Forty Years of Vegetation Change on the Missouri River Floodplain

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Comparative inventories in 1969 and 1970 and in 2008 of vegetation from 30 forest stands downstream of Garrison Dam on the Missouri River in central North Dakota showed (a) a sharp decline in cottonwood regeneration; (b) a strong compositional shift toward dominance by green ash; and (c) large increases in invasive understory species, such as smooth brome, reed canary grass, and Canada thistle. These changes, and others discovered during remeasurement, have been caused by a complex of factors, some related to damming (altered hydrologic and sediment regimes, delta formation, and associated wet–dry cycles) and some not (diseases and expansion of invasive plants). Dominance of green ash, however, may be short lived, given the likelihood that the emerald ash borer will arrive in the Dakotas in 5–10 years, with potentially devastating effects. The prospects for recovery of this valuable ecosystem, rich in ecosystem goods and services and in American history, are daunting.

Keywords: riparian, cottonwood, deltas, restoration, reservoirs

Although dam building continues globally, the era of dam building in North America is over (Graf 1999). The ecological effects of dams, however, will continue apace for decades or even centuries unless those dams are removed or reregulated or their effects are mitigated by extensive and expensive restoration projects (e.g., planting trees, stocking fish, constructing nesting islands; see, e.g., Gore and Shields 1995, Galat et al. 1998, NRC 2002). Some 75,000 dams have been built in the continental United States; all watersheds in the nation larger than about 2000 square kilometers have one or more dams altering water flow (Dynesius and Nilsson 1994, Graf 1999). The most rapid increases in reservoir storage occurred between the late 1950s and the late 1970s (Graf 1999). The Great Plains and Rocky Mountain regions have some of the highest ratios of reservoir storage capacity to annual runoff in North America; these dammed regions have therefore experienced the greatest changes in river discharge (Graf 2006).

The holistic science of large-river ecology that developed during the last few decades of the twentieth century followed (and, to a considerable extent, was stimulated by) the dam-building era on the world's waterways (e.g., Ward and Stanford 1979, Vannote et al. 1980, Nilsson 1981, Williams and Wolman 1984, Power et al. 1988, Junk et al. 1989, Bayley 1991, Scott et al. 1996, Stanford et al. 1996, Poff et al. 1997, Galat et al. 1998, Sparks et al. 1998, Osterkamp and Hupp 2010). Therefore, most of what we have learned about the natural functioning of river ecosystems, and especially about complex land and water interactions, has been learned out of necessity from the study of ecologically impaired rivers. The scarcity of unregulated rivers—such as the Fiume Tagliamento, a reference river for the European Alps (Ward et al. 1999)—that could serve as experimental references or as restoration targets, has made predictions of regulated-river behavior in most regions less certain. Because of the lack of such large reference rivers in the Great Plains, it is necessary to conduct long-term studies and monitoring to test predictions about rivers in this region. Our science would benefit from periodic checks on the concepts and theories of river-ecosystem behavior that have developed from these predictions. In the present study, we attempted to accomplish this by resampling riparian forests studied 40 years ago and by evaluating the accuracy of the hypotheses made at that time.

One of the first studies in which the long-term effects of dams on riparian vegetation in the drylands of North America were predicted (Johnson et al. 1976) was conducted in 1969 and 1970, within a 166-kilometer (km)–long remnant floodplain reach of the heavily regulated Missouri River in North Dakota, between Garrison Dam (closed in 1953), which formed Lake Sakakawea, and Oahe Reservoir (filled about 1960), which was formed by Oahe Dam, downstream in South Dakota (figure 1). The six mainstem dams on the Missouri River operated by the Corps of Engineers can store up to 90.5 cubic kilometers of water, more capacity than any other river system in the United States.

Riparian forests in drylands are especially valued for their high biodiversity; these forests may cover only 1% of

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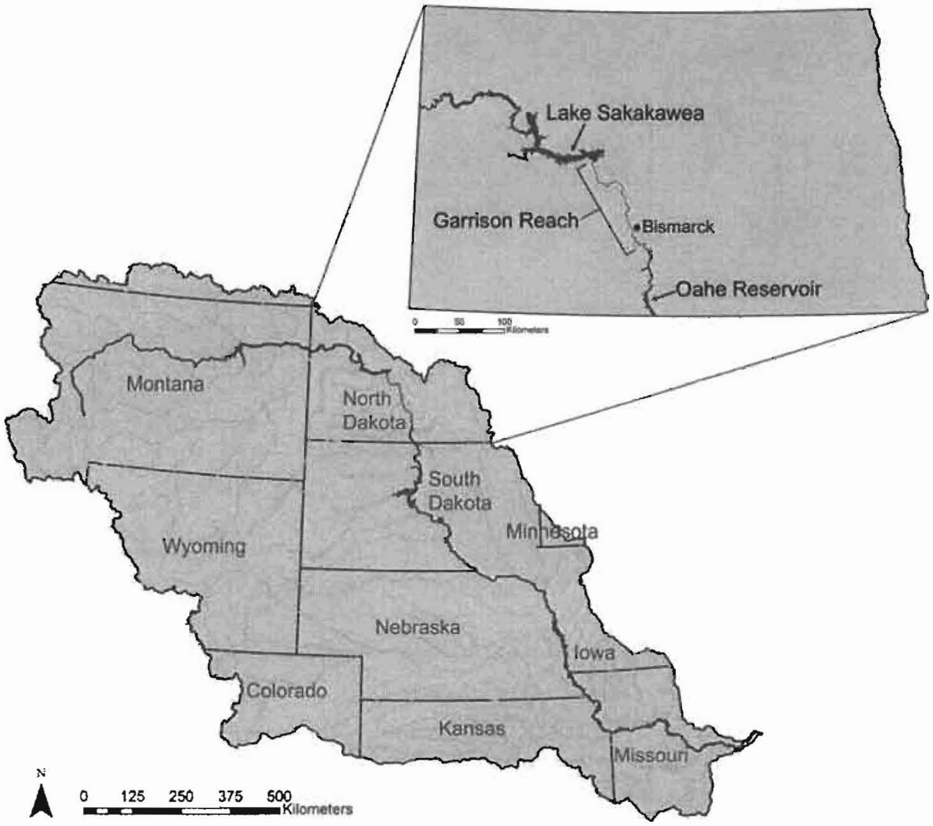

Figure 1. Map of the Missouri River (in dark blue) and watershed in central North America. The enlarged map of North Dakota shows the Garrison Reach of the Missouri River flanked by Lake Sakakawea and Oahe Reservoir. Source: US Army Corps of Engineers.

the landscape area but support—for example—more bird species than all other vegetation types combined (Ohmart 1994). Hibbard (1972) found that riparian forests in the Garrison Reach provided nesting habitat for a wide range of bird species, from open-country birds in the youngest, post-flood cottonwood–willow communities, to shrub-loving bird species in middle-aged cottonwood communities, to forest-dwelling birds in the most-mature forests. Some bird species, such as cavity-nesting woodpeckers, are reliant on cottonwood trees, specifically because of their large size and hollow trunks and branches (Sedgwick and Knopf 1992). About half of the species of birds that nest in the middle Missouri River forests are Neotropical migrants (Liknes et al. 1994). Riparian forests also function as corridors and habitat connectors, facilitating the mobility of organisms across landscapes and sustaining biodiversity (Hilty et al. 2006).

Dams and riparian vegetation: Initial hypotheses

Two specific hypotheses about the long-term effects of dams on riparian vegetation on the Missouri River floodplain were made by Johnson and colleagues (1976).

Hypothesis 1. The lack of cottonwood regeneration downstream of dams on the Missouri River is caused by major reductions in peak flows and channel dynamics (meandering and widening), after which the river ceases to create sandbars necessary for seedling establishment. Johnson and colleagues (1976) forecast a rather bleak future for the tree species *Populus deltoides* Bartr. ex Marsh. and its minor associate, the peach-leaf willow (*Salix amygdaloides* Anderss.). Large storage dams were seen as an ecological "game changer" because they cut peak flows and reduced the formation of flood-deposited point bars downriver that are needed to regenerate cottonwood and other pioneering species that initiate forest succession on floodplains. The Missouri River dams were predicted to sharply reduce cottonwood forest area, changing it from the historically dominant community occupying three-quarters of the floodplain area into a minor community relegated to small patches in river-marginal locations. Cottonwood is well adapted for success on active floodplains. Its many adaptations included voluminous seed dispersal by wind and water, timed with receding flows and exposure of fresh alluvium; rapid seed germination and root and height growth that enable tolerance to flooding, drought, and sedimentation; tolerance to low soil fertility on sandbars; and the ability to reproduce vegetatively after physical damage (Braatne et al. 1996).

A shortage of sandbar habitat for cottonwood regeneration would be less serious if cottonwood could maintain itself in established stands. Johnson and colleagues (1976) and others observed, however, that established cottonwood communities appeared not to be self-maintaining; cottonwood seedlings were absent in cottonwood-forest understories, probably because of reduced light levels and the negative effect of leaf-litter buildup on seed germination. A sharp decline in reproduction, as was forecast for a species that cannot maintain itself in established stands, is indeed a recipe for a slow death.

Identification of a cottonwood problem on regulated rivers by Johnson and colleagues (1976) spawned a plethora of similar ecological studies on the numerous cottonwood-dominated rivers in central and western North America. The assessments for the future of forests on dammed rivers from many of these studies were more dire than were those for the Missouri River. Descriptors like *imminent decline* (Howe and

Knopf 1991), *collapse* (Rood and Mahoney 1990), *survival... in jeopardy* (Bradley and Smith 1986), and *abrupt forest decline* (Rood and Heinze-Milne 1989) were used to characterize the status of cottonwood on other rivers. Therefore, the cottonwood problem, apparently first detected on the Missouri River, has now been suspected or confirmed on dozens of dammed, meandering-type rivers in the drylands of North America. Some dammed, braided-type rivers in the American West, however, have undergone channel narrowing and short-term cottonwood forest expansion (Johnson 1994, 1998, Friedman et al. 1998).

Hypothesis 2. Evidence of declining reproduction of box elder and American elm, coupled with high reproduction densities of green ash, suggests declining diversity in late-successional forest stands. Johnson and colleagues (1976) observed that the short-lived cottonwood forests were likely to be replaced by combinations of four late-successional species—green ash, *Fraxinus pennsylvanica* var. *lanceolata* (Borkh.) Sarg.; box elder, *Acer negundo* L.; American elm, *Ulmus americana* L.; and bur oak, *Quercus macrocarpa* Michx.—that all (except bur oak) reproduce abundantly in the understory of cottonwood forests. Because of a dynamic, meandering channel and natural successional processes, the preregulation floodplain was a mosaic of forests of different ages and species mixes, ranging from young, thick stands of cottonwood to forests older than 100 years that had lost the cottonwood component and were populated by late-successional tree species.

Johnson and colleagues (1976) thought that the cessation of channel meandering caused by Garrison Dam would shift the floodplain-forest composition over time away from cottonwood and toward these late-successional species. But as hypothesis 2 suggests, there were indications from field data that in the post-dam environment, two of the four late-successional species—elm and box elder—showed signs of low survival of reproduction, possibly caused by the cessation of spring moisture recharge from overbank flooding. An increased rate of mortality of established trees from disease, flooding, or drought (discussed later) was not forecast. Ultimately, as the hypothesis suggests, chronic reproductive failure of elm and box elder would favor green ash, the only late-successional species that at the time exhibited a balanced population structure. The demise of elm and box elder would produce a decline in biodiversity across the floodplain, especially in cottonwood forests midway through succession, a period when all tree species grow together—cottonwood in the overstory and the late-successional species in the understory.

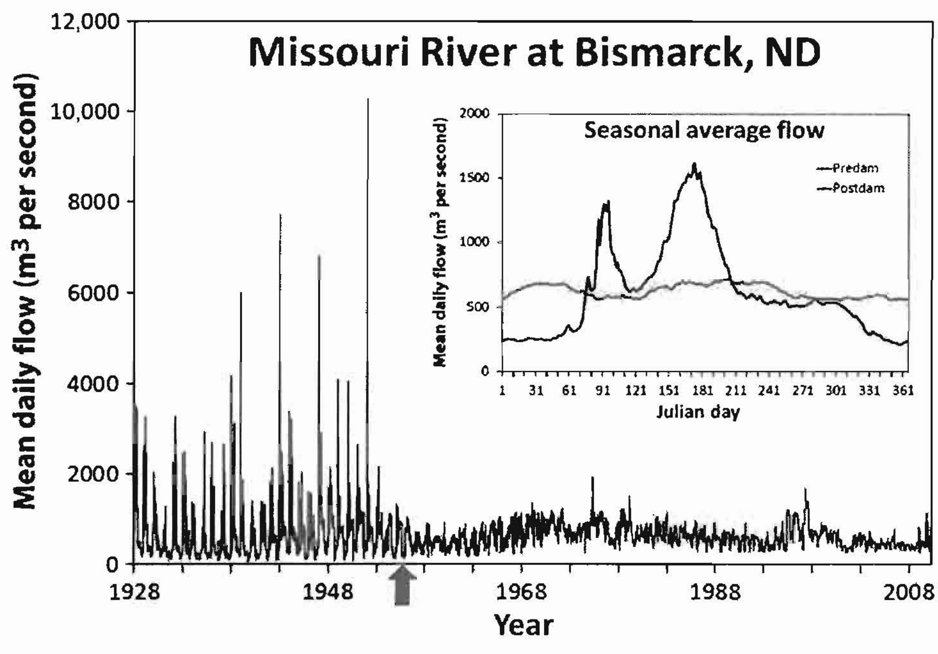

Figure 2. Daily hydrograph for the period of record for the Bismarck, North Dakota, gauge (no. 06342500) on the Missouri River. The insert is streamflow for the same data set averaged for each Julian day (1 January–31 December). The red arrow points to the year in which Lake Sakakawea was filled for the first time. Source: US Geological Survey National Weather Information System. Abbreviation: m^3, cubic meters.

The Garrison Reach study area

Major changes have occurred in the broader physical and biological environment of the Garrison Reach study area since dam construction. Hydrology, channel structure, land and water cover, and delta formation top the list.

Hydrologic and sediment regime. The filling of Lake Sakakawea behind Garrison Dam began in the fall of 1953. The reservoir eliminated approximately 23,000 hectares each of riparian forests and of cropland. The river below the dam was subjected to a controlled-release regimen and began to adjust to this major alteration of sediment and flow. The average daily flow of the Missouri River was nearly identical before and after the dam's construction at the US Geological Survey gauging station in Bismarck: The flow in the predam period (1928–1952) was 623.2 cubic meters (m^3) per second, and it was 624.2 m^3 per second in the postdam period (1953–2010). The flow regime, however, changed markedly after the dam's construction. During the predam period, approximately two-thirds of the annual peaks were greater than 2500 m^3 per second (figure 2). The instantaneous annual peak of record occurred in 1952 (14,150 m^3

per second) just before the dam's closure. No postdam peak of record has exceeded 2500 m^3 per second; the highest was 1951 m^3 per second in 1975.

The seasonal flow patterns changed markedly after the dam's construction. For example, the large peak flows between April and July in the predam period disappeared in the postdam period (inset in figure 2). Over the period of record, the relatively flat postdam hydrograph showed higher winter flows but generally lower summer flows than during the predam period.

Virtually all of the sediment that enters Lake Sakakawea remains there. The annual suspended-sediment load transported by the Missouri River past Bismarck declined by almost an order of magnitude following the closure of Garrison Dam (USACE 1951, 1957, 1965, 1970, 1976). Postdam sources of sediment for the Garrison Reach are primarily from tributaries and erosion of the riverbed and banks of the Missouri itself.

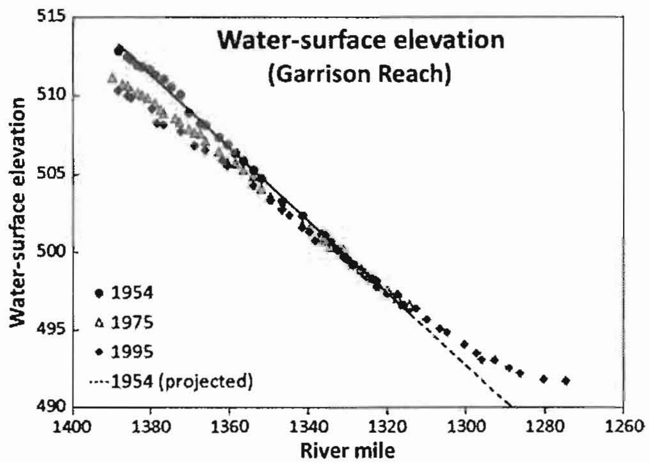

Figure 3. Elevation (in meters) above mean sea level of the river surface under steady flow (1050 cubic meters per second) through the Garrison Reach of the Missouri River in North Dakota. Water-surface elevation is used as a proxy for riverbed elevation. Elevation downstream of river mile 1315 in 1954 was estimated by linear regression of upstream observations. Source: data from Paul Boyd, US Army Corps of Engineers.

Riverbed elevation. The shape of the longitudinal curve of riverbed elevation (using water-surface elevation as a proxy) through the Garrison Reach has changed since Garrison Dam's construction. When the reservoir was filled (1954), riverbed elevation throughout the reach had assumed a relatively straight line, indicating a uniform slope (figure 3). Postdam sampling (in 1975 and 1995) showed a pronounced downcutting of the river channel below the dam, caused by sediment-hungry, clear-water releases. This effect attenuated with distance until at the midpoint of the reach, downcutting was negligible. From midreach downstream, however, the riverbed has aggraded such that the river current has slowed, and sediment has dropped out at the confluence with Oahe Reservoir. The slope in the reservoir-delta region eventually approached zero (figure 3). The riverbed below the dam (river mile 1388) has degraded 2.6 meters (m) in 40 years, whereas it has aggraded near Oahe Reservoir (river mile 1289) by 2.5 m. The rate of degradation has slowed, probably because of a coarsening of the riverbed (Livesey 1963, Williams and Wolman 1984).

Overall, the upper section of the curve has flattened out from channel incision, whereas the lower section has aggraded and flattened out through sedimentation. Channel incision is known to reduce channel meandering and to lower floodplain groundwater levels, whereas channel aggradation generally raises the water table, reduces flow conveyance, and increases flooding (Schumm 2005). Therefore, only the middle section of the reach (the hinge point in the stream gradient) has retained its predam elevation. Alteration of the channel slope by dams bordering remnant riverine reaches negatively impacts their underlying physical environment and ecological function (Ligon et al. 1995, Graf 2006).

Historic land- and water-cover changes. The Garrison Reach was mapped at three points in time using ArcGIS (Esri, Redlands, California) to compare pre- and postdam land-cover conditions. Digital, georeferenced images of the 1892 Missouri River Commission maps, including their vegetation-type designations, were obtained from the US Army Corps of Engineers. Geographic information system (GIS) maps for the 1950s (1955 and 1956) were produced from black-and-white aerial photographs at 1:20,000 scale obtained from the US Department of Agriculture (USDA) Aerial Photography Field Office. The mid-1950s maps were considered to be predam snapshots, given the short time interval between the filling of the reservoir (1954) and the photography dates. Land-cover maps for 2006 were based on county mosaic orthophotography (in true color) from the National Agricultural Imagery Project, obtained from the USDA National Resources Conservation Service Geospatial Data Gateway. Details of the procedures used in mapping land cover are available in Dixon and colleagues (2010).

A time series of GIS maps revealed changes since 1892. Two sets of maps—one for a relatively narrow floodplain section (figure 4) and a second for a relatively wide floodplain section (figure 5)—reflect the range of conditions in the Garrison Reach. Both river sections exhibit a loss of channel complexity, a decrease in active channel width, and a decrease in the number of open sandbars between the pre- and postdam maps; they also exhibited a conversion of most of the natural upland grassland and about a quarter of the forest on the floodplain to agriculture during the predam period, as well as an expansion of grassland (especially visible in figure 5) and development of wooded islands from sandbars between the pre- and postdam dates of the snapshots. The narrow section shows little channel meandering across the time series, whereas major differences

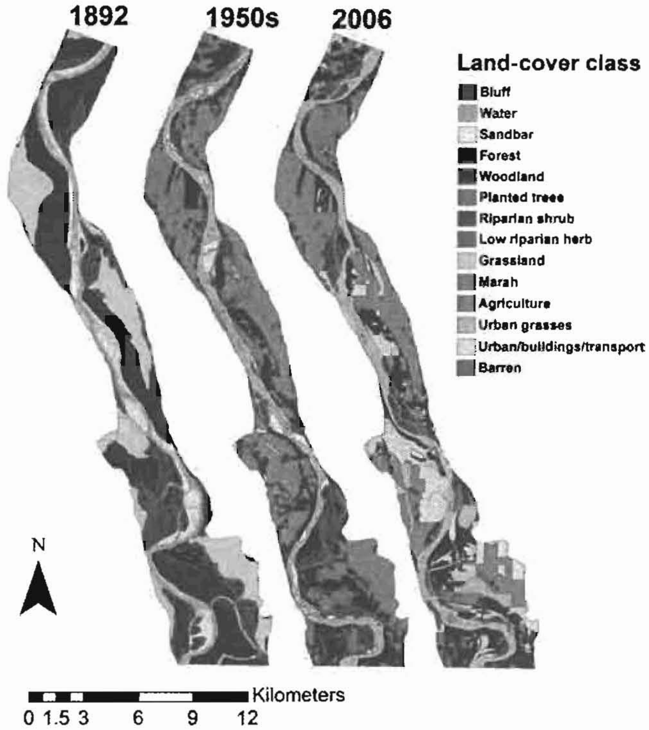

Figure 4. Geographic information system maps of land and water cover for a relatively narrow floodplain reach of the Missouri River at three points in time.

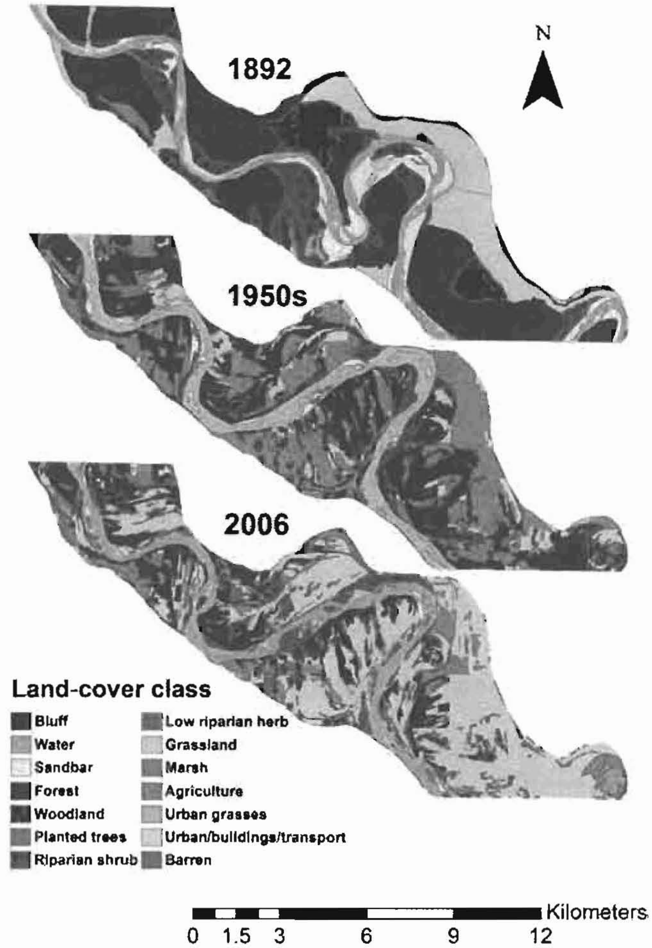

Figure 5. Geographic information system maps of land and water cover for a relatively wide floodplain reach of the Missouri River at three points in time.

are visible in the channel's location in the wide floodplain section between the two predam maps but not between the postdam-period maps. Flood protection enabled the expansion of urban land near Bismarck and Mandan (figure 4) during the postdam period.

The areal extent of forest types on the floodplain also shifted during the 1892–2006 period. The cottonwood forests that had established before Garrison Dam was built were considerably more extensive than were the postdam cottonwood forests in 2006 (figure 6). The postdam cottonwood forests were, for the most part, located near the main river channel, in contrast to the predam cottonwoods, which were more widely distributed across the floodplain. Dixon and colleagues (2010) found that the rate of cottonwood establishment has slowed during the postdam period.

Reservoir delta. Potential impacts of a delta forming south of Bismarck were neither forecast nor discussed by Johnson and colleagues (1976). Sedimentation (aggradation) occurs wherever flowing water that is transporting sediment contacts the still water of the reservoir margin. The point of confluence frequently shifts from near the South and North Dakota state line during the low-reservoir stage to as much as 70 river km upstream, near the Burleigh–Emmons county line when the reservoir is full (figure 7). The river deposits sediment sporadically along this 70-km reach, depending on the reservoir stage. The aerial image in figure 7 shows splays of sediment scattered throughout this reach; however, because the reservoir is most often maintained near full pool to create maximum head for power generation, the delta is best developed near the Burleigh–Emmons county line.

Reservoir deltas have been termed "novel" riverine habitats because on unregulated rivers, deltas are transient features associated with tributary confluences (Stevens et al. 2001, Johnson 2002). They are highly dynamic and ecologically complex, but they are poorly studied. The areas of natural river upstream of the reservoir at full pool were thought to be largely outside the influence of the reservoir. However, we have learned with time from the Garrison Reach and from other rivers (Schumm 2005) of three types of physical changes upstream of reservoirs: channel aggradation, reduced channel conveyance, and rising river and groundwater levels. The first two of these cause the third. Aggradation occurs when sediment accumulates in the channel and raises the riverbed elevation at the river–reservoir confluence. As the slope of the channel flattens out and flow velocity drops, a backup effect causes the river stage to rise and sediment deposition to occur farther upstream. When high flows occur in river sections with restricted conveyance, especially during cold winters with heavy ice buildup

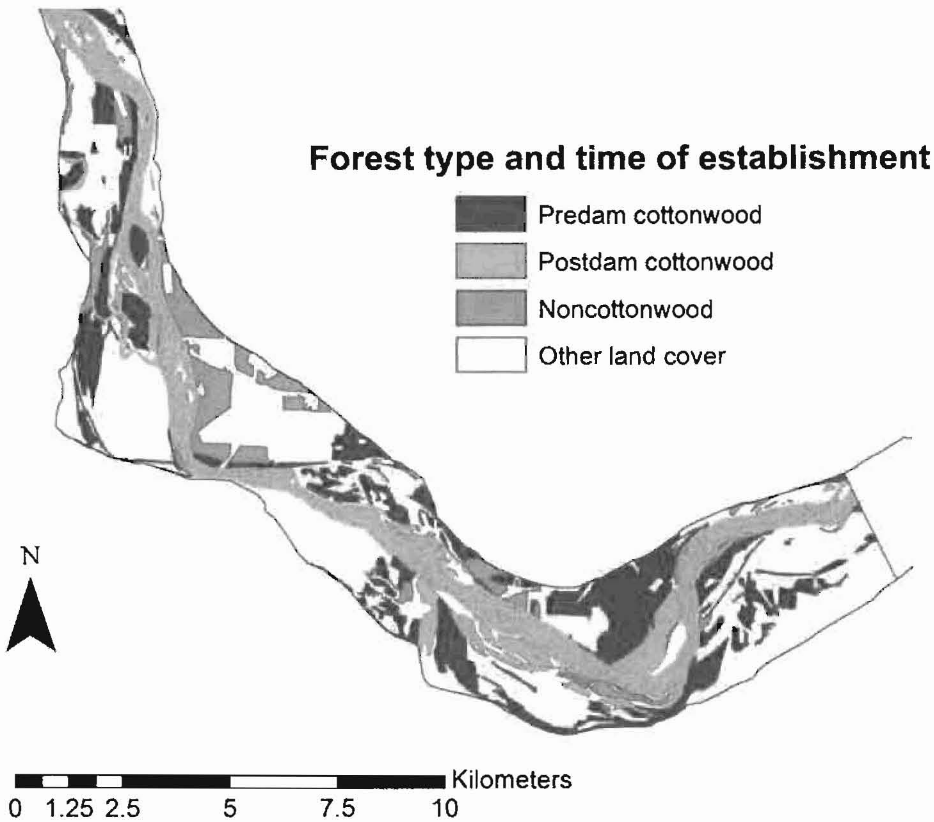

Figure 6. Forest age classes and the period of establishment for a typical section of the Garrison Reach of the Missouri River in North Dakota.

and jams, backup can be severe and can cause considerable property damage many kilometers upstream, as occurred near Bismarck in March 2010. The net effect of sedimentation and backup is hydration of the floodplain well upstream of the predelta, full-pool reservoir margin.

Forty years of vegetation change

The best test of hypotheses 1 and 2 are the remeasurement data from the 34 stands of forest in the Garrison Reach.

Field sampling of riparian vegetation. Stands 1–10 were sampled in the summer of 1969, whereas Stands 11–34 were sampled in the summer of 1970. The method used to sample vegetation in 2008 was identical to those of Johnson and colleagues (1976) and Keammerer (1972), except that tree-seedling density was not estimated in 2008 and that four more herbaceous-layer plots were sampled for each stand in 2008.

Thirty of the 34 stands were resampled in the summer of 2008. One of the four unsampled stands (Stand 31, near Bismarck) had been converted to suburban land use. Permission was not granted to resample the three other stands (Stands 9, 18, and 22); however, they had remained forested.

Forest population structure. The results from the remeasured stands confirmed a key observation about cottonwood: It does not reproduce successfully in its own forests. The population structure of a young cottonwood stand (Stand 28) in 1970 assumed a negative exponential form, typical of a balanced population (Meyer 1952) that could be self-maintaining over time (figure 8 insert). Forty years later, however, the size structure of the population had shifted strongly to a normal distribution, with the peak numbers of trees in larger size classes. A sizable gap in the smallest size classes indicated no population ingrowth. The mean diameter of cottonwood trees during the period nearly doubled from 15.5 centimeters (cm) diameter at breast height (DBH) to 31.5 cm DBH; the largest cottonwood tree sampled in Stand 28 in 1970 was 30 cm DBH, whereas the DBH of the largest cottonwood sampled in 2008 was 70 cm. The same shift in cottonwood size structure was evident when the size classes of all 22 remeasured stands in which cottonwood was present were averaged at both sampling dates (figure 8). The mean DBH in these stands was 32.8 cm in 1969 and 1970 and 48.2 cm in 2008. Cottonwood is slowly but certainly on the way out in established stands on the Missouri River floodplain.

Late-successional species exhibited widely varying trends in basal area (cross-sectional area of trees at 1.3 m above the ground expressed on a unit area basis) over the remeasurement period. American elm underwent the largest change within the group of late-successional species (figure 9). Elm was historically a major canopy tree on the floodplain; Johnson and colleagues (1976) found elm basal area to have been second only to that of cottonwood. Because of Dutch elm disease (*Ophiostoma ulmi* [Buisman] Nannf.), however, elm has been nearly eliminated as a member of the mature forest community (figure 9). Forests that were once dominated by elm have now, at best, a few large trees remaining.

The decline of box elder dominance was less dramatic than that of elm (figure 9). The basal area of box elder declined in the large majority of stands; small increases were largely confined to young cottonwood stands. The largest declines occurred in middle-aged forests in which late-successional species would be expected to be increasing, not decreasing, as cottonwoods undergo natural thinning.

Green ash basal area increased in most stands, including young cottonwood stands, whereas only a few stands experienced modest to large decreases (figure 9). Overall, the postcottonwood forest community has been reduced to a

Figure 7. Aerial photograph of the Missouri River mainstem delta south of Bismarck, North Dakota. The horizontal yellow line corresponds to the border between Burleigh and Emmons Counties and the approximate northern boundary of the full pool of Oahe Reservoir. Photograph: US Department of Agriculture, National Agriculture Imagery Program.

green-ash dominated community with box elder as a waning codominant.

Forest succession in real time. The successional trajectories of the large majority of the remeasured stands with cottonwood present were, as was expected, toward increasing proportions of late-successional species. The *rate of succession* is defined here as the proportional increase in the importance value of late-successional species. *Importance value* is the sum of the relative values of frequency, density, and dominance (basal area) (Curtis and McIntosh 1951) and is a measure of the relative ecological importance of species in a plant community.

Stands that experienced slow rates of succession (the shortest arrows in figure 10) generally occurred near the ends of the stand gradient. For example, 40 years was insufficient for late-successional species to colonize and grow to tree size (i.e., more than 10 cm DBH) in the nutrient-poor, young cottonwood stands. Among the older stands, the last few giant cottonwood trees (1–2 m DBH) mostly survived through the remeasurement period, despite broken branches and tops.

The most rapid succession rates (the longest arrows in figure 10) occurred in middle-aged forests (the middle portion of figure 10). The stands with abundant elm and box elder in 1969 and 1970 (Stands 2 and 7) exhibited slow succession because of the high mortality of these species during the remeasurement period. In contrast, Stands 12 and 17, in which ash was the dominant late-successional species and in which elm was absent or uncommon in 1969 and 1970, exhibited the highest rates of succession. The decline of elm in all stands and box elder in many stands had the effect of slowing the natural shift in relative importance from pioneer to late-successional species and to delay the time at which late-successional species would dominate cottonwood compositionally. The expectations during succession that late-successional species should increase and that pioneer species should decrease with time were not observed in many of the remeasured stands.

Five stands (marked in red in figure 10) experienced *reverse succession*, defined as a decrease in the importance of late-successional species. Three of these (Stands 3, 6, and 8) experienced high mortality in the Oahe delta region caused by rising groundwater. Two of the five stands (Stands 14 and 32) had been managed for wildlife by cutting the smaller trees, most often of late-successional species more desirable for firewood.

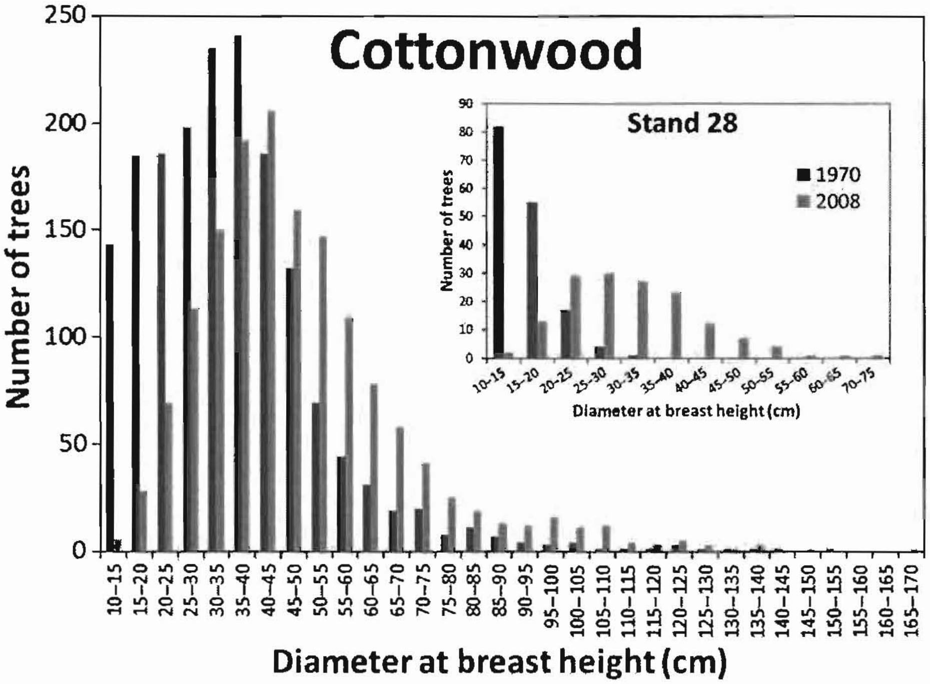

Figure 8. Size structure changes of cottonwood between the measurement in 1969 and 1970 and that in 2008, averaged for all resampled stands. The insert is the size structure of cottonwood trees for a single remeasured stand (Stand 28).

Overall, a complex pattern of succession has developed in Missouri River forests of predam origin. Flooding from reservoir backup and exotic plant diseases have altered the normal development of late-successional species by reducing their regeneration, growth rates, and survival.

Trends in tree reproduction. The mean seedling density across all stands in 1969 and 1970 was approximately 1 seedling per square meter (m^2) for box elder and 6 seedlings per m^2 for ash and elm (table 1). These seedling densities were several orders of magnitude greater than the tree densities in the same stands. Box elder and elm sapling densities were a fourth of that for ash (table 1).

The reproduction of late-successional species has decreased sharply since the 1969 and 1970 measurement. Box elder and elm seedling ubiquity dropped from 31 to 6 stands and from 22 to 15 stands, respectively (table 1). Ash ubiquity declined less, from 33 to 25 stands. Box elder sapling density declined from 1596 saplings per hectare to 250 saplings per hectare (table 1). Elm sapling reductions were even greater. Ash experienced major reductions in seedling presence and sapling density but still remained at much higher densities than box elder and elm.

Changes in herbaceous vegetation. The most-striking changes in the herbaceous layer involved three invasive species. Smooth brome (*Bromus inermis* Leyss), of Eurasian origin (Vogl et al. 1996), was present in about half of the stands in 1969 and 1970; its relative cover was low, averaging 5.4% in occupied stands (figure 9). By 2008, smooth brome was present in all but one remeasured stand, and its average relative cover had risen to 34.4%. In 10 of the 30 stands, relative cover by smooth brome exceeded 50% (figure 9).

Canada thistle (*Cirsium arvense* [L.] Scop.) and reed canary grass (*Phalaris arundinacea* L.) were more restricted geographically than the ubiquitous smooth brome. Canada thistle, also of Eurasian origin, is a noxious weed in many Great Plains states (Stubbendieck et al. 2003) but was not sampled in the large majority of stands in 1969 and 1970. Where it did occur, it exhibited relative cover values less than 5% (figure 9). By 2008, it had spread to nearly all stands and had reached cover values up to 25%. It also exhibited a strong longitudinal pattern of occurrence, with low cover values nearer the dam and high cover values associated with the Oahe delta (figure 9).

Reed canary grass is a hybrid between North American and Eurasian genotypes (Reinhardt-Adams and Galatowitsch 2005). It has expanded rapidly in shallow wetlands throughout the northern Great Plains, displacing many native wetland plants. It was absent from riparian forests in 1969 and 1970 but is now quite abundant and concentrated in the Oahe delta region. Cover values ranged widely, from several percent to 75% (figure 9).

1969 and 1970 hypotheses: Right or wrong?

New data from the Garrison Reach generally support hypothesis 1. GIS maps clearly show that the river channel has moved very little in the nearly 60 years since Garrison Dam's construction. This contrasts sharply with the extensive channel meandering mapped in the predam period (figure 5). The expansive swaths of early-successional forests mapped in 1892 cannot be sustained by a fixed channel and the low postdam regeneration rate observed. Cottonwood communities of postdam origin have been mostly confined to comparatively small patches near the main river channel highly vulnerable to erosion.

Reduced peak flows in the Garrison Reach following damming triggered the near-channel expansion of cottonwood reproduction (figure 4). Channel narrowing is a well-known mechanism of forest regeneration on confined sections of meandering rivers during periods of low flow, when banks and islands are exposed (Friedman et al. 1996). Without channel movement or further narrowing in the future, similar

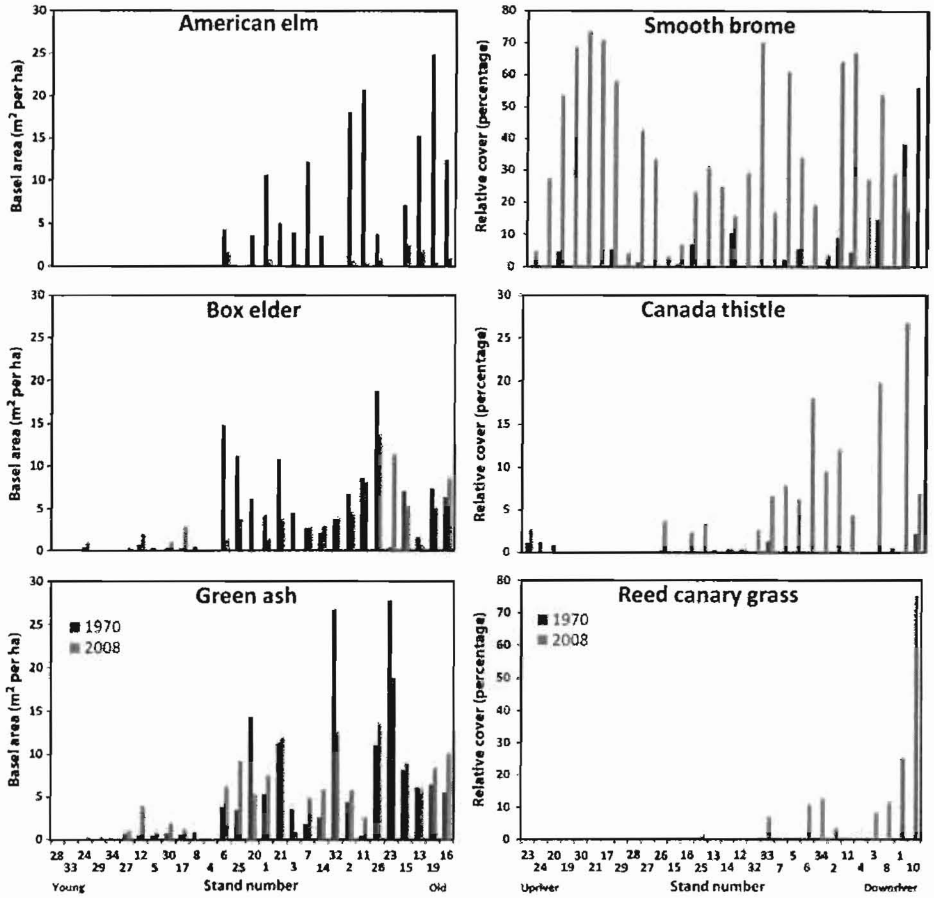

Figure 9. Changes in basal area for three late-successional tree species (left column) and changes in cover for three invasive herbaceous species (right column) over a 40-year period in the Garrison Reach of the Missouri River floodplain. Abbreviations: ha, hectares; m², square meters.

sapling category (hypothesis 2) was only a short-term bottleneck or was a chronic recruitment problem that would eventually slow the successional advance of box elder and elm. The remeasurement data show that the unbalanced age structure has continued, leading to our acceptance of hypothesis 2—that biodiversity in successionally mature stands will continue to decline. Neither species appears able to maintain its predam prominence on the floodplain in the postdam environment but for very different reasons, as is discussed below.

Green ash has emerged as the dominant late-successional species, as was predicted by Johnson and colleagues (1976). Major declines in all size classes of American elm and box elder foretell their greatly reduced roles in the future floodplain forests. Elm will eventually be extirpated in the region by Dutch elm disease unless resistant trees are found and propagated. Johnson and colleagues (1976) did not discuss the potential effects of the disease because none were apparent in natural forests at the time of their study; however, some street trees in Bismarck had succumbed to the disease by 1969. The loss of elm from the ecosystem will have long-term consequences for the biodiversity, productivity, and resilience of late-successional forests on this and other floodplains (e.g., Hale et al. 2008).

pulses of cottonwood regeneration are unlikely to be repeated. The rate of cottonwood regeneration has declined in recent decades (Dixon et al. 2010). The proximity of these river-marginal patches to the main channel also makes them more vulnerable to erosion from ice and high flows than would have been the case for predam patches that established on the inside of dynamic river bends. Stabilization of riverbanks is common in the Garrison Reach, which further limits channel movement, point bar formation, and forest regeneration (Florsheim et al. 2008). Fifty-two percent of the banks have been stabilized in the urban areas of the reach, whereas 21% have been stabilized in rural areas (Angradi et al. 2004).

The remeasurement data clearly show the void of reproduction within established stands, steadily increasing tree size, and aging population structure of cottonwood. The remeasured stands and the historic land- and water-cover mapping together provide strong evidence that cottonwood is indeed a fugitive species on the Missouri River floodplain that is dependent on cut-and-fill alluviation during high flows to form new recruitment sites.

It could not have been known from a single measurement in 1969 and 1970 whether the low recruitment into the

The cause of box elder decline is less obvious. Johnson and colleagues (1976) hypothesized that overbank flooding may have periodically provided essential moisture and nutrient-rich silt to enable the roots of late-successional species to reach the capillary fringe of the water table in the semiarid climate. Xerification of the floodplain now that floods have ceased could be lowering the survivorship of all but the larger and more deeply rooted box elder trees. Browsing by cattle and deer is a second likely factor reducing recruitment into box elder populations. Deer and cattle are both numerous on the floodplain; other studies have shown browsing to be a major factor affecting the composition and structure of riparian forests (e.g., Scott and Auble 2002).

In summary, the two hypotheses of Johnson and colleagues (1976) have been largely borne out by the remeasurement data—that is, a sharp decline in cottonwood regeneration caused by the cessation of flooding and a depauperization of the late-successional forest community and floodplain landscape.

Surprises

Although ash appears to be the current winner on the successional racetrack, its dominant position may be short lived, given the appearance and westward movement of a "great equalizer": the emerald ash borer (*Agrilus planipennis* Fairmaire). This Asian insect was first found in Detroit, Michigan, and Windsor, Ontario, in 2002, associated with urban trees (Poland and McCullough 2006). To date, tens of millions of ash trees have been killed as the pest outbreak has expanded from the Detroit area west to Minnesota, east to Maryland, and south to West Virginia (Moser et al. 2009). The borer often attacks stressed trees first, but when beetle populations are high, even the healthiest ash trees are killed. All North American species of ash are susceptible to mortality by the insect. Foresters are not sanguine about the prospects for containment because of the widespread nature of ash and the potential for inadvertent transport of the pest via firewood.

A second surprise after 40 years was the rapid formation and impact of the Oahe delta. Groundwater has been rising in the affected area, causing considerable mortality of established trees. Of the six native tree species on the floodplain, only peach-leaf willow can withstand chronic flooding. Even cottonwood, which is remarkably well adapted to life along rivers, rarely survives flooding throughout the growing season. Field notes from the 2008 remeasurement show a high mortality rate of trees in most stands (Stands 1, 2, 3, 6, 8, and 10) south of Bismarck in the affected area. There was no evidence of abnormal rates of tree mortality in the 1969 and 1970 survey of the same stands. Sedimentation in the delta area will continue, and unless streamflow and groundwater backup are relieved by channelization or flood-scale releases from Garrison Dam, such as those that occurred in summer 2011, water tables are likely to increase further or stabilize at high levels during high-reservoir stages.

The survival prospects for these forests are poor. The complete replacement of some forests that were well developed in 1969 by grassland had already occurred in 2008 (e.g., Stand 10;

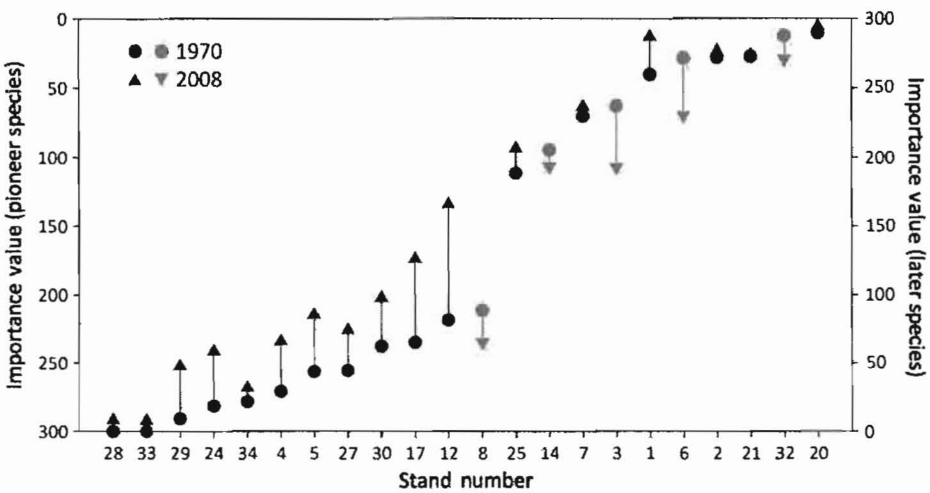

Figure 10. Successional trajectories for all remeasured stands over a 40-year period (stands with cottonwood present in 1969 and 1970). The circles represent the 1969 and 1970 importance values for pioneer species (cottonwood, left ordinate) and late-successional species (elm, ash, and box elder; right ordinate). The triangles represent the importance values for each group of species in 2008. The red color signifies reverse succession (increased importance values for pioneer species over time) and the black signifies forward (normal) succession (decreased importance values of pioneer species over time). The stands are arranged by decreasing importance value of cottonwood and willow in 1969 and 1970. The ordinates of the graph are scaled differently.

Table 1. Density of reproduction of late-successional tree species in occupied stands at two time periods on the Missouri River floodplain.

	Seedlings				Saplings			
	1969–1970[a]		2008		1969–1970[a]		2008	
Species	Number per square meter	Number of occupied stands	Number per square meter	Number of occupied stands	Number per hectare	Number of occupied stands	Number per hectare	Number of occupied stands
Green ash	6.6	33		25	6043	33	163	9
Box elder	1.0	31		6	1596	33	250	3
American elm	6.4	22		15	1405	27	73	4

Note: Seedling density was not estimated in 2008. Thirty-four stands were sampled in 1969 and 1970, and 30 of those were resampled in 2008.
[a]From Johnson (1971).

figure 11). The conversion process is accelerated by wildfires, which are primarily caused accidentally by recreationists, that occur commonly now because more grassland has been planted in the Oahe Game Management Area. Most of the cropland within the boundary of the management area has been planted with various mixtures of native, warm-season grasses (Jeb Williams, North Dakota Game and Fish Department, personal communication, 9 August 2011). Many wetter sites, some of which were forested in 1969 and 1970 within the boundary, have also converted naturally—assisted by fire—to mixtures of reed canary grass and prairie cordgrass (figure 11).

The future vegetation of the area south of Bismarck affected by the delta will be dominated by wet grassland, not forest and agriculture as it was in 1969 and 1970. The high water table and increased flooding during high-reservoir stages and fires during low-reservoir stages will open the forest canopy, facilitating grassland establishment and heavy weed growth, except on some of the higher ground that currently supports midsuccessional, high-diversity cottonwood forests.

At the opposite (northern) end of the Garrison Reach, channel degradation, not aggradation, has occurred. Any ecological effects of degradation, such as increased tree mortality from a lowered water table, were not apparent from the remeasurement data. However, other measurements should be taken to determine whether more-subtle effects, such as tree growth decline, a lowering of floodplain lake and wetland levels, and restricted lateral movement of the incised channel, are detectable, as they have been found to be on the lower Missouri River (NRC 2002).

Conclusions

The changes on the Missouri River floodplain over the past 40 years follow a century and a half of substantial human influences, the most important of these being the extensive clearing of timber for agriculture; the cutting of massive volumes of timber for steamboat fuel; the removal of snags; channelization and levee construction; bank stabilization; and, most recently, the building of large dams (Schneiders 1999). Concern in the United States over the declining health of this river system is evidenced by two major reports by the National Research Council in the last decade in which the collective impacts and approaches needed for ecosystem recovery were reviewed (NRC 2002, 2011). The new findings from the Garrison Reach describe both the continuing and other, unforeseen stressors on what remains of the ecological legacy in remnant reaches confined between reservoirs. River

Figure 11. Conversion of a successionally mature riparian forest to a grassland dominated by reed canary grass. The forest was killed by reservoir backup during high-reservoir stages and by wildfire during low-reservoir stages. The left photograph is of Carter Johnson in Stand 10 in 1969. Photograph: Janet Johnson. The right photograph is of Carter Johnson in same stand in 2008. Photograph: Michael L. Scott.

engineering, agriculture, and urbanization are not the only causes of the declining health of riparian forests. Diseases and insect pests imported from around the world have been (and may continue to be) an important cause of the decline of the trees that naturally replace short-lived cottonwoods and contribute so much to forest biodiversity.

Perhaps the most surprising consequence of the dams has turned out to be the areal extent and the impacts of deltas in the contact zone between river and reservoir. Almost a quarter of the Garrison Reach's floodplain forests—once thought to be safe from permanent flooding—are now dead or dying as a result of rising groundwater. The environmental benefits of this novel delta ecosystem dominated by low-diversity grassland—much of it planted—pale in comparison to those of the high-diversity riparian forests being lost. As the world's reservoir systems age, the effects of delta formation and expansion will become more evident and problematic, as they have in the Garrison Reach. Studies are needed in order to identify problems and to find solutions that will minimize the effects of deltas on the riparian ecosystems associated with most dammed river systems worldwide (Johnson 2002).

Mounting, cumulative impacts make the restoration of the riparian ecosystems of the Missouri River doubtful. More and more cards are stacked against the natural river ecosystem as impacts diversify and magnify. Although some of these impacts were predictable, others—largely stochastic in nature (pest invasions and tree diseases)—were not. If ash and elm are functionally extirpated, true restoration will be impossible; however, reactivating key ecological processes, such as flooding and cut-and-fill alluviation, in the reach could recover much of the biodiversity and function of the cottonwood community (see Rood et al. 2003) that historically dominated the floodplain.

The major lesson from this long-term research is that a second, more insidious wave of impacts of damming follows the initial acute impacts associated with the filling of large reservoirs. The second wave affects the remnant forests that survived downstream of the dams or in gaps between the reservoirs. These slow-to-develop environmental changes, such as channel incision, bank stabilization, and delta formation, are the product of flow and sediment alteration. Other impacts not directly associated with damming can be as serious as physical environmental changes in influencing ecological processes and biodiversity, such as the expansion of invasive plants, agricultural and urban expansion, and the introduction of insect pests and diseases. What started out 40 years ago as predominantly a cottonwood-regeneration problem on the Missouri River floodplain has expanded into a potential riparian-forest catastrophe with increasingly daunting prospects for recovery.

Postscript. During the publication phase of this article, unprecedented moisture in the upper Missouri River basin triggered record-breaking flow releases from the US Army Corps of Engineers dams. The extent to which these flows will rejuvenate the impaired elements of the river ecosystem discussed in this article are as yet unknown but should be a high priority for study when the flood waters have receded.

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