwood recruitment sites. Thus, the post-dam

delta has maintained some of the physical environmental conditions that have largely been lost in remnant reaches of the dammed Missouri River.

The favorability of the delta environment for cottonwood recruitment was mainly due to the natural hydrograph and large sediment load of the White River. Because the White River has no dams, the timing and delivery of water and sediment to its delta were relatively unimpaired. For example, streamflow into the delta exhibited the spring pulses and summer drawdowns typical of pre-development rivers in the Great Plains. Therefore, the flow and sediment dynamics that sustain the growth and reproduction of riparian forests along free-flowing rivers were largely functioning on the delta, although they were affected by the more unnatural water regime of Fort Randall Reservoir.

Because of the natural flow and sediment dynamics of the White River, it would be inaccurate to describe the delta as an entirely novel ecosystem with a unique assemblage of biotic and environmental conditions (Morse et al. 2014). While the presence of a persistent, well-developed delta is a novel element in the river system, the vegetation communities that have developed on this delta are largely similar to those occurring along natural river reaches. Thus, the delta is best described as a semi-natural ecosystem that supports native riparian vegetation communities and exhibits many of the abiotic and biotic conditions found on natural floodplains.

Changes in land use also favored the recruitment and expansion of cottonwood forests on the delta. Prior to construction of Fort Randall Dam, much of the floodplain that is now occupied by the delta was privately owned and used as hay, pasture, or crops. In the decades after the reservoir filled, many cultivated fields were abandoned because of increased flood frequency and deposition of sediment and coarse woody debris. One

landowner stated that a field previously cultivated as hay was abandoned when flood deposition of driftwood hindered operation of harvesting equipment (personal communication, Edward Byre II). Another landowner described the increased frequency and severity of backup flooding from ice jamming along the long, flattened gradient. The flooding was so severe one year that it killed some of his neighbor's cattle (personal communication, Randall Holmquist). Ice tended to break up first in the upper reaches and jam against unbroken ice farther downstream (Appendix Figure 18; Beltaos and Prowse 2001).

The floodplain 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 (USCFC 1987). After the delta was transferred into public ownership, rates of forest clearing declined, and cottonwoods colonized abandoned fields where the river deposited new sediments. Most of the cottonwood forest expansion on the delta in recent decades occurred in old fields, in areas larger than those created by point bar formation alone. Because the delta floodplain is now in public ownership, it will likely remain relatively undeveloped, with minimal land use impacts on existing cottonwood forests.

Longitudinal environmental gradient

Physical properties

The hydrologic and sediment regimes of the White River and its delta differed, thereby producing differences in vegetation between the two subreaches. The hydrology of the delta was largely controlled by reservoir stages (rather than by river discharge) that changed an average of ~four vertical meters during the growing season (May-October;

USGS gaging station 06442996). Reservoir stages recharged and stabilized the delta water table and maintained subirrigated conditions for most of the growing season. Impacts of the reservoir were most extreme at the distal end of the delta where reservoir pools frequently inundated younger alluvial surfaces and gradually lessened upstream. High rates of sedimentation due to the calm water of the reservoir flattened the stream gradient, reducing streamflow velocities and leading to accumulation of fine textured sediments, conditions that helped retain soil moisture in the delta. The transition subreach, which occurred between the delta and riverine subreaches, was the upstream most point where the reservoir visibly influenced the environment. The reservoir influenced the transition subreach in several ways, including increased frequency of backup flooding due to the reduced gradient and low flow capacity of the channel in downstream portions of the delta, and increased severity of flooding associated with winter ice jams (Appendix Figure 18).

The environment of the delta and transition subreaches contrasted with that of the White River, which was controlled by upstream conditions (rather than by the reservoir). Moisture conditions on the White River floodplain were mainly influenced by streamflow, spring flooding, and sediment deposition, and were more variable than on the delta. Peak flows typically occurred in the spring and early summer, and were followed by considerable water table declines in mid- to late summer. In late summer, overbank flows were rare and the floodplain environment dried out. The White River meandered slowly across its floodplain forming soils of different textures and elevations and high topographic diversity. Additionally, the White River had a steeper stream gradient and greater flow velocities than the portion of the river that flowed through the delta.

Vegetation patterns

Vegetation established in accordance with the different hydrogeomorphic environments along the White River-White River delta continuum. Plant species favored by subirrigated or hypoxic soils over long time periods comprised a larger proportion of the flora in the downstream direction. The wettest portions of the delta near the reservoir supported emergent wetland vegetation, primarily cattails (*Typha* L. spp.), and sometimes peachleaf willow and sandbar willow. Willows that co-occurred with cattails, however, often exhibited signs of flood stress, including production of adventitious roots (Appendix Figure 19) and stunted growth. Cottonwood was intolerant of the chronically saturated soils and high water levels on the lower extremes of the delta, and was present only along natural levees or on surfaces far enough above the water table not to be chronically flooded by the reservoir. Although hypoxic soils restricted cottonwood establishment on the lower fringes of the delta, it grew faster under moderately subirrigated conditions on the middle and upper portions of the delta than along the White River, as evidenced by significantly greater growth rates in some of the young age classes.

Riparian plant species favored by water table decline during the growing season (e.g., cottonwood, Russian olive) comprised a larger proportion of the flora in the upstream direction. As the influence of the reservoir diminished, cottonwood and other riparian plants adapted to a more natural hydrologic regime dominated the floodplain. Nine non-wetland species, including American plum, eastern red-cedar, and poison ivy, were restricted to sites along the White River subreach, but only two species were restricted to the delta and/or transition subreaches, indicating that a wider range of

moisture conditions along the White River supported a more diverse assemblage of species. These findings are consistent with observations of riparian vegetation zonation on natural floodplains, whereby plant species are distributed according to moisture tolerances (Hupp and Osterkamp 1985, Harris 1987, Auble et al. 1994, Amlin and Rood 2001, Van Eck et al. 2004, Lite et al. 2005, Merigliano 2005). Compositional differences between the two subreaches also may have been partially due to the wider range of stand ages along the White River than on the delta. Delta stands may have contained fewer species than riverine stands because they were younger, and may accumulate more species over time.

Woodland age class distribution on the delta

The environmental conditions under which cottonwood reproduced on the White River delta differed from that along the historical White River and Missouri River floodplains. Cottonwood forests on natural floodplains typically formed even-aged, arcuate bands on the inside of river curves (Everitt 1968, Johnson et al. 1976, Noble 1979, Bradley and Smith 1986, Braatne et al. 1996, Rood et al. 2007). These bands generally were youngest on point bars on the inside of river curves and increased in age with distance from the channel. Each band originated from a particular seedling establishment event, usually following a flood. With meander migration, the river channel moved away from the establishment band, and with sediment deposition associated with greater surface roughness from new vegetation, the surface aggraded. With subsequent flooding and channel meandering, older bands continued to aggrade and occur farther from the current channel. Because the river moved most frequently over shorter distances (Wolman and Leopold 1957), few stands located near the channel

escaped erosion and attained sufficient age to reach the oldest age classes. In contrast, older forests near the floodplain edge were relatively protected from the meandering river and persisted for longer periods.

On the contemporary (2012) White River delta, 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 floodplain edge. This pattern can be explained by the highly depositional environment of the delta, where there was very little erosion or channel movement during the post-dam period. Progressive sedimentation flattened the stream gradient, reducing the velocity of stream flows and the capacity (power) of the single-thread river to erode its banks and initiate channel movement (Bagnold 1966). Additionally, the fine textured sediments transported by the White River formed cohesive banks that were often colonized by vegetation, further increasing resistance to erosion (Wynn and Mostaghimi 2006). Consequently, stands bordering the river channel were relatively protected from scour and persisted throughout the post-dam period. Also, stands located near the channel often occurred on natural levees with a slightly higher elevation and probably coarser sediments than the surrounding floodplain, and were thus more protected from prolonged reservoir inundation that can cause mortality.

Stand persistence and bank resistance to erosion along the river channel also impeded channel movement, point bar formation, and the establishment of new stands on the inside of river curves. Seedling establishment was instead largely limited to recent, unvegetated sediment deposits that were predominately located behind the levees and near the wooded edge of the floodplain or in abandoned fields. Historically, higher

surfaces that were farther from the channel were used more for agriculture because they were drier. With increased flooding and the related abandonment of many agricultural fields, these surfaces were among the main open sites for colonization by cottonwood. This trend will likely continue over time, up to the point that all fields are forested, as continued sedimentation and flattening of the gradient allow overbank flows to deposit sediment farther from the channel.

Turnover of vegetation

Although the area of woodland on the delta increased over the post-dam period, this expansion was curtailed at times by mortality from high stages of Fort Randall Reservoir. Up to nine percent of the total woodland area was lost following flood years (1997 and 2011) and a high water year (2010) on the Missouri River. Woodland losses were concentrated in the lower portions of the delta where there was prolonged flooding behind natural levees and on younger alluvial surfaces closer to the reservoir. Vegetation turnover between low and high pool cycles was common in the lower delta; consequently, a high proportion of the delta's woodland area was in the youngest age classes.

During the record Missouri River flood of 2011 (Grigg et al. 2011, Dixon et al. 2015), vegetation on the delta was flooded for over three months, far exceeding the typical duration of peak flows on the pre-development Missouri River (one to several weeks; NRC 2002a). By late July, inundated cottonwoods showed signs of flood stress, including precocious leaf senescence (yellowing) and scattered mortality (Appendix Figure 9). Many trees succumbed to flood-related mortality up to two years later, probably due to prolonged hypoxic conditions (Appendix Figure 10). These findings are

consistent with previous studies that documented cottonwood intolerance to continual flooding during the growing season (Regehr et al. 1975, Amlin and Rood 2001, Nielsen et al. 2010). Flood-related mortality in 2011 may have been exacerbated by saturated conditions in 2010, which was also a high water year on the Missouri River. Saturated conditions for two years in a row may have killed trees that would have otherwise tolerated one year of inundation.

Willow mortality was also observed following the 2011 flood, although it was less widespread than cottonwood mortality. While willow species are more flood tolerant than *Populus* spp. and often thrive under saturated conditions (Hosner 1960, Pereira and Kozlowski 1977, Noble 1979, Busch et al. 1992, Stromberg et al. 1997, Everson and Boucher 1998, Amlin and Rood 2001), many failed to survive in locations where plants were entirely submerged or nearly submerged for the majority of the growing season. Mortality patterns of cottonwood and willow suggest that a reduction in the maximum reservoir water levels could reduce the amount of vegetation mortality during high pool cycles, thus allowing woody communities and associated biodiversity to persist (Johnson 2002, Volke et al. 2015).

Flood-related woodland mortality or damage for a given measurement interval amounted to less than 10 percent of the total pre-flood woodland area. Although not inconsequential, periodic mortality may not be an entirely negative phenomenon, as mortality events and subsequent cottonwood re-colonization may help maintain areas of young cottonwood forests in the delta system like river meandering and channel widening or narrowing used to do during the pre-dam era (Johnson et al. 1976, Scott et al. 1996, Johnson et al. 2012). Along the historical Missouri River, forest mortality regularly

occurred during large floods when the channel moved many kilometers, eroding large areas of floodplain forest (Johnson 1992, NRC 2002a). As was often noted by Lewis and Clark in their journals, the Missouri River channels were littered with coarse woody debris ranging from massive cottonwood trunks to sawyers and brush, indicating that forest and floodplain destruction was common on the pre-dam river (Coues 1893). This process created new alluvial surfaces suitable for colonization by pioneer seedlings and helped maintain young forest age classes on newly forming floodplain surfaces. While the primary cause of woodland mortality on the delta (submergence and prolonged inundation) was different than along the historical Missouri River (erosion), it may double as a means to maintain young stands on the delta.

Novel environmental conditions following a mortality event on the delta may have a substantial long-term influence on future vegetation composition. During large floods on the historical Missouri River, vegetation near the channel was generally removed and replaced by bare alluvial deposits, the ideal seedbed for cottonwood and willow (Johnson 1992). In contrast, flood-killed vegetation on the delta was only partially removed from the site, leaving behind abundant standing dead and downed woody debris from the former stand. Further, lowering of heightened reservoir levels was often delayed until after the peak seed dispersal period of cottonwood and willow (May-June), favoring colonization by other species that disperse seeds later in the season. Observations two years after the 2011 flood documented that cottonwood and willow recolonized some sites where there was mortality (Appendix Figure 11), but were absent from other sites colonized by Canada thistle (Appendix Figure 20), an exotic herbaceous species that often thrives in disturbed environments (Van Bruggen 1985). While woodland expanded

on the delta over time, these observations suggest that increased frequency and duration of flood events like the one that occurred in 2011 could remove native riparian vegetation and stimulate establishment and expansion of ruderal and exotic species. Thus, adjustment of reservoir operations to a more natural hydrograph could not only encourage establishment and persistence of native woody riparian vegetation, but also prevent proliferation of undesirable species, such as saltcedar (*Tamarix* spp.), which is beginning to be identified in parts of South Dakota (Nagler et al. 2011).

Mixed-age stands on the delta

Although the pioneer species of cottonwood, peachleaf willow, sandbar willow, and yellow willow were absent or extremely rare in the understory of cottonwood forests along the White River, they frequently occupied the understory of cottonwood forests on the White River delta and in the river-delta transition subreach. As understory components, pioneer species occurred with varying abundance across the range of stand ages on the delta and transition subreaches, in stands up to 160 years old. These findings are in sharp contrast to the large body of literature that has documented the pioneer, even-aged nature of cottonwood forests along rivers in North America (Everitt 1968, Johnson et al. 1976, Noble 1979, Bradley and Smith 1986, Rood and Mahoney 1990, Stromberg et al. 1991, Johnson 1994, Friedman et al. 1995, Braatne et al. 1996, Scott et al. 1997, Auble and Scott 1998, Mahoney and Rood 1998, Cooper et al. 1999, Dykaar and Wigington 2000, Johnson et al. 2012). For example, in an inventory of cottonwood stands along the Missouri River in North Dakota, Keammerer (1972) did not find a single cottonwood, peachleaf willow, sandbar willow, or yellow willow seedling in the forest understory. Likewise, Everitt (1968) and Noble (1979) noted that on meandering river

floodplains in the Great Plains, cottonwoods were distributed in distinct bands, each band being of uniform age and originating from a specific flood event. From these studies and those that followed, it is clear that establishment of riparian cottonwoods and related pioneer species is restricted to moist, bare sites that are exposed to full sunlight. In natural rivers, these conditions occur on active alluvial surfaces, such as point bars, bank attached bars, or mid-channel bars.

On the White River delta, however, conditions for pioneer recruitment were sometimes met within established stands of cottonwood trees. Recent sedimentation within many delta stands buried understory vegetation and litter, creating large areas of moist, bare substrate under the forest canopy. Seedlings of pioneer species, particularly cottonwood, often established on these sediments where partial overstory mortality or tree felling by beaver allowed more light to reach the forest floor. Cottonwood and willow recruitment was also observed under the partially flood-killed canopy along the upper Mississippi River following the 1993 flood (Yin 1998).

Recruitment of cottonwood and willow within delta stands was likely further facilitated by elevated groundwater levels adjacent to Fort Randall Reservoir, especially during years of average or slightly above average reservoir stages. Along natural rivers in this region, pioneer recruitment is typically restricted to a six week window during the period of seed dispersal coinciding with receding spring flows and exposure of recently deposited alluvium (Mahoney and Rood 1998). Beyond this recruitment window, seed germination is limited to moist surfaces immediately adjacent to the lowering stream margins that are prone to scour by subsequent high flows and ice. High reservoir stages likely delayed or prevented seasonal groundwater declines on the nearby delta (Simons

and Rorabaugh 1971), thereby increasing the area and persistence of suitable recruitment sites. Therefore in wet years, germination may have been possible for the full length of the seed dispersal period (~10 weeks; Johnson 1994) increasing the opportunities for seedling establishment. Once established, elevated water tables may have protected developing seedlings from drought stress, which is a common cause of mortality (Johnson 1994, Mahoney and Rood 1998). Moreover, seedlings that colonized existing stands were more likely to be protected from subsequent scour that is a common cause of mortality for seedlings on exposed surfaces near the channel margins.

In 25 percent of delta stands, conditions remained sufficiently favorable to allow younger cottonwood cohorts to recruit into the overstory population. Mixed-age stands were dominated by younger trees, with only a few remaining trees from the original stand. Because cottonwood is intolerant of shade (McClendon and McMillen 1982, Shafroth et al. 1995), successive recruitment events were limited to stands where prolonged reservoir inundation exceeded the flood tolerance of cottonwood (2-3 growing season months; Amlin and Rood 2001), resulting in near complete mortality of the overstory. Historical aerial photos suggest that at some locations, development of mixed-age stands was facilitated by past forest clearing followed by flooding, which opened up stands to enable cottonwood recruitment.

These findings show that reproduction of cottonwood and willow sometimes occurred on new alluvial surfaces formed by vertical accretion within stands rather than by erosional and depositional processes along the channel margins. Formation of uneven-aged stands of cottonwood trees spanning 16-37 years of age has rarely been documented along rivers, although extended cottonwood recruitment periods have been observed on a

young island (Merigliano 1998), in a filling arroyo (Friedman et al. 2005), and during the processes of channel narrowing (Friedman et al. 1996) and channel abandonment (Stella et al. 2011).

Given that cottonwood forests along the mainstem Missouri River are now aging in place with few opportunities to reproduce (Dixon et al. 2012, Johnson et al. 2012, Scott et al. 2013), it is notable that new cottonwoods have recruited within some existing stands on the White River delta. These findings indicate that, unlike remnant forests along the Missouri, pioneer delta forests may be, to some degree, self-maintaining, even in the absence of erosion and channel migration. Although some stands on the delta may have a relatively short life span, especially those located within the reservoir margins, evidence suggests that eventual replacement of these forests is possible. Thus, even if forests are periodically lost following prolonged inundation events, the area of cottonwood forest on the delta is likely to remain relatively stable or increase over time.

Similarity of the White River delta to the White River

Aside from brief descriptions in the journals of Lewis and Clark (Coues 1893) and Patrick Gass (MacGregor 1997), and witness tree records from the 1890s public land surveys, little is known about the pre-dam vegetation on what is now the White River delta. Witness tree records indicated that the floodplain was dominated by cottonwoods, with a few scattered American elms. The survey notes also indicated that the mouth of the White River was dominated by willows.

Due to the paucity of pre-dam data, the cottonwood forest community along the contemporary White River serves as the best reference for the pre-dam conditions on what is now the White River delta. Because the White River's hydrologic and sediment

regimes remain largely undisturbed, it maintains natural cottonwood forest dynamics that should closely match the pre-settlement condition. However, livestock grazing, which is common in the basin, probably influences vegetation along the river (Kauffman and Krueger 1984, Auble and Scott 1998, Patten 1998, Belsky et al. 1999, NRC 2002b, Scott et al. 2003), but its effects on the White River's cottonwood forests have not been quantified. Clearing for agriculture is a cause of forest removal along the White River.

Cottonwood forests on the delta and along the river developed via similar successional trajectories. The youngest stands were dominated by high densities of cottonwood and willow. The older stands were dominated by cottonwood and green ash, with scattered Russian olive, American elm, and box elder. All but two of the species that occurred on the delta were also present along the White River, indicating a high degree of vegetation community similarity. Moreover, the woody plant communities in each subreach were dominated by native species; Russian olive was the only exotic woody species that occurred within the study reach.

Early successional stands of pioneer seedlings and saplings (cottonwood, peachleaf willow, and sandbar willow) were common throughout the White River and delta subreaches. Pioneer seedling and sapling densities were not statistically different between the two subreaches, indicating that the early successional plant community was very similar along the White River-White River delta continuum.

The overstory vegetation on the delta and along the White River was nearly identical. All of the tree species that occurred on the delta also occurred along the White River, and exhibited similar ranges of frequency, density, and dominance among stands of comparable age. The Bray-Curtis similarity score based on mean species importance

values indicated that the overstory vegetation was 85 percent similar. Likewise, the Spearman's rank correlation coefficient (r_s) based on mean species importance values indicated that the rank order abundance of overstory species was nearly identical between the delta and the White River. Collectively, these findings indicate that the delta provided a similar environment and supported a similar assemblage of native woody species as the White River.

Despite the many similarities, there were some compositional differences between the delta and the White River, especially in the understory. Specifically, the delta supported a greater proportion of wetland affiliated species (e.g., willows) than the river, and the river supported a greater proportion of non-wetland species (e.g., poison ivy) than the delta. These compositional differences are likely explained by increased moisture availability on the delta (due to the reservoir), which favored plants that tolerate or require persistent moisture throughout the growing season.

Compositional differences also may have been due to the greater proportion of younger stands on the delta relative to the White River. Younger stands that are often closer to the channel and on lower topographic positions naturally support a greater proportion of moisture tolerant, pioneer species than later successional stands on higher surfaces. Species richness tends to be lowest in younger stands where the understory is undeveloped and mid- and later successional species are absent (Johnson et al. 1976). Hence, it was expected that some later successional species that occurred along the White River would be absent or rare on the delta. Further, the chronic sedimentation in the delta environment likely prevented more upland, later successional species from establishing.

Similarity of the White River delta to Missouri River remnant reaches

Due to the scarcity of pre-dam studies, it is impossible to know the exact composition of cottonwood forests that historically dominated the Missouri River floodplain. General descriptions of the pre-settlement flora are available from the reports of early explorers, including Lewis and Clark (Coues 1893) and Audubon (1897), and also from General Land Office surveys that took place in the mid- to late 1800s. A more formal study by Johnson (1950) investigated the cottonwood forest successional sequence near Vermillion, South Dakota, but only measured the dominant species. Wilson (1970) likewise provided a discussion of cottonwood forest succession along this reach. Studies by Weaver (1960) and Stevens (1945) described the vegetation along the river in and around Nebraska and in North Dakota, but presented little quantitative information about species abundances or the relative proportions of vegetation types on the pre-dam floodplain. None of these early studies provided a substantial tally of the pre-dam flora.

Most of what is known about the composition of pre-dam cottonwood forests has been derived from studies that took place over 15 years after the onset of river regulation along the Garrison reach in North Dakota (Keammerer et al. 1975, Johnson et al. 1976). Although the impacts of flow regulation on vegetation were already underway (e.g., cessation of flooding, decreased channel movement), these studies provided the best available reference for pre-dam cottonwood forests along the Missouri River. A more recent inventory of remnant cottonwood forests (Dixon et al. 2010) also provided insight to the historical composition of pre-dam forests, especially the overstory community, as many of the existing forests established prior to or shortly after dam closure.

The woody plant community on the contemporary White River delta was similar to that along the Garrison reach of the Missouri River in 1969-1970. Woody plant species richness on the delta was greater than or equal to that of the Garrison reach, depending on stand age. The overstory composition at the two sites was nearly identical, with the exception of bur oak, which did not occur on the delta but was present in low numbers along the Garrison reach. The absence of bur oak on the delta is likely explained by its sensitivity to chronically wet soil, as evidenced by its tendency to occur on higher floodplain surfaces and in upland mesic ravines (Johnson et al. 1976).

Although there was a high degree of similarity in the overstory vegetation on the delta and along the Garrison reach, there were some differences in the understory vegetation. Most notably, the delta understory had a higher proportion of wetland affiliated species than that of the Garrison reach. Likewise, upland species were more common along the Garrison reach than on the delta. These differences are likely partly explained by environmental differences between the two sites. At the time of the Garrison study, flow regulation had already been underway for over 15 years. Johnson et al. (1976) suggested that the effects of flow regulation, including channel incision and cessation of flooding, created a more xeric environment that favored species able to persist under drier conditions. Further, in the absence of flooding, it was expected that mortality would be highest for species with wetland affinities. These effects were probably most apparent for the understory vegetation, which responds more rapidly to changing environmental conditions. In contrast, the White River delta was an aggrading system with frequent overbank flooding and a high water table, and consequently supported a vegetation community that included wetland species. These environmental differences likely explain

some of the variation in community composition between the delta and the Garrison reach.

The differences in understory composition also may be partially due to natural biogeographic variation in species abundances. The Garrison reach is located over 500 rkm upstream (to the ~north) of the White River delta and is characterized by slightly different climate and soils, factors which influence the distribution and abundance of plant species (Gleason 1926). Although only plant species with ranges common to both sites were included in the analysis, it is possible that some species were more common at one site than the other due to regional environmental differences that influenced the availability of propagules and the growth and survival of recruitment.

The woody plant communities occurring on the contemporary White River delta and Gavins Point reach of the Missouri River were also similar. Woody plant species richness on the delta was lower than or equal to species richness along the Gavins Point reach, depending on stand age. The majority (75 percent) of species that occurred on the delta were also present along the Gavins Point reach. Not all of the species present along the Gavins Point reach, however, occurred on the White River delta. Many of the species that were absent from the delta were non-wetland species, such as American plum and eastern red-cedar. Despite a few compositional differences, these findings are further evidence that the delta supported native cottonwood forest communities similar to those found in remnant reaches of the Missouri River.

As in the Garrison reach, compositional differences between the delta and Gavins Point vegetation are likely partly explained by environmental differences between the two sites. At the time of the Gavins Point study, flow regulation had been in progress for

over 50 years. Due to the cumulative effects of the six upstream dams, hydrologic alterations along the Gavins Point reach are the most extreme of any of the Missouri River remnant reaches (Galat and Lipkin 2000). Post-dam changes include channel degradation (USACE 2004) and significant declines in annual peak flows (Galat and Lipkin 2000), both processes that strongly contribute to xerification of the floodplain. These alterations likely explain the greater proportion of non-wetland species along the Gavins Point reach.

Floristic differences between the delta and the Gavins Point reach also may be due to biogeography. The Gavins Point reach is located over 200 rkm to the southeast of the delta, in a region with a milder and wetter climate, different soils, and greater species richness on the floodplain and in the surrounding landscape (Dixon et al. 2010). Given these factors, it was expected that certain species had a greater probability of occurring at one site or the other.

Some of the compositional differences between the White River delta and the Gavins Point reach also may be due to differences in land use patterns and land use intensities in the surrounding landscape. While the area surrounding the delta has remained relatively undeveloped, the area surrounding the Gavins Point reach has undergone a substantial amount of urban and agricultural expansion during the last century (Dixon et al. 2010, Dixon et al. 2012). Thus, species that benefit from land use change, such as eastern red-cedar, may have had a higher probability of occurring in the Gavins Point reach than on the delta. Xerification of the floodplain further enabled colonization by upland species. A combination of land use, environmental, and

biogeographic effects likely explains the compositional differences between the delta and Gavins Point reach vegetation.

The high similarity between the woody plant community on the White River delta and those along the White River and remnant reaches of the Missouri River supports the observation that the vegetation on the delta was similar to pre-dam types. Reservoir deltas associated with unregulated or lightly regulated contributing rivers, such as the White River, may be more successful sites for recovery of cottonwood forests than would be parcels of the Missouri River floodplain in remnant reaches, as they retain many natural riverine processes such as overbank flooding, sedimentation, and spring flood pulses and summer drawdown. These processes, known to help maintain healthy riparian ecosystems, would be a missing ingredient for success in restoring riparian forests on remnant floodplains.

A recently released cottonwood management plan (USACE 2011) proposes to preserve existing stands and to reestablish new stands along the Missouri River on retired cropland and along created fluvial features such as side channels, oxbow lakes, and backwaters. This is a welcome and long-awaited program that, if implemented, could potentially help solve a problem first reported 40 years ago. While this approach would help to maintain cottonwood and willow trees on the floodplain, it probably would not restore the cottonwood forest ecosystem, particularly the high species diversity known to exist in pre-regulation stands. Pre-regulation forests were established on relatively low floodplain surfaces and were repeatedly aggraded by alluviation from floods. As a result, these communities supported a significant proportion of wetland affiliated species. This species diversity cannot be restored by tree planting on relatively high, former floodplain

surfaces where most farming is practiced. Moreover, it would be a daunting and expensive task for generations of managers to secure the land, plant several hundred hectares each year within remnant reaches (Dixon et al. 2012), and manage weeds and animal depredation on an increasingly larger area (Novotny and Johnson 2007). Hence, reservoir deltas provide new opportunities to counterbalance losses of high biodiversity riparian ecosystems along the Missouri River.

The future of the delta

If recent trends continue, the area of the delta will likely increase, albeit at a declining rate. Continued sediment inputs from the White River will extend and aggrade the "sediment wedge," allowing the delta to expand up and down gradient. The downstream portions of the delta located within the reservoir margins may aggrade up to the maximum reservoir pool. As the delta expands, the environmental moisture gradient along the White River-White River delta continuum will also lengthen. The lowest portions of the delta that are currently occupied by cattails and willows will trap sediment and aggrade, creating a more favorable environment for cottonwood establishment and survival. With continued expansion and aggradation of delta surfaces, cottonwood and other moisture sensitive plants will expand downstream. Likewise, progressive flattening of the gradient in the upstream direction will increase the frequency and duration of backup flooding and overbank flows that deliver new sediment to the floodplain. Some or all of the transition subreach may become increasingly similar to the delta environment (increasingly flattened channel gradient and subirrigated conditions), facilitating expansion of woodland in the upstream direction. Over time, woodland also may expand laterally on the floodplain, to a maximum extent from valley wall to valley wall.

Current trends indicate that the rates of delta and woodland expansion will continue to decline over time, especially as abandoned fields become occupied with cottonwood-willow communities and the availability of open sites diminishes. In the absence of channel migration and erosion, periodic inundation similar to the magnitude observed during the 2011 flood may eventually be one of the only means to remove (kill) older forests and maintain significant portions of the delta in young forest, which will otherwise be restricted to the youngest alluvial surfaces at the delta fringes. Without periodic flooding from the reservoir and channel movement, the future delta might exhibit low cottonwood recruitment and aging cottonwood forests similar to the Missouri River's mainstem remnant reaches.

Of course, current trends may not continue in the future due to expected changes in regional climate and increased water demands in the Missouri River basin. Climate change will likely alter precipitation regimes and produce more variable moisture conditions in the basin (Stone et al. 2001, Ojima and Lackett 2002, Palmer et al. 2008). Reservoir water levels will therefore likely exhibit greater interannual variability, which will affect the multiple designated uses of the Missouri River reservoirs (USACE 2006), along with the hydrogeomorphic dynamics of reservoir deltas and related vegetation communities. A warmer climate will likely increase demands for irrigation withdrawals in the basin, potentially reducing the amount of water stored in the Missouri River system. With decreased reservoir storage and increased reservoir level variability, the functional delta would shift down gradient and vegetation turnover on the lower delta would become more frequent. For these reasons and other unanticipated environmental

changes in the Missouri River basin, it is difficult to predict the future trajectories of the Missouri River reservoir deltas and associated vegetation communities.

Advantages of deltas for restoration

The successful establishment of pioneer forests on the White River delta indicates that other deltas forming in Missouri River reservoirs also may be favorable locations for recovery or restoration of native pioneer forests. A preliminary survey of nine reservoir deltas along the Missouri River, including the White River delta, proposed that reservoir deltas may offer distinct advantages over mainstem, remnant reach restoration sites or at least should be considered within the mix of ecological restoration solutions (Volke et al. 2015). The advantages of reservoir deltas are:

1) **Large land area** – The Missouri River's reservoir deltas currently occupy over 1,000 km^2, more than twice the area of cottonwood dominated forest currently in remnant reaches.
2) **High proportion in public land** – Much of the delta land is under public ownership (state and federal), hence, large-scale restorations can be conducted more easily and effectively than on the patchwork of public and private lands comprising the Missouri River floodplain.
3) **More natural hydrologic and sediment regimes** – Deltas associated with unregulated or lightly regulated contributing rivers, such as the White River, retain many natural riverine processes such as overbank flooding, sedimentation, and spring flood pulses and summer drawdown.

4) **Often dominated by cottonwood and willow** – The early successional plant community, including cottonwood and willow, has been establishing under current reservoir operations on most deltas.
5) **High potential to expand** – Deltas have a high potential to expand riparian forests, especially if reservoir management is modified to minimize backup effects and elevated groundwater conditions, and more closely mimic the natural hydrologic regime.
6) **Provide shallow aquatic habitat** – Deltas provide shallow aquatic habitat for native fish and other aquatic species that is in short supply in the modern Missouri River.

Restoration options

The expansion of woodland on the White River delta during the post-dam era represents passive restoration (natural recovery) of native riparian vegetation. Woodland expansion appears to have been driven by inadvertent environmental changes brought about by the presence of Fort Randall Reservoir. This is in contrast to active restoration, which includes deliberate approaches such as re-regulation of dams, removal of non-native plants and weeds, planting programs, or habitat improvement for targeted species (Kauffman et al. 1997). There are several options to enhance riparian forest establishment on Missouri River reservoir deltas.

Current reservoir management does not consider the effects of reservoir pool dynamics on the ecological condition of deltas. Both natural forest establishment and stand survival could be improved by slight modification of reservoir storage rules to better mimic the natural flow regime: higher water in spring and lower water in summer

and fall. Declining water levels during the seed dispersal period (June-July) would increase recruitment of cottonwood and willow on exposed sand and mud flats (Mahoney and Rood 1998). A second modification of current reservoir operation rules would be to prohibit the occasional prolonged high stage conditions that exceed the flood tolerance of cottonwood (2-3 growing season months; Amlin and Rood 2001). Likewise, a small, permanent reduction in maximum reservoir levels could reduce vegetation turnover between low and high pool cycles, thus creating more permanent woody communities and higher associated biodiversity (Johnson 2002). This method could be improved by first removing undesirable plants, such as the noxious Canada thistle that has been observed on the White River delta, followed by prescribed restorative reservoir water levels. A similar approach has been employed along other rivers (Taylor et al. 1999, Cooper and Andersen 2012). Adjusting storage reservoir water level regimes, however, may have consequences for operational objectives, such as hydropower production. Thus, any ecological benefits would have to be weighed against operational costs.

The establishment and expansion of pioneer forests on deltas could be enhanced by planting cottonwood and willow trees. This has been suggested as one potential restoration option in remnant reaches of the Missouri River (Johnson 1992, NRC 2002a, USACE 2011) and has been used along degraded rivers in the American West (Friedman et al. 1995, Taylor and McDaniel 1998, Taylor et al. 1999, Sprenger et al. 2002, Bhattacharjee et al. 2006, Golet et al. 2008, Bunting et al. 2013). The ideal sites for planting on deltas would be bottoms currently unvegetated or sparsely vegetated, and located upstream of the normal operating reservoir pool in locations that are protected from prolonged reservoir inundation. Planting of native riparian trees should supplant

establishment of non-native and undesirable plants, as has been suggested for restoration of dewatered reservoirs following dam removal (Shafroth et al. 2002, Michel et al. 2011). Additionally, sites that are currently occupied by undesirable plants (e.g., Canada thistle or common reed [*Phragmites australis* (Cav.) Trin. ex Steud.]) could be mechanically or chemically treated and then planted with fast-growing pioneers to outcompete weeds and initiate natural successional processes (Taylor and McDaniel 1998). Survival of cottonwood-willow plantings could be improved through reservoir management.

Finally, land managers should prioritize riparian forests on deltas to maximize their restoration potential. Land uses that typically result in the loss of forest area or impede forest expansion on deltas include clearing of woody vegetation for pasture or cultivation, planting food plots for game species, and permanent cultivation of the floodplain. Restrictions on these activities could improve the establishment and survival of pioneer forests over the long-term.

Research needs

Much more needs to be learned about the potential importance of reservoir deltas in the restoration or recovery of large regulated river ecosystems. There is surprisingly little information regarding the physical and ecological processes that shape these emerging deltas, and only very limited information exists regarding the value of deltas to aquatic and terrestrial species (Volke et al. 2015). Before specific restoration recommendations can be formulated, study of post-dam forest recruitment patterns on reservoir deltas needs to be completed using remote sensing and field investigations. Future studies should seek to quantify the current composition and extent of vegetation on deltas and the hydrogeomorphic dynamics of deltas as they relate to vegetation

patterns. This information is needed to determine how passive and active restoration on deltas could improve establishment and survival of pioneer forests.

CONCLUSIONS

1) The formation of Fort Randall Reservoir in 1953 initiated major changes to the physical template of the lower White River, creating a novel delta that did not exist in the pre-dam period. The delta was a highly depositional environment where the channel and floodplain aggraded by as much as 12 m during the post-dam period. Additional physical changes due to chronic sedimentation included flattening of the stream gradient, narrowing of the active channel, formation of prominent natural levees adjacent to the active channel, and producing and exposing bare sediments throughout the delta. These geomorphic features and conditions provided the physical template upon which cottonwood forests developed, albeit differently than they did historically along the free-flowing Missouri River. The hydrogeomorphic dynamics on the delta were largely maintained by the natural flow and sediment regimes of the White River interacting with the stage dynamics of Fort Randall Reservoir.
2) The area of riparian woodland on the delta increased by about 50 percent during the post-dam period. Whereas the pre-dam bottomland in what is now delta was dominated by older woodland, the post-dam delta was dominated by younger woodland. Woodland expansion was curtailed at times by mortality caused by high reservoir stages.
3) Cottonwood forests similar to pre-dam types established on the post-dam White River delta. The woody plant community in these new forests was largely composed of native species that also occurred along the natural White River and along remnant reaches of the Missouri River. Hence, the delta community was not an entirely novel assemblage of species, but rather, an analogue of the natural river system.

4) Distribution patterns of plant species followed a longitudinal environmental moisture gradient along the White River-White River delta continuum, ranging from relatively dry, riverine conditions along the White River that frequently supported non-wetland species, to relatively wet, lacustrine conditions in the lower delta that favored wetland affiliated species, especially willows. These patterns indicate that reservoir water levels maintained subirrigated conditions during the growing season that supported a high proportion of wetland affiliated species. The accumulation of finer textured soils in the delta also may have contributed to a higher proportion of wetland affiliated species. In contrast, the White River exhibited a more dynamic, seasonable moisture regime and supported a comparatively greater number of non-wetland species.
5) Reservoir deltas like the one forming at the confluence of the White River and Fort Randall Reservoir offer new opportunities to counterbalance losses of high biodiversity riparian ecosystems along the Missouri and other regulated rivers. Riparian ecosystems in western North America occupy only a small percentage of the total land area, but are vital to maintaining regional biodiversity and ecological services. The majority of the length of the Missouri River in the Dakotas was inundated by reservoirs and the floodplain forest was destroyed. What remains is aging and losing biodiversity in the absence of natural flow and sediment regimes, especially flooding. Deltas offer promise as recruitment sites for the pioneer cottonwood community; hence, deltas are one bright spot in a rather dark future for biodiversity along the Missouri River and probably other regulated river systems.
6) Natural forest establishment and stand survival on reservoir deltas could be improved by passive and active restoration efforts, including modification of reservoir storage

rules to better mimic the natural flow regime. Because deltas represent some of the more geomorphically active and hydrologically dynamic environments remaining in regulated rivers, they may offer distinct advantages over mainstem, remnant reach restoration sites, or at least should be considered within the mix of ecological restoration solutions.

7) There is surprisingly little information regarding the physical and ecological processes that shape emerging reservoir deltas. Further study of the potential of deltas to assist in the recovery of riverine and riparian ecosystems and to raise the level of ecosystem services provided to the public on regulated rivers is urgently needed.

APPENDIX A: FIGURES

Appendix Figure 1. Cottonwood forests along the White River in South Dakota upstream of stand 87. Note the bands of Russian olive adjacent to the active channel. Date: June 24, 2013.

Appendix Figure 2. Cottonwood forests (near stand 58) along the White River in South Dakota. Note the bands of Russian olive adjacent to the active channel and the numerous bank-attached and mid-channel bars. Date: July 3, 2013.

Appendix Figure 3. A 63 year old cottonwood forest (stand 49) along the White River in South Dakota. Note the abundant riverbank grape and cover by riparian shrubs in the understory. Date: July 1, 2013.

Appendix Figure 4. A 71 year old cottonwood forest (stand 52) on an attached island along the White River in South Dakota. Note the high cover and diversity of woody understory vegetation. Date: June 18, 2013.

Appendix Figure 5. A 33 year old cottonwood forest (stand 39) along the White River in South Dakota, with evidence of livestock grazing. Note the relatively open canopy and dominance of smooth brome in the understory. Date: June 28, 2013.

Appendix Figure 6. Downstream view of the White River delta in South Dakota near rkm 3 during the record Missouri River flood of 2011. Fort Randall Reservoir is in the background. Date: August 10, 2011.

Appendix Figure 7. Aerial view of the distal end of the White River delta at the confluence of the White and Missouri Rivers on Fort Randall Reservoir in South Dakota. Date: August 15, 2014. Photo credit: Gray Tappan.

Appendix Figure 8. Recent sediment deposits in a middle age cottonwood forest on the White River delta (Gammon Bottoms) in South Dakota. Note the buried tree root flares and the scarcity of understory vegetation. Date: August 1, 2011.

Appendix Figure 9. Flooded young cottonwood and willow trees at the distal end of the White River delta in South Dakota during the record Missouri River flood of 2011. Note the yellowing leaves and scattered mortality. Date: July 18, 2011.

Appendix Figure 10. Photograph of the White River delta in South Dakota in June 2013, showing riparian woodland mortality (grey colored standing dead trees) caused by the 2011 Missouri River flood.

Appendix Figure 11. Extensive overstory mortality on the White River delta (near stand 22) in South Dakota following the Missouri River flood of 2011. Note the post-2011 flood recruitment of cottonwood and peachleaf willow in the understory. Date: May 30, 2013.

Appendix Figure 12. Extensive mortality of riparian vegetation on the distal end of the White River delta in South Dakota following the record Missouri River flood of 2011. Date: October 1, 2011.

Appendix Figure 13. Cottonwood recruitment in an abandoned agricultural field in the transition subreach upstream of the White River delta (Byre Bottoms) in South Dakota. Date: June 17, 2011.

Appendix Figure 14. Dense peachleaf willow saplings (stand 71) on the lower White River delta in South Dakota. Date: June 11, 2013.

Appendix Figure 15. Early successional cottonwood and sandbar willow on a lateral bar (stand 11) along the White River in South Dakota. Date: August 2, 2011.

Appendix Figure 16. Cottonwood seedlings in a tree size stand on the White River delta (Neugebauer Bottoms) in South Dakota. A snag created a small opening in the forest canopy, allowing sunlight to reach recent sediment deposits in this stand. Date: August 16, 2011.

Appendix Figure 17. Cottonwood seedlings in a tree size stand on the White River delta (Gammon Bottoms) in South Dakota. Tree felling by beaver created a small opening in the forest canopy, allowing sunlight to reach recent sediment deposits in this stand. Date: August 17, 2011.

Appendix Figure 18. Large ice scar on an old cottonwood tree in the transition subreach just upstream of the White River delta (near stand 1) in South Dakota. Date: June 7, 2011.

Appendix Figure 19. Adventitious roots growing from the base of a peachleaf willow sapling on the lower White River delta (near stand 19) in South Dakota. Note the sediment accumulation at the base of the trunk. Date: June 3, 2013.

Appendix Figure 20. A thirteen year old cottonwood forest on the White River delta (stand 26) in South Dakota with dense post-2011 flood recruitment of Canada thistle in the understory. Date: June 10, 2013.

APPENDIX B: TABLES

Appendix Table 1. Overstory species composition in the 35 stands along the lower White River and on the White River delta in South Dakota. The dashes indicate no applicable data.

Species	Frequency	Relative Frequency (%)	Density (trees/ha)	Relative Density (%)	Dominance (m²/ha)	Relative Dominance (%)	Importance Value (200)	Importance Value (300)
White River delta								
Stand 2								
Box elder	5.0	3.2	3.6	1.9	0.06	0.3	2.2	5.4
Cottonwood	97.5	61.9	140.7	73.8	20.28	96.7	170.5	232.4
Green ash	55.0	34.9	46.5	24.4	0.61	2.9	27.3	62.2
Total	157.5	100.0	190.8	100.0	20.96	100.0	200.0	300.0
Stand 3								
Cottonwood	100.0	74.1	242.3	65.0	21.46	78.9	143.9	218.0
Green ash	27.5	20.4	34.9	9.4	0.53	1.9	11.3	31.7
Russian olive	7.5	5.6	95.5	25.6	5.21	19.2	44.8	50.3
Total	135.0	100.0	372.7	100.0	27.20	100.0	200.0	300.0
Stand 6								
Cottonwood	100.0	93.0	817.8	98.1	18.13	99.1	197.2	290.3
Peachleaf willow	7.5	7.0	15.6	1.9	0.16	0.9	2.8	9.7
Total	107.5	100.0	833.4	100.0	18.30	100.0	200.0	300.0
Stand 8								
Cottonwood	100.0	100.0	507.2	100.0	11.56	100.0	200.0	300.0
Total	100.0	100.0	507.2	100.0	11.56	100.0	200.0	300.0
Stand 15								
Cottonwood	100.0	97.6	444.1	98.7	41.20	99.9	198.6	296.2

Green ash	2.5	2.4	2.8	0.6	0.02	0.1	0.7	3.1
Russian olive	0.0	0.0	2.8	0.6	0.02	0.1	0.7	0.7
Total	102.5	100.0	449.8	100.0	41.25	100.0	200.0	300.0
Stand 16								
Cottonwood	100.0	93.0	227.4	98.1	5.25	99.1	197.2	290.3
Green ash	2.5	2.3	1.4	0.6	0.02	0.4	1.0	3.3
Peachleaf willow	5.0	4.7	2.9	1.3	0.03	0.5	1.8	6.4
Total	107.5	100.0	231.7	100.0	5.30	100.0	200.0	300.0
Stand 17								
Cottonwood	100.0	59.7	69.9	73.8	10.94	92.8	166.5	226.2
Green ash	20.0	11.9	7.1	7.5	0.16	1.4	8.9	20.8
Peachleaf willow	42.5	25.4	16.0	16.9	0.64	5.4	22.3	47.7
Russian olive	5.0	3.0	1.8	1.9	0.05	0.4	2.3	5.3
Total	167.5	100.0	94.8	100.0	11.79	100.0	200.0	300.0
Stand 20								
Cottonwood	100.0	52.6	82.9	65.4	3.17	65.6	131.0	183.7
Green ash	15.0	7.9	6.4	5.0	0.10	2.0	7.0	14.9
Peachleaf willow	55.0	28.9	28.7	22.6	1.32	27.4	50.0	79.0
Russian olive	20.0	10.5	8.8	6.9	0.24	5.0	11.9	22.5
Total	190.0	100.0	126.7	100.0	4.83	100.0	200.0	300.0
Stand 21								
Cottonwood	100.0	66.7	81.9	83.8	3.07	80.8	164.6	231.3
Peachleaf willow	50.0	33.3	15.9	16.3	0.73	19.2	35.4	68.7
Total	150.0	100.0	97.8	100.0	3.80	100.0	200.0	300.0
Stand 26								
Cottonwood	96.2	59.5	181.1	76.9	3.14	75.9	152.8	212.3
Peachleaf willow	65.4	40.5	54.3	23.1	1.00	24.1	47.2	87.7
Total	161.5	100.0	235.4	100.0	4.14	100.0	200.0	300.0

Transition								
Stand 1								
American elm	–	–	3.1	6.5	0.05	0.4	6.9	–
Box elder	–	–	0.2	0.4	<0.01	0.0	0.5	–
Cottonwood	–	–	19.3	41.3	11.84	96.9	138.2	–
Green ash	–	–	23.8	50.9	0.31	2.6	53.4	–
Russian olive	–	–	0.4	0.9	<0.01	0.1	0.9	–
Total	–	–	46.8	100.0	12.21	100.0	200.0	–
Stand 10								
American elm	30.0	17.6	29.9	8.2	2.64	7.3	15.5	33.2
Box elder	20.0	11.8	36.8	10.1	0.49	1.3	11.5	23.2
Cottonwood	12.5	7.4	11.5	3.2	18.52	51.3	54.5	61.8
Green ash	95.0	55.9	271.8	74.7	14.28	39.5	114.2	170.1
Peachleaf willow	7.5	4.4	9.2	2.5	0.11	0.3	2.8	7.2
Yellow willow	5.0	2.9	4.6	1.3	0.06	0.2	1.4	4.4
Total	170.0	100.0	363.9	100.0	36.10	100.0	200.0	300.0
White River								
Stand 9								
Cottonwood	85.0	49.3	54.7	44.7	19.91	91.5	136.2	185.4
Green ash	87.5	50.7	67.7	55.3	1.85	8.5	63.8	114.6
Total	172.5	100.0	122.4	100.0	21.76	100.0	200.0	300.0
Stand 39								
Cottonwood	100.0	96.4	185.5	99.1	12.37	99.8	198.9	295.3
Peachleaf willow	3.7	3.6	1.7	0.9	0.02	0.2	1.1	4.7
Total	103.7	100.0	187.3	100.0	12.39	100.0	200.0	300.0
Stand 40								
American elm	2.5	1.8	2.6	0.6	0.11	0.4	1.0	2.8

Box elder	10.0	7.3	15.8	3.8	0.79	2.9	6.6	13.9
Cottonwood	17.5	12.7	18.4	4.4	11.72	42.9	47.3	60.0
Green ash	100.0	72.7	376.7	89.4	12.80	46.9	136.3	209.0
Hackberry	2.5	1.8	2.6	0.6	0.16	0.6	1.2	3.0
Honey locust	2.5	1.8	2.6	0.6	0.10	0.4	1.0	2.8
Peachleaf willow	2.5	1.8	2.6	0.6	1.62	6.0	6.6	8.4
Total	137.5	100.0	421.4	100.0	27.29	100.0	200.0	300.0
Stand 41								
Cottonwood	100.0	90.0	213.3	97.2	18.22	99.1	196.4	286.4
Russian olive	11.1	10.0	6.1	2.8	0.16	0.9	3.6	13.6
Total	111.1	100.0	219.4	100.0	18.37	100.0	200.0	300.0
Stand 43								
Cottonwood	100.0	74.1	390.8	88.8	22.55	95.4	184.1	258.2
Russian olive	35.0	25.9	49.5	11.3	1.09	4.6	15.9	41.8
Total	135.0	100.0	440.3	100.0	23.64	100.0	200.0	300.0
Stand 47								
American elm	5.0	3.0	4.3	1.3	0.49	1.2	2.5	5.5
Cottonwood	60.0	36.4	64.0	18.8	30.70	77.3	96.1	132.4
Green ash	100.0	60.6	273.0	80.0	8.51	21.4	101.4	162.0
Total	165.0	100.0	341.2	100.0	39.71	100.0	200.0	300.0
Stand 49								
American elm	3.8	2.6	1.7	1.0	0.02	0.1	1.0	3.6
Cottonwood	96.2	64.1	138.7	79.8	19.85	97.4	177.2	241.3
Green ash	7.7	5.1	3.3	1.9	0.06	0.3	2.2	7.4
Honey locust	3.8	2.6	1.7	1.0	0.04	0.2	1.2	3.7
Russian olive	38.5	25.6	28.4	16.3	0.40	2.0	18.3	44.0
Total	150.0	100.0	173.8	100.0	20.37	100.0	200.0	300.0

Stand 51								
American elm	3.1	1.9	2.9	0.8	0.04	0.1	0.9	2.7
Cottonwood	71.9	42.6	111.6	29.7	31.89	83.9	113.6	156.2
Green ash	93.8	55.6	261.5	69.5	6.08	16.0	85.5	141.1
Total	168.8	100.0	376.0	100.0	37.99	100.0	200.0	300.0
Stand 52								
Box elder	10.0	5.6	8.7	2.5	0.15	0.2	2.7	8.3
Cottonwood	100.0	55.6	249.2	71.3	58.32	96.0	167.3	222.8
Green ash	60.0	33.3	78.7	22.5	1.43	2.4	24.9	58.2
Peachleaf willow	10.0	5.6	13.1	3.8	0.84	1.4	5.1	10.7
Total	180.0	100.0	349.8	100.0	60.74	100.0	200.0	300.0
Stand 58								
Cottonwood	100.0	62.2	265.9	75.9	16.04	90.3	166.2	228.4
Green ash	0.0	0.0	3.1	0.9	0.05	0.3	1.2	1.2
Honey locust	3.6	2.2	3.1	0.9	0.04	0.2	1.1	3.3
Russian olive	57.1	35.6	78.2	22.3	1.64	9.2	31.5	67.1
Total	160.7	100.0	350.3	100.0	17.76	100.0	200.0	300.0
Stand 84								
Cottonwood	100.0	81.8	215.1	94.4	22.98	99.2	193.7	275.5
Green ash	18.5	15.2	10.5	4.6	0.16	0.7	5.3	20.5
Russian olive	3.7	3.0	2.1	0.9	0.02	0.1	1.0	4.0
Total	122.2	100.0	227.7	100.0	23.15	100.0	200.0	300.0
Stand 86								
Cottonwood	–	–	119.1	93.2	20.99	98.1	191.2	–
Green ash	–	–	7.9	6.2	0.37	1.7	7.9	–
Peachleaf willow	–	–	0.8	0.6	0.04	0.2	0.8	–
Total	–	–	127.8	100.0	21.40	100.0	200.0	–

Stand 87								
Cottonwood	100.0	64.9	98.1	79.2	15.31	96.2	175.4	240.2
Green ash	50.0	32.4	24.5	19.8	0.57	3.6	23.4	55.8
Peachleaf willow	4.2	2.7	1.3	1.0	0.04	0.2	1.3	4.0
Total	154.2	100.0	123.9	100.0	15.92	100.0	200.0	300.0

Appendix Table 2. Sapling layer species composition in 34* stands along the lower White River and on the White River delta in South Dakota.

Species	Frequency (%)	Relative Frequency (%)	Percent Cover	Relative Percent Cover	Density (saplings/ha)	Relative Density (%)	Importance Value	Relative Importance Value
White River delta								
Shrub size stands								
Stand 4								
Cottonwood	50.0	35.3	4.2	27.5	1666.7	14.2	77.0	25.7
Sandbar willow	91.7	64.7	11.1	72.5	10083.3	85.8	223.0	74.3
Total		100.0	15.3	100.0	11750.0	100.0	300.0	100.0
Stand 12								
Cottonwood	33.3	26.7	0.3	2.3	291.7	3.0	31.9	10.6
Sandbar willow	91.7	73.3	14.1	97.7	9541.7	97.0	268.1	89.4
Total		100.0	14.4	100.0	9833.3	100.0	300.0	100.0
Stand 22								
Peachleaf willow	66.7	57.1	10.1	69.3	625.0	31.3	157.7	52.6
Sandbar willow	50.0	42.9	4.5	30.7	1375.0	68.8	142.3	47.4
Total		100.0	14.5	100.0	2000.0	100.0	300.0	100.0
Stand 23								
Cottonwood	100.0	47.1	6.6	54.8	6875.0	44.5	146.4	48.8
Peachleaf willow	87.5	41.2	1.1	9.0	3250.0	21.1	71.2	23.7
Sandbar willow	25.0	11.8	4.4	36.2	5312.5	34.4	82.4	27.5
Total		100.0	12.1	100.0	15437.5	100.0	300.0	100.0
Stand 71								
Cottonwood	100.0	45.5	3.7	8.8	1650.0	7.3	61.6	20.5

Peachleaf willow	100.0	45.5	38.2	91.2	20850.0	92.1	228.7	76.2
Sandbar willow	20.0	9.1	0.0	0.0	150.0	0.7	9.8	3.3
Total		100.0	41.9	100.0	22650.0	100.0	300.0	100.0
Stand 83								
Cottonwood	100.0	42.1	2.6	11.8	4375.0	12.4	66.4	22.1
Peachleaf willow	100.0	42.1	18.3	84.7	30500.0	86.5	213.3	71.1
Sandbar willow	37.5	15.8	0.8	3.5	375.0	1.1	20.3	6.8
Total		100.0	21.6	100.0	35250.0	100.0	300.0	100.0
Tree size stands								
Stand 2								
Green ash	75.0	56.3	8.5	56.9	541.7	56.5	169.7	56.6
Riverbank grape	33.3	25.0	5.3	35.0	83.3	8.7	68.7	22.9
Sandbar willow	8.3	6.3	0.2	1.4	291.7	30.4	38.1	12.7
Yellow willow	16.7	12.5	1.0	6.7	41.7	4.3	23.5	7.8
Total		100.0	15.0	100.0	958.3	100.0	300.0	100.0
Stand 3								
Green ash	91.7	84.6	34.5	95.0	916.7	100.0	279.6	93.2
Riverbank grape	16.7	15.4	1.8	5.0	0.0	0.0	20.4	6.8
Total		100.0	36.4	100.0	916.7	100.0	300.0	100.0
Stand 6								
Cottonwood	25.0	15.8	0.6	2.7	125.0	2.3	20.8	6.9
Green ash	91.7	57.9	17.7	83.0	5083.3	93.1	234.0	78.0
Riverbank grape	41.7	26.3	3.0	14.3	250.0	4.6	45.2	15.1
Total		100.0	21.3	100.0	5458.3	100.0	300.0	100.0
Stand 8								
Cottonwood	41.7	71.4	9.1	70.3	416.7	62.5	204.3	68.1
Sandbar willow	8.3	14.3	1.2	9.0	41.7	6.3	29.6	9.9

Yellow willow	8.3	14.3	2.7	20.6	208.3	31.3	66.2	22.1
Total		100.0	12.9	100.0	666.7	100.0	300.0	100.0
Stand 15								
False indigo	8.3	8.3	0.6	4.3	41.7	6.3	18.9	6.3
Green ash	66.7	66.7	13.9	95.4	500.0	75.0	237.1	79.0
Riverbank grape	16.7	16.7	0.0	0.3	83.3	12.5	29.5	9.8
Russian olive	8.3	8.3	0.0	0.0	41.7	6.3	14.6	4.9
Total		100.0	14.5	100.0	666.7	100.0	300.0	100.0
Stand 17								
False indigo	16.7	15.4	0.2	1.1	125.0	11.5	28.0	9.3
Green ash	33.3	30.8	11.8	76.6	291.7	26.9	134.3	44.8
Riverbank grape	8.3	7.7	2.7	17.4	0.0	0.0	25.1	8.4
Sandbar willow	41.7	38.5	0.0	0.0	625.0	57.7	96.2	32.1
Yellow willow	8.3	7.7	0.8	4.9	41.7	3.8	16.4	5.5
Total		100.0	15.3	100.0	1083.3	100.0	300.0	100.0
Stand 20								
Cottonwood	8.3	4.5	1.6	13.1	41.7	0.6	18.2	6.1
Green ash	33.3	18.2	3.3	26.8	166.7	2.5	47.5	15.8
Peachleaf willow	25.0	13.6	1.8	15.1	83.3	1.3	30.0	10.0
Sandbar willow	83.3	45.5	3.4	27.8	5958.3	91.1	164.4	54.8
Yellow willow	33.3	18.2	2.1	17.2	291.7	4.5	39.8	13.3
Total		100.0	12.1	100.0	6541.7	100.0	300.0	100.0
Stand 21								
Sandbar willow	91.7	100.0	6.8	100.0	19541.7	100.0	300.0	100.0
Total		100.0	6.8	100.0	19541.7	100.0	300.0	100.0
Stand 26								
Cottonwood	37.5	60.0	7.5	66.7	187.5	50.0	176.7	58.9
Peachleaf willow	12.5	20.0	3.8	33.3	125.0	33.3	86.7	28.9

Sandbar willow	12.5	20.0	0.0	0.0	62.5	16.7	36.7	12.2
Total		100.0	11.3	100.0	375.0	100.0	300.0	100.0
Transition								
Tree size stands								
Stand 1								
Green ash	50.0	100.0	14.3	100.0	875.0	100.0	300.0	100.0
Total		100.0	14.3	100.0	875.0	100.0	300.0	100.0
Stand 10								
Box elder	8.3	4.8	3.7	9.0	83.3	3.9	17.7	5.9
Chokecherry	16.7	9.5	3.3	7.9	708.3	33.3	50.8	16.9
Green ash	58.3	33.3	16.6	40.5	708.3	33.3	107.1	35.7
Riverbank grape	58.3	33.3	14.1	34.4	375.0	17.6	85.4	28.5
Woodbine	8.3	4.8	0.1	0.2	83.3	3.9	8.9	3.0
Yellow willow	25.0	14.3	3.3	8.0	166.7	7.8	30.1	10.0
Total		100.0	41.1	100.0	2125.0	100.0	300.0	100.0
White River								
Shrub size stands								
Stand 11								
Cottonwood	100.0	48.0	23.6	42.9	13166.7	28.3	119.2	39.7
Peachleaf willow	8.3	4.0	0.0	0.0	166.7	0.4	4.4	1.5
Sandbar willow	100.0	48.0	31.4	57.1	33166.7	71.3	176.4	58.8
Total		100.0	55.0	100.0	46500.0	100.0	300.0	100.0
Stand 75								
Cottonwood	87.5	46.7	5.6	35.4	4437.5	20.2	102.3	34.1

Sandbar willow	100.0	53.3	10.3	64.6	17562.5	79.8	197.7	65.9
Total		100.0	15.9	100.0	22000.0	100.0	300.0	100.0
Stand 76								
Cottonwood	100.0	53.3	16.6	85.8	7875.0	58.6	197.7	65.9
False indigo	12.5	6.7	0.6	3.2	250.0	1.9	11.8	3.9
Sandbar willow	75.0	40.0	2.1	11.0	5312.5	39.5	90.5	30.2
Total		100.0	19.4	100.0	13437.5	100.0	300.0	100.0
Stand 85								
Cottonwood	100.0	47.1	33.1	81.0	4937.5	50.0	178.1	59.4
Russian olive	25.0	11.8	2.0	4.9	187.5	1.9	18.6	6.2
Sandbar willow	87.5	41.2	5.8	14.1	4750.0	48.1	103.3	34.4
Total		100.0	40.9	100.0	9875.0	100.0	300.0	100.0
Tree size stands								
Stand 9								
Chokecherry	16.7	12.5	3.0	15.2	41.7	2.2	29.9	10.0
False indigo	25.0	18.8	0.3	1.3	708.3	37.8	57.8	19.3
Green ash	75.0	56.3	12.8	64.6	1083.3	57.8	178.6	59.5
Riverbank grape	16.7	12.5	3.8	19.0	41.7	2.2	33.7	11.2
Total		100.0	19.8	100.0	1875.0	100.0	300.0	100.0
Stand 39								
None	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Total		0.0	0.0	0.0	0.0	0.0	0.0	0.0
Stand 40								
Green ash	66.7	57.1	14.1	77.5	625.0	75.0	209.7	69.9
Riverbank grape	50.0	42.9	4.1	22.5	208.3	25.0	90.3	30.1
Total		100.0	18.2	100.0	833.3	100.0	300.0	100.0

Stand 41								
False indigo	12.5	33.3	0.5	18.2	125.0	28.6	80.1	26.7
Russian olive	12.5	33.3	1.9	68.2	0.0	0.0	101.5	33.8
Western snowberry	12.5	33.3	0.4	13.6	312.5	71.4	118.4	39.5
Total		100.0	2.8	100.0	437.5	100.0	300.0	100.0
Stand 43								
Eastern red-cedar	25.0	18.2	0.1	0.5	125.0	3.3	22.0	7.3
Riverbank grape	12.5	9.1	0.3	0.9	0.0	0.0	10.0	3.3
Russian olive	50.0	36.4	20.4	76.2	500.0	13.3	125.9	42.0
Western snowberry	50.0	36.4	6.0	22.4	3125.0	83.3	142.1	47.4
Total		100.0	26.8	100.0	3750.0	100.0	300.0	100.0
Stand 47								
American plum	12.5	33.3	0.0	0.0	62.5	33.3	66.7	22.2
Chokecherry	12.5	33.3	0.0	0.0	62.5	33.3	66.7	22.2
Green ash	12.5	33.3	1.4	100.0	62.5	33.3	166.7	55.6
Total		100.0	1.4	100.0	187.5	100.0	300.0	100.0
Stand 49								
Eastern red-cedar	12.5	4.8	0.0	0.0	62.5	2.0	6.8	2.3
Golden currant	25.0	9.5	0.0	0.0	250.0	8.2	17.7	5.9
Green ash	37.5	14.3	6.1	21.1	1000.0	32.7	68.0	22.7
Riverbank grape	87.5	33.3	8.6	29.5	687.5	22.4	85.2	28.4
Russian olive	75.0	28.6	11.8	40.4	125.0	4.1	73.1	24.4
Western snowberry	25.0	9.5	2.6	9.0	937.5	30.6	49.2	16.4
Total		100.0	29.1	100.0	3062.5	100.0	300.0	100.0
Stand 51								
Chokecherry	10.0	5.9	1.6	3.8	150.0	9.1	18.8	6.3
Green ash	80.0	47.1	29.5	70.7	1100.0	66.7	184.5	61.5
Riverbank grape	80.0	47.1	10.6	25.4	400.0	24.2	96.7	32.2

Total		100.0	41.7	100.0	1650.0	100.0	300.0	100.0
Stand 52								
Box elder	62.5	20.0	29.6	53.0	1125.0	23.1	96.1	32.0
Chokecherry	50.0	16.0	3.4	6.0	1312.5	26.9	49.0	16.3
Fragrant sumac	62.5	20.0	0.8	1.3	750.0	15.4	36.7	12.2
Golden currant	12.5	4.0	0.0	0.0	62.5	1.3	5.3	1.8
Green ash	37.5	12.0	6.0	10.7	375.0	7.7	30.4	10.1
Riverbank grape	87.5	28.0	16.1	28.9	1250.0	25.6	82.5	27.5
Total		100.0	55.9	100.0	4875.0	100.0	300.0	100.0
Stand 58								
Eastern red-cedar	12.5	12.5	0.2	2.4	62.5	12.5	27.4	9.1
False indigo	12.5	12.5	0.0	0.0	62.5	12.5	25.0	8.3
Riverbank grape	12.5	12.5	1.4	13.4	62.5	12.5	38.4	12.8
Russian olive	62.5	62.5	8.6	84.1	312.5	62.5	209.1	69.7
Total		100.0	10.3	100.0	500.0	100.0	300.0	100.0
Stand 84								
Cottonwood	12.5	12.5	1.5	5.6	0.0	0.0	18.1	6.0
Green ash	75.0	75.0	24.2	90.8	687.5	78.6	244.4	81.5
Riverbank grape	12.5	12.5	0.9	3.5	187.5	21.4	37.5	12.5
Total		100.0	26.6	100.0	875.0	100.0	300.0	100.0
Stand 86								
Chokecherry	12.5	100.0	0.0	0.0	250.0	100.0	0.0	0.0
Total		100.0	0.0	0.0	250.0	100.0	0.0	0.0
Stand 87								
Green ash	62.5	100.0	10.8	100.0	187.5	100.0	300.0	100.0
Total		100.0	10.8	100.0	187.5	100.0	300.0	100.0

*The seedling and sapling layers of stand 16 were not sampled; thus, only 34 stands were included in this table.

Appendix Table 3. Seedling layer species composition in 34* stands along the lower White River and on the White River delta in South Dakota.

Species	Frequency (%)	Relative Frequency (%)	Percent Cover	Relative Percent Cover	Density (seedlings/ha)	Relative Density (%)	Importance Value	Relative Importance Value
White River delta								
Shrub size stands								
Stand 4								
Box elder	4.2	2.6	1.0	2.2	416.7	0.5	5.3	1.8
Cottonwood	62.5	38.5	10.8	24.1	26250.0	30.1	92.7	30.9
False indigo	4.2	2.6	5.0	11.1	416.7	0.5	14.2	4.7
Sandbar willow	87.5	53.8	13.0	29.1	58333.3	67.0	149.9	50.0
Woods' rose	4.2	2.6	15.0	33.4	1666.7	1.9	37.9	12.6
Total		100.0	44.8	100.0	87083.3	100.0	300.0	100.0
Stand 12								
Cottonwood	87.5	50.0	4.2	16.4	131250.0	65.5	131.8	43.9
Sandbar willow	87.5	50.0	21.7	83.6	69166.7	34.5	168.2	56.1
Total		100.0	25.9	100.0	200416.7	100.0	300.0	100.0
Stand 22								
Peachleaf willow	4.2	100.0	1.0	100.0	416.7	100.0	300.0	100.0
Total		100.0	1.0	100.0	416.7	100.0	300.0	100.0
Stand 23								
Cottonwood	56.3	47.4	2.5	26.0	6666.7	40.1	113.4	37.8
Peachleaf willow	56.3	47.4	6.1	63.6	9333.3	56.1	167.1	55.7
Sandbar willow	6.3	5.3	1.0	10.4	625.0	3.8	19.4	6.5
Total		100.0	9.6	100.0	16625.0	100.0	300.0	100.0

Stand 71								
Cottonwood	15.0	27.3	3.7	17.7	3000.0	20.7	65.7	21.9
Peachleaf willow	40.0	72.7	17.0	82.3	11500.0	79.3	234.3	78.1
Total		100.0	20.7	100.0	14500.0	100.0	300.0	100.0
Stand 83								
Cottonwood	18.8	16.7	2.3	11.8	1250.0	4.8	33.3	11.1
Peachleaf willow	81.3	72.2	9.4	47.6	22500.0	85.7	205.5	68.5
Sandbar willow	12.5	11.1	8.0	40.6	2500.0	9.5	61.2	20.4
Total		100.0	19.7	100.0	26250.0	100.0	300.0	100.0
Tree size stands								
Stand 2								
American elm	4.2	2.4	1.0	2.8	416.7	0.9	6.2	2.1
Box elder	25.0	14.6	1.7	4.7	5833.3	12.4	31.8	10.6
Green ash	70.8	41.5	3.2	9.2	26666.7	56.6	107.3	35.8
Peachleaf willow	12.5	7.3	2.3	6.6	1250.0	2.7	16.6	5.5
Riverbank grape	25.0	14.6	8.5	24.1	2916.7	6.2	45.0	15.0
Sandbar willow	16.7	9.8	3.0	8.5	3750.0	8.0	26.2	8.7
Western snowberry	8.3	4.9	3.0	8.5	2083.3	4.4	17.8	5.9
Woodbine	8.3	4.9	12.5	35.5	4166.7	8.8	49.2	16.4
Total		100.0	35.2	100.0	47083.3	100.0	300.0	100.0
Stand 3								
American elm	4.2	2.6	1.0	5.3	416.7	0.2	8.1	2.7
Box elder	8.3	5.1	1.0	5.3	833.3	0.4	10.8	3.6
Green ash	100.0	61.5	10.6	56.5	212916.7	94.5	212.5	70.8
Riverbank grape	45.8	28.2	5.2	27.6	10416.7	4.6	60.4	20.1
Woodbine	4.2	2.6	1.0	5.3	833.3	0.4	8.3	2.8
Total		100.0	18.8	100.0	225416.7	100.0	300.0	100.0

Stand 6								
Green ash	75.0	90.0	16.3	60.9	9166.7	100.0	250.9	83.6
Riverbank grape	8.3	10.0	10.5	39.1	0.0	0.0	49.1	16.4
Total		100.0	26.8	100.0	9166.7	100.0	300.0	100.0
Stand 8								
American elm	4.2	6.7	1.0	12.5	416.7	3.4	22.6	7.5
False indigo	4.2	6.7	1.0	12.5	833.3	6.9	26.1	8.7
Green ash	20.8	33.3	1.0	12.5	2500.0	20.7	66.5	22.2
Riverbank grape	8.3	13.3	1.0	12.5	2916.7	24.1	50.0	16.7
Roughleaf dogwood	4.2	6.7	1.0	12.5	416.7	3.4	22.6	7.5
Western snowberry	16.7	26.7	2.0	25.0	4583.3	37.9	89.6	29.9
Yellow willow	4.2	6.7	1.0	12.5	416.7	3.4	22.6	7.5
Total		100.0	8.0	100.0	12083.3	100.0	300.0	100.0
Stand 15								
Cottonwood	58.3	35.0	1.0	2.6	312500.0	87.1	124.7	41.6
False indigo	4.2	2.5	10.0	26.2	416.7	0.1	28.8	9.6
Green ash	54.2	32.5	2.5	6.6	30416.7	8.5	47.6	15.9
Riverbank grape	41.7	25.0	13.7	35.8	13750.0	3.8	64.7	21.6
Western snowberry	4.2	2.5	1.0	2.6	833.3	0.2	5.3	1.8
Woodbine	4.2	2.5	10.0	26.2	833.3	0.2	28.9	9.6
Total		100.0	38.2	100.0	358750.0	100.0	300.0	100.0
Stand 17								
American elm	12.5	6.7	1.0	6.4	1250.0	1.6	14.6	4.9
Cottonwood	4.2	2.2	1.0	6.4	833.3	1.1	9.7	3.2
Green ash	62.5	33.3	2.7	17.0	27500.0	35.1	85.4	28.5
Riverbank grape	41.7	22.2	1.4	8.9	10000.0	12.8	43.9	14.6
Russian olive	33.3	17.8	4.6	29.5	5000.0	6.4	53.6	17.9
Sandbar willow	25.0	13.3	4.0	25.5	32500.0	41.5	80.3	26.8
Woodbine	8.3	4.4	1.0	6.4	1250.0	1.6	12.4	4.1

Total		100.0	15.7	100.0	78333.3	100.0	300.0	100.0
Stand 20								
Green ash	25.0	18.8	1.0	7.1	7083.3	11.7	37.6	12.5
Riverbank grape	29.2	21.9	1.0	7.1	4166.7	6.9	35.9	12.0
Russian olive	33.3	25.0	2.5	17.9	7916.7	13.1	56.0	18.7
Sandbar willow	41.7	31.3	8.5	60.7	40833.3	67.6	159.6	53.2
Yellow willow	4.2	3.1	1.0	7.1	416.7	0.7	11.0	3.7
Total		100.0	14.0	100.0	60416.7	100.0	300.0	100.0
Stand 21								
Sandbar willow	70.8	54.8	1.8	66.6	16956.5	58.8	180.2	60.1
Western snowberry	58.3	45.2	0.9	33.4	11904.8	41.2	119.8	39.9
Total		100.0	2.7	100.0	28861.3	100.0	300.0	100.0
Stand 26								
Cottonwood	6.3	25.0	1.0	25.0	625.0	25.0	75.0	25.0
Riverbank grape	6.3	25.0	1.0	25.0	625.0	25.0	75.0	25.0
Russian olive	6.3	25.0	1.0	25.0	625.0	25.0	75.0	25.0
Sandbar willow	6.3	25.0	1.0	25.0	625.0	25.0	75.0	25.0
Total		100.0	4.0	100.0	2500.0	100.0	300.0	100.0
Transition								
Tree size stands								
Stand 1								
American elm	12.5	9.4	1.0	2.0	1250.0	1.1	12.4	4.1
False indigo	25.0	18.8	12.5	24.4	8333.3	7.1	50.2	16.7
Green ash	29.2	21.9	3.6	7.0	24583.3	20.9	49.8	16.6
Peachleaf willow	12.5	9.4	1.0	2.0	6250.0	5.3	16.6	5.5
Riverbank grape	16.7	12.5	6.3	12.2	5416.7	4.6	29.3	9.8
Western snowberry	29.2	21.9	19.4	37.9	67916.7	57.8	117.6	39.2

Woods' rose	8.3	6.3	7.5	14.6	3750.0	3.2	24.1	8.0
Total		100.0	51.3	100.0	117500.0	100.0	300.0	100.0
Stand 10								
American elm	25.0	11.8	1.7	2.4	3750.0	9.2	23.3	7.8
Box elder	4.2	2.0	10.0	14.2	416.7	1.0	17.2	5.7
Chokecherry	8.3	3.9	32.5	46.2	10416.7	25.5	75.6	25.2
Cottonwood	8.3	3.9	1.0	1.4	833.3	2.0	7.4	2.5
Green ash	58.3	27.5	4.5	6.4	9583.3	23.5	57.3	19.1
Peachleaf willow	4.2	2.0	1.0	1.4	416.7	1.0	4.4	1.5
Riverbank grape	41.7	19.6	12.3	17.5	2916.7	7.1	44.2	14.7
Western snowberry	4.2	2.0	1.0	1.4	416.7	1.0	4.4	1.5
Woodbine	45.8	21.6	5.4	7.6	10416.7	25.5	54.7	18.2
Yellow willow	12.5	5.9	1.0	1.4	1666.7	4.1	11.4	3.8
Total		100.0	70.3	100.0	40833.3	100.0	300.0	100.0
White River								
Shrub size stands								
Stand 11								
Cottonwood	70.8	54.8	11.1	60.3	46250.0	69.8	185.0	61.7
Sandbar willow	54.2	41.9	6.3	34.2	19166.7	28.9	105.1	35.0
Western snowberry	4.2	3.2	1.0	5.4	833.3	1.3	9.9	3.3
Total		100.0	18.4	100.0	66250.0	100.0	300.0	100.0
Stand 75								
Cottonwood	43.8	31.8	8.0	33.7	22500.0	32.4	97.9	32.6
Peachleaf willow	12.5	9.1	10.0	42.1	5625.0	8.1	59.3	19.8
Sandbar willow	81.3	59.1	5.8	24.3	41250.0	59.5	142.8	47.6
Total		100.0	23.8	100.0	69375.0	100.0	300.0	100.0

Stand 76								
Cottonwood	37.5	60.0	2.3	31.8	8125.0	65.0	156.8	52.3
Green ash	6.3	10.0	1.0	13.6	625.0	5.0	28.6	9.5
Sandbar willow	12.5	20.0	3.0	40.9	3125.0	25.0	85.9	28.6
Woodbine	6.3	10.0	1.0	13.6	625.0	5.0	28.6	9.5
Total		100.0	7.3	100.0	12500.0	100.0	300.0	100.0
Stand 85								
Chokecherry	6.3	11.1	1.0	4.7	625.0	11.1	26.9	9.0
Cottonwood	12.5	22.2	1.0	4.7	1250.0	22.2	49.1	16.4
False indigo	12.5	22.2	7.5	34.9	625.0	11.1	68.2	22.7
Riverbank grape	6.3	11.1	1.0	4.7	625.0	11.1	26.9	9.0
Sandbar willow	12.5	22.2	10.0	46.5	1875.0	33.3	102.1	34.0
Woodbine	6.3	11.1	1.0	4.7	625.0	11.1	26.9	9.0
Total		100.0	21.5	100.0	5625.0	100.0	300.0	100.0
Tree size stands								
Stand 9								
American elm	12.5	3.9	2.3	2.8	2500.0	1.9	8.6	2.9
Chokecherry	29.2	9.2	10.3	12.2	10833.3	8.3	29.7	9.9
False indigo	12.5	3.9	5.7	6.7	833.3	0.6	11.3	3.8
Green ash	79.2	25.0	5.9	7.0	31250.0	23.9	55.9	18.6
Poison ivy	16.7	5.3	12.5	14.8	7083.3	5.4	25.5	8.5
Riverbank grape	54.2	17.1	26.6	31.5	9583.3	7.3	55.9	18.6
Western snowberry	41.7	13.2	6.5	7.7	23333.3	17.8	38.7	12.9
Woodbine	70.8	22.4	14.8	17.5	45416.7	34.7	74.5	24.8
Total		100.0	84.6	100.0	130833.3	100.0	300.0	100.0
Stand 39								
False indigo	6.3	6.7	1.0	9.8	625.0	1.1	17.6	5.9
Green ash	6.3	6.7	1.0	9.8	625.0	1.1	17.6	5.9

Western snowberry	81.3	86.7	8.2	80.5	55000.0	97.8	264.9	88.3
Total		100.0	10.2	100.0	56250.0	100.0	300.0	100.0
Stand 40								
American elm	25.0	16.2	2.0	11.3	3636.4	8.0	35.6	11.9
Green ash	50.0	32.4	1.7	9.4	15416.7	34.1	76.0	25.3
Riverbank grape	45.8	29.7	1.8	10.2	7391.3	16.4	56.3	18.8
Western snowberry	8.3	5.4	3.0	17.0	5000.0	11.1	33.4	11.1
Woodbine	20.8	13.5	4.2	23.8	13333.3	29.5	66.8	22.3
Woods' rose	4.2	2.7	5.0	28.3	416.7	0.9	31.9	10.6
Total		100.0	17.7	100.0	45194.3	100.0	300.0	100.0
Stand 41								
Chokecherry	6.3	5.6	5.0	11.9	1250.0	1.0	18.4	6.1
Green ash	6.3	5.6	1.0	2.4	625.0	0.5	8.4	2.8
Western snowberry	93.8	83.3	31.1	73.9	121250.0	98.0	255.2	85.1
Woodbine	6.3	5.6	5.0	11.9	625.0	0.5	17.9	6.0
Total		100.0	42.1	100.0	123750.0	100.0	300.0	100.0
Stand 43								
Chokecherry	6.3	3.1	5.0	12.8	1250.0	1.4	17.3	5.8
Green ash	43.8	21.9	8.6	21.9	14375.0	15.6	59.4	19.8
Riverbank grape	56.3	28.1	6.4	16.5	10000.0	10.9	55.5	18.5
Western snowberry	75.0	37.5	13.8	35.2	63750.0	69.4	142.1	47.4
Woodbine	18.8	9.4	5.3	13.6	2500.0	2.7	25.7	8.6
Total		100.0	39.1	100.0	91875.0	100.0	300.0	100.0
Stand 47								
American elm	37.5	13.0	2.3	10.6	8125.0	12.3	35.9	12.0
American plum	25.0	8.7	5.5	25.0	10625.0	16.0	49.7	16.6
Chokecherry	37.5	13.0	2.3	10.6	6250.0	9.4	33.1	11.0
Eastern red-cedar	6.3	2.2	1.0	4.5	625.0	0.9	7.7	2.6
Golden currant	6.3	2.2	1.0	4.5	625.0	0.9	7.7	2.6

Green ash	62.5	21.7	1.0	4.5	15000.0	22.6	48.9	16.3
Riverbank grape	68.8	23.9	2.5	11.1	11875.0	17.9	53.0	17.7
Western snowberry	31.3	10.9	5.4	24.5	10625.0	16.0	51.4	17.1
Woodbine	12.5	4.3	1.0	4.5	2500.0	3.8	12.7	4.2
Total		100.0	22.0	100.0	66250.0	100.0	300.0	100.0
Stand 49								
American elm	6.3	2.3	5.0	6.1	625.0	0.6	8.9	3.0
Chokecherry	37.5	13.6	3.0	3.6	6250.0	5.8	23.1	7.7
Eastern red-cedar	6.3	2.3	5.0	6.1	625.0	0.6	8.9	3.0
Fragrant sumac	12.5	4.5	18.0	21.9	5625.0	5.3	31.7	10.6
Golden currant	6.3	2.3	5.0	6.1	625.0	0.6	8.9	3.0
Green ash	31.3	11.4	2.6	3.2	8750.0	8.2	22.7	7.6
Riverbank grape	68.8	25.0	14.4	17.4	24375.0	22.8	65.2	21.7
Russian olive	6.3	2.3	1.0	1.2	1250.0	1.2	4.7	1.6
Western snowberry	50.0	18.2	18.1	22.0	50000.0	46.8	87.0	29.0
Woodbine	31.3	11.4	3.6	4.4	5000.0	4.7	20.4	6.8
Woods' rose	18.8	6.8	6.7	8.1	3750.0	3.5	18.4	6.1
Total		100.0	82.4	100.0	106875.0	100.0	300.0	100.0
Stand 51								
American elm	5.0	2.1	1.0	6.9	500.0	0.7	9.7	3.2
Chokecherry	15.0	6.3	1.0	6.9	2500.0	3.4	16.6	5.5
Green ash	65.0	27.1	1.3	9.0	11000.0	15.1	51.2	17.1
Poison ivy	5.0	2.1	1.0	6.9	1000.0	1.4	10.4	3.5
Riverbank grape	55.0	22.9	2.2	15.1	10500.0	14.4	52.4	17.5
Western snowberry	25.0	10.4	1.0	6.9	3000.0	4.1	21.4	7.1
Woodbine	65.0	27.1	6.0	41.4	44500.0	61.0	129.5	43.2
Woods' rose	5.0	2.1	1.0	6.9	0.0	0.0	9.0	3.0
Total		100.0	14.5	100.0	73000.0	100.0	300.0	100.0

Stand 52								
American elm	25.0	4.4	2.0	3.6	3125.0	2.0	10.0	3.3
Box elder	12.5	2.2	3.0	5.4	1250.0	0.8	8.4	2.8
Chokecherry	56.3	9.9	6.6	11.8	14375.0	9.1	30.7	10.2
Eastern red-cedar	6.3	1.1	1.0	1.8	625.0	0.4	3.3	1.1
Fragrant sumac	50.0	8.8	3.6	6.5	8750.0	5.5	20.8	6.9
Golden currant	12.5	2.2	1.0	1.8	1250.0	0.8	4.8	1.6
Green ash	81.3	14.3	2.0	3.6	16250.0	10.3	28.2	9.4
Poison ivy	6.3	1.1	1.0	1.8	625.0	0.4	3.3	1.1
Riverbank grape	100.0	17.6	15.2	27.3	32500.0	20.6	65.4	21.8
Western snowberry	87.5	15.4	4.9	8.8	26875.0	17.0	41.2	13.7
Woodbine	87.5	15.4	6.9	12.3	43750.0	27.7	55.4	18.5
Woods' rose	43.8	7.7	8.6	15.4	8750.0	5.5	28.6	9.5
Total		100.0	55.7	100.0	158125.0	100.0	300.0	100.0
Stand 58								
False indigo	18.8	9.7	2.3	18.3	2500.0	6.5	34.5	11.5
Green ash	31.3	16.1	1.0	7.9	8125.0	21.0	45.0	15.0
Honey locust	6.3	3.2	5.0	39.3	625.0	1.6	44.1	14.7
Riverbank grape	62.5	32.3	1.4	11.0	16875.0	43.5	86.8	28.9
Russian olive	37.5	19.4	1.0	7.9	6250.0	16.1	43.3	14.4
Western snowberry	6.3	3.2	1.0	7.9	1250.0	3.2	14.3	4.8
Woodbine	31.3	16.1	1.0	7.9	3125.0	8.1	32.0	10.7
Total		100.0	12.7	100.0	38750.0	100.0	300.0	100.0
Stand 84								
Green ash	56.3	36.0	1.0	7.9	6875.0	9.6	53.5	17.8
Poison ivy	6.3	4.0	1.0	7.9	625.0	0.9	12.8	4.3
Riverbank grape	31.3	20.0	1.0	7.9	4375.0	6.1	34.0	11.3
Western snowberry	56.3	36.0	4.7	36.8	56875.0	79.8	152.7	50.9
Woodbine	6.3	4.0	5.0	39.5	2500.0	3.5	47.0	15.7

Total		100.0	12.7	100.0	71250.0	100.0	300.0	100.0
Stand 86								
American elm	6.3	7.1	1.0	1.8	625.0	1.2	10.1	3.4
Golden currant	6.3	7.1	5.0	8.8	625.0	1.2	17.1	5.7
Poison ivy	37.5	42.9	30.3	53.4	31250.0	58.1	154.4	51.5
Riverbank grape	12.5	14.3	5.5	9.7	2500.0	4.7	28.6	9.5
Western snowberry	18.8	21.4	10.0	17.6	16875.0	31.4	70.4	23.5
Woods' rose	6.3	7.1	5.0	8.8	1875.0	3.5	19.4	6.5
Total		100.0	56.8	100.0	53750.0	100.0	300.0	100.0
Stand 87								
Chokecherry	18.8	9.7	1.0	2.7	2000.0	1.7	14.1	4.7
Green ash	75.0	38.7	11.1	29.9	67333.3	57.9	126.5	42.2
Riverbank grape	62.5	32.3	9.0	24.3	17500.0	15.1	71.6	23.9
Western snowberry	25.0	12.9	8.0	21.6	21250.0	18.3	52.8	17.6
Woods' rose	12.5	6.5	8.0	21.6	8125.0	7.0	35.0	11.7
Total		100.0	37.1	100.0	116208.3	100.0	300.0	100.0

*The seedling and sapling layers of stand 16 were not sampled; thus, only 34 stands were included in this table.

Appendix Table 4. Stand location, species, diameter, and age of each tree cored along the lower White River and on the White River delta in South Dakota.

Stand number	Species	Diameter (cm)	Age (years)
White River delta			
2	Cottonwood	45.7	37
2	Cottonwood	44.0	41
2	Cottonwood	32.6	47
2	Cottonwood	30.4	47
2	Cottonwood	27.3	48
2	Cottonwood	34.6	48
2	Cottonwood	54.1	48
2	Cottonwood	39.4	49
2	Cottonwood	43.0	49
2	Cottonwood	41.4	49
2	Cottonwood	47.1	50
2	Cottonwood	40.2	50
2	Cottonwood	39.9	52
2	Green ash	11.6	15
2	Green ash	10.3	16
2	Green ash	11.2	16
2	Green ash	13.9	17
2	Green ash	10.8	18
2	Green ash	14.5	36
2	Green ash	15.3	37
3	Cottonwood	38.4	22
3	Cottonwood	31.5	27
3	Cottonwood	15.4	33
3	Cottonwood	32.3	33
3	Cottonwood	45.0	35
3	Cottonwood	21.7	35
3	Cottonwood	21.5	36
3	Cottonwood	30.7	36
3	Cottonwood	29.1	36
3	Cottonwood	34.5	36
3	Cottonwood	38.0	36
3	Cottonwood	67.1	36
3	Cottonwood	54.5	42
3	Cottonwood	31.4	43

3	Cottonwood	38.9	44
3	Cottonwood	39.5	44
3	Cottonwood	43.1	46
3	Green ash	10.6	23
6	Cottonwood	16.4	17
6	Cottonwood	16.1	18
6	Cottonwood	10.7	18
6	Cottonwood	16.0	18
6	Cottonwood	15.8	18
6	Cottonwood	16.6	18
6	Cottonwood	15.0	18
6	Cottonwood	15.2	18
6	Cottonwood	17.8	18
6	Cottonwood	15.5	18
6	Cottonwood	13.1	18
6	Cottonwood	13.3	18
6	Cottonwood	11.8	18
6	Cottonwood	14.2	19
6	Cottonwood	25.7	19
6	Cottonwood	12.1	19
6	Cottonwood	21.7	19
6	Cottonwood	23.2	19
6	Cottonwood	11.3	19
6	Cottonwood	33.5	33
6	Peachleaf willow	11.0	17
8	Cottonwood	12.8	10
8	Cottonwood	17.7	11
8	Cottonwood	14.8	11
8	Cottonwood	22.1	12
8	Cottonwood	20.5	12
8	Cottonwood	11.5	12
8	Cottonwood	22.3	12
8	Cottonwood	19.1	12
8	Cottonwood	13.7	12
8	Cottonwood	17.5	13
8	Cottonwood	13.5	13
8	Cottonwood	15.8	13
8	Cottonwood	29.8	13
8	Cottonwood	21.1	14

8	Cottonwood	13.2	14
8	Cottonwood	16.2	14
8	Cottonwood	13.9	14
8	Cottonwood	14.6	14
8	Cottonwood	13.5	14
8	Cottonwood	12.5	14
8	Cottonwood	19.3	14
8	Cottonwood	21.9	14
8	Cottonwood	23.0	15
8	Cottonwood	11.2	16
9	Cottonwood	63.5	107
9	Cottonwood	70.5	121
9	Cottonwood	79.5	134
9	Green ash	10.9	23
9	Green ash	15.5	30
9	Green ash	12.9	43
9	Green ash	20.2	46
9	Green ash	18.2	48
9	Green ash	10.3	53
9	Green ash	21.1	54
9	Green ash	19.8	57
9	Green ash	13.6	57
9	Green ash	12.2	60
9	Green ash	27.6	63
9	Green ash	20.4	65
9	Green ash	21.9	74
9	Green ash	20.2	77
15	Cottonwood	23.3	42
15	Cottonwood	20.1	43
15	Cottonwood	21.2	43
15	Cottonwood	34.0	44
15	Cottonwood	24.9	44
15	Cottonwood	22.8	45
15	Cottonwood	29.2	45
15	Cottonwood	27.2	45
15	Cottonwood	37.9	45
15	Cottonwood	29.1	46
15	Cottonwood	38.7	46
15	Cottonwood	37.1	47

15	Cottonwood	41.7	47
15	Cottonwood	31.8	47
15	Cottonwood	32.4	47
15	Cottonwood	36.5	48
15	Cottonwood	36.5	48
15	Cottonwood	32.1	49
15	Russian olive	5.6	16
16	Cottonwood	11.9	9
16	Cottonwood	12.2	9
16	Cottonwood	25.4	10
16	Cottonwood	16.5	10
16	Cottonwood	12.2	11
16	Cottonwood	16.9	11
16	Cottonwood	11.4	13
16	Cottonwood	18.4	13
16	Cottonwood	20.8	13
16	Cottonwood	16.8	14
16	Cottonwood	18.5	14
16	Cottonwood	14.3	14
16	Cottonwood	21.7	14
16	Cottonwood	14.9	14
16	Cottonwood	19.3	14
16	Cottonwood	16.4	15
16	Cottonwood	12.1	15
16	Cottonwood	14.2	15
16	Green ash	13.0	15
16	Peachleaf willow	10.0	16
17	Cottonwood	55.8	35
17	Cottonwood	43.0	37
17	Cottonwood	51.9	37
17	Cottonwood	42.4	38
17	Cottonwood	45.2	38
17	Cottonwood	35.4	39
17	Cottonwood	56.7	41
17	Cottonwood	46.5	43
17	Cottonwood	62.2	44
17	Cottonwood	45.3	45
17	Cottonwood	32.1	45
17	Cottonwood	35.2	45

17	Cottonwood	60.4	45
17	Peachleaf willow	27.0	33
17	Peachleaf willow	24.8	36
17	Russian olive	11.6	10
19	Peachleaf willow	14.8	12
19	Peachleaf willow	20.6	12
20	Cottonwood	19.7	9
20	Cottonwood	19.6	9
20	Cottonwood	24.7	9
20	Cottonwood	22.2	9
20	Cottonwood	11.0	11
20	Cottonwood	21.5	11
20	Cottonwood	13.0	11
20	Cottonwood	20.1	12
20	Cottonwood	11.6	12
20	Cottonwood	10.1	12
20	Cottonwood	20.9	13
20	Cottonwood	21.9	13
20	Cottonwood	16.7	13
20	Cottonwood	19.1	14
20	Cottonwood	49.1	35
20	Cottonwood	52.5	36
20	Green ash	15.7	12
20	Green ash	13.0	13
20	Peachleaf willow	41.4	39
20	Russian olive	19.5	13
21	Cottonwood	15.9	8
21	Cottonwood	13.7	8
21	Cottonwood	23.5	9
21	Cottonwood	19.4	9
21	Cottonwood	23.4	10
21	Cottonwood	18.7	11
21	Cottonwood	14.3	11
21	Cottonwood	10.1	11
21	Cottonwood	14.2	11
21	Cottonwood	18.7	11
21	Cottonwood	39.6	11
21	Cottonwood	21.0	12
21	Cottonwood	22.5	12

21	Cottonwood	14.3	12
21	Cottonwood	15.0	13
21	Cottonwood	18.8	13
21	Cottonwood	14.2	13
21	Cottonwood	31.2	21
21	Cottonwood	44.0	45
21	Peachleaf willow	21.7	20
21	Peachleaf willow	24.7	28
22	Peachleaf willow	15.5	12
22	Peachleaf willow	9.9	12
22	Peachleaf willow	15.4	13
22	Peachleaf willow	11.5	13
22	Peachleaf willow	10.6	13
23	Cottonwood	13.5	13
23	Cottonwood	17.4	14
23	Peachleaf willow	31.6	32
26	Cottonwood	12.0	10
26	Cottonwood	10.2	12
26	Cottonwood	10.5	12
26	Cottonwood	10.7	12
26	Cottonwood	16.2	12
26	Cottonwood	12.6	12
26	Cottonwood	13.9	13
26	Cottonwood	12.8	13
26	Cottonwood	11.5	13
26	Cottonwood	18.7	13
26	Cottonwood	16.6	13
26	Cottonwood	11.9	13
26	Cottonwood	13.4	13
26	Cottonwood	12.4	14
26	Cottonwood	15.4	14
26	Cottonwood	35.9	36
26	Peachleaf willow	12.2	13
26	Peachleaf willow	11.6	13
26	Peachleaf willow	11.0	13
26	Peachleaf willow	10.4	15
26	Peachleaf willow	16.8	16

Transition

1	American elm	15.3	14
1	American elm	17.7	16
1	Cottonwood	64.9	135
1	Cottonwood	96.0	148
1	Green ash	11.1	14
1	Green ash	15.8	16
1	Green ash	11.9	16
1	Green ash	12.5	17
1	Green ash	16.3	17
1	Green ash	10.9	20
1	Green ash	15.2	20
10	American elm	34.2	53
10	Green ash	12.9	16
10	Green ash	10.5	17
10	Green ash	11.8	23
10	Green ash	10.8	25
10	Green ash	10.9	25
10	Green ash	15.8	29
10	Green ash	23.7	55
10	Green ash	26.1	65
10	Green ash	30.5	79
10	Green ash	33.4	79
10	Green ash	31.4	84
10	Green ash	23.0	85
10	Peachleaf willow	11.5	12

White River

39	Cottonwood	11.1	21
39	Cottonwood	11.7	30
39	Cottonwood	20.4	31
39	Cottonwood	16.4	31
39	Cottonwood	16.4	31
39	Cottonwood	12.2	31
39	Cottonwood	22.2	31
39	Cottonwood	17.4	32
39	Cottonwood	18.8	32
39	Cottonwood	20.6	32
39	Cottonwood	11.0	33

39	Cottonwood	21.5	34
39	Cottonwood	23.0	34
39	Cottonwood	17.5	34
39	Cottonwood	17.3	35
39	Cottonwood	21.9	38
39	Cottonwood	32.8	42
39	Cottonwood	34.0	42
39	Cottonwood	19.7	44
39	Cottonwood	33.5	52
40	Cottonwood	50.7	83
40	Cottonwood	76.4	83
40	Cottonwood	53.8	84
40	Cottonwood	87.0	84
40	Cottonwood	54.9	85
40	Cottonwood	58.0	85
40	Cottonwood	60.6	85
40	Cottonwood	108.8	85
40	Cottonwood	57.0	85
40	Cottonwood	81.8	88
40	Cottonwood	136.3	115
40	Green ash	12.5	35
40	Green ash	18.7	38
40	Green ash	16.2	39
40	Green ash	20.3	44
40	Green ash	48.7	52
40	Green ash	20.7	55
40	Green ash	15.5	56
40	Green ash	16.8	57
41	Cottonwood	19.9	37
41	Cottonwood	25.4	37
41	Cottonwood	25.5	38
41	Cottonwood	23.6	39
41	Cottonwood	18.7	50
41	Cottonwood	40.6	50
41	Cottonwood	25.9	52
41	Cottonwood	24.6	53
41	Cottonwood	39.6	54
41	Cottonwood	30.0	55
41	Cottonwood	43.9	55

41	Cottonwood	41.2	55
41	Cottonwood	24.5	55
41	Cottonwood	33.0	56
41	Cottonwood	28.8	56
41	Cottonwood	16.0	58
43	Cottonwood	22.7	30
43	Cottonwood	21.2	31
43	Cottonwood	29.1	31
43	Cottonwood	24.7	34
43	Cottonwood	34.0	34
43	Cottonwood	26.4	34
43	Cottonwood	28.1	35
43	Cottonwood	19.9	35
43	Cottonwood	25.9	36
43	Cottonwood	31.8	36
43	Cottonwood	31.9	36
43	Cottonwood	30.7	36
43	Cottonwood	26.7	36
43	Cottonwood	19.6	37
43	Cottonwood	19.8	39
43	Russian olive	16.5	24
43	Russian olive	19.7	39
47	Cottonwood	62.8	132
47	Cottonwood	71.4	133
47	Cottonwood	88.8	134
47	Cottonwood	52.4	134
47	Cottonwood	81.2	136
47	Cottonwood	63.0	140
47	Cottonwood	69.4	142
49	Cottonwood	43.1	53
49	Cottonwood	79.9	54
49	Cottonwood	48.0	55
49	Cottonwood	39.2	61
49	Cottonwood	40.1	61
49	Cottonwood	35.8	61
49	Cottonwood	48.7	62
49	Cottonwood	49.3	63
49	Cottonwood	43.9	63
49	Cottonwood	53.0	63

49	Cottonwood	41.6	65
49	Cottonwood	31.1	67
49	Cottonwood	31.0	68
49	Cottonwood	59.7	68
49	Cottonwood	54.3	75
49	Peachleaf willow	20.6	13
49	Russian olive	10.4	10
49	Russian olive	10.8	10
49	Russian olive	14.4	13
51	Cottonwood	60.5	56
51	Cottonwood	46.3	57
51	Cottonwood	30.9	58
51	Cottonwood	53.9	59
51	Cottonwood	65.5	61
51	Cottonwood	60.6	65
51	Cottonwood	60.0	66
51	Cottonwood	32.8	72
51	Cottonwood	44.2	72
51	Cottonwood	36.2	73
51	Cottonwood	77.0	73
51	Cottonwood	37.9	74
51	Cottonwood	50.8	74
51	Green ash	11.7	33
51	Green ash	12.3	35
51	Green ash	11.3	38
51	Green ash	16.4	41
51	Green ash	27.6	49
51	Green ash	28.7	55
52	Cottonwood	33.0	41
52	Cottonwood	64.1	67
52	Cottonwood	38.2	70
52	Cottonwood	55.9	70
52	Cottonwood	42.7	71
52	Cottonwood	31.3	72
52	Cottonwood	40.2	72
52	Cottonwood	34.5	76
52	Green ash	10.1	38
52	Green ash	10.5	39
52	Green ash	20.5	43

52	Peachleaf willow	23.0	54
52	Peachleaf willow	31.1	54
58	Cottonwood	14.8	29
58	Cottonwood	30.1	31
58	Cottonwood	27.0	31
58	Cottonwood	15.5	32
58	Cottonwood	34.0	33
58	Cottonwood	23.1	33
58	Cottonwood	28.6	34
58	Cottonwood	36.7	34
58	Cottonwood	33.5	34
58	Cottonwood	23.0	34
58	Cottonwood	25.4	34
58	Cottonwood	21.0	34
58	Cottonwood	36.7	39
58	Cottonwood	34.5	41
58	Cottonwood	37.0	44
58	Russian olive	12.2	23
65	Green ash	20.3	35
84	Cottonwood	25.0	51
84	Cottonwood	36.0	52
84	Cottonwood	32.7	53
84	Cottonwood	33.6	53
84	Cottonwood	24.5	53
84	Cottonwood	26.1	54
84	Cottonwood	26.6	54
84	Cottonwood	29.7	54
84	Cottonwood	51.3	54
84	Cottonwood	31.3	55
84	Cottonwood	31.7	55
84	Cottonwood	31.2	55
84	Cottonwood	28.6	57
84	Cottonwood	62.2	57
84	Cottonwood	44.7	58
84	Green ash	18.2	42
85	Cottonwood	11.0	7
85	Cottonwood	8.5	7
85	Cottonwood	10.8	8
85	Cottonwood	15.2	8

85	Cottonwood	14.7	8
86	Cottonwood	43.8	57
86	Cottonwood	46.7	61
86	Cottonwood	37.9	62
86	Cottonwood	50.3	64
86	Cottonwood	42.5	65
86	Cottonwood	44.6	65
86	Cottonwood	46.0	67
86	Cottonwood	40.2	67
86	Cottonwood	50.5	93
87	Cottonwood	48.3	45
87	Cottonwood	25.5	47
87	Cottonwood	34.8	48
87	Cottonwood	36.5	48
87	Cottonwood	34.1	50
87	Cottonwood	29.7	50
87	Cottonwood	21.2	50
87	Cottonwood	36.1	52
87	Cottonwood	57.7	52
87	Cottonwood	24.5	53
87	Cottonwood	29.8	53
87	Cottonwood	26.0	54
87	Cottonwood	28.3	55
87	Cottonwood	43.8	64
87	Green ash	20.5	21
87	Green ash	19.6	44

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