Alterations of Riparian Ecosystems Caused by River Regulation

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An estimated two-thirds of the fresh water flowing to the oceans is obstructed by approximately 40,000 large dams (defined as more than 15 m in height) and more than 800,000 smaller ones (Petts 1984, McCully 1996). Many additional rivers are constrained by artificial levees or dikes. These hydrological alterations—to ensure water for agricultural, industrial, and domestic purposes; for hydroelectricity; or for flood protection—have changed ecosystem structures and processes in running waters and associated environments the world over. In this article, we discuss the global-scale ecological changes in riparian ecosystems resulting from dam operations.

Comparative studies of free-flowing and regulated rivers have increased our understanding of the environmental effects of dams (Rosenberg et al. 1995). The first studies concentrated on large reservoirs; reaches downstream from dams were of subsequent concern. Early work also focused on aquatic systems. By the 1980s rivers were viewed in a larger perspective, as central elements in entire catchment areas (Ward 1997). In this process, the importance of riparian ecosystems successively attracted more attention (Naiman and Décamps 1997).

Riparian ecosystems occupy the ecotone between upland and aquatic realms (Figure 1). More precisely, the riparian ecosystem can be defined as the stream channel between the low- and high-water marks plus the terrestrial landscape above the high-water mark (where vegetation may be influenced by elevated water tables or extreme flooding and by the ability of the soils to hold water; Naiman et al. 1993). Natural riparian ecosystems include a variety of community types, including strips of spruce forest on periodically frozen ground with dense moss carpets, floodplain landscapes with deciduous trees and shrubs on heterogeneous substrates, and deltas with distinct plant zonation and well-developed forests having diverse animal communities. Some floodplain landscapes, such as those in South America, Europe, Africa, and Asia, cover tens of thousands of km^2 of land (Welcomme 1979, Petts 1984).

DAM OPERATIONS HAVE CAUSED GLOBAL-SCALE ECOLOGICAL CHANGES IN RIPARIAN ECOSYSTEMS. HOW TO PROTECT RIVER ENVIRONMENTS AND HUMAN NEEDS OF RIVERS REMAINS ONE OF THE MOST IMPORTANT QUESTIONS OF OUR TIME

Riparian areas are particularly sensitive to variation in the hydrological cycle and serve as good indicators of the environmental change that is caused by dam operations. Moreover, riparian processes have a central ecological role in most landscapes. Riparian ecosystems offer habitats for many species, function as filters between land and water, and serve as pathways for dispersing and migrating organisms (Naiman and Décamps 1997). Riparian ecosystems also have many economic and recreational values.

Dams are affecting riparian ecosystems all over the world. Consider the 139 regulated and free-flowing rivers in the United States, Canada, Europe, and former USSR that exceed 350 m^3/s in mean annual discharge. Eighty-five of them, representing 77% of the total water discharge, were strongly or moderately regulated and fragmented by dams (Dynesius and Nilsson 1994).

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Figure 1. Riparian zone in the free-flowing Lais River, a tributary to the Vindel River in the Ume River system, northern Sweden. This riparian system shows a distinct zonation of plants, going from mixed forest to willow (**Salix** *spp.*) *shrubs to vegetation of sedges* (**Carex** *spp.*) *and water horsetail* (**Equisetum fluviatile**). *Photo: C. Nilsson.*

Effects of dams and regulations on riparian zones

Many environmental effects of dams are immediate and obvious. For example, dams obstruct migration pathways for fish, and reservoirs trap waterborne sediment. Other environmental effects are gradual and subtle, making them difficult to predict. If a river is regulated, for example, the flood extent and the nutrient loads will certainly change but the exact nature of these changes and their magnitudes and time periods often remain unforeseeable. Every river is unique in terms of its flow patterns, the landscapes it flows through, and the species it supports, implying that the design and operating pattern of every dam is also unique. So are the effects of the dam on the river and its associated ecosystems (Johnson 1998).

In most cases, dams are built to ensure less variable flows in the rivers downstream, which is attained by increasing fluctuations of water levels in the reservoir behind the dam. Welcomme (1979) described this as a change from "flood-rivers" to "reservoir-rivers." In other cases, dams are built to facilitate diversions of water, which can leave the channels permanently or intermittently dry or at least strongly reduce flows. Conversely, dams are often built in arid areas with pronounced periods of rain and drought to ensure water availability during the dry season.

In addition to modifying the environment at the dam site proper, a dam affects riparian communities upstream by raising water levels and modifying water-level fluctuations and downstream by altering flow regimes. Many rivers have been turned into chains of storage reservoirs and run-of-river impoundments without any rapids left. This includes the Volga, Mississippi, Paraná, and most hydroelectric rivers in northern Sweden. One dam controls the water up to the next dam so that the upstream and downstream effects of dams overlap (Figure 2).

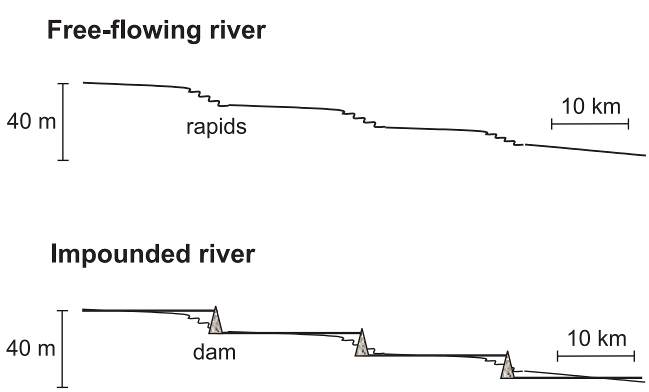

Figure 2. Most free-flowing rivers consist of series of rapids and slow-flowing stretches. In strongly impounded rivers, dams have been erected on the rapids, converting the rivers into stairs of reservoirs or impoundments and dams. In such rivers, one dam controls the water level up to the nearest dam upstream.

Upstream effects

The dams on Earth keep back approximately 10,000 km^3 of water. This is equivalent to five times the volume of water in all the rivers in the world (Chao 1995) or to a 10 cm deep layer of water spread on all the dry land in the world (Pielou 1998). Storing all this water cannot be made without far-reaching environmental consequences. These include habitat loss resulting from inundation and also the formation of new riparian zones.

Inundation of habitats. The most general upstream effect of a dam is that the water volume increases and inundates terrestrial and riparian areas (Figure 3). In some cases, dams have increased the volume of an existing lake but, often, running waters have been converted to reservoirs, which lead to permanent loss of habitats. This effect is especially profound where reservoirs are close to mountains, in dry areas, or in the far north where river valleys are usually the most productive landscape elements. Because many species in these environments are restricted to valley bottoms, large-scale impoundment of water is likely to extinguish entire populations. The initial effect of inundation on plants is through the root system. The waterlogged soil becomes anoxic and this leads to oxygen stress and eventual elimination of the primary root system. Many plants have special adaptations to cope with oxygen stress in soils, including the formation of aerated tissue and adventitious roots (Junk and Piedade 1997). Some species will immediately cease growth and die if the plants are entirely inundated. Others will respond by enhanced shoot elongation that restores contact with the open air (Blom and Voesenek 1996).

Inundation not only leads to the loss of organisms but also introduces environmental problems. Some inundated areas were cleared of woody vegetation before damming but in many cases, especially in old dam construction projects, land was inundated together with its existing vegetation. For example, in the Tucuruí project in the Amazon, 20 million m^3 of high-quality timber were inundated (Barrow 1988). It may take a long time for all this organic matter to decompose. When flooded soils and vegetation decompose, they release greenhouse gases (CO_2 and CH_4), which contribute to global warming (see St. Louis et al. 2000), and methylmercury, which accumulates in predatory fish (Rosenberg et al. 1997).

Decomposition of flooded soils also releases nutrients such as nitrogen and phosphorous that may temporarily increase aquatic productivity. For example, increased growth of floating aquatic vegetation like giant salvinia (*Salvinia molesta*), water hyacinth (*Eichhornia crassipes*), and water lettuce (*Pistia stratiotes*) is a common phenomenon in tropical manmade lakes (Petr 1978). Riparian vegetation was controlled in the Senegal River by periodic drought and brackish water. Regulation of the river led to stable water levels and freshwater conditions in the Guiers Lake situated in the coastal delta. As a result, giant salvinia, coontail (*Ceratophyllum demersum*), and bulrush (*Typha australis*) increased rapidly (Cogels et al. 1997). Excessive growth of plants may reduce access to drinking water for stock, taint potable water, usurp reservoir volume, cause evapotranspirative loss, and foul pump intakes.

New riparian zones. Impounded areas eventually develop new shorelines within the range of regulated water-level fluctuations. These shorelines can vary from several kilometer wide zones in large reservoirs to approximately 1 m wide strips along run-of-river impoundments with limited water-level fluctuations. The succession of shoreline communities on pre-upland river margins depends not only on the interplay between erosion and sedimentation of substrates and invasion and extinction of organisms, but also on the duration, timing, and frequency of regulated water levels. In the tropics, terrestrial grasses may grow on reservoir shorelines during periods of drawdown. Grass vegetation on the new shoreline around the Kariba Reservoir on the Zambezi River, for example, provides grazing for large herbivores (Baxter 1977).

Figure 3. Two contrasting types of storage reservoirs. (top) Barrier Lake on the Kananaskis River, Alberta, Canada. This shoreline is a strip of barren land. The Kananaskis River belongs to the catchment of the Nelson River. (bottom) The Koka Reservoir on the Awash River, Ethiopia. Floating vegetation of water hyacinth (Eichhornia crassipes) *is seen in the foreground. Photos: courtesy of Mats E. Johansson (top) and Kristoffer Hylander (bottom).*

The situation is different in northern temperate regions. Most years the entire reservoir shoreline is above water only during late winter and usually covered by ice and snow. Nilsson et al. (1997) modeled vegetation development on new shorelines in northern Sweden by using chronosequences of 43 storage reservoirs and 45 run-of-river impoundments (Figure 4). Shorelines along the storage reservoirs had low diversity in their early stages fol-

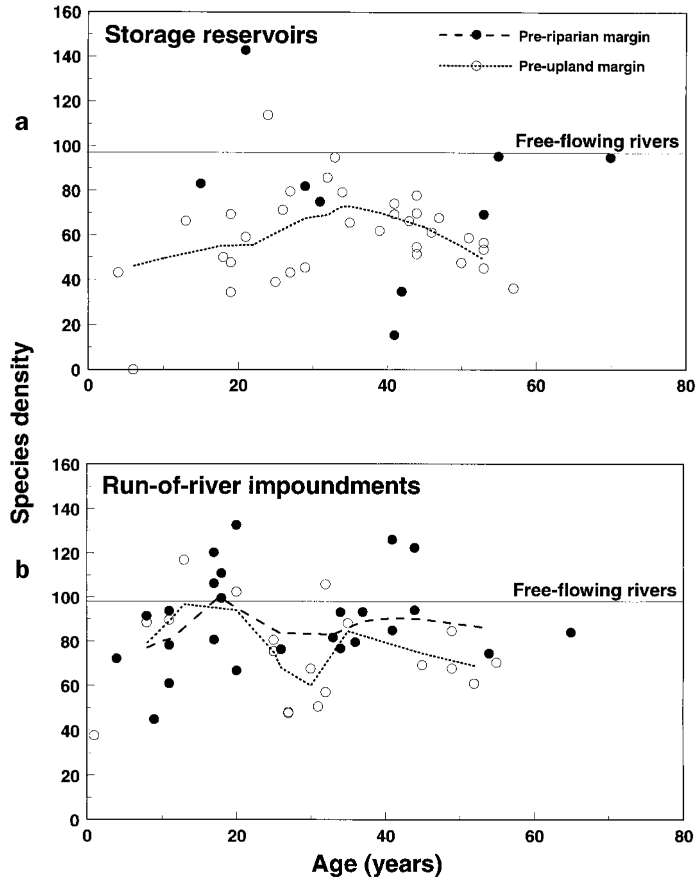

Figure 4. Temporal changes in riparian species density in reservoirs in northern and central Sweden. (a) Storage reservoirs. (b) Run-of-river impoundments. Preriparian margins overlap with the range of pristine water-level fluctuations, whereas pre-upland margins were formed when water levels were raised at the onset of regulation to intersect former upland soils. The diversity of plant species rebounds during the first 20 or 30 years after a dam is built and then tapers off. The subsequent scarcity of new species may be attributed to either a gradual depletion of seeds over the decades or a slow deterioration (soil erosion) of the habitat. Curves were smoothed with LOWESS regressions (Trexler and Travis 1993). Horizontal lines indicate the mean values of species richness for adjacent, free-flowing rivers. Modified from Nilsson et al. (1997).

lowed by a recovery phase, which lasted for approximately 30 years, but never reached predam values of species density. After 30 years, species density declined such that 50-year-old reservoirs had levels of species density similar to young reservoirs. Erosion of fine-grade substrates and a reduction of the available species pool because of constraints on dispersal likely played a role in this development pattern (Nilsson et al. 1997). Vegetation cover was extremely low throughout the study period. Species density and plant cover in run-of-river impoundments recovered to levels more similar to those before damming but absolute numbers of species were lower because regulated shorelines were narrower than natural riparian zones (Nilsson et al. 1997).

On a smaller scale, shoreline vegetation shows considerable variation between years, depending on between-year differences in water-level fluctuations. This situation has been reported from the Rybinsk Reservoir on the upper Volga River in Russia (Ekzertsev 1979) and the Gardiken Reservoir on the upper Ume River in northern Sweden (Nilsson and Keddy 1988). In reservoirs with low water-level fluctuations, shoreline vegetation can persist and develop similar to that of lakes. Ekzertzev (1979) reported that reservoirs on the Volga River that are filled to a constant level every year and hold a constant summer water level might develop stable plant communities within 5–10 years. The shallow parts of the reservoirs acquire the most luxuriant growth. The plant communities change with marked water-level changes.

Downstream effects

Many regulated rivers have storage reservoirs in the headwater regions, and downstream from these regions there is an intact channel with a regulated flow. In such rivers, a single reservoir can affect the flow in almost the entire river. Such a change will modify the riparian zone and its communities and might also lead to salinization and invasion of exotic species.

Hydrology and geomorphology. A common downstream effect of large dams is that the flood peak, and hence the frequency of overbank flooding, is reduced and sometimes displaced in time (Petts 1984). Furthermore, increased water use and evaporation losses following the formation of large reservoirs often reduce downstream discharge. Altered hydrology downstream of dams also reduces groundwater recharge in the riparian zone resulting in a falling groundwater table. These changes reduce the extent of the active floodplain.

Dams also change geomorphologic processes such as sediment cycling. Reservoirs may trap large masses of the sediment previously transported farther downstream. For example, a dam built across the Maujira River, a tributary to the Gadavari River in India, lost 60% of its storage capacity in 43 years because of siltation (Dogra 1986). The water released from a reservoir tends to restore its original load of sediment and nutrients, resulting in increased erosion downstream of the dam. This erosion leads to channel simplification and reduced geomorphologic activity in the river bed, for example, a lack of point-bar deposition and reduced river meandering (Johnson 1992) and a slower build-up of deltas and coastline erosion. Coastal marshes of the Mississippi River in Louisiana have experienced substantial losses as sediment deposition has declined following flood control and navigation practices (Nyman et al. 1990). Another example is the construction of dams on major rivers that drain into the Black Sea (Don, Kuban, Dniepr, and Dniester rivers), where reduced transport of sediment into the sea has changed the morphology of its coastline (Mee 1992). English et al. (1997) reported that the Slave River delta of Great Slave Lake, Northwest Territories, Canada, was markedly reduced after impoundment of the Peace River at Hudson's Hope, British Columbia.

Although regulation by dams usually reduces sediment transport, some regulated rivers still suffer from heavy siltation. This occurs in several Chinese rivers narrowed by dikes that exclude extensive parts of their floodplains from flooding. The siltation leads to an elevation of the riverbed and increased overbank flooding (Dudgeon 1995).

Riparian communities. Riparian communities within semi-arid and subarctic regions, where floods are extremely important for watering, fertilizing, cleaning, and sowing the land, are generally most severely altered by impoundment because water is so scarce. Low-altitude areas are generally more sensitive to water regulation than high-altitude areas because the terrain is flatter and small alterations in flow may affect vast areas (Petts 1984).

Eliminating or reducing the perturbing effects of floods and lowered groundwater levels that follow river regulation changes the species composition of riparian forests to that of forest types more characteristic of unflooded upland areas (Décamps et al. 1988). Many upland species are normally excluded from growing in and near free-flowing river channels because of intolerance to sedimentation, erosion, submersion, physical damage, and low soil fertility (Johnson 1994). Riparian pioneer species, on the other hand, are adapted to or need such processes; they have easily dispersed seeds, rapid germination, and rapid root and height growth (Johnson 1994). Changes in the hydrological regime start a new succession of riparian communities (Figure 5). For example, lowered groundwater levels resulting from river regulation can cause a decline in the reproduction of pioneers followed by a successive dieback of mature individuals (Stromberg et al. 1996). Lack of regeneration leads the succession toward older, less productive states, which also affects wildlife negatively (Nilsson and Dynesius 1994). Thomas (1996) reported several cases of such degradation along African rivers (e.g., Tana and Turkwel Rivers in Kenya, Jubba River in Somalia, Pongolo River in South Africa, Hadejia River in Nigeria; Figure 6). Rood et al. (1994) found a drastic decline in riparian cottonwood (*Populus angustifolia*, *Populus balsamifera*, and *Populus deltoides*) along the St. Mary River in Alberta, Canada, which was probably caused by drought-induced mortality following river regulation.

Even if floods remain, changes in their timing may be sufficient to cause environmental change. Atwell (1970) found that delayed flooding would negatively affect reproduction and feeding patterns of many animal species. Animals breeding adjacent to water suffer from destruction of eggs and larvae. Amphibians, crocodiles, and birds are strongly affected (see Dudgeon 2000). Movement patterns for populations of large herbivores are closely related to the flooding regime. Without normal floods, the floodplain is accessible to grazing during a longer period and will not be properly rested. Moreover, biomass production of the river is closely linked to the seasonal coupling and uncoupling of the floodplain (Bonetto et al. 1989). For example, many fish species have evolved in concurrence with this seasonality; hydrological changes will have adverse effects on their reproduction and growth.

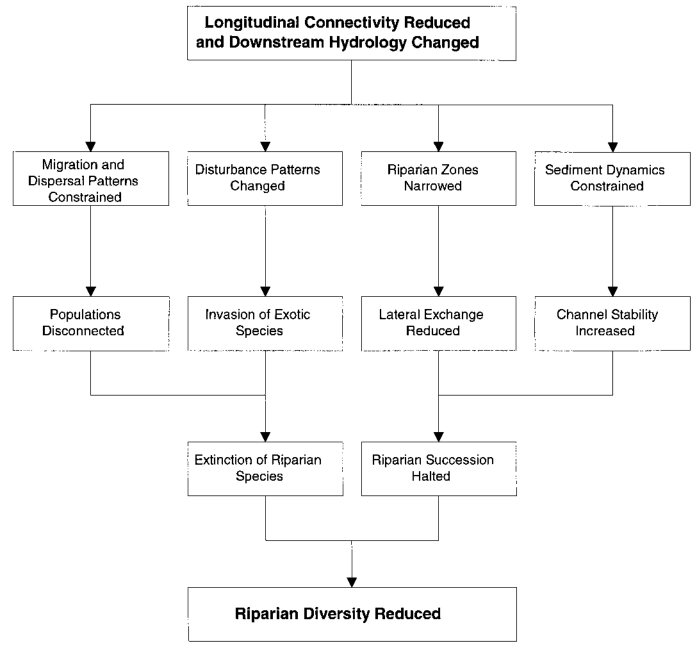

Figure 5. Overview of riparian succession following a reduced flooding regime downstream from dams. The figure summarizes four scenarios of change that may occur individually or in various combinations. Obstructions to dispersal disconnect riparian populations, whereas changed disturbance regimes may favor the spread of exotics. This eventually results in the extinction of native riparian species. When riparian zones are narrowed and sediment dynamics constrained, the aquatic riparian system becomes stabilized and the riparian succession is halted. The final result of any scenario is a reduction of riparian diversity. The majority of changes occur during the first decades after damming.

Riparian wetlands, deltas, and estuaries are usually highly productive and have high species numbers but may degrade following river regulation (Foote et al. 1996). Regulation of the Macquarie River in Australia has decreased the amount of water entering the downstream Macquarie marshes. The result has been a degradation of the wetland and a pronounced impact on species numbers and densities of waterbirds in the marsh area (Kingsford and Thomas 1995).

Community dynamics are also governed by geomorphologic processes. For example, channel migration is a major determinant of riparian vegetation patterns in many regions of the world. Some species may disappear

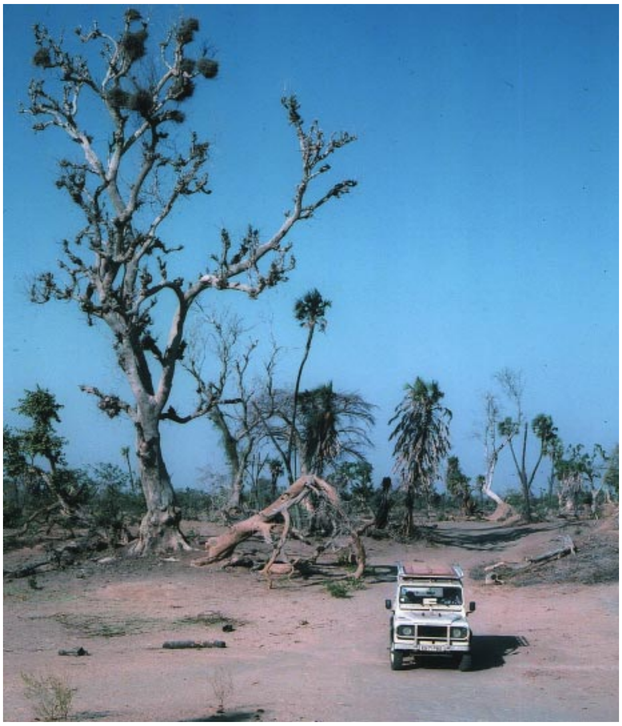

Figure 6. Dying **Mitragyna/Acacia nilotica** *riparian woodland along the dry Burum Gana Channel of the Hadejia River, northeast Nigeria. This woodland is dominated by acacia* **(Acacia nilotica), Mitragyna inermis** *(Rubiaceae), tamarind* **(Tamarindus indica),** *jackal-berry* **(Diospyros mespiliformis)**, *and ogwango* **(Khaya senegalensis)**. *Upstream dam construction, drought, and natural channel changes have left large areas of the Hadejia-Jama'are floodplain desiccated, degrading riparian forests and other wetland ecosystems (Thomas 1996). Photo: courtesy of Bill Adams.*

when regulation by dams changes the geomorphology. Auble et al. (1997) reported that the cottonwood *P. deltoides* along Boulder Creek on the Colorado Plains does not establish in the absence of erosion and bare soil. By simulating the effects of altered flow and meandering rates on the compositional dynamics of floodplain forests in the upper Missouri River, Johnson (1992) found that the pioneer cottonwood forest that still exists after regulation cannot be maintained by the low meandering rates and eventually will be replaced by later successional species.

Salinization. Dieback of the native tree, black box (*Eucalyptus largiflorens*), is an increasing problem on the floodplains of the lower Murray River in southern Australia. A primary cause of the dieback appears to be salinization of floodplain soils caused by reduced flooding frequency in the Murray River. This dieback happens because naturally saline groundwater comes to the surface when floodplain water is not recharged by floodwater (Jolly et al. 1993).

Problems with waterlogging and soil salinization are also common in many semi-arid and arid areas where dams are built to provide water for irrigation (Figure 7). Irrigation of soils of low permeability can cause the sometimes saline groundwater table to rise. Salt accumulates in the topsoil as water evaporates. This process has happened in some formerly very fertile areas (e.g., the Indus plains in Pakistan; Dogra 1986).

The Aral Sea in Kazakhstan and Uzbekistan is another example of devastation from altered river hydrology. Large land areas needed irrigation to support a growing cotton industry. Increasing amounts of water were abstracted from Amu Dar'ya and Syr Dar'ya, the two largest tributaries of the Aral Sea. This caused an 80% decrease of water volume of the Aral Sea in less than 40 years (Figure

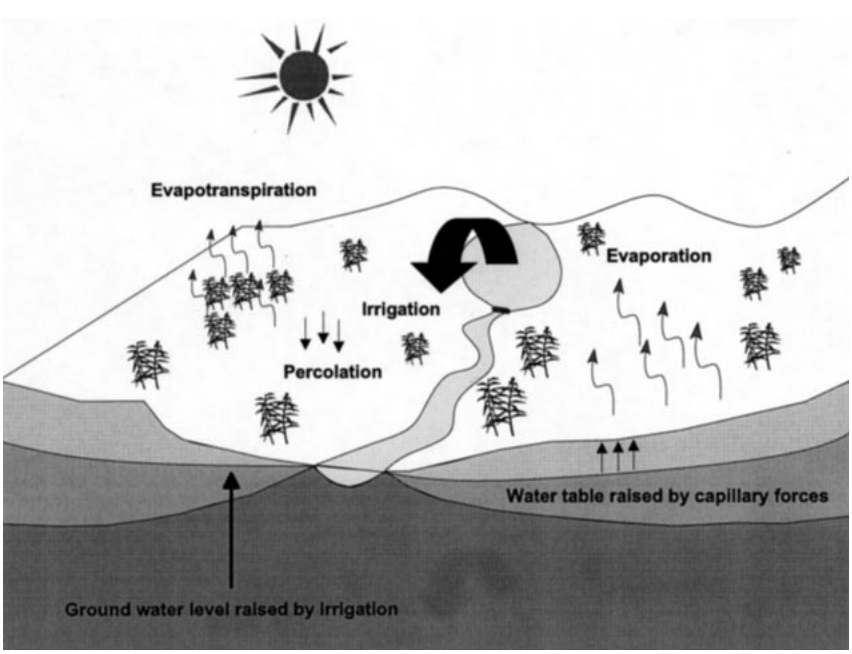

Figure 7. Schematic diagram of the process of salinization that follows from irrigation in arid lands. Water is allowed to infiltrate and percolate into the soil of areas under crop cultivation. Ultimately such irrigation projects suffer from two undesirable side effects: salinization and waterlogging of the soil. The irrigated area is subject to very heavy soil-water losses through evapotranspiration. Salts contained in the irrigation water remain in the soil and increase in concentration. Percolation of large volumes of water causes a rise in the water table and may, in time, bring the zone of saturation close to the surface. This phenomenon is called waterlogging. When the water table rises to the point at which upward capillary action can bring water to the surface, evaporation is increased and salinization is intensified.

8) and an increase in salinity from 8–10 g/L to 30 g/L over the first three decades (Aladin and Plotnikov 1993). The Aral Sea is now saltier than the ocean (Stone 1999). Its shrinkage has affected the region immensely. Flora and fauna have suffered massive losses. Enormous amounts of salt and dust are blown onto agricultural land in the Aral region from the 3.6 million hectares of exposed seabed, causing deterioration of both human health and soil fertility (Stone 1999).

Invasion by exotic species. Riparian zones are generally vulnerable to invasion by exotic species because rivers are dynamic and have recurrent disturbances, water is available all year-round, and rivers form a natural network for dispersal across the landscape (Planty-Tabacchi et al. 1995). These patterns are often even more pronounced in regulated rivers where natural communities are further disturbed. Water regulation of most river systems in South Africa has stabilized the natural hydrological regimes and caused alien aquatic plants such as water hyacinth, parrot's feather (*Myriophyllum aquaticum*), giant salvinia, and fairy moss (*Azolla filiculoides*) to spread. This has lead to reduced water movement, reduced water oxygenation, water loss through evaporation, and loss of light penetration (Ashton et al. 1986).

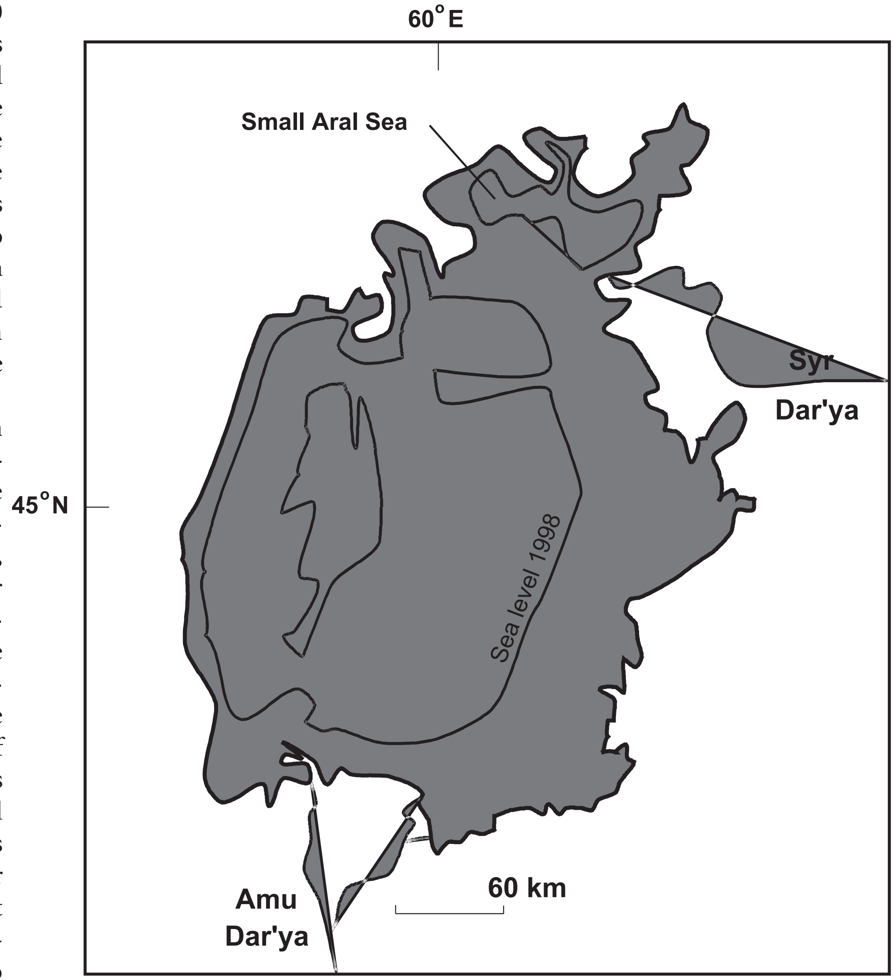

Figure 8. General map of the Aral Sea in Kazakhstan and Uzbekistan in Central Asia showing shorelines in 1960 (thick black line) and 1998. Massive irrigation schemes were planned and constructed in this region when it was part of the Soviet Union. Most of the water flowing in the Amu Dar'ya and Syr Dar'ya Rivers that maintained the Aral Sea was diverted to irrigate cotton, and river water no longer reaches the sea. Modified from Stone (1999).

A genus of tree species that has spread dramatically along regulated rivers is the tamarisk (*Tamarix* spp.). The genus consists of 54 species with origins in North Africa, the Mediterranean, and the Middle East. The tamarisk has been introduced to Australia and the United States where it has replaced native trees and associated bird fauna (Ellis 1995). The tree has invaded thousands of hectares of riparian habitat in the southwestern United States by tolerating drought better than the natural riparian vegetation (Cleverly et al. 1997). Dams and irrigation projects have facilitated the spread of the tamarisk by creating large-scale changes in river systems.

The Himalayan balsam (*Impatiens glandulifera*) is a successful herbaceous invader of riparian systems. It was imported from the Himalayas to beautify European gardens and has rapidly spread along European rivers. In the Czech Republic, this balsam occupies 56% of the length of large river systems (Pysek and Prach 1995). Similarly, the purple loosestrife (*Lythrum salicaria*), a herbaceous perennial native to Eurasian fens and riversides, is extremely successful in many parts of North America, where it has invaded almost any kind of wetland habitat. In many cases, it has formed dense, homogeneous stands that restrict native plants (Hight and Drea 1991).

Future needs and directions

It may be difficult to insert new knowledge about the effects of hydrological alterations on riparian ecology into the policymaking process (Rosenberg et al. 1995). Strong economical and political interests supportive of river regulation exist, which tend to minimize the ecological effects of dams and contribute to the postaudit parts of hydroelectric projects receiving little financial support compared to the planning and construction phases (Rosenberg et al. 1997). A better understanding of the effects of hydrological alterations is needed to evaluate the changes caused by

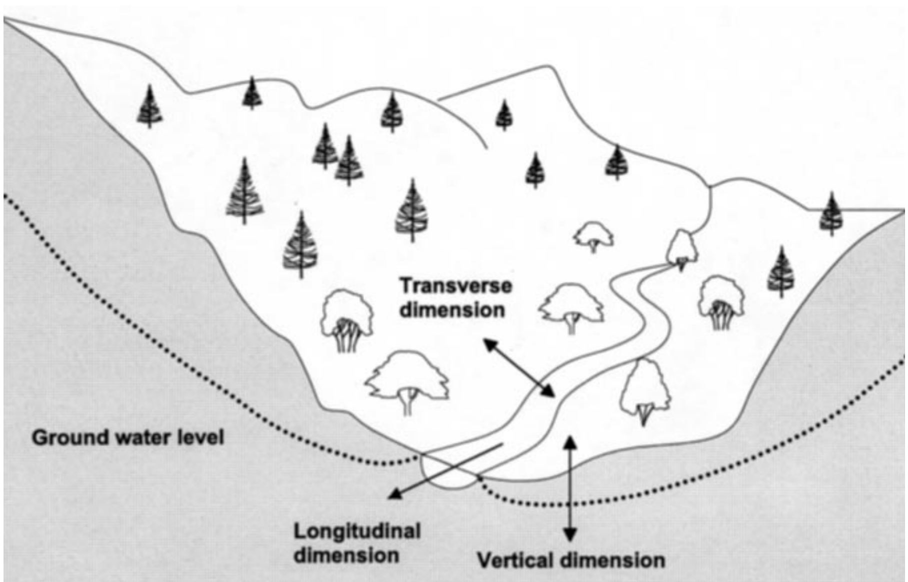

Figure 9. Schematic illustration showing the three spatial dimensions in which riparian ecosystems interact with their hypothetical environments. The longitudinal dimension includes processes such as dispersal of riparian plants by water and nutrient transport by salmon from the sea to the riparian zone. The transverse dimension includes feeding movements of animals such as a bear slaughtering a fish or a beaver cutting trees in the riparian zone. The vertical dimension includes transport of nutrients brought by upwelling water from the area under the floodplain to the root zone of riparian trees.

already built projects and to predict the outcomes of planned projects. Such knowledge is also a prerequisite for ecological restorations that are now becoming increasingly common. Hitherto, there seems to be no example of a water-regulation project for which the effects on riparian processes have been described in reasonable detail before construction; all developments have been pursued with little understanding or appreciation of the ecological consequences to riparian zones (Naiman et al. 1993).

Biological and physical processes in riparian zones occur at a variety of spatiotemporal scales. To date, free-flowing and regulated rivers have been studied on somewhat different scales. The more recent developments in the ecology of riparian systems along free-flowing rivers have focused on entire rivers or catchment areas (e.g., Ward 1997), whereas knowledge of the effects of hydrological alterations still emphasizes local case studies (i.e., individual dams). This difference in scale is probably because dams are controversial and research funding is, therefore, related to the immediate area of individual projects rather than entire river systems with multiple dams (and dam operators). To alleviate this discrepancy, there is a need to increase both the spatial and temporal scales at which regulated riparian systems are studied. In other words, the effects of regulated riparian systems on local and regional scales, over short and long time periods, should be disentangled. Basically, the studies of large-scale effects of hydrological alterations on riparian processes can take three directions—studies of effects within catchment areas, differences in effects between catchment areas, and changes with time.

Effects within catchment areas.

This direction includes effects on longitudinal linkages (along the river) and on transverse linkages (across the river; Figure 9). An important subject for the longitudinal axis is the linkage between upstream and downstream reaches, especially in rivers with multiple dams where upstream and downstream effects may overlap. The transverse axis involves the connections with surrounding environments. This dimension may also include the vertical dimension of Ward (1997), that is, interactions between the stream and the area under the stream channel and floodplain that contributes to the stream (Figure 9).

One good example of a connection between riparian habitats in the upstream and downstream reaches of a river is the seed that is eroded from an upstream site, transported downstream, and finally deposited on a floodplain close to the coast where it may germinate and give rise to a new plant population (e.g., the distribution of alpine plants along rivers far outside the normal distribution range). An example of a connection in the upstream direction is the Pacific salmon (*Onchorhynchus* spp.) moving marine-derived nutrients from the sea to the riparian vegetation in the upstream reaches of the river (Ben-David et al. 1998). Except for such anecdotal examples, however, most connections along the longitudinal gradient remain unknown. It is important to improve this knowledge, especially to understand how the location, number, size, and operation of dams affect their impact on longitudinal connections. A few predictions are given in the serial discontinuity concept of Ward and Stanford (1983).

Effects on transverse linkages are somewhat better understood because they are closely related to regulated water-level regimes. The interactions between longitudinal and transverse dimensions, however, deserve more study. For example, the erection of multiple dams is known to impoverish riparian communities (e.g., Nilsson et al. 1997). The relative importance of downstream dispersal and habitat alteration in causing this change is, however, not known. To elaborate on such questions, further information is needed about the distribution of species along rivers. Different groups of species show different distributions of species richness along rivers, and these patterns may change differently following flow regulation (Ward and Stanford 1983). This observation also raises the question of whether species diversity patterns in different groups are correlated and change in similar ways as a result of flow regulation. Such relationships may imply that there are indicator groups that can serve as surrogates for overall species diversity when evaluating effects of hydrological alterations and designing specific management programs.

Effects between catchment areas. Evaluation of global variation in the effects of hydrological alterations is essential for improving the forecasting of individual cases, especially if these imply new combinations of environmental variables. Rivers vary in catchment geochemistry, hydrology, topography, climate, and vegetation development. They have different floras and faunas and they have been subjected to many more human impacts than flow regulation. This variation certainly affects responses to river regulation and it explains why, even though the same riparian processes are affected wherever a dam is built, individual responses may differ considerably between regions (Jansson et al. 2000). Comparisons between different catchment areas are important.

One factor that deserves more study on a global scale is variation in natural flooding between regions and, consequently, in sensitivity of different floodplains to alterations in flooding (Poff et al. 1997). In the Amazon, for example, a well-developed floodplain forest can withstand 230 days of annual flooding (Junk and Piedade 1997), whereas riparian forests near the mountains in northern Sweden can withstand only about 15 days (Wassén 1966). Changes in the timing and duration of flooding regimes may alter processes such as erosion and sedimentation, water currents and wave action, organism dispersal and migration, groundwater recharge, and successional processes in the riparian corridor. It is a huge task to sort out global variation in the responses of all these processes. Such comparisons also require care in the choice of variables. It is more important to compare the relative duration of flooding then the absolute duration of flooding in evaluating the responses of riparian forests to altered water-level regimes, for example.

Time scales. Although some information is available on the development of riparian communities along regulated water bodies, their future and more stable states are not known. One reason is that most studies of succession after dam closure are on rivers that have been regulated for only a few decades. Moreover, most ecological studies last for only a few years, so simply studying a river that has been regulated for a long time is no guarantee that useful information about long-term changes is being provided. Some information on the long-term development of riparian corridors affected by river regulation can be gained by retrospective studies based on historical evidence (e.g., Johnson 1994). Another possibility is to use chronosequence studies where a temporal trend is inferred by studying different-aged sites (Nilsson et al. 1997). A third approach would be to predict environmental change using mathematical models, but comprehensive ecosystem models are still lacking.

In addition to these three types of studies, long-term monitoring will be the only reliable method to detect, assess, and validate predicted changes in riparian ecosystems and thus provide a useful basis for adaptive management of riparian systems. More complete assessments of the effects of hydrological alterations on riparian ecosystems, however, will be difficult to achieve because hydrological alterations usually displace riparian zones. To regain a riparian vegetation structure in the new location, riparian trees have to complete at least one life cycle; this period will be long enough to make it difficult to distinguish between natural dynamics, succession initiated by river regulation, and succession initiated by global change.

In summary, riparian zones belong to the most diverse, productive, and dynamic systems in the world. They are greatly impacted by humans. The demands of increasing human populations on water resources threaten to impair riparian ecosystems to the point where environmental and human health is at great risk. How to protect river environments and human needs of rivers remains one of the most important questions of our time.

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