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RIPARIAN ECOSYTEMS OF SEMI-ARID NORTH AMERICA: DIVERSITY AND HUMAN IMPACTS

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Abstract: Riparian ecosystems in the semi-arid West of North America are diverse but have many similarities. The mountainous landscape with wide range of latitude, longitude, and elevation offers diverse opportunities for streamside vegetation. All riparian ecosystems in the region are dependent on supplemental water, usually from the shallow, valley alluvial aquifer. Western riparian ecosystems provide several ecological services. They stabilize streambanks, trap sediment, improve water quality, and help control or modulate hydrologic processes. They function as habitat for many western animal species, serving as a small mesic island or strip within an arid landscape. They also serve as recreational sites for humans. Riparian systems are controlled by interacting hydrologic and geomorphic processes. Floods may alter river channel characteristics and the extent of riparian vegetation while enhancing recruitment of riparian species and recharging the alluvial water table. Geomorphic features, such as canyons and valleys, control the size of the riparian zone, as well as depth of the water table. Driving variables may differ from north to south, especially hydrology. For example, northern riparian zones are influenced by ice scour, while southern zones often have flash floods. Riparian systems occur along spatial and temporal gradients. Along elevational gradients, riparian vegetation may change from simple deciduous forests to mixed deciduous to coniferous and possibly alpine wetlands. Differences among channel, terrace, and upland plant communities decrease with increasing elevation as moisture stress decreases. Temporal gradients occur within a location in the riparian zone as early pioneer communities such as cottonwood/willow give way to late successional communities such as mesquite or sagebrush, often a consequence of sediment accumulation. Many similarities among western riparian ecosystems exist because several dominant genera (e.g., *Populus*) are common throughout the West, and many geomorphic and hydrologic processes that influence riparian establishment are similar. Western riparian ecosystems have been greatly altered by human activity. Major factors include natural resource use, urbanization, alteration of stream flows through dam construction and ground-water withdrawal, modification of biotic conditions through grazing, agriculture, and introduction of non-native species, and alteration within watersheds. Better understanding of the ecology of western riparian ecosystems will increase potential for restoration and protection of remaining areas.

Key Words: riparian, western North America, semi-arid, floods, gradients, human alteration

INTRODUCTION

Riparian ecosystems in an arid region appear to be an anomaly. In country that boasts no more than 8–35 cm of annual precipitation and has a potential evapotranspiration (ET) rate often more than ten times precipitation, mesic plant communities are possible only where a river or other water source provides a moisture subsidy. Riparian systems therefore are uncommon ecosystems, making up less than 1–3% of the landscape, but nevertheless, they are linked hydrologically to the rest of the landscape (Naiman and Decamps 1997). Their importance has produced a great deal of research describing not only the communities but also their role as a service ecosystem and the processes that create and maintain them. This introductory paper to the symposium on Semi-Arid Riparian Ecosystems held by the Society of Wetland Scientists offers a general description of the diversity of riparian ecosystems in the arid-West of North America and the many stressors that alter them. It illustrates similarities and differences of function, structure, and process in riparian ecosystems across the West, an area for purposes of this discussion generally extending west from the 100th meridian to the crest of the Cascades and Sierras and south from southern Canada to northern Mexico.

Western rivers often feed from high alpine meadows and snow fields and end in closed basins (lakes or playas) or large rivers that lead toward the sea. Some watersheds such as the Colorado, Missouri, and Columbia cover a large percentage of the arid West and thus include environments of great variety: high-to-low elevations, north-south and east-west gradients, and steep-to-shallow terrain. Consequently, when discussing riparian ecosystems of the arid West, there is no standard description other than that the riparian zone essentially encompasses those alluvial sediment deposits where river and alluvial ground water supplement that available from local precipitation (Gregory et al. 1991). The diversity of environments found throughout the West results in a diversity of vegetation communities, a diversity that occurs not only across great distances or elevations but also within kilometers or less in single river reaches. This diversity, especially in community structure and composition, increases the value of these ecosystems as fish and wildlife habitat and creates a wide range of ecological services and functions.

The importance of riparian ecosystem services and functions, many being beneficial to humans, was a primary reason for organizing the symposium on Semi-Arid Riparian Ecosystems. Many people recognize these services and functions and have worked toward a better understanding of riparian systems; research papers in this volume are examples of this. However, others have ignored their importance and show little respect for maintenance or enhancement of riparian ecosystems in the West and elsewhere.

Functions of riparian ecosystems may vary with system characteristics, including vegetation structure, composition, and abundance; ecological diversity; and landscape position. Riparian vegetation stabilizes sediments that compose streambanks and the floodplain, thus preventing excessive soil erosion. By trapping or filtering sediment, nutrients, and pollutants transported during floods, riparian vegetation reduces downstream sediment loads and improves water quality. Dense stands of riparian vegetation in the floodplain also reduce downstream flooding by causing the river to spread while slowing its velocity, which in turn, enhances ground-water recharge. Riparian vegetation tends to prevent the river from down-cutting or cutting a straight path (channelizing), thus promoting a sinuous course, ground-water recharge, and maintenance of an elevated water table (a form of positive feedback).

Riparian ecosystems function as the transition zone, ecotone, or buffer between the riverine aquatic system and uplands (Naiman and Decamps 1997). As a transition zone, they remove materials from surface and subsurface flow that may enter the watercourse from hillslopes (Lowrence et al. 1984, Cooper et al. 1987, Hill 1996). The width and density of riparian vegetation directly influence the amount of soil and sediment lost to the river from eroding, poorly-managed upland areas and also the rate of immobilization of fertilizers, pesticides, and other natural, applied, or spilled contaminants that may be present. Fortunately, wide riparian zones are commonly found in broad floodplains where many non-point source pollution-generating conditions (e.g., agriculture) occur.

Riparian ecosystems, although often narrow bands of territory, are vital to maintaining biodiversity of the more extensive, adjoining uplands (Naiman et al. 1993). A high percentage of the animal species in arid regions need riparian habitats for some stage of their life cycles (Brinson et al. 1981, Kondolf et al. 1996). Riparian ecosystems are often the sole available habitat for amphibians and invertebrates that require moist conditions. Structurally complex riparian vegetation communities provide many different habitats and support a diverse array of animal species. Different groups of animals occupy or use the different "layers" of vegetation, and this multi-story arrangement is often present nowhere else in arid landscapes (Anderson et al. 1983, Hunter et al. 1987). Canopies of plants growing on streambanks provide shade, cooling stream water, while roots stabilize and create overhanging banks, providing habitat for fish and other aquatic organisms.

Recreational use of riparian areas is growing. People are drawn to these areas where cool, shady environments along flowing streams are prime camping and picnicking sites. The use of riparian ecosystems by birds, wildlife, and fish also attracts birders, naturalists, hunters, and anglers.

CONTROLLING FACTORS

Riparian ecosystems may influence many hydrologic and geomorphic conditions, but they also are a product of these conditions. The interaction between riparian vegetation and hydrologic and geomorphic processes demonstrates a strong synergy that makes understanding riparian ecosystem processes a complex task, one amply illustrated by several papers in this issue.

Hydrologic Conditions

The primary reason most western riparian ecosystems exist is the presence of relatively abundant water. Most riparian plants are wetland or facultative wetland species (Sabine 1994) that cannot survive on local rainfall, requiring a supplemental supply of river water or shallow ground water. The extent, density, vigor, and species composition of riparian vegetation depend on volume and timing of stream flows (Stromberg 1993, Auble et al. 1994, Stromberg and Patten 1996, Scott et al. 1993, 1996, 1997). Watershed characteristics, precipitation, and other climatic factors influence the volume and timing of these flows. Rapid spring snowmelt or intense thunderstorms can produce periodic flooding, while background "base flow" conditions result from gradual release of ground water and snowmelt. Need for natural flow regimes to maintain riparian communities and enhance their recovery is a common conclusion of many recent riparian studies (Poff et al. 1997).

Periodic floods, such as spring runoff, influence establishment of riparian plant seedlings. High flows scour portions of the floodplain and redeposit sediments, allowing tree seedlings to germinate and grow on bare sandbars without competition from established plants, especially herbs (Friedman et al. 1995, Scott et al. 1997, Stromberg et al. 1997, Osterkamp 1998). Most native riparian plant species disperse seeds as annual high flows subside (Auble et al. 1994). In the arid Southwest, cottonwoods and willows release seeds in March and April as winter floods recede. In the northern Rockies (e.g., Montana), cottonwoods disperse seed in late May and June coincident with spring high flows from snowmelt. Gradually decreasing flows following flood peaks keep flood-deposited soils moist as seedlings put down roots (Rood and Mahoney 1995). As plants mature, they continue to depend on the shallow alluvial aquifer or ground water from valley slopes, which collects in the floodplain (Dawson and Ehleringer 1991, Flanagan et al. 1992).

Landscape Characteristics

Geomorphic factors interacting with hydrologic and vegetation conditions produce different river types. The vegetation and climate of a river's watershed greatly influence the volume, sediment load, and timing of stream flows. Watersheds with little vegetation cover, such as those of the desert Southwest, release water almost immediately after a storm (Graf 1988). Forested watersheds enhance ground-water recharge, resulting in slower water release. Watersheds with many evergreen plants, such as chaparral shrublands in California and Arizona or coniferous forests of western mountains, may use water throughout the year, reducing the total amount of runoff. Watersheds with winter deciduous or dormant plants like aspen or grasses may release more water to streams in winter, often with an elevated nutrient load, than summer unless the water is stored as snow (Longstreth and Patten 1975). Topography and soil cover also significantly affect runoff and sediment load. For example, in the watershed of the Paria River in southern Utah where vegetation cover is limited, summer storms, often short-term convection or orographic storms, produce sediment-laden floods, while extended winter frontal storms produce low sediment-load floods (Graf et al. 1991). Steep terrain, exposed bedrock, or thin, stony soils produce greater streamflow volumes more quickly than gentle slopes and deep organic soils.

Different river types and associated channels produce different conditions for establishment and maintenance of riparian vegetation. Reaches of aridland rivers are straight, meandering, or braided (Graf 1988). Braided reaches are most common in arid regions and are characterized by abundant bedload. Braided streams range from steep to low gradient, but they require erodible banks to facilitate development of mid-channel bars. Reaches of rivers may alternate from braided to meandering or are compound rivers that have a low flow meandering channel and high flow braided channel. These varying conditions produce a dynamic system within which riparian vegetation may establish when portions of the channel or channel margin are sufficiently stable and elevated. Braided rivers usually are a consequence of flood events where the channel is widened and filled with bedload material (Graf 1988). Following floods, riparian recruitment may occur on islands, point bars, or channel margins, often narrowing the channel and enlarging the floodplain. This process has been shown to be common on many Great Plain rivers (Friedman et al. 1996, Osterkamp 1998). This process, which may take years, gradually returns the river from one with braided channels to one with a meandering channel.

Some arid-region rivers occur in geologically young valleys or resistant canyons that do not have erodible margins. These rivers often have little room for channel-margin sediment accumulation, a condition necessary for establishment of extensive riparian vegetation (Scott et al. 1996). Reaches along a portion of the upper Missouri River in Montana and the Colorado River in Grand Canyon exemplify large rivers with constrained channels, while many mid-to-high elevation, steep gradient rivers in the West (e.g., upper Gallatin River in Montana and upper Salt River in Arizona) typify small to medium sized constrained rivers.

Different riparian ecosystem types are related to different river types. High-elevation, steep-gradient streams often support alder communities near the river, grading away from the channel into box elder and cottonwood, or possibly conifer forests (e.g., spruce (*Picea* spp.)). Where high elevation valleys broaden and rivers meander, extensive stands of shrub willow may characterize the riparian community. At lower elevations, narrow canyons may only support riparian species above spring flood stage. These canyons, Grand Canyon being a primary example, occur near the lower end of the watershed and thus are impacted by water accumulation from many tributaries and large floods. In lower elevation, broad valleys, the river may migrate in response to spring or other large floods, often passing through a braided channel condition following a flood, prior to returning to it sinuous course. These changes may result in a sequence of different-aged riparian forest representing different locations of the stream channel as it migrated across the valley.

GRADIENTS ACROSS WESTERN RIPARIAN SYSTEMS

The range of environments found throughout the arid West creates a diversity of riparian ecosystems because the factors that shape these environments change over space and time, resulting in spatial and temporal gradients in riparian ecosystem form and function. For example, the seasonal source and condition of water available for riparian vegetation development varies from north-to-south latitudes and high-to-low elevations. Also, discharge patterns of rivers that alter the environment within which riparian vegetation must establish and survive differ spatially (e.g., Hill et al. 1991, Stromberg 1993, Auble et al. 1994, Scott et al. 1996). As an introduction to an issue addressing ecosystem processes, community dynamics, riparian ecophysiology, etc., recognition of differences and similarities among the wide range of riparian ecosystems found in the West is essential.

Much of the arid West is characterized by the Basin and Range Province described by Fenneman (1931). The region extends over 12° latitude from semi-tropical, hot deserts of Arizona to edges of the boreal forest in northern Montana and southern Canada. This variety of conditions creates extensive geographic (spatial) gradients to which riparian plants must adapt. In a discussion of Rocky Mountain vegetation, Peet (1988) demonstrates how elevational (or longitudinal) gradients and moisture gradients control vegetational communities found throughout the mountains and valleys. Similar, but more detailed, gradients were demonstrated for the Santa Catalina Mountains in Arizona (Whittaker and Neiring 1965, 1975). In both examples, riparian or wetland communities were placed tightly along the wet or moist axis of the diagrams, sometimes dropping out at high elevations. This moisture/elevational gradient is one of several environmental gradients that determine the occurrence of aridland riparian vegetation. Other geographic or spatial gradients, in addition to elevational gradients, that may also be associated with moisture include latitudinal gradients (i.e., north/south differences) and river-to-upland (lateral) gradients. Processes associated with time, such as succession, also create temporal gradients in structure and composition that, when associated with geographical or spatial gradients, result in a very complex set of riparian communities throughout the West.

Elevational Gradients

Elevational (longitudinal) gradients in the Rocky Mountains clearly show the relationship between abiotic driving variables and corresponding vegetation. The environmental/elevational gradient approach used by Whittaker and Neiring (1965, 1975) and others shows primary conditions that alter vegetation along an elevational gradient. Most of these conditions relate to moisture and temperature differences, the primary factors found to control lower and upper timberline, respectively (Griggs 1938).

The differences between riparian and upland vegetation communities diminish with increasing elevation. For example, the water-availability (moisture) gradient from stream to upland is steep in the desert or in low elevation arid valleys and becomes less steep (almost non-existent) at higher elevations. Riparian zone temperatures are influenced more by the stream at low, hotter elevations than at cooler, high elevations. Evapotranspiration (ET) demands decrease with elevation and the requirement for supplemental water for plant survival decreases. This corresponds with increasing precipitation (mostly orographic) that reduces the differential in ambient water available to riparian and upland plants. Concomitant with reduced ET demands, cooler temperatures, and increased precipitation, stream gradients increase, depth to bedrock decreases, and watershed size decreases. Ground water, moving under a shallow soil layer, helps maintain some upland plants and is the primary recharge source for the streams. Availability of deep alluvium at higher elevations exists but is uncommon except in low gradient subalpine valleys (Patten 1968). Consequently, differences between channel margin, riverine terrace, and upland vegetation diminish. An elevation/moisture triangle is used to depict elevational convergence of vegetation as the steepness of the moisture gradient from stream to upland decreases (Figures 1 and 2).

Woody vegetation sampled at the channel, adjacent terrace, and upland along elevational gradients on four mountain ranges in Arizona (Valenciano 1992) were used to create Figure 1. The lower elevation shows a wide difference in channel to upland vegetation, that is, cottonwood to Sonoran Desert scrub. The high elevation location on the triangle shows that moisture conditions along the stream and upland have converged, and woody species found in riparian forests are the same as, or similar to, those in the upland. Changes along an elevational gradient in New Mexico

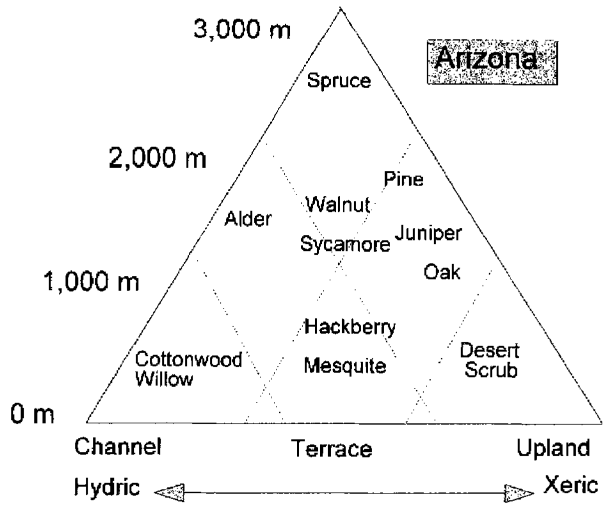

Figure 1. Riparian communities in Arizona relative to valley location (channel, terrace, and upland) and elevation. The hydric/xeric gradient from channel to upland becomes less distinct with elevation, resulting in little difference between channel and upland vegetation.

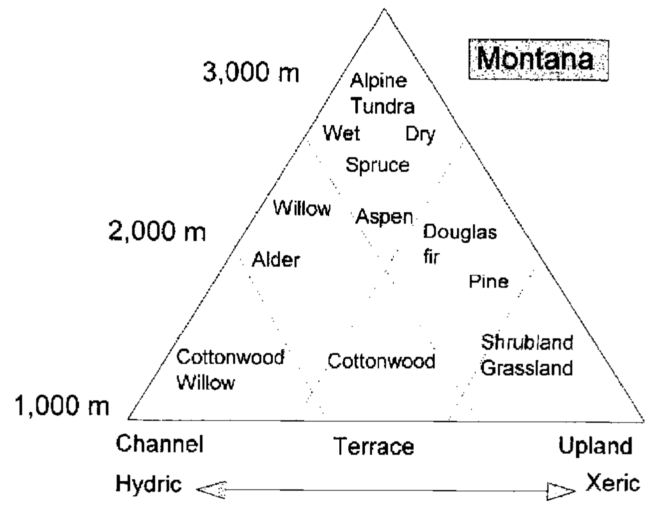

Figure 2. Riparian communities in Montana relative to valley location (channel, terrace, and upland) and elevation.

show similar patterns (Freeman and Dick-Peddie 1970).

I have created a similar elevational triangle for the mountainous region near Yellowstone National Park based on my own research and observations (Figure 2). The convergence of vegetation along gradients at mid- and upper elevations is not as clear as in Arizona. Broad upper elevation valleys may support extensive shrub willow communities; however, when valleys are narrow and stream gradients steep, upland trees are found along the rivers (e.g., Engelmann spruce (*Picea engelmannii* Engelm.)). Similar elevational triangles showing differences and similarities between riparian and non-riparian vegetation could be developed for other areas of the arid West, an indication that the influence of aridity decreases with increasing elevation. Also, with increasing latitude, mean temperatures are cooler and atmospheric moisture stress decreases. Consequently, high elevation riparian community types occur at lower elevations at higher latitudes. However, two factors complicate this concept. Low elevation riparian communities in southern latitudes (e.g., cottonwood (*Populus*)/willow (*Salix*)) may occur near sea-level, but this is not possible in the northern latitudes where the lowest locations are 300–500 m above sea-level. The longer growing season in southern latitudes, along with other hydrologic factors, may allow development of a mixed deciduous riparian forest at mid-elevations, a riparian community type not found farther north, although similar genera may occur mixed with mid-elevation coniferous riparian communities in northern latitudes (Figure 3).

Latitudinal Gradients

To emphasize latitudinal differences in driving variables and corresponding riparian ecosystems, comparisons are made between northern (e.g., Montana) and southern (e.g., Arizona) extremes of the arid western U.S. (Table 1). Riparian vegetational changes along elevational gradients for these regions are shown in Figures 1 and 2.

Hydrology as a riparian driver in northern Rocky Mountain states is quite different from that in southern states. Factors such as snow and ice play a more predominant role in the north than the south, and storm events can be quite different between these regions.

Snow and Local Storms. Northern Rocky Mountain states usually have extensive regional snow accumulation that does not melt until late April to June. Snow accumulates both in the mountains and valleys. Late spring rains and warm weather melt the snowpack, causing a reliable springtime or early summer hydrographic peak. Recruitment of many riparian species is

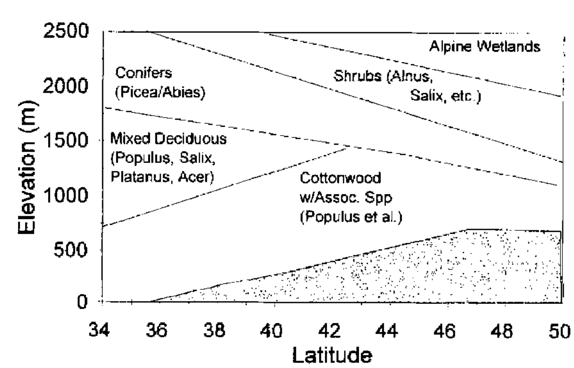

Figure 3. Riparian communities along elevational and latitudinal gradients in the arid West.

Table 1. Similarities and differences between northern and southern hydrologic and geomorphic variables that drive riparian ecosystem structure. Central Rocky Mountain and Great Plains locations may be intermediate.

Montana (northern states)	Arizona (southern states)
Hydrology	
Regional Heavy Snow Accumulation	Local Heavy Snow Accumulation
Spring Snowmelt Hydrographs	Snowmelt on Larger Streams Feeding from Mountains (often regulated)
Local Storm Effects (uncommon)	Local Storm Effects (common)
Flash Flooding (uncommon)	Flash Flooding (common)
Ice Formation/Scour	No Ice
Flow Variability Low	Flow Variability High
Flow Predictability High	Flow Predictability Low
Geomorphology	
Spring Sediment and Snowmelt Sediment Trapped in Ice	High Watershed Erosion (limited cover) Much Sediment with Flash Floods (much bedload)
Point Bar Formation and Bank Erosion (common with spring floods, braided channels variable)	Point Bar Formation and Bank Erosion (variable) (braided channels common following floods)

triggered by or coincides with this spring peak (Scott et al. 1993).

Snow accumulation in southern Rocky Mountain states is usually on the high mountains, a consequence of winter frontal storms. This snowpack may melt any time as a result of warm, late winter or early spring weather or rainstorms. High flows in southern states thus occur from February through March, triggering riparian vegetation recruitment (Stromberg et al. 1991, Stromberg et al. 1993a).

Except for summer orographic storms, heavy local storms have little effect on stream flows in northern regions, while summer convective storms may cause flash floods in southern regions. Annual hydrographs in the central Rockies often show the effects of summer mountain precipitation, having a peak in spring and then again in later summer. Summer peaks in central and northern regions are usually not so great as to override riparian recruitment events that were enhanced by spring peaks. This often is not the case in the south or south-central regions where extensive and intensive summer storms may cause flash floods that scour seedlings of riparian plants that had established only a few months earlier (Graf et al. 1991). Only when high winter/spring flows that trigger riparian recruitment in the south are followed by a relatively dry summer, and no large floods the next year or two, is recruitment of spring seed-dispersal species such as cottonwood and willow mostly successful (Stromberg et al. 1991). Other native species such as arrowweed (*Tessaria sericea* (Nutt.) Shinners), seepwillow (*Baccharis salicifolia* (R. and P.) Pers.), and the non-native salt cedar (*Tamarix chinensis* Lour.) disperse seeds from late spring well into summer and thus take advantage of summer floods (Stromberg 1998).

Runoff of snowmelt in both northern and southern states is captured by large reservoirs. The difference being that many rivers in lower elevation valleys in the south are dewatered by water impoundments and diversions, while most reservoirs in the north are regulated for hydropower and flood control, which normally allows flow-through. This flow-through usually reduces the peak flow and may elevate the base flow (Hirsh et al. 1990, Dynesius and Nilsson 1994). Unlike lower order rivers in the northern plains (e.g., Missouri River), most higher order rivers flowing out of mountains into broad alluvial valleys in the north are not regulated or altered except for occasional small impoundments and irrigation take-out canals. Only during extreme drought years might these take-outs significantly affect stream flow and riparian recruitment, maintenance, and survival. Many rivers in the southern Sierras (e.g., Bishop Creek) have multiple, small impoundments for hydropower. Constant but reduced flows below these impoundments have enhanced riparian vegetation encroachment into the channel in the upper reaches, while lower reaches are dewatered with little vegetation (Harris et al. 1987).

Ice Formation. Northern riparian ecosystems may normally not be scoured by flash floods, but they are greatly affected by ice formation in the winter. Ice forms on the surface of rivers of all sizes in the northern Rockies during extreme cold periods. As temperatures change, ice may break up, causing gorging of the river. When the river gorges, the ice is elevated and scours the bank at levels equal to or well above those of spring floods (Smith 1980). Scouring not only damages existing trees but may remove much of the riparian vegetation (Johnson 1994). Consequently, successful recruitment of woody riparian vegetation along northern streams may only occur above the ice scour zone (Scott et al. 1997). A moving ice gorge may also have sufficient eroding and cutting energy to alter channel morphology. There is little evidence of ice being a major factor in riparian establishment and survival in the southern Rocky Mountains and Southwest.

Geomorphic influences also are quite different between northern and southern regions. These differences may be closely tied to hydrologic phenomena, as well as local and regional geologic characteristics.

Sediment. Many riparian species require bare moist soil with little vegetative competition for seed germination and establishment (Stromberg et al. 1991, Scott et al. 1996). Development of these barren locations along streams is often the consequence of sediment scour and fill processes during high flow events (Leopold et al. 1964) or sediment deposition along river channels and islands during normal flows when deposition occurs in flow-attenuated locations, such as downstream from vegetation. Cold climate and snow and ice create differences in sediment transport from north to south. Many south-central to southern rivers have a coarse, sandy bedload produced by erosion in washes and tributaries. This bedload may move in pulses in response to large storm events or snowmelt (Graf 1988). Northern rivers, especially in mountain valleys, often have gravel- or cobble-lined channels; fine erosional materials produced by tributaries are limited because of greater vegetation cover than in the south. However, fine sediment carried by northern rivers in winter may temporarily be held in ice deposited on the river terrace or along the channel by gorging. As the ice melts, some sediment is transported downstream, while some is deposited on the terrace, gradually accumulating over time and burying riparian vegetation. Deposition of fine sediments (e.g., silt) on terraces, islands, and elevated floodplains occurs during overbank flows in both north and south regions (Leopold et al. 1964). These deposits aggrade the floodplain, enhancing development of species that do not require a shallow water table.

Flash floods, common in the central and southern regions of the arid West, cause channel erosion and entrainment of much of the bedload. Intensive snowmelt events in the north may result in similar processes. During flood recession, transported sediment will build the floodplain through deposition on the elevated terrace, if overbank flow, or on the inside of a curve, aggrading on the point bar (Leopold et al. 1964). Sediment will also form elevated deposits across the widened active channel. For example, Friedman (1993) described three depositional units following a flood on a braided river in the Great Plains: channel bed, stable bars of various elevations, and terraces. Some of these depositional units may be sufficiently above the water table to prevent riparian recruitment. Others may be so close to the stream base-flow level as to allow scour and/or burial of any new recruitment by high frequency floods (e.g., 2-year-return flood) (Stromberg et al. 1991). When recruitment of riparian vegetation on new depositional surfaces is successful, the floodplain tends to enlarge as the channel narrows. Coalescence of vegetated islands in braided rivers, to each other or the floodplain, accentuates channel narrowing (Friedman et al. 1996, Hupp and Osterkamp 1996, Stromberg et al. 1997).

Stream-to-Upland Gradients

The elevation triangles (Figures 1 and 2) are based on samples or descriptions of three points along the vegetational gradient from channel-vegetation to upland-vegetation. This lateral gradient is related primarily to soil moisture availability (e.g., depth to the alluvial water table) and sediment deposition within the floodplain. The latter phenomenon at an early stage (0.5- to 1-m sediment depth) creates appropriate conditions for establishment of riparian species because roots of these plants will remain within reach of the alluvial water table, usually closely equivalent to stream level, at least near the stream. Sediment deposition greater than 1 m may prevent shallow rooted riparian species from establishing (e.g., Shafroth et al. 1995) and enhances establishment of terrace species that can tolerate greater depths to water, rely on local precipitation for moisture, or become established in the absence of physical disturbance (e.g., mesquite or sacaton grass in Arizona, and red osier dogwood and mesic grasses in Utah or Montana). Streamside vegetation often includes obligate wetland species (Sabine 1994) such as rush (*Scirpus*) and cattail (*Typha*); thus, the stream-to-upland gradient may be a continuum from hydric to mesic to xeric species. In extremely hot dry climates, this gradient may be only 10 to 100 m long and readily identifiable. The steepness of this gradient from emergent aquatic plants to woody trees to scrub/grass vegetation is controlled by valley geomorphology; it may be truncated by a narrow valley or extended across broad alluvial basins. In cooler or mesic climates (e.g., southeastern United States), the gradient is extensive (several kms) and often difficult to discern, as one deciduous forest type blends into another.

Like community structure, species richness varies along the stream-to-upland gradient. Gregory et al. (1991) showed in the Sierras and Cascades that species richness along this gradient peaks in the riparian zone back from the channel edge where water is available from a shallow water table and the surface is not constantly disturbed by frequent floods. Valenciano (1992) showed a similar peak in species richness in montane Arizona, whereas others have shown richness peaks in the active channel/channel edge wetland herbaceous community, especially when the floodplain maintains a wetland character for some time (Stromberg et al. 1997).

Temporal Gradient

The fluvial and geomorphic processes that result in the geographic or spatial stream-to-upland gradients also create temporal gradients. Most stream channels are not static channels but, rather, respond to dynamic changes in the landscape (e.g., Campbell and Green 1968, Irvine and West 1979). Both large and small streams change their meander patterns across floodplains, scouring the outside curve while depositing sediment on the point-bar on the inside of the meander curve. Braided channels, while not following this pattern, also are dynamic and create changing islands of sediment within the channel. Flood events of increasing magnitude erode and deposit and change channel patterns at increasing rates (Stromberg et al 1997). If recruitment locations such as point-bars or islands remain relatively stable and continue to accumulate sediment, using space-for-time substitution, it is possible to study stream-to-upland gradients at these locations to understand temporal gradients, as successional processes at one point over time tend to mimic the stream-to-upland gradient. This concept does not always work well if the processes that created early stages of a successional gradient are altered (e.g., flood peaks and sediment availability are reduced by upstream dam construction).

Our studies over a ten-year period on the Hassayampa River, a small unregulated river west of Phoenix, Arizona, well illustrate this space-for-time approach. During this period, a low-terrace location near the river gradually accumulated sediment. Consequently, as its height above the river or thalweg increased, primary successional species (e.g., cottonwood and willow) began to mature, and secondary species (e.g., mesquite (*Prosopis*)) occupied the understory. In time, unless a major flood event (e.g., > 25-year interval) scours the location and "resets the clock," the site will become a high-terrace, mesquite bosque.

Probably one of the most often described successional processes occurring along meandering rivers and mimicking a river-to-upland gradient is the arcuate pattern of riparian forests that result from point-bar migration, sediment accumulation, bar elevation, and cutbank erosion, all occurring at a bend or meander in a river (Bradley and Smith 1984, Scott et al. 1996). A location on the point-bar may first be invaded by coyote willow (*Salix exigua* Nutt.), then by cottonwood, and eventually, as the cottonwood matures, more drought-tolerant or deeper rooted riparian species, those considered to be late successional species (Boggs and Weaver 1994). Examples of these include mesquite in the Southwest, box elder (*Acer negundo* L.) in the Central Rockies, and sagebrush and upland grasses or the non-native Russian olive (*Elaeagnus angustifolia* L.) in the northern Rockies.

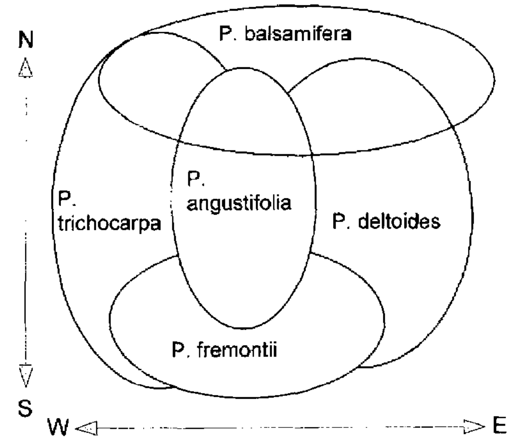

Figure 4. Conceptual model of distribution of *Populus* species in the arid West along longitudinal and latitudinal gradients. Hybridization is common in areas of overlap.

GEOGRAPHIC SIMILARITIES

Although driving variables may differ geographically, riparian vegetation communities found throughout the arid West may have similar structure and functions. Structural similarities occur because they are related, in part, to successional processes driven by common, widespread, fluvial-geomorphic processes. For example, point-bars, channel margin, and island deposits provide exposed sediment that supports young riparian plants along meandering and braided rivers throughout the region. Also, sediment accumulation on terraces accompanies aging of riparian vegetation and establishment of later successional species. One common thread throughout most mid- and low elevation riparian vegetational communities in the arid West is the presence of cottonwood (*Populus*) as a keystone species. Cottonwood species found along streams have been shown to have similar recruitment requirements (e.g., high flows coincident with seed dispersal and extended periods of wetted streamside sediment) (Bradley and Smith 1984, Scott et al. 1996, 1997, Shafroth et al. 1995, Stromberg et al. 1997, Auble et al. 1998, Mergliano 1998, Rood et al. 1998, Shafroth et al. 1998). Two groups of cottonwood occur in the West (Braatne et al. 1996), often hybridizing where their ranges overlap (Figure 4). These are the narrow leaf cottonwood (*P. angustifolia* James), balsam poplar (*P. balsamifera* Du Roi), and black cottonwood (*P. trichocarpa Hook.*) group, and the plains cottonwood (*P. deltoides* Marshall) and Fremont cottonwood (*P. fremontii* S. Wats.) group. Species may also hybridize across groups (e.g., several of the *Populus* species in the northern Rockies and Great Plains (Great Plains Flora Association 1986, Rood and Mahoney 1995)).

The group including narrow leaf cottonwood reproduces asexually through root sprouts more readily than the group including Fremont cottonwood (Rood et al. 1994). The advantage of asexual reproduction is obvious when conditions do not encourage sexual reproduction. For example, during the forty years that Rush Creek in the eastern Sierras was mostly dewatered, black cottonwood barely survived until a perennial flow was reestablished, after which, this species quickly began to reestablish stands through root sprouting (Stromberg and Patten 1989). Why these groups have developed these different capabilities is open to conjecture. The group that root-sprouts tends to occur in more northern or colder climates with a shorter growing season than the group with little asexual reproduction (Rood et al. 1994). Possibly, slow growth of seedlings in colder climates makes young trees more susceptible to scour (both ice and sediment), while longer growing seasons result in rapid development of young trees, which have greater resilience to scour.

Where several cottonwood species occupy the same riparian zone, they may demonstrate different tolerances to moisture stress. Narrow leaf and plains cottonwood recruited on a gravel bar along the Yellowstone River near Billings, Montana following the 1997 100-year flood. Survival and vigor of narrow leaf cottonwood is greater than plains cottonwood on elevated areas of the bar, but plains cottonwood is more vigorous in depressions with fine sediments (pers. observ.). Adjacent islands with mature narrow leaf, plains, and black cottonwood show similar patterns with plains cottonwood in moist depressions (e.g., secondary channels), narrow leaf cottonwood on elevated terraces, and black cottonwood on intermediate sites.

Willow trees often are associated with cottonwood throughout the arid-region riparian forests, and willow becomes one of the dominant riparian shrubs at high elevations where tree forms of cottonwood and willow decrease or are absent. Another woody genus that tends to demonstrate commonality among riparian associations is alder (*Alnus* spp.). In many cases, alder species are only found immediately adjacent to the active channel.

HUMAN IMPACTS

People influence riparian ecosystems by using and managing land and water and by introducing or removing plant and animal species. Natural resource development (e.g., mining, forestry, and agriculture), has both direct and indirect effects on the abundance, structure, composition, productivity, and functional integrity of riparian ecosystems.

Changes in Water Availability

Population growth in the West depended primarily on the easy availability of water. From the 100th meridian to the crests of the Sierras and Cascades, the western United States is largely semi-arid. Droughts are a fact of life and climate, and the ability of ranchers, farmers, and communities to survive depends on the control and delivery of water. Consequently, very few western rivers remain free-flowing. Rivers have been managed regionally to produce water for irrigation, generate hydroelectric power, and for flood control. Large dams have been constructed on most of the West's large rivers, and the resulting water impoundments cover a large part of their original channels and floodplains. Hydrologic modification of most rivers and associated ground-water aquifers has, in turn, altered riparian ecosystems (Busch and Smith 1995).

Dams on large rivers like the Colorado, Missouri, Snake, and Columbia have greatly altered downstream ecosystems (Ligon et al. 1995, Collier et al. 1996). They impound spring floods that would scour channels, deposit sediment, and produce riparian vegetation along the high water zone (e.g., Johnson 1991). To satisfy agriculture, water held behind dams is released in large quantities primarily during the summer (dry) season when crops require supplemental water. These water releases do not coincide with normal high flow periods for the river, so riparian vegetation that disperses seeds in the spring will have insufficient flows for germination; seedlings that germinate in spring under lower flows may be scoured away by higher, managed summer releases (Fenner et al. 1985, Rood and Mahoney 1990, 1995, Johnson 1992, Dominick and O'Neill 1998, Mahoney and Rood 1998). In contrast to these riparian ecosystems that appear to be collapsing, some have been expanded by flow regulation. In braided rivers of the Great Plains, reduction of spring flood peaks through dam regulation have resulted in widespread narrowing of channels. Channel narrowing has resulted in extensive establishment of cottonwood, willow, and salt cedar in areas that once were active channels (Johnson 1994, 1998, Friedman et al. 1996, 1997, 1998).

Some dams (e.g., along the upper Missouri River) are operated on a "flow-of-the-river" policy; that is, the amount of water flowing into the impoundment is released at the same time from the dam, especially during high flows. The impoundment is used to ensure downstream water during dry periods and to control major floods if it has the capacity. Unfortunately, although timing and amount of water may be sufficient for recruitment and maintenance of riparian vegetation, the river carries little sediment below the dam, except for that entering from tributaries. Because sediment deposits, usually carried by floods, are so important for recruitment, riparian vegetation is greatly reduced or lost (Scott et al. 1997).

Ground-water withdrawal also affects stream flow throughout much of the West. In most cases, surface flow is hydraulically connected to the alluvial water table. When wells for irrigation, mining, or municipal use are drilled adjacent to the river, or even away from the river in the aquifer recharge zone, a "cone of ground-water depression" caused by water withdrawal will develop (Friedman et al. 1997, Scott et al. 1999). Either way, the result often is a drop in the water table and reduced stream flow. This reduces the vigor of riparian vegetation and ultimately can cause its death and prevent re-establishment. Examples of this effect are becoming increasingly common in the Southwest where limited rainfall cannot replenish the ground-water extraction "overdraft" (Stromberg et al. 1992, 1996).

To move water downstream and to develop floodplain lands, many western rivers have been channelized, the lower Colorado River being a prime example (Ohmart et al. 1988). This alters the hydrology of the valley or floodplain, often preventing overbank floods, reducing ground-water recharge, and eliminating riparian recruitment sites. More drought-tolerant species such as mesquite may survive this alteration, but species such as cottonwood and willow are lost.

Land Uses in the Watershed

Riparian ecosystem condition reflects the cumulative effects of all activities that influence hydrologic conditions in watersheds. Watersheds throughout much of the West are mountainous, and landscape modifications on steep terrain may quickly affect down slope and downstream ecosystems. Multiple resource uses on mountains and in valleys have modified both the quantity and quality of water entering rivers from these areas. Sometimes, the results of land use can be subtle, while in other cases, downstream impacts on riparian ecosystems can be dramatic.

Timber Harvest. Timber harvest in the West is commonly achieved through clear-cutting of forests. Rain falling on these large, cleared areas causes increased soil erosion and more rapid water runoff (Sidle et al. 1985, Swanson et al. 1987). Flood flows often become larger and flashier and carry increased sediment. Percolation of rainfall and snowmelt into the ground is reduced and, with it, the base flows that sustain riparian vegetation during the dry season.

The recent practice of leaving a buffer zone between clear-cuts and streams has reduced some of the negative impacts of watershed forest cutting. Buffer strips help to reduce sedimentation rates and provide for the continued ecological interactions between streams and riparian vegetation that maintain fish habitat and aquatic food webs (Kauffman 1988). However, most buffer zones are inadequate to prevent all adverse impacts of clear cutting and are often too narrow to accomplish their intended effects.

Riparian forests also are directly affected by timber cutting. Cottonwood forests along rivers of the Plains, for example, are cut for wood products. This direct loss of habitat diminishes the ability of the riparian ecosystem to sustain wildlife and carry out the other valuable ecological functions discussed previously (Grant 1986).

Grazing. Riparian ecosystems offer water, shade, and food for domestic livestock. Cattle and sheep congregate in riparian areas, particularly during hot or dry periods when upland forage production is low and water is locally unavailable. Grazing in riparian areas disrupts the reproductive cycle of riparian trees such as cottonwoods, whose broadleaved seedlings and saplings are as palatable to cattle as grasses and other herbaceous cover. Domestic livestock concentrated in bottomlands for extended periods destroy riparian ground cover, destabilize streambanks, and thus increase sediment loads to streams (Armour et al. 1991, Elmore 1992, Feller 1998).

Where managed for high visibility or high density, native wildlife populations also have damaged riparian ecosystems. In some national parks and urban greenbelts, deer, elk, and even bison populations have expanded well beyond the long-term carrying capacity of the "protected" area (Patten 1993). Lacking natural (or human) predators and unable to emigrate seasonally or permanently, these animals cause the same problems as concentrated domestic livestock. Even in relatively unconfined environments, wildlife managed to maximize hunter satisfaction can decimate riparian vegetation.

Agriculture. Irrigated agriculture is traditionally the greatest water-consumptive activity in the West. Stream diversion for irrigation may reduce surface flows to a level insufficient to maintain riparian vegetation, while ground-water pumping lowers local and regional water tables and reduces stream flow, either of which can eliminate or weaken riparian vegetation.

Many broad alluvial valleys historically had rich soils and shallow water tables and, so, were extensively cleared for agriculture. Clearing of riparian vegetation to make way for fields causes direct loss of wildlife habitat and water- and sediment-buffering ability. Some uneconomic farm lands now lay fallow and are being restored to riparian vegetation. Remaining agricultural activity on floodplain lands is sustained by irrigation and fertilization to compensate for losses in natural fertility and regionally low precipitation.

Mining. Hardrock mining is common in mountainous parts of the West. Softrock mining, especially strip-mining for coal, occurs more commonly in grasslands and deserts of Montana, Wyoming, and Arizona. Extraction of sand and gravel aggregate materials from floodplains and remnants of Pleistocene river terraces and outwash plains is another common form of mining and is closely tied to rapidly expanding human developments.

Hardrock operations, such as open pit copper mining, generally disrupt the landscape surface while appropriating natural valleys for waste or leach pads and tailings ponds. Such operations can consume all available water, usually obtained through extensive ground-water pumping. Valley filling locally destroys riparian ecosystems by burying the entire area with overburden rubble or exhausted tailings. Ground-water pumping lowers the water tables of some nearby, unburied streams. Mines also may intercept the deep water table, disrupting regional aquifers and reducing stream and spring flows over a large area (Nelson et al. 1991).

Mining also produces chemical contaminants that find their way into streams. These include naturally occurring heavy metals such as copper, lead, and arsenic (the direct outputs of mining) or compounds used for ore leaching such as cyanide and sulfuric acid. Acid outflow from tailings lowers stream pH (i.e., high acidity), kills plants and animals in affected stream reaches, and prevents the re-establishment of the aquatic biota (Nelson et al. 1991).

Strip-mining for coal, when carried out near rivers, can contaminate them and cause channel alterations. Although most coal transport is accomplished via truck or train, some is transported in slurry pipe lines, which requires large amounts of water (often a 50/50 mix), in most cases from deep aquifers. In some cases, withdrawal of even deep water may reduce surface flows or dry up shallow wells.

Sand and gravel mining destroys the riparian vegetation that is removed during excavation, but it also indirectly jeopardizes the rest of the local riparian ecosystem. Whether undertaken directly within a river channel or on the adjacent floodplain, aggregate removal can lower water tables and reduce or eliminate surface flows (Friedman et al. 1997, Scott et al. 1999). Some gravel pits must be continually pumped to provide access to sand and gravel deposits. Nearby channels dry up or migrate toward these low-lying basins. The lowered water table may be beyond the reach of riparian plant roots, and trees growing along dried-up or abandoned channels are likewise left without sufficient water. Especially near fast-growing urban areas, riparian and river ecosystems are left cratered and fragmented by this widespread but little-regarded activity.

Urbanization and Road Development

The western United States is experiencing massive population growth, primarily in urban areas including metropolitan Las Vegas, Phoenix, Denver, Salt Lake City, Portland, and Seattle, as well as in smaller cities and mountain communities. Expanding population centers directly impact stream-side lands that once supported riparian ecosystems and continually increase their demands on a decidedly finite water supply. As a result, many (perhaps most) urban riparian ecosystems are already gone, and the survival of many remaining fragments is in doubt. Even small communities have impacts on stream and riparian ecosystems (Medina 1990).

Many western towns were founded along rivers because of the ready water source and (along major waterways) the transportation potential. Even where stream navigation is impractical, highways and railroads follow river valleys, often the gentlest available grades. Cities expanded along these major transportation routes, often directly within floodplains. Some riverfront property is valued for aesthetic reasons, some for commercial and industrial convenience, but riverfront development directly competes with riparian ecosystems for the critical strip of bottomland. Belatedly realizing their loss, some towns have attempted to preserve or even restore riparian areas (Kondolf and Keller 1991). However, ever-increasing land values bring development pressures and elimination of natural biological communities in favor of up-market concrete ones. Runoff from these hardened urban watersheds is immediate and intense (Graf 1988), sometimes actually lowering nearby riparian water tables as it causes rapid erosion and downcutting in stream channels.

Stream water or ground water used by cities often is disposed of in the form of treated sewage effluent. In extremely arid regions where rivers have been totally or largely dewatered, returning effluent to a depleted channel can reestablish and maintain riparian vegetation (Stromberg 1993b). The potential for using effluent for riparian restoration and maintenance is great throughout the West. Although it may not meet some current clean water standards for a short distance downstream, biological processes in a recovered, effluent-dependent riverine/riparian ecosystem may ultimately improve downstream water quality sufficiently to meet necessary standards.

When valley bottom and riverside roadways were small and less traveled, impacts on rivers and associated riparian areas were proportionately minor, but as highways expanded from small tracks to multi-lane freeways, the impacts increased. Widening existing, traditionally located highways has sometimes required redirecting rivers and constricting stream flows (Patten 1989). Established riparian ecosystems were destroyed while re-engineered channels are too steep-sided or fast-flowing to allow new ones to become established. Minor roads constructed to facilitate rapid mineral and timber resource extraction are rarely constructed for long-term stability, increasing erosion potential and reducing riparian vegetation cover and stream water quality.

Recreation

The popularity of riparian recreation sites leaves them vulnerable to over-use and misuse (Johnson and Carothers 1982). Motorized recreation has major impacts on many riparian resources. When stream flows are low, channels may become thoroughfares for four-wheel drive and all-terrain vehicles, to the detriment of riparian vegetation and soils. Every human presence leaves its mark, but riparian ecosystems are resilient and rebound easily if use is limited. Continuous or repeated, intense recreation (e.g., ski resorts in mountain valleys), like uncontrolled or constant domestic livestock grazing, causes the most ruinous impacts.

Biological Alterations

Plants may be deliberately imported as ornamentals, food or fiber sources, or for some other functional purpose. Many are accidentally introduced through careless transport of propagules or with associated species. Intensive or poorly timed livestock grazing and dam-induced changes in flood timing and magnitude often favor the survival of introduced species (e.g., salt cedar) and allows thriving exotics to displace native species.

One introduced riparian species that continues to be recommended as an ornamental and distributed by commercial plant nurseries is Russian-olive, which successfully competes with native riparian species, especially along more northern rivers (Shafroth et al. 1995). As long as it continues to be planted in urban and rural settings, a seed source will always be available and it will be difficult to control or remove from western riparian ecosystems.

Tamarisk, or salt cedar, was introduced from the Near East to the Southwest as an ornamental shrub over 100 years ago (Brock 1984). It was highly touted as a streambank stabilizer and an efficient, drought-tolerant windbreak during the Dust Bowl era. However, it now has overrun floodplains from Texas to California and north to Wyoming and eastern Montana, occupying over 500,000 ha of riparian habitat. Along the lower Colorado River, it occupies up to 90% of the area originally dominated by cottonwood-willow riparian forests (Ohmart et al. 1988).

Salt cedar is very difficult to remove from human-impacted riparian areas. It produces incredible numbers of tiny, wind-dispersed seeds throughout the growing season. It can repeatedly resprout after fire, cutting, or browsing, and it tenaciously survives in very wet, very dry, or very salty soils (Sala and Smith 1996, Gladwin and Roelle 1998, Smith et al. 1998). In other words, salt cedar has the ability to use the conditions now prevalent on western streams and rivers: overgrazing, salty irrigation runoff, and dams preventing normal spring floods. It can now out-compete most native riparian trees and shrubs in the desert Southwest, and this domination produces a simplified community of weedy exotic plants (Everitt 1998), lacking the multi-story structure and high biological diversity of native riparian woodlands (Stromberg 1998). Salt cedar ecosystems are also particularly flammable, and few native riparian species can tolerate fire (Busch and Smith 1995). Only along free-flowing rivers, where grazing and agriculture are eliminated or managed at sustainable levels, are cottonwood and willow likely to reclaim lost territory.

Herbaceous exotics are also becoming prevalent in many riparian understory communities (Stromberg and Chew 1997). They may create dense ground cover that excludes native species and increases fuel for fires. Maintenance of an exotic ground cover may be enhanced by grazing in riparian areas.

CONCLUSION

The environments of the semi-arid West are highly diverse. Mountains, valleys, broad plains, and deep canyons all play a role in creating opportunities for a diversity of riparian ecosystems. Western riparian ecosystems appear to differ considerably if one views them locally because variation in sediment supply, valley geometry, and flow create diverse riverine environments. At a coarser scale, the relation between climate and elevation produces sharp elevational contrasts in riparian environments. High alpine meadows may support small shrub or herb wetland/riparian areas; broad valleys with deep alluvium allow river meandering and opportunities for constant changes in dense riparian forests; and desert washes with ephemeral flows support xeroriparian plants. All sorts of conditions fall between these examples.

Aridity is a constant in this landscape. Most species found along western rivers could not survive away from the river and the shallow alluvial water table that supports mesic vegetation in a region characterized by semi-arid or xeric plant species. Consequently, western riparian zones offer a diversity of vegetation richness and structure that contrasts with most upland areas. It is a zone that is used by many associated species and contributes to regional biodiversity.

Rivers and their associated riparian areas link much of the West. These linear strands offer migration routes and tend to enhance genetic continuity throughout the region. Cottonwoods are probably the best expression of this continuity, creating similarities among western riparian areas. Although several cottonwood species are found throughout the region, sorting themselves longitudinally and latitudinally, where their ranges overlap, hybridization is common, indicating a common developmental evolution.

Keystone genera such as cottonwood also are found to have common requirements for recruitment and survival across most of the West. These needs often are tied to evolutionary development of the species or genus in association with external environmental drivers. Common for most western rivers is winter or spring flooding that enhances recruitment conditions for riparian species, many species disseminating seeds at this time. Also, most riparian species are phreatophytic and thus must grow in areas where the water table is shallow and decline following floods is small.

Riparian ecosystems in the semi-arid West have been threatened for more than a century. Development of resource extractive industries from timber and mining to agriculture and grazing have greatly altered valley landscapes and water conditions. Most rivers are dammed, and natural stream flows are now things of the past. Many efforts to restore western riparian ecosystems have not been very successful; however, knowledge about riparian ecosystem functions has improved, which has led to increased efforts and greater successes (Briggs and Cornelius 1998). Unless we begin to reverse past changes in many of the driving variables needed for riparian recruitment and survival, restoration success will not continue to improve, and western riparian areas will become even a smaller part of the landscape than they are now.

LITERATURE CITED

Anderson, B.W., R.D. Ohmart, and J. Rice. 1983. Avian and vegetation community structure and their seasonal relationships in the lower Colorado River Valley. Condor 85:392–405.

Armour, C.L., D.A. Doff, and W. Elmore. 1991. Effects of livestock grazing on riparian and stream ecosystems. Fisheries (Bethesda, MD) 16:7–11.

Auble, G.T., J.M. Friedman, and M.L. Scott. 1994. Relating riparian vegetation to present and future streamflow. Ecological Applications 4:544–554.

Auble, G.T. and M.L. Scott. 1998. Fluvial disturbance patches and cottonwood recruitment along the upper Missouri River, Montana. Wetlands 18:546–556.

Boggs, K. and T. Weaver. 1994. Changes in vegetation and nutrient pools during riparian succession. Wetlands 14:98–109.

Braatne, J.H., S.B. Rood, and P.E. Heilman. 1996. Life history, ecology and conservation of riparian cottonwoods in North America. p. 57–86. *In* R.F. Stettler, H.D Bradshaw, Jr., P.E. Heilman, and T.M. Hinckley (eds.) Biology of *Populus* and Its Implications for Management and Conservation. NRC Research Press, Ottawa, Ontario, Canada.

Bradley, C.E. and D.G. Smith. 1986. Plains cottonwood recruitment and survival on a prairie meandering river floodplain, Milk River, southern Alberta and northen Montana. Canadian Journal of Botany 64:1433–1442.

Briggs, M.K. and S. Cornelius. 1998. Opportunities for ecological improvement along the lower Colorado River and delta. Wetlands 18:513–529.

Brinson, M.M., B.L. Swift, R.C. Plantico, and J.S. Barclay. 1981. Riparian ecosystems: their ecology and status. U.S. Fish and Wildlife Service Biological Services Program, Washington, DC, USA. FWS/OBS-81/17.

Brock, J.H. 1984. *Tamarix* spp. (salt cedar), an invasive exotic woody plant in arid and semi-arid riparian habitats of western USA. p. 27–44. *In* L. de Wall, L. Child, P. Wade, and J. Brock (eds.) Ecology and Management of Invasive Riverside Plants. John Wiley and Sons, New York, NY, USA.

Busch, D.E. and S.D. Smith. 1995. Mechanisms associated with decline of woody species in riparian ecosystems of the southwestern United States. Ecological Monographs 65:347–370.

Campbell, C.J. and W. Green. 1968. Perpetual succession of stream-channel vegetation in a semi-arid region. Journal Arizona Academy of Sciences 5:86–98.

Collier, M., R.H. Webb, and J.C. Schmidt. 1996. Dams and rivers: a primer on the downstream effects of dams. U.S. Geological Survey Circular 1126.

Cooper, J.R., J.W. Gilliam, R.B. Daniel, and W.P. Robard. 1987. Riparian areas as filters for agricultural sediment. Journal of the Soil Science Society of America 51:416–420.

Dawson, T.E. and J.R. Ehleringer. 1991. Streamside trees that do not use stream water. Nature 350:335–337.

Dominick, D.S. and M.P. O'Neill. 1998. Effects of flow augmentation on stream channel morphology and riparian vegetation: upper Arkansas River Basin, Colorado. Wetlands 18:591–607.

Dynesius, M. and C. Nilsson. 1994. Fragmentation and flow regulation of river systems in the northern third of the world. Science 266:753–762.

Elmore, W. 1992. Riparian responses to grazing practices. p. 442–457. *In* R.B. Naiman (ed.) Watershed Management: Balancing Sustainability and Environmental Change. Springer-Verlag, New York, NY, USA.

Everitt, B.L. 1998. Chronology of the spread of tamarisk in the central Rio Grande. Wetlands 18:658–668.

Feller, J.M. 1998. Recent developments in the law affecting livestock grazing on western riparian areas. Wetlands 18:646–657.

Fenneman, N.M. 1931. Physiography of Western United States. McGraw-Hill Publishing Co., New York, NY, USA.

Fenner, P., W.W. Brady, and D.R. Patton. 1985. Effects of regulated water flows on regeneration of Fremont cottonwood. Journal of Range Management 38:135–138.

Flanagan, L.B., J.R. Ehleringer, and T.E. Dawson. 1992. Water sources of plants growing in woodland, desert, and riparian communities: evidence from stable isotope analysis. United States Forest Service General Technical Report INT-289:43–47.

Freeman, C.E. and W.A. Dick-Peddie. 1970. Woody riparian vegetation in the Black and Sacramento Mountain ranges of southern New Mexico. Southwestern Naturalist 15:145–164.

Friedman, J.M., W.R. Osterkamp, and W.M. Lewis, Jr. 1996. Channel narrowing and vegetation development following a Great Plains flood. Ecology 77:2167–2181.

Friedman, J.M., W.R. Osterkamp, M.L. Scott, and G.T. Auble. 1998. Downstream effects of dams on channel geometry and bottomland vegetation: regional patterns in the Great Plains. Wetlands 18: 619 633.

Friedman, J.M., M.L. Scott, and G.T. Auble. 1997. Water management and cottonwood forest dynamics along prairie streams. p. 49–71. *In* F. Knopf and F. Samson (eds.) Ecology and Conservation of Great Plains Vertebrates. Ecological Studies 125. Springer-Verlag, New York, NY, USA.

Friedman, J.M., M.L. Scott, and W.L. Lewis, Jr. 1995. Restoration of riparian forest using irrigation, artificial disturbance, and natural seedfall. Environmental Management 19:547–557.

Gladwin, D.N. and J.E. Roelle. 1998. Survival of plains cottonwood (*Populus deltoides* subsp. *monilifera*) and salt cedar (*Tamarix ramosissima*) seedlings in response to flooding. Wetlands 18:669–674.

Graf, J.B., R.H. Webb, and R. Hereford. 1991. Relation of sediment load and floodplain formation to climatic variability, Paria River drainage basin, Utah and Arizona. Geological Society of America Bulletin 103:1405–1415.

Graf, W.L. 1988. Fluvial Processes in Dryland Rivers. Springer-Verlag, New York, NY, USA.

Grant, G.E. 1986. Downstream effects of timber harvest activities on the channel and valley floor morphology of western Cascade streams. Ph.D. Dissertation. Johns Hopkins University, Baltimore, MD, USA.

Great Plains Flora Association. 1986. Flora of the Great Plains. University of Kansas Press, Lawrence, KS, USA.

Gregory, S.V., F.J. Swanson, W.A. McKee, and K.W. Cummins. 1991. An ecosystem perspective of riparian zones. Bioscience 41: 540–551.

Griggs, R.F. 1938. Timberlines in the northern Rocky Mountains. Ecology 19:548–564.

Harris, R.R., C.A. Fox, and R.J. Risser. 1987. Impacts of hydroelectric development on riparian vegetation in the Sierra Nevada region, California. Environmental Management 11:519–527.

Hill, A.R. 1996. Nitrate removal in stream riparian zones. Journal Environmental Quality 25:743–755.

Hill, M.T., W.S. Platts, and R.L. Beschta. 1991. Ecological and geomorphological concepts for instream and out-of-channel flow requirements. Rivers 2:198–210.

Hirsch, R.M., J.F. Walker, J.C. Day, and R. Kallio. 1990. The influence of man on hydrologic systems. p. 329–359. *In* M.G. Wolman and H.C. Riggs (eds.) The Geology of North America, Volume 0-1. Surface Water Hydrology. Geological Society of America, Boulder, CO, USA.

Hunter, W.C., B.S. Anderson, and R.D. Ohmart. 1987. Avian communtiy structure changes in a mature floodplain forest after extensive flooding. Journal Wildlife Management 51:495–502.

Hupp, C.R. and W.R. Osterkamp. 1996. Riparian vegetation and fluvial geomorphic processes. Geomorphology 14:277–295.

Irvine, J.R. and N.E. West. 1979. Riparian tree species distribution and succession along the lower Escalante River, Utah. Southwest Naturalist 24:331–346.

Johnson, R.R. 1991. Historic changes in vegetation along the Colorado River in the Grand Canyon. p. 178–206. *In* National Research Council. Colorado River Ecology and Management. National Academy Press, Washington, DC, USA.

Johnson, R.R. and S.W. Carothers. 1982. Riparian habitats and recreation: interrelationships in the Southwest and Rocky Mountain region. U.S. Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO, USA. Eisenhower Consortium Bulletin 12:1–31.

Johnson, W.C. 1992. Dams and riparian forests: case study from the upper Missouri River. Rivers 3:229–242.

Johnson, W.C. 1994. Woodland expansion in the Platt River, Nebraska: patterns and causes. Ecological Monographs 64:45–84.

Johnson, W.C. 1998. Adjustment of riparian vegetation to river regulation in the Great Plains, USA. Wetlands 18:608–618.

Johnson, W.C. R.L. Burgess, and W.R. Keammerer. 1976. Forest overstory vegetation and environment on the Missouri River floodplain in North Dakota. Ecological Monographs 64:45–84.

Kauffman, J.B. 1988. The status of riparian habitats in Pacific Northwest forests. p. 45–55. *In* K.J. Raedeke (ed.) Streamside Management: Riparian Wildlife and Forestry Interactions. Institute of Forest Resources, University of Washington, Seattle, WA, USA. Contribution 59.

Kondolf, G.M., R. Kattelmann, M. Embury, and D.C. Erman. 1996. Status of riparian habitat. In Sierra Nevada Ecosystem Project: Final Report to Congress. Center for Water Wildlands Research, University of California, Davis, CA, USA.

Kondolf, G.M. and E.A. Keller. 1991. Management of urbanizing watersheds. p. 27–40. *In* J. DeVries and S. Conard (eds.) California Watersheds at the Urban Interface. California Water Research Center Report 75.

Leopold, L.B., M.G. Wolman, and J.P. Miller. 1964. Fluvial Processes in Geomorphology. W.H. Freeman and Co., San Francisco, CA. USA.

Ligon, F.K., W.E. Dietrich, and W.J. Trush. 1995. Downstream ecological effects of dams, a geomorphic perspective. Bioscience 45: 183–192.

Longstreth, D.J. and D.T. Patten. 1975. Conversion of chaparral to grass in central Arizona: effects on selected ions in watershed runoff. American Midland Naturalist 93:25–34.

Lowrence, R., J. Fail, Jr., O. Hendrickson, R. Leonard, Jr., and L. Rasmussen. 1984. Riparian forests as nutrient filters in agricultural watersheds. Bioscience 34:374–377.

Mahoney, J.M. and S.B. Rood. 1998. Streamflow requirements for cottonwood seedling recruitment—an integrative model. Wetlands 18:634–645.

Medina, A.L. 1990. Possible effects of residential development on streamflow, riparian plant communities and fisheries in small mountain streams in central Arizona. Forest Ecological Management 33/34:351–361.

Merigliano, M.F. 1998. Cottonwood and willow demography on a young island, Salmon River, Idaho. Wetlands 18:571–576.

Naiman, R.J. and H. Decamps. 1997. The ecology of interfaces: riparian zones. Annual Review of Ecology and Systematics 28: 621–658.

Naiman, R.J., H. Decamps, M. Pollock. 1993. The role of riparian corridors in maintaining regional biodiversity. Ecological Applications 3:209–212.

Nelson, R.L., M.L. McHenry, and W.S. Platts. 1991. Mining. American Fisheries Society Special Publication 19:425–457.

Ohmart, R.D., B.W. Anderson, and W.C. Hunter. 1988. The ecology of the lower Colorado River from Davis Dam to the Mexico-United States boundry: a community profile. U.S. Fish and Wildlife Biological Report 85:1–296.

Osterkamp, W.R. 1998. Processes of fluvial island formation, with examples from Plum Creek, Colorado and Snake River, Idaho. Wetlands 18:530–545.

Patten, D.T. 1968. Dynamics of the shrub continuum along the Gallatin River in Yellowstone National Park. Ecology 49:1107–1112.

Patten, D.T. 1989. Effects of phased highway improvements, browsing and moisture stress on the riparian ecosystem along the Upper Gallatin River, Montana. p. 185. *In* R.E. Gresswell, B.A. Barton, and J.L. Kersher (eds.) Proceedings of a Workshop on Riparian Resource Management, 8–11 May 1989, Billings, MT. U.S. Bureau of Land Management, Billings, MT, USA.

Patten, D.T. 1993. Herbivore optimization and overcompensation, does response of western rangelands to native herbivory support these theories? Ecological Applications 3:35–36.

Peet, R.K. 1988. Forests of the Rocky Mountains. p. 61–101. *In* M.G. Barbour and D.W. Billings (eds.) North American Terrestrial Vegetation. Cambridge University Press, New York, NY, USA.

Poff, N.L., J.D. Allan, M.B. Bain, J.R. Karr, K.L. Prestgaard, B.D. Richter, R.E. Sparks, and J.C. Stromberg. 1997. The natural flow regime: a paradigm for river conservation and restoration. Bioscience 47:769–784.

Rood, S.B., C. Hillman, T. Sanche, and J.M. Mahoney. 1994. Clonal reproduction of riparian cottonwoods in southern Alberta. Canadian Journal of Botany 72:1766–1770.

Rood, S.B., A.R. Kalishchuk, and J.M. Mahoney. 1998. Initial cottonwood seedling recruitment following the flood of the century of the Oldman River, Alberta, Canada. Wetlands 18:557–570.

Rood, S.B. and J.M. Mahoney. 1990. Collapse of riparian poplar forests downstream from dams in western prairies: probably causes and prospects for mitigation. Environmental Management 14: 451–464.

Rood, S.B. and J.M. Mahoney. 1995. River damming and riparian cottonwoods along the Marias River, Montana. Rivers 5:195–207.

Sabine, B.J. (ed.). 1994. National list of plant species that occur in wetlands—Regions 4, 5, and 8. Resource Management Group, Inc., Grand Haven, MI, USA.

Sala, A. and S.D. Smith. 1996. Water use by *Tamarix ramosissima* and associated phreatophytes in a Mojave Desert floodplain. Ecological Applications 6:888–898.

Scott, M.L., G.T. Auble, and J.M. Friedman. 1997. Flood dependency of cottonwood establishment along the Missouri River, Montana. Ecological Applications 7:677–690.

Scott, M.L., J.M. Friedman, and G.T. Auble. 1996. Fluvial process and the establishment of bottomland trees. Geomorphology 14: 327–339.

Scott, M.L., P.B. Shafroth, and G.T. Auble. 1999. Responses of riparian cottonwoods to alluvial water declines. Environmental Management 23: (in press).

Scott, M.L., M.A. Wondzell, and G.T. Auble. 1993. Hydrograph characteristics relevant to the establishment and growth of western riparian vegetation. p. 237–246. *In* H.J. Morel-Seytoux (ed.) Proceedings of the thirteenth annual American Geophysical Union Hydrology Days. Hydrology Days Publications, Atherton, CA, USA.

Shafroth, P.B., G.T. Auble, and M.L. Scott. 1995. Germination and establishment of the native plains cottonwood (*Populus deltoides* Marshall subsp. *monilifera*) and the exotic Russian-olive (*Elaeagnus angustifolia* L.). Conservation Biology 9:1169–1175.

Shafroth, P.B., G.T. Auble, J.C. Stromberg, and D.T. Patten. 1998. Establishment of woody riparian vegetation in relation to annual patterns of streamflow, Bill Williams River, Arizona. Wetlands 18: 577–590.

Sidle, R.C., A.J. Pierce, and C.L. O'Loughlin. 1985. Hillslope stability and land use. Water Resources Monograph 11. American Geophysical Union, Washington, DC, USA.

Smith, D. 1980. River ice processes: thresholds and geomorphic effects in northern and mountain rivers. p. 323–343. *In* D.R. Coats and J.D. Vitek (eds.) Thresholds in Geomorphology. Allen and Unwin, Boston, MA, USA.

Smith, S.D., D.A. Devitt, A.Sala, J.R. Cleverly, and D.E. Busch. 1998. Water relations of riparian plants from warm desert regions. Wetlands 18:687–696.

Stromberg, J.C. 1993. Instream flow models for mixed deciduous riparian vegeetation within a semiarid region. Regulated Rivers: Research and Management 8:225–235.

Stromberg, J.C. 1998. Functional equivalency of salt cedar (*Tamarix chinensis*) and Fremont cottonwood (*Populus fremontii*) along a free-flowing river. Wetlands 18:675–686.

Stromberg, J.C. and M.K. Chew. 1997. Herbaceous exotics in Arizona's riparian ecosystems. Desert Plants 13:11–17.

Stromberg, J.C., J. Fry, and D.T. Patten. 1997. Marsh development after large floods in an alluvial, arid-land river. Wetlands 17:292–300.

Stromberg, J.C. and D.T. Patten. 1989. Early recovery of an eastern Sierran riparian system following forty years of stream diversion. p. 399–404. *In* Proceedings of the California Riparian Systems Conference, U.S. Forest Service, Berkeley, CA, USA. General Technical Report PSW-110.

Stromberg, J.C. and D.T. Patten. 1996. Instream flow and cottonwood growth in the eastern Sierra Nevada of California, USA. Regulated Rivers: Research and Management 12:1–12.

Stromberg, J.C., D.T. Patten, and B.D. Richter. 1991. Flood flows and dynamics of Sonoran riparian forests. Rivers 2:221–223.

Stromberg, J.C., B.D. Richter, D.T. Patten, and W.G. Wolden. 1993a. Response of a Sonoran riparian forest to 10-year return flood. Great Basin Naturalist 53:18–30.

Stromberg, J.C., M.R. Sommerfeld, D.T. Patten, J. Fry, C. Kramer, F. Amalfi, and C. Christian. 1993b. Release of effluent into the upper Santa Cruz River, southern Arizona: ecological considerations. p. 81–92. *In* M. Wallace (ed.) Proceedings of the Symposium on Effluent Use and Management. American Water Resources Association, Tucson, AZ, USA.

Stromberg, J.C., R. Tiller, and B. Richter. 1996. Effects of groundwater decline on riparian vegetation of semiarid regions: The San Pedro, Arizona. Ecological Applications 6:1133–131.

Stromberg, J.C., J.A. Tress, S.D. Wilkins, and S. Clark. 1992. Response of velvet mesquite to groundwater decline. Journal of Arid Environments 23:45–58.

Swanson, F.J., L.E. Benda, S.H. Duncan, G.E. Grant, W.F. Megahan, L.M. Reid, and R.R. Ziemer. 1987. Mass failures and other processes of sediment production in Pacific Northwest forest landscapes. p. 9–38. *In* E.O. Salo and T.W. Cundy (eds.) Streamside Management, Forestry and Fishery Interactions. Institute of Forest Resources, University of Washington, Seattle, WA, USA. Contribution 57.

Valenciano, D. 1992. Elevational and cross-sectional gradients in montane riparian plant communities of sub-Mogollon Arizona: a comparison to adjacent upland communities. M.S. Thesis. Arizona State University, Tempe, AZ, USA.

Whittaker, R.H. and W.A. Neiring. 1965. Vegetation of the Santa Catalina Mountains, Arizona. II. A gradient analysis of the south slope. Ecology 46:429–452.

Whittaker, R.H. and W.A. Neiring. 1975. Vegetation of the Santa Catalina Mountains, Arizona. V. Biomass, production and diversity along the elevation gradient. Ecology 56:771–790.

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