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Riparian vegetation diversity along regulated rivers: contribution of novel and relict habitats

W. CARTER JOHNSON
Department of Horticulture, Forestry, Landscape, and Parks, South Dakota State University, Brookings, SD, U.S.A.

SUMMARY

1. The creation and maintenance of spatial and temporal heterogeneity by rivers flowing through floodplain landscapes has been disrupted worldwide by dams and water diversions. Large reservoirs (*novel ecosystems*) now separate and isolate remnant floodplains (*relict ecosystems*). From above, these appear as a string of beads, with beads of different sizes and string connections of varying lengths.
2. Numerous studies have documented or forecast sharp declines in riparian biodiversity in relict ecosystems downstream from dams. Concurrently, novel ecosystems containing species and communities of the former predam ecosystems have arisen along all regulated rivers. These result from the creation of new environments caused by upper reservoir sedimentation, tributary sedimentation and the formation of reservoir shorelines.
3. The contribution of novel habitats to the overall biodiversity of regulated rivers has been poorly studied. Novel ecosystems may become relatively more important in supporting riverine biodiversity if relict ecosystems are not restored to predam levels. The Missouri River of the north-central U.S.A. is used to illustrate existing conditions on a large, regulated river system with a mixture of relict and novel ecosystems.

Keywords: delta, Missouri River, remnant floodplain, reservoir, riparian biodiversity, shoreline

Introduction

A central tenet of landscape ecology is that pattern affects process (Forman & Godron, 1986). The rates and trajectories of ecological processes, such as productivity and ecological succession, depend on the spatial patterning of the environment (Wiens, 1999, 2002). This concept is perhaps best represented by river ecosystems. The normally high biodiversity present on natural floodplains is created and sustained by high environmental heterogeneity in space and time (Hupp, 1988; Gould & Walker, 1997; Ferreira & Stohlgren, 1999). This heterogeneity is generated largely by the river network, as it creates valley topography forming strong spatial gradients in substrate, temperature and moisture (Ward *et al*., 1999). The natural flow regime, including droughts and deluges, periodically restructures the floodplain environment enabling diverse mixtures of species to persist side by side, some adapted to stability and others adapted to instability (Johnson, Burgess & Keammerer, 1976; Brown, 1997; Poff *et al*., 1997).

Flow regulation by dams has disrupted the natural pulse flow regime of most rivers and has altered the processes that sustain biodiversity (Junk, Bayley & Sparks, 1989; Ward & Stanford, 1995; Stanford *et al*., 1996; Tockner, Malard & Ward, 2000). Dams have fragmented the world's major rivers into disjunct, largely disconnected ecosystems. This is particularly true where rivers are managed for diverse objectives, such as navigation, irrigation, flood control and recreation. McCully (1996) has estimated that approximately 40 000 large dams (>15 m in height) and over 800 000 small dams have been built on rivers worldwide, indicating the pervasive effects of dams on the ecology of rivers.

Correspondence: W. Carter Johnson, Department of Horticulture, Forestry, Landscape, and Parks, South Dakota State University, Brookings, SD 57007, U.S.A. E-mail: carter_johnson@sdstate.edu

Reservoirs now separate and isolate remnant floodplains. From above, these may appear as a string of beads, with beads of different sizes and string connections of varying lengths. The beads (reservoirs and associated habitats) have been termed *novel* habitats (Stevens *et al*., 2001) within the river system, i.e. they represent environments and biotic communities largely absent from the preregulated river (Table 1). In addition to the lacustrine habitats created by the dams, other novel habitats have formed on most river systems as the reservoirs have aged. These include riverine deltas formed at the upper reservoir connection to the mainstem river, lacustrine deltas formed where tributaries enter the reservoirs themselves, and reservoir shorelines.

Remnant floodplains existing above, between, or below reservoirs, have been termed *relict* habitats (Stevens *et al*., 2001). They have retained their predam physiognomy of river channel and exposed floodplain (Table 1). The extent to which relict reaches have retained predam levels of native biodiversity varies considerably among rivers and reaches, depending on the magnitude of flow and sediment alteration by upstream dams and the degree of agriculturalisation and urbanisation of the floodplain. However, if native biodiversity is to be found in regulated river systems, it is likely concentrated in relict reaches that possess a legacy of preregulation channel and floodplain dynamics.

The distinction between relict and novel habitats is not always sharp. For example, the uppermost portions of reservoirs may include a mixture of relict and novel elements (Fig. 1). Nilsson, Jansson & Zinko (1997) applied the terms 'preupland' and 'preriparian' to distinguish the different origins of plant communities on regulated rivers.

The distribution of native biodiversity along mainstem, regulated rivers is likely to be a distinctly chequered pattern with low values for novel habitats associated with river 'beads' and high values for relict habitats associated with river 'strings'. However, the distribution pattern of species and communities probably is changing and will continue to do so. Reservoirs are ageing, evidenced by enlarging deltas with wetland and aquatic vegetation not unlike that of the former river and floodplain. The shorelines of some reservoirs, such as Lake McConaughy on the North Platte River (U.S.A) discussed below, have developed relatively diverse, well-structured woody vegetation. Biodiversity and spatial heterogeneity of novel habitats may be increasing. In contrast, many projections for relict habitats and reaches below dams are for spatial homogenisation and biodiversity decline unless flow variability and cut-and-fill alluviation are recovered at least to threshold levels.

A key question is the extent to which probable increases in biodiversity in novel habitats may compensate for expected losses of species or shifts in community structure and composition in relict reaches, assuming that river processes will be incompletely restored to recover predam levels of biodiversity. This question cannot be answered at present, but raising the issue of shifting biodiversity on regulated river systems would seem to be useful at this time, particularly if it stimulates field research on the subject.

The purpose of this paper is to outline the prospect of shifting biodiversity associated with regulated rivers. Too few comprehensive studies have been completed to form hard conclusions. Adequate data and insights are in print, however, to develop reasonable hypotheses about spatial and temporal patterns of plant biodiversity associated

Table 1 Characteristics of relict and novel habitats of regulated mainstem rivers

	Relict (remnant) reaches	Novel habitats/reaches
Relationship to reservoirs	Above/below/between reservoirs (not permanently flooded)	Associated with reservoirs
Types	a. Unregulated (headwaters) b. Tributary replenished (unregulated tributaries) c. Tributary non-replenished (regulated tributaries) d. Channelised	a. Reservoir shorelines b. Mainstem deltas c. Tributary deltas

with novel and relict habitats. This discussion is illustrated using examples from central and western North America, with an emphasis on the better-studied Missouri River in the north-central U.S.A. While these examples cited below exhibit many of the characteristics of regulated rivers worldwide, they do not represent all cases. For example, on the lower Snake River in Idaho and the Volga River in Russia, reservoirs are essentially contiguous, forming stair steps with virtually no strings of intervening relict floodplain.

Relict ecosystems

Numerous studies have measured or forecasted sharp declines in biodiversity downstream of dams (e.g. Johnson *et al*., 1976; Petts, 1980; Bayley, 1991; Ligon, Dietrich & Trush, 1995; Poff *et al*., 1997). Native aquatic organisms such as fish have declined in warm-water rivers because of the cold, clear water releases from dams, restrictions to movement caused by the dams themselves, altered hydrological regime, and disconnections between river and floodplain, among others (Stanford *et al*., 1996).

Vegetation has changed dramatically below most large dams. This is particularly true for forests dominated by *Populu*s in the central and western U.S.A. (Patten, 1998), and three patterns are apparent (Friedman *et al*., 1998). *Populus* and its highly associated biodiversity has failed to regenerate downstream of dams on meandering rivers in cooler climates, producing more homogeneous and impoverished forest cover (Rood & Mahoney, 1990; Johnson, 1992; Scott, Auble & Friedman, 1997). Contrastingly, along braided, sand bed rivers, dams and water diversions have caused channel narrowing and native *Populus* expansion, possibly increasing biodiversity, at least for the short-term (Nadler & Schumm, 1981; Johnson, 1994). Thirdly, some rivers in hot, semiarid regions have become dominated by exotic woody species (*Tamarix, Elaeagnus*) that are better adapted to river regulation than the native *Populus* or have colonised rivers with natural flow regimes unfavourable for *Populus* (Ohmart, Anderson & Hunter, 1988). The rate at which biodiversity has or will decline below dams is poorly known, but is expected to be relatively rapid unless key riverine features, such as flow variability and cut-and-fill alluviation, are restored (Stanford *et al*., 1996).

Novel ecosystems

Deltas

Studies of the vegetation forming novel habitats on regulated river systems are few. The paucity of data probably results from the rather recent appearance of significant delta areas on mainstem reservoirs. Also, these new habitats are neither distinctly riparian nor lacustrine, so may have been passed over by scientists either interested in lakes or rivers. Vegetation of deltas forming in natural lakes or in estuaries has been studied more thoroughly (e.g. Kandus & Adamoli, 1993; Golub & Barmin, 1995; Vadineanu *et al*., 1998), but extrapolation to reservoirs may be tenuous because of the greater water surface fluctuations behind hydroelectric dams (Hill, Keddy & Wisheu, 1998).

The rate at which reservoirs accumulate silt and grow deltas should depend largely on the sediment yields of contributing watersheds and the volume of the reservoirs relative to inflow (Baxter & Glaude, 1980). Run-of-the-river reservoirs may not develop significant deltas because most sediment is flushed through the dam. Storage reservoirs in dry climates should produce rapidly growing mainstem deltas, such as the delta, discussed below, forming in upper Lake McConaughy on the North Platte River in the Great Plains. Undammed tributaries should grow deltas in reservoirs much faster than dammed tributaries that retain sediment. Nilsson (1996) has raised similar questions regarding the biological influence of free-flowing versus dammed tributaries on river mainstems. As discussed more thoroughly below for the Missouri River, deltas forming where unregulated tributaries enter large storage reservoirs often provide the best or only near-shore habitat for the establishment of woody riparian vegetation.

Kingsley Dam, forming Lake McConaughy was completed in 1941. A ring of native riparian vegetation dominated by *Populus* formed near maximum pool level soon after the reservoir filled (Fig. 1). Structurally, the vegetation associated with the reservoir delta strongly resembles that of the river upstream (Fig. 1). The delta has assumed a multi-channelled form with considerable spatial heterogeneity in vegetation structure, ranging from tall *Populus* trees closer to the river and shorter vegetation towards the reservoir. The short vegetation ranges from plant communities dominated by shallow water emergents (*Typha*, *Scirpus*, *Polygonum*) to young woody communities of *Populus* and *Salix*.

The vegetation of Lake McConaughy delta is dynamic both spatially and temporally. It expands and contracts in area over short time periods (i.e. 5–10 years) in response to reservoir levels. When the reservoir drops below normal levels during the growing season, vegetation expands onto exposed substrate. When water levels return to normal summer pool elevation, intolerant vegetation dies and vegetation zones shift landward. This high turnover of plants probably is typical of reservoir deltas in response to complex interactions between wet/dry weather cycles and reservoir operations.

At longer time scales, however, this delta appears to be aggrading and forming more land above normal maximum pool level. Aggradation is suggested by the presence of *Populus* growing on new land forming in the delta. *Populus* does not tolerate continual flooding during the growing season and must establish on bare surfaces above water (Braatne, Rood & Heilman, 1996). The mechanism for aggradation is the greater surface roughness contributed by delta vegetation which slows inflow (thus raising stage) and captures sediment on higher surfaces (Pasternack & Brush, 1998). Flooding upstream of deltas during high river flow is a well-known phenomenon often alleviated by channelisation to increase conveyance (Baxter & Glaude, 1980).

Thus, the long-term trend has been for vegetation to increase in area and in structural complexity as this delta has grown and as aggradation has produced greater topographical variability. Despite high turnover of plants in the short term, a longer-term trend of increasing the area of woody vegetation in a range of age classes is apparent. Although field sampling has not been conducted on the Lake McConaughy delta, aerial photographs and ground reconnaissance suggest that the vegetation of the delta is taking on many of the characteristics of the vegetation of the river channel upstream.

Shorelines

Nilsson and co-workers have contributed considerable data and insight into the broad biodiversity patterns of shoreline vegetation around reservoirs, particularly in Sweden (e.g., Nilsson *et al*., 1997; Nilsson & Berggren, 2000). The greatest differences exist between run-of-the-river reservoirs and storage reservoirs, with the former generally more diverse because they often contain elements of the predam riparian communities (i.e. ecological legacies). In contrast, storage reservoirs have usually destroyed pre-existing natural riparian vegetation, requiring shoreline vegetation to develop anew around reservoir margins at higher elevations, often on poor soils and without riparian seed banks.

While no similarly comprehensive studies have been conducted on western U.S. reservoir margins, there is evidence of both similarities and differences with the Swedish data. For example, along the middle Snake River in Idaho and Oregon, most reservoirs are run-of-the-river in type and have developed relatively diverse vegetation along their margins, probably more diverse structurally and compositionally than the riparian vegetation that they have replaced. This condition has developed because of the introduction of many riparian tree species not part of the presettlement flora, which was dominated by *Salix* spp. and *Celtis reticulata* Torr. Some of these introduced trees are eastern North American (*Populus deltoides* Bart., *Acer saccharinum* L., *Ulmus* spp.), while others are Eurasian (*Elaeagnus angustifolia* (L.), *Tamarix* spp.). Riparian woodland dominated by introduced trees also has increased substantially along the banks and islands of relict reaches between reservoirs (Johnson *et al*., 1995; Dixon & Johnson, 1999).

The above pattern for the middle Snake River applies to other reservoirs in the semiarid portions of the west, particularly in the south-west (Friedman *et al*., 1998). Conditions around reservoirs in the Great Plains, however, differ sharply from those in more arid environments. For example, the shoreline vegetation around Lake McConaughy, as mentioned above, is comprised largely of native species, particularly the native *Populus* and *Salix*. More extreme conditions, however, occur around the Missouri River reservoirs in the northern Great Plains, around which woody vegetation has largely failed to establish successfully, except at tributary junctions. As discussed more fully below, the steep, unstable banks, long fetches, and changeable water levels of large storage reservoirs along this river largely preclude the establishment of riparian vegetation.

Missouri River

The Missouri River of the north-central U.S.A. exhibits a mixture of relict and novel habitats. Approximately one-third of the river's length is occupied by storage reservoirs (novel habitats), one-third comprised of relict floodplain-unchannelised sections, and one-third comprised of relict floodplain-channelised sections (Fig. 2). Although data are incomplete, riparian plant diversity appears to vary among reaches, from the highest values associated with lightly regulated conditions that retain biotic legacy of the predammed river, to the lowest values associated with novel reservoir habitat.

Relict ecosystems

Natural floodplain – lightly regulated
Less than 100 km of unregulated river occurs above the most upstream storage reservoir on the Missouri River. However, one reach in particular occurs sufficiently downstream of a comparatively small reservoir to retain many predam flow and vegetation characteristics. This occurs between Great Falls, Montana and Fort Peck Reservoir (Fig. 2), which includes the National Wild and Scenic reach.

Forests of *Populus* dominate the riparian zone; their status and potential for regeneration in the postdam environment have been well studied. Scott, Auble and Friedman (1997) have found that the majority of the existing forests, particularly in reaches where the channel is confined, established after large floods. While floods still occur, they are of reduced magnitude and therefore produce less frequent regeneration events. *Populus* forests will persist in the reach but will diminish in area unless larger floods are prescribed (Bovee & Scott, 2002). Nonetheless, this reach will continue to support at least modest levels of native *Populus* forest relatively rich in woody plant diversity, especially if summer stock grazing is reduced.

Natural floodplain – replenished
In some reaches below the large mainstem dams, sediment and flow variability curtailed by the dam are replenished by large, unregulated tributaries. This is the case where the Yellowstone River enters the Missouri River in extreme western North Dakota between two large reservoirs (Fig. 2). The Yellowstone actually has more flow than the Missouri at the confluence. The Yellowstone River has no water storage reservoirs, but a significant proportion of its drainage area has been dammed, and low-head mainstem dams divert water for irrigation (Helfrich *et al*., 1999).

The Yellowstone sharply improves the conditions in the Missouri for native organisms. Its abundant silt load and naturally varying hydrology sustain near preregulation conditions in the Missouri. Because of the replenishing effects of the Yellowstone, this reach experiences lateral channel movement, riparian vegetation establishment (primarily *Populus*), and successful reproduction of important warm-water, native fishes such as sturgeon and paddlefish (Ryckman, 2000).

Natural floodplain – unreplenished
Other tributaries entering the Missouri between dams are smaller than the Yellowstone and as such fail to contribute sufficient flow variability and sediment to sustain native communities. An example is the well-studied reach between Lake Sakakawea and Oahe Reservoir (Fig. 2). Vegetation studies confirm the high spatial and temporal diversity of floodplain vegetation that occurred as a legacy of predam river dynamics. The dynamic river channel initiated a succession of forest vegetation beginning with young *Populus* and *Salix* forests and ending with later-successional forests of *Fraxinus*, *Acer*, *Ulmus*, and *Quercus* (Johnson *et al*., 1976). The forest understory vegetation was rich, with approximately 220 species of vascular plants, 80% of which were native (Keammerer, Johnson & Burgess, 1975).

While this reach still retains considerable ecological legacy, biodiversity is expected to decline as the pioneer, early successional elements of both the vegetation and of the associated animal communities drop out (Hibbard, 1972), succumbing to the disappearance of the predam processes of channel meandering and overbank flow (Reily & Johnson, 1982). Johnson (1992) estimated that the once dominant *Populus* would become a minor component of the vegetation of the floodplain approximately 100 years after dam closure. The rate at which other biodiversity elements will decline in the future without efforts to restore key riverine processes is largely unknown.

Channelised floodplain
The section of the Missouri River downstream of the last dam (approximately one-third of the river's

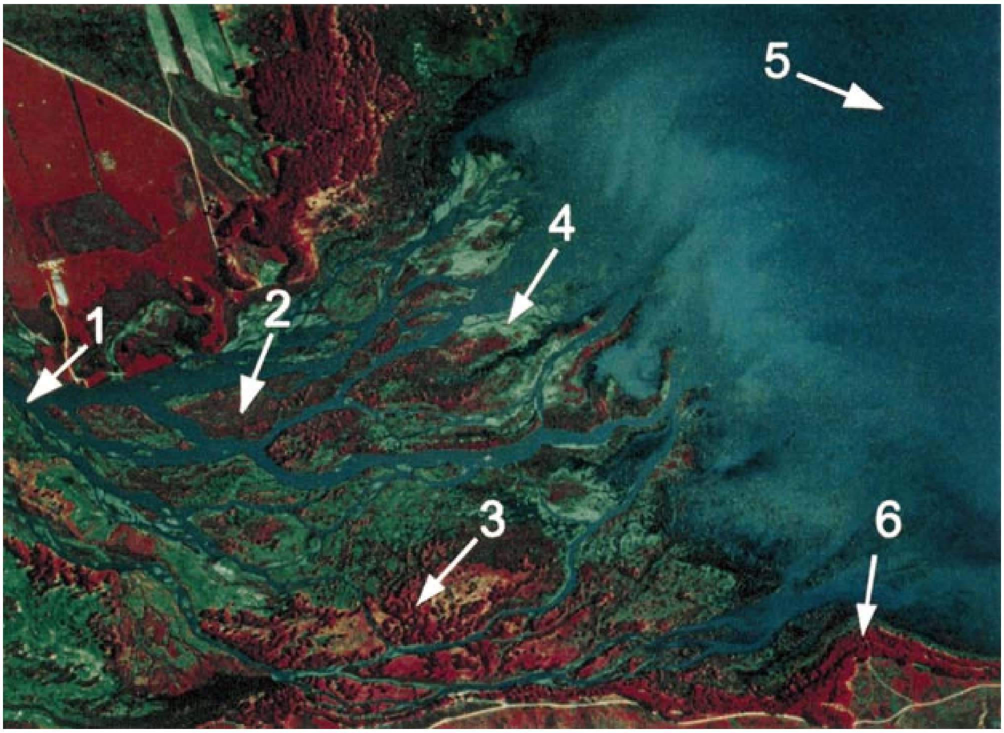

Fig. 1 Colour-infrared aerial photograph (16 May 1988) of the delta on upper Lake McConaughy (right) fed by the North Platte River (left). *Relict habitats*: 1, channel of North Platte River; 3, relict island with *Populus* forest; *Novel habitats*: 2, reservoir delta with young *Populus* and *Salix* stands; 4, reservoir delta with mixed emergents of *Typha* and *Polygonum*; 5, open reservoir; 6, reservoir shoreline with *Populus* forest.

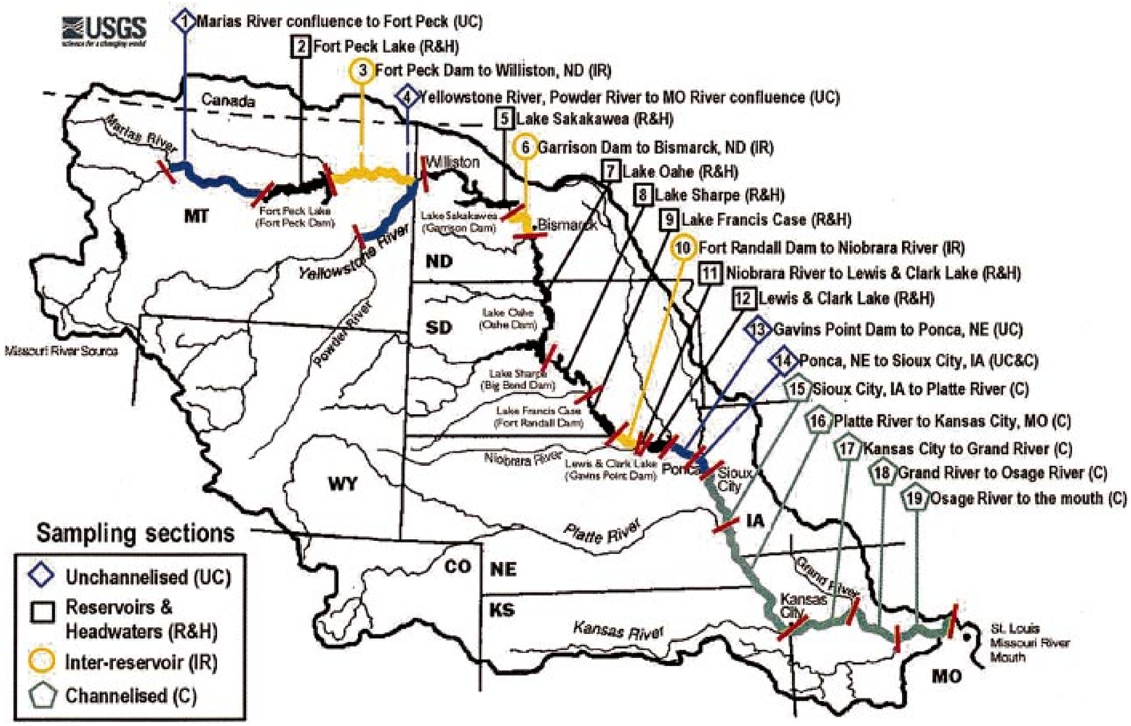

Fig. 2 Location of reservoirs, relict-unchannelised, and relict-channelised reaches for the Missouri River, U.S.A. (printed with permission of the U.S. Geological Survey).

length) has been channelised to enable navigation by boats and barges (Fig. 2). Nearly continuous levees protect the floodplain from overbank flows, and side channels have been blocked converting the formerly multichannelled river into a single, stationary thread (Hesse, 1996). Channel degradation has lowered the floodplain's water table, effectively de-watering the floodplain of marshes and lakes (Galat, Robinson & Hesse, 1996). Floodplain protection has stimulated the clearing of the native forest vegetation, leaving only small remnant patches with little new regeneration. Overall, populations of both native terrestrial and aquatic organisms have been decimated by river regulation, agricultural activities, and industrialisation; however, significant natural resources remain.

Small-scale habitat improvements in the channelised section are underway to reverse the historic declines in biodiversity (Galat *et al*., 1998). Side channels (chutes) have been re-established on several large river bottoms (Boyer Chute, Hamburg Bend, Lisbon Bottoms) to create shallow water habitat for warm-water fishes. The managed areas are part of the Big Muddy National Wildlife Refuge that totals approximately 25 000 ha (U.S. Fish & Wildlife Service, 1999). The effectiveness of these local projects in increasing the populations of native organisms (particularly fishes) adapted to riverine conditions, without systemic improvements in the river's sediment and flow regime, is unknown at this time.

Novel ecosystems

Reservoir deltas – mainstem

Mainstem deltas have become more visible with time. Vegetation has become sufficiently established and large enough in area to restrict flow through the delta during high flow events. This has caused flooding upstream of the river-delta confluence, most notably in Pierre, South Dakota and in Bismarck, North Dakota, associated with Lake Sharpe and Lake Oahe, respectively (Fig. 2). The mainstem delta associated with Lewis and Clark Lake occupies an especially large proportion of the reservoir compared with the other, much larger mainstem reservoirs. Recreational boating interests have decried the shallow water and expanding wetland, while waterfowl hunters and fishermen have welcomed and adapted to the changes.

No quantitative studies of vegetation have been published on the Missouri's mainstem deltas. Field observations and aerial photographs indicate, however, that the nature of the deltas and their vegetation are strongly affected by the operations of the reservoirs. The large storage reservoirs such as Oahe and Sakakawea have highly variable pool levels, ranging as much as 10–12 m between wet and dry periods. This creates high plant recruitment during low reservoir levels but high plant mortality after refilling. Yet, as these reservoir deltas enlarge, they may aggrade more significantly and develop higher surfaces for woody plant establishment that can survive the wet-dry cycles, similar to that observed on the Lake McConaughy delta. *Populus* regeneration requires either summer drawdown or sub-irrigated land lying above high pool levels. *Populus* cannot withstand prolonged root submergence during the growing season (Braatne *et al*., 1996). Deltas on the Missouri's small reservoirs with comparatively stable pool levels, such as Lewis and Clark Lake, have developed mostly herbaceous wetland vegetation. Much of this delta is comprised of floating mats of *Typha*, similar to those described world-wide by Sasser *et al*. (1995) and Klosowski & Tomaszewicz (1993).

Reservoir deltas – tributaries

Many small tributaries empty into the Missouri's reservoirs. As with mainstem deltas, tributary deltas are beginning to form and to support wetland vegetation. The Niobrara River delta, forming in Lewis and Clark Lake, is one of the largest and best developed of the reservoir deltas. Because of the stable reservoir levels, the delta is dominated by emergent aquatic species such as *Typha*. In contrast, the White River delta, forming in Lake Francis Case, is smaller but is developing woodland communities (Fig. 3). The White River is one of the few unregulated rivers of its size in the Great Plains (Friedman *et al*., 1998). It contributes a heavy sediment load to Lake Francis Case with considerable potential to enlarge the delta. Tributary deltas appear to be forming very slowly in large reservoirs because they often enter very deep water.

Reservoir shorelines

Riparian vegetation generally has failed to establish along the shorelines of the Missouri reservoirs. The large size of the reservoirs killed all pre-existing wetland vegetation. Any new establishment must

Fig. 3 Confluence of the White River (upper left) and the Missouri River in central South Dakota, U.S.A. LANDSAT – ETM + image (12 June 1999) provided by D. Greenlee of EROS Data Center. *Novel habitats*: 1, mixed emergent; 3, young *Populus-Salix* forest; 4, Lake Francis Case (Missouri River); *Relict habitats*: 2, White River.

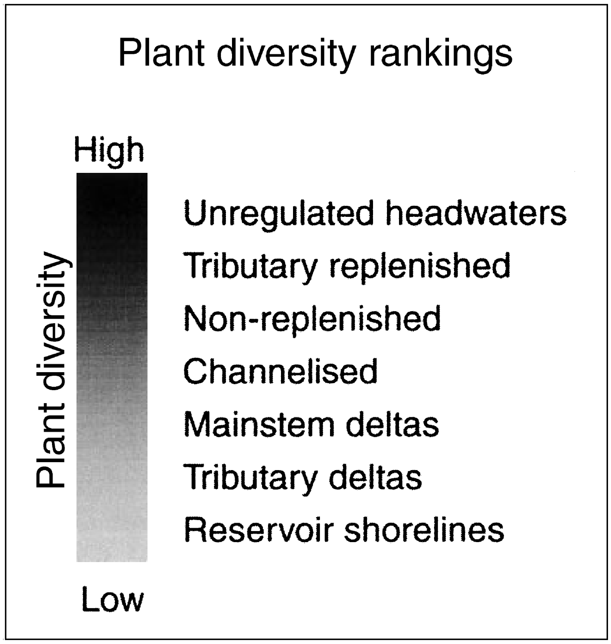

Fig. 4 Estimated plant diversity rankings for mainstem habitats along regulated rivers.

form from propagules dispersed to new soils. While colonisation often occurs, establishment is prohibited by massive wave action from the windy climate and large fetch. Millions of dollars have been spent to stabilise these reservoir shorelines by using physical structures and vegetation to reduce bank collapse and reservoir sedimentation; however, these attempts largely have failed. These barren, unstable reservoir shorelines contrast with the vegetated, comparatively stable Swedish shorelines (Nilsson, 1981).

Riparian vegetation has established naturally, however, in certain portions of these large reservoirs. The best examples occur in association with small, often ephemeral, tributaries which have created flatter topography, contribute some sediment and occur in coves protected from wave action. Thus, novel shoreline plant communities have formed successfully as small, isolated patches associated with pre-existing drainages. However, these represent only a tiny fraction of the total reservoir shoreline.

General biodiversity patterns

I propose biodiversity rankings for habitats associated with large, regulated rivers such as the Missouri (Fig. 4). These rankings are only estimates based on scattered information available from the Missouri and from other river systems such as the North Platte and Snake rivers discussed above. No complete inventory of higher plants and animals has been conducted for any single segment of the Missouri River and its floodplain. We should expect relict ecosystems with the greatest ecological legacy to currently hold the highest proportion of their predevelopment complement of native riparian species. Among the relict habitats, unregulated (or lightly regulated) reaches should retain the highest percentage of species and communities, followed by replenished reaches and then by unreplenished reaches. Among the relict reaches, channelised reaches should have the greatest losses of communities and shifts in native species because of the engineered channel and often more intensive use of the floodplain for agriculture and industry (Fig. 4).

Novel habitats begin with riparian biodiversity at or near zero. Thus, as a group, they should differ more from predevelopment biodiversity than do relict habitats. These all rank below relict habitats in this scheme (Fig. 4). Mainstem deltas should rank the highest among novel habitats because larger deltas form more quickly than most tributary deltas in reservoirs. The latter, however, should accumulate species faster than reservoir shorelines, many of which have been extremely slow to develop riparian communities. Thus, the strongest contrasts in biodiversity should be between shorelines along large reservoirs and the floodplains of the unregulated headwaters or lightly regulated mainstem reaches, such as the National Wild and Scenic reach of the Missouri River.

These rankings may change positions with time, as more species establish. The deltas could shift the most, possibly surpassing channelised and non-replenished reaches if the latter have not benefited from restoration and continue to lose early and mid-successional species and communities. Unregulated headwaters should maintain their lead position unless more dams are built or human activity on the floodplain increases substantially. Tributary-replenished reaches should maintain high levels of biodiversity as long as the tributary continues to contribute high flow variability and sediment to the mainstem. Considerable swapping of positions among the middle four categories (Fig. 4) could occur in the next century depending on the extent to which relict reaches are restored and novel habitats create spatial and temporal heterogeneity, a prerequisite for harbouring large numbers of riparian species.

Conclusions

Maximum biodiversity along regulated rivers occurs in unregulated, lightly regulated and replenished sections. High biodiversity in these relict sections is the product of relatively natural flow and sediment supply and a legacy of native species. Such sections should be a high priority for preservation as a means to maintain natural riverine physical processes and to protect remnant floodplain vegetation from overexploitation or conversion to agriculture. Unfortunately, rich floodplain forest continues to be cleared on the Missouri River floodplain, despite its increasing scarcity.

Non-replenished relict sections should be high priorities for restoration. Most contain a considerable legacy of species and communities formed and shaped during preregulation time periods. These communities still are rich in biodiversity but soon may lose early and mid-successional elements because of chronic flow and sediment depletions. Restoration of the key process of cut-and-fill alluviation must occur before the expected biodiversity decline can be reversed. This will require whole-system changes in reservoir operations and removal of channel stabilisation structures.

Reservoirs in many large river systems are beginning to show their ages by the appearance of expanding deltas. Some deltas are topographically heterogeneous and therefore support varied wetland vegetation, including woody communities. Such deltas appear to be creating environmental conditions that support vegetation structurally similar to that initially killed during reservoir formation.

Reservoir deltas are both understudied and undermanaged. Their contribution to overall riverine biodiversity is virtually unknown. Moreover, few deltas are managed to enhance vegetation heterogeneity or wildlife and fishery values. For example, a small, permanent reduction in maximum reservoir pool levels could dramatically reduce vegetation turnover between low and high pool cycles, thus creating more permanent, woody communities and higher associated biodiversity. Current reservoir management does not consider the effects of reservoir pool dynamics on the ecological condition of mainstem and tributary deltas. Channelisation of deltas to reduce upstream flooding may limit the extent to which the delta creates topographical heterogeneity and harbours biodiversity.

Deltas are mostly or completely under public ownership. Thus, publicly owned deltas can provide exceptional recreational experiences and less-restrictive, more comprehensive management than is possible on most private land. Deltas may become future riverine 'wilderness' areas. Some have already become sufficiently extensive and rugged for recreationists to literally become lost in the complex of channels and rank vegetation. The degree to which novel habitats become valuable to riverine conservation depends largely on the extent to which relict ecosystems are preserved or restored in the future.

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