Importance of low-flow and high-flow characteristics to restoration of riparian vegetation along rivers in arid south-western United States

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SUMMARY

- 1. Riparian vegetation in dry regions is influenced by low-flow and high-flow components of the surface and groundwater flow regimes. The duration of no-flow periods in the surface stream controls vegetation structure along the low-flow channel, while depth, magnitude and rate of groundwater decline influence phreatophytic vegetation in the floodplain. Flood flows influence vegetation along channels and floodplains by increasing water availability and by creating ecosystem disturbance.
- 2. On reference rivers in Arizona's Sonoran Desert region, the combination of perennial stream flows, shallow groundwater in the riparian (stream) aquifer, and frequent flooding results in high plant species diversity and landscape heterogeneity and an abundance of pioneer wetland plant species in the floodplain. Vegetation changes on hydrologically altered river reaches are varied, given the great extent of flow regime changes ranging from stream and aquifer dewatering on reaches affected by stream diversion and groundwater pumping to altered timing, frequency, and magnitude of flood flows on reaches downstream of flow-regulating dams.
- 3. As stream flows become more intermittent, diversity and cover of herbaceous species along the low-flow channel decline. As groundwater deepens, diversity of riparian plant species (particularly perennial species) and landscape patches are reduced and species composition in the floodplain shifts from wetland pioneer trees (*Populus*, *Salix*) to more drought-tolerant shrub species including *Tamarix* (introduced) and *Bebbia*.
- 4. On impounded rivers, changes in flood timing can simplify landscape patch structure and shift species composition from mixed forests composed of *Populus* and *Salix*, which have narrow regeneration windows, to the more reproductively opportunistic *Tamarix*. If flows are not diverted, suppression of flooding can result in increased density of riparian vegetation, leading in some cases to very high abundance of *Tamarix* patches. Coarsening of sediments in river reaches below dams, associated with sediment retention in reservoirs, contributes to reduced cover and richness of herbaceous vegetation by reducing water and nutrient-holding capacity of soils.
- 5. These changes have implications for river restoration. They suggest that patch diversity, riparian plant species diversity, and abundance of flood-dependent wetland tree species such as *Populus* and *Salix* can be increased by restoring fluvial dynamics on flood-suppressed rivers and by increasing water availability in rivers subject to water diversion or withdrawal. On impounded rivers, restoration of plant species diversity also may hinge on restoration of sediment transport.

6. Determining the causes of vegetation change is critical for determining riparian restoration strategies. Of the many riparian restoration efforts underway in south-western United States, some focus on re-establishing hydrogeomorphic processes by restoring appropriate flows of surface water, groundwater and sediment, while many others focus on manipulating vegetation structure by planting trees (e.g. Populus) or removing trees (e.g. Tamarix). The latter approaches, in and of themselves, may not yield desired restoration outcomes if the tree species are indicators, rather than prime causes, of underlying changes in the physical environment.

Keywords: arid, flood hydrograph, Gila River basin, groundwater, plant species richness, Populus, restoration, riparian vegetation, river floodplain, Salix, Tamarix

Introduction

Stream flow regimes can be characterised both in terms of their low-flow and high-flow components (Sanz & del Jalon, 2005). In dry regions, there is high variance between the low flow and high flow extremes, and the streams undergo periods of drought and intense flooding (Capon, 2003; Bunn et al., 2006). Perennial stream flow, often taken for granted in humid regions, is a rare commodity in arid regions, and many streams that do not receive water from the regional aquifer have surface water only intermittently or ephemerally. Where surface flow is intermittent, groundwater levels in the stream alluvium show strong seasonal declines, and water is less available to riparian phreatophytes, which are plants that extract water from aquifers or the capillary fringe above the water table (Meinzer, 1927). Floods influence riparian biota by creating ecosystem disturbance, driving geomorphic change, and altering availability of resources including water, light and nutrients (Bendix & Hupp, 2000). In arid regions, floods tend to have high magnitude but short duration. The rapidly peaking and receding waters of small floods create minor disturbance and provide a transitory water source. Floods of greater magnitude and longer duration can shape vegetation structure for decades (Friedman & Lee, 2002), and mediate water availability both through short-term hydrologic processes (overbank soil wetting, groundwater recharge) and longer-term geomorphic processes (channel incision, floodplain aggradation and degradation, deposition of course versus fine sediments; Shentsis & Rosenthal, 2003; Malmon, Reneau & Dunne, 2004).

The south-western United States has been undergoing rapid human population increase and

experiencing the increased pressure on the region's freshwater ecosystems that such growth entails (Maddock & Hines, 1995). Regionally, irrigated agriculture continues to consume the largest fraction of the water used (Pitt, 2001; Fig. 1). Municipal and industrial sectors (e.g. power plant cooling) use increasingly larger shares and are the primary water use categories on some rivers (Fitzhugh & Richter, 2004). Typically, hydrologic alterations are greater on low-altitude (and higher-order) alluvial rivers and streams than on the mountain tributaries that are farther from large population centres.

Within the Gila River Basin of Arizona, the San Pedro is one of the few rivers that remains undammed and retains extensive segments with perennial flow. Some rivers in this basin, such as the Santa Cruz near Tucson, Arizona, have dry channels and deep groundwater levels caused by decades of pumping from the stream and regional aquifers (Logan, 2002). The flow in some of the Gila's tributaries, including the Agua Fria and Salt River near Phoenix, Arizona, is completely diverted into canals (Graf, 1982, 2000; Springer et al., 1999). Reaches of others, such as the Lower Verde and portions of the Salt, retain their full flow rate but are modified by a series of dams that allow for water and delivery to downstream (Beauchamp, Stromberg & Stutz, 2007). The Gila ultimately flows into the Colorado River, which itself rarely now flows to its delta, with a large per cent of its water captured in reservoirs (Briggs & Cornelius, 1998; Graf, 1999; Glenn et al., 2001). The response of riverine ecosystems to these changes is complex. Some large wetland complexes have been converted to dry, open lands or replaced by irrigated farmland and cities, and many aquatic and riparian species have become rare or endangered (Miller, 1961; Deacon, Minckley & Udall,



Fig. 1 Irrigated agriculture is a common land use in the floodplain of many rivers in south-western United States, including this reach of the Gila River in Arizona. Photo source is the United States Geological Survey.

1991; Patten, 1998; Stromberg *et al.*, 2004; Cowley, 2006). Some riparian zones, however, now have increased abundance of marshland or forests (Stevens *et al.*, 1995; Shafroth, Stromberg & Patten, 2002a).

In this paper we address relationships between stream flow regimes and riparian vegetation of the arid south-western United States, focussing mainly on rivers within Arizona's Gila River drainage basin (Fig. 2). Specifically, we examine relationships of low flows and high flows with plant species diversity, plant species composition and landscape heterogeneity. We begin with an overview of two regional rivers that may function as reference ecosystems for restoration (Wissmar & Beschta, 1998), and then address vegetation changes on reaches that have been hydrologically altered by stream diversion, groundwater pumping and dam operation. We conclude by summarising riparian ecosystem restoration efforts, and discuss the merits of a process-based, hydrogeomorphic approach to restoration.

Reference rivers

Two well-studied reference rivers in the Gila Basin are the San Pedro and Hassayampa. From its headwaters near Sonora, Mexico, the San Pedro flows north for 225 km to its confluence with the Gila River, passing through the Chihuahuan and Sonoran Desert biomes. Portions of the San Pedro river are affected by

groundwater pumping for agricultural, municipal and industrial use (copper mining), but some segments retain perennial flow, particularly where there is inflow of groundwater from the regional (basin-fill) aquifer to the riparian aquifer and where shallow bedrock underlies the river bed and acts as a dam over which the water must flow. Stream flow is impeded only by small (and seasonally temporary) diversion structures. Although agricultural activities have occurred along the river for centuries, much of the San Pedro River corridor remains undeveloped, leading The Nature Conservancy, the principal nongovernmental nature protection organisation in the U.S.A., to deem it as one of their 'last great places' and the American Bird Conservancy to declare it a 'globally important bird area'. The Hassayampa River also is an undammed, interrupted perennial river, i.e. one with alternating segments of perennial and intermittent to ephemeral flow. Although much of the river has ephemeral flow, an 8-km perennial stretch of the Hassayampa in the Sonoran Desert near Wickenburg, Arizona, was purchased by The Nature Conservancy. This area is managed as a preserve, and provides important habitat for many plant and animal species that depend on riparian habitat. The Hassayampa and San Pedro Rivers both are in the Basin and Range Physiographic Province which is characterised by topographic complexity and large altitudinal range in the catchment (Hunt, 1967).

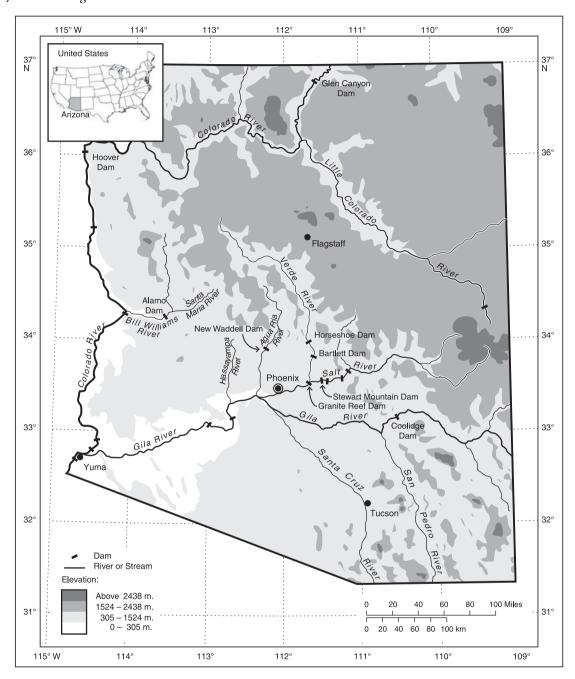


Fig. 2 Major rivers, streams, and dams in Arizona. Map adapted from the Arizona Geographic Alliance.

Low-flow periods, riparian plants and drought stress

The flow regime of a river varies with many factors, including climate, drainage area, geology, proximity to major tributaries and proximity to groundwater recharge sites. Many rivers in the arid south-west of the United States naturally flow intermittently or ephemerally, given the low precipitation rates. As rivers emerge from the wetter mountains into the arid basins, the surface water often rapidly drains into deep alluvial aquifers, creating intermittent to ephemeral flow. Geological strata that restrict flow from the regional (basin-fill) aquifer to the riparian (stream) aquifer can also contribute to intermittent flows. In reaches with intermittent flow, no-flow days are most common in early summer (May and June) between the winter run-off season and the late summer monsoonal rain and flood season, and in late autumn (October and November) prior to the winter rainy season. In such reaches, the stream often loses water to the aquifer, and the groundwater in the stream alluvium tends to be deep with its level highly fluctuating. In ephemeral reaches, the stream flows only for short periods following storm events, and the surface water and groundwater typically are not hydraulically connected.

Low-flow conditions and high-flow conditions both can be characterised by the magnitude, duration, frequency, timing and rate of change of flow, and by their temporal and spatial variability (Poff *et al.*, 1997; Richter *et al.*, 1997, 1998). With respect to low-flow conditions, the stream base flow rate (i.e. the flow that is derived from groundwater) determines the amount of stream water present during dry seasons. The duration of periods with no surface flow (i.e. the degree of stream intermittency, or hydroperiod) controls vegetation structure along the low-flow channel of desert rivers (Stromberg *et al.*, 2005). The timing and frequency of no-flow periods also may influence channel vegetation, but this issue remains to be investigated.

Stream beds and floodplains of desert alluvial rivers often are composed of coarse sediments, resulting in a high degree of hydraulic connectivity between surface water and groundwater and tight coupling between stream stage and aquifer water levels. Mean annual flow rate and stream stage thus are of importance to floodplain vegetation as indicators of water level in the riparian aquifer (Stromberg & Patten, 1990; Smith et al., 1991; Rood et al., 1995; Willms et al., 1998). At larger spatial scales, the length and spatial distribution of perennial versus intermittent reaches are important to riparian vegetation as they influence factors such as the spatial extent of aquifer recharge by flood flows.

Depth to groundwater (or to saturated soils), intraannual and inter-annual fluctuation in water table level, and groundwater decline rate influence the abundance, age structure, and composition of phreatophytic vegetation on river floodplains and terraces (Stromberg *et al.*, 1992; Busch & Smith, 1995; Stromberg, Tiller & Richter, 1996; Mahoney & Rood, 1998; Scott, Shafroth & Auble, 1999; Castelli, Chambers & Tausch, 2000; Scott, Lines & Auble, 2000a; Horton, Kolb & Hart, 2001a,b; Amlin & Rood, 2002, 2003; Cooper, D' Amico & Scott, 2003a; Elmore, Mustard & Manning, 2003; Lite & Stromberg, 2005; Naumburg *et al.*, 2005). Although well studied, some aspects of this relationship, including effects on phreatophytic riparian vegetation of timing (e.g. growing season or dormant season) of groundwater decline, need further investigation.

The phreatophytic trees that grow along rivers of the south-western United States encompass a diverse group of species that differ widely in root depth and architecture, water use rate, tolerance for drought and capacity to shift between seasonally varying water sources (Smith et al., 1998). Goodding willow (Salix gooddingii Ball), a common pioneer tree along Sonoran Desert rivers, is an obligate phreatophyte, with groundwater essential to its survival and forming a primary component of its water supply. Fremont cottonwood (Populus fremontii S. Wats.) is also considered to be an obligate phreatophyte although it does use other water sources (Busch, Ingraham & Smith, 1992; Smith et al., 1998; Leffler & Evans, 1999; Snyder & Williams, 2000; Horton et al., 2001a,b; Potts & Williams, 2004). Velvet mesquite (Prosopis velutina Woot.), a deep-rooted tree that is common on river floodplains and terraces as well as in desert uplands, is a facultative phreatophyte; when growing in riparian settings it utilises deep (groundwater) and shallow (rain and flood water) water sources, but in desert uplands it can survive on rainfall alone (Stromberg, Wilkins & Tress, 1993a; Scott et al., 2000b, 2003; Snyder & Williams, 2003). In general the dichotomy between obligate and facultative is somewhat arbitrary, in that species may vary in their dependence on groundwater depending on climatic conditions and geomorphic setting.

Populus fremontii and Salix gooddingii both are relatively shallow-rooted, drought-intolerant tree species. (Horton et al., 2001b; Glenn & Nagler, 2005). Because fine roots of these trees are concentrated in the capillary fringe, just above the water table, they are sensitive to fluctuation in water table depth, particularly on coarse soils with a narrow capillary fringe. Groundwater decline during the dry season in hot summers can strand roots above the water level, reduce productivity and, in some cases, cause death. Seasonal declines of 1 m, for example, can kill saplings of cottonwood and willow (Shafroth, Stromberg & Patten, 2000). Although small populations of these species, composed of a small number of age classes, occur along dry stream reaches, dense, multi-aged mixed forests of P. fremontii and *S. gooddingii* are sustained where groundwater under the floodplain is shallow (averaging less than about 3 m deep) and levels fluctuate little (typically <1 m year⁻¹) (Stromberg, Patten & Richter, 1991; Shafroth *et al.*, 1998, 2000; Scott *et al.*, 1999, 2000a; Horton *et al.*, 2001a,b; Lite & Stromberg, 2005).

Water relationships of riparian shrubs are less well known. Seep-willow baccharis [Baccharis salicifolia (Ruiz & Pavón) Pers.] and narrowleaf willow (Salix exigua Nutt.), common shrubs along low-flow channels and on low floodplains, are relatively shallowrooted and may be obligate phreatophytes (Gary, 1963; Williams et al., 1998). Rubber rabbitbrush [Ericameria nauseosus (Pallas ex Pursh) Nesom & Baird], a species that roots to about 4 m, is phreatophytic in some, but not all, settings (Toft, 1995; Elmore et al., 2003). Water sources of burrobrush (Hymenoclea spp.), a small shrub that occurs along perennial as well as ephemeral streams, have not been studied. Burrobrush, like other xeroriparian species, may rely on transitory flood water (de Soyza, Killingbeck & Whitford, 2004).

Herbaceous species in desert river floodplains vary widely in their water relations and water sources. Inflowing groundwater creates the continuously saturated soils that sustain hardstem bulrush [Schoenoplectus acutus (Muhl. ex Bigelow) A.& D. Lövel, torrey rush (Juncus torreyi Coville), and other macrophytes along channels of perennial reaches of the San Pedro River (Stromberg et al., 1996). Big sacaton (Sporobolus wrightii Munro ex Scribn.), a perennial bunch grass that grows on floodplains and terraces, is a deep-rooted (to 4 m) facultative phreatophyte that uses different water sources by season (Scott et al., 2000b, 2003; Tiller, 2004). Many of the annual plants in desert riparian corridors are sustained by seasonal flood water, and others by rainfall (Bagstad, Stromberg & Lite, 2005), or some combination thereof.

The diversity and composition of herbaceous plants in the riparian corridor both vary along lateral topographic gradients as a function of water availability. During the summer dry season, diversity typically declines laterally across the floodplain, paralleling increases in depth to groundwater (Lite, Bagstad & Stromberg, 2005); composition changes from wetland to upland species along these same gradients (Stromberg *et al.*, 1996). Following seasonal rains and floods, the spatial patterns can shift, with herbaceous species having low diversity on

flood-scoured surfaces and becoming increasingly diverse with increasing distance above or away from the channel (Stromberg, in press).

Amid the Sonoran and Chihuahuan desert environments, as in arid and semi-arid regions throughout the world, perennial river flows, shallow groundwater, periodic flood flows, and the high soil moisture they provide and disturbance they create are critical for sustaining riparian plant species and maintaining high species diversity (Tabacchi et al., 1996; Rundel & Sturmer, 1998; Fossati, Pautou & Peltier, 1999; Ali, Dickinson & Murphy, 2000). For example, a total of 340 vascular plant species were recorded within the 135 ha Nature Conservancy's Hassayampa River Preserve (Wolden, Stromberg & Patten, 1994) and 608 species were recorded in the 19 291 ha San Pedro National Riparian Conservation Area (Makings, 2005) with an additional 200 species along the river's lower reaches. In contrast, sectors of the Sonoran Desert without perennial streams harbour fewer species (Bowers & McLaughlin, 1982).

Not all of the plant species that occur along desert rivers are obligately dependent on the water resources of the riparian corridor. One-third of the species in the floras of the Hassayampa and San Pedro River do rely on supplemental riparian water sources, as inferred from having a wetland designation from obligate wetland through facultative upland. However, twothirds of the species are classified as upland species (i.e. those with no formal wetland designation according to the National PLANTS data base [USDA-NRCS, 2002]), and many of these are desert annuals that rely on rainfall when growing in the riparian corridor and desert upland alike. Because these rivers are well connected to their catchments, with the riparian zones abutting upland plant communities and receiving inflows from tributaries and upstream reaches, their riparian corridors support this wide range of regional upland species.

High flows, riparian plants and flood disturbance

Floods in the south-western United States tend to occur in three seasons, and each seasonal type has different climatic drivers and leaves a different signature on the landscape. Floods that occur during the late summer monsoonal thunderstorm season can have great magnitude (with high instantaneous peaks) but short duration; they transport and deposit

fine sediment and can inundate substantial areas of the floodplain for short periods. Floods that occur in winter following regional Pacific storms or in fall after tropical storms can have longer duration; such floods can erode extensive areas of river floodplains and terraces, deposit thick sediment lenses, and elevate stream flows and groundwater in the stream alluvium for several months postflood (Minckley & Clark, 1984; Huckleberry, 1994; Stromberg, Fry & Patten, 1997; Bagstad *et al.*, 2005).

From a demographic perspective, floods can be viewed as agents that cause mortality of plants (Friedman, Osterkamp & Lewis, 1996; Stromberg et al., 1997) while also creating opportunities for establishment of pioneer species (Scott, Friedman & Auble, 1996). Populus fremontii and S. gooddingii are short-lived pioneer trees with temporally specialised reproduction strategies adapted to the regional climatic flood pattern. They annually produce large numbers of tiny wind- and water-dispersed seeds, a common strategy for establishment in frequently disturbed environments (Braatne, Rood & Heilman, 1996; Karrenberg, Edwards & Kollmann, 2002). Establishment tends to occurs in years with wet winters and springs. Large winter floods have the geomorphic capacity to scour and redeposit sediments, thereby creating seed beds for these plants to establish without competition from an existing overstory. Seeds of both species are viable only during a brief period in spring, and germinate as the high winter flows decline and expose bare, damp sediments (Fenner, Brady & Patton, 1984). Salix gooddingii disperses seeds somewhat later in the season than P. fremontii (although the seed dispersal periods overlap), and, as flood waters recede, establishes on sites that are slightly lower and closer to the stream. The frequency of years with suitable establishment conditions varies from several times per decade to less than once per decade (Stromberg et al., 1991; Shafroth et al., 1998; Stromberg, 1998).

From a landscape perspective, floods create a shifting mosaic of patches, with each patch associated with specific geomorphic surfaces and hydrologic conditions and supporting different types or age classes of vegetation (Harris, 1987; Hupp & Osterkamp, 1996; Higgins, Rodgers & Kemper, 1997; Hughes, 1997; Ward *et al.*, 2001). In dry regions, these patch dynamics are rapid. On the Hassayampa, we observed the re-distribution of patches

after large winter floods scoured and redistributed sediments and created a mosaic of surfaces of different elevations above the water table (Stromberg et al., 1997). Patches of riverine marsh developed in areas of the widened channel with saturated soils and shallow surface water (although these were soon replaced by other patches following sediment accretion during a subsequent flood), young patches composed of Populus and Salix occupied sediment deposits that had moist surfaces, while Hymenoclea shrublands developed on deep sediment deposits that were too high above the water table to sustain wetland trees. Over time, recurring floods create multiple patches composed of Populus and Salix trees, each typically consisting of trees of a similar age (cohort) that established during the same flood event.

Floods also influence community attributes such as species diversity. Plants with an annual life-span comprise the majority of species in the flora of Southwestern riparian corridors (65% of species in the San Pedro floodplain, Bagstad et al., 2005; 58% of species at the Hassayampa River Preserve, Wolden et al., 1994). Many of these species are riparian ruderals with a suite of life-history characteristics including short life span, high seed production, and high allocation to reproductive effort, that adapt for life in disturbed environments (Grime, 1973, 1977). Diversity and cover of herbaceous plants thus typically increase seasonally after small (1- to 3-year recurrence interval floods; Bagstad et al., 2005) and medium (10year recurrence interval flood; Stromberg et al., 1993b) floods. Floods create the bare mineral soils on which the ruderals establish by scouring litter, redistributing sediments and reducing abundance of competitive dominants (Nilsson et al., 1999; Xiong et al., 2001b; Xiong, Nilsson & Johansson, 2001a), and by providing the water (and perhaps nutrients) that stimulates their germination and growth. In a fashion consistent with the intermediate disturbance hypothesis (Connell, 1979), species diversity can decline after larger, more erosive floods, but subsequently levels often increase to higher values than were observed before the flood (Bagstad et al., 2005).

Floods also increase diversity by creating spatial heterogeneity in the floodplain. This allows for high species turnover along environmental gradients and thus for high beta diversity of plant species (Whittaker, 1972; Nilsson *et al.*, 1989; Nichols,

Killingbeck & August, 1998; Ward, 1998; Gould & Walker, 1999; Capon, 2005). Complex spatial gradients of tree canopy cover, litter cover, and soil texture and nutrient content are created as fluvial processes such as sediment transport interact with vegetation to drive forest succession. As a result of flood-driven accretion, floodplains typically increase in elevation with distance from the channel, which creates gradients of inundation frequency, scour intensity, soil moisture and distance to saturated soils (Lyon & Sagers, 1998; Ward & Tockner, 2001). Along these topographic hydrogradients, there are compositional shifts from shallow-rooted, rhizomatous, floodadapted hydrophytes and wetland ruderals on low fluvial surfaces, to deeper-rooted perennials and raindependent annuals on high floodplains and terraces (Stromberg et al., 1996; Williams et al., 1999; Auble, Scott & Friedman, 2005; Bagstad et al., 2005).

Many physical factors, including flood intensity, groundwater availability, rainfall surface and amounts and seasonality, and temperature, vary over the length of a river, and collectively these factors create spatial patterns in the riparian community (Tabacchi et al., 1996; Ward et al., 2001). The San Pedro River has provided an excellent laboratory for longitudinal studies. The total stream power during floods of a given recurrence interval in the San Pedro increases with distance downstream as catchment size and drainage density increase and then ultimately decline as stream channel gradient decreases, following a common pattern of many rivers (Church, 2002). Woody plant species diversity does not change along this gradient, as it does on some rivers in the western United States (Bendix, 1997), but the vegetation does change in species composition and age structure. Woody pioneer species increase in diversity at sites with higher flood intensity, while more competitive (late-successional) species decrease (Lite et al., 2005); additionally, the forest stands become increasingly dominated by younger trees in the lower reaches.

Landscape heterogeneity also varies over the length of desert rivers, in association with changes in low-flow and high-flow components of the stream flow regime. Along the San Pedro River, the number of vegetation patches in the floodplain varied as a function of flood stream power (greater at sites with more intense disturbance), while the number of different patch types varied as a function of site water

availability (greater at wetter sites). Overall, the riparian areas of the higher altitude reaches of the San Pedro River, where stream power is low, groundwater is shallow, and floodplains are narrow but rainfall is high and temperatures low, have high herbaceous cover and high small-scale species diversity. Riparian sites in the more arid reaches at lower altitude, in contrast, have less herbaceous cover and lower small-scale diversity but have wider floodplains and greater flood disturbance, and thus support a greater number of species across the floodplain (Lite *et al.*, 2005).

Changes to low-flow conditions and plant responses

The main anthropogenic actions that alter low-flow characteristics are stream flow diversion, groundwater pumping from near-stream areas (typically intercepting the riparian aquifer), groundwater pumping from areas far from the stream (intercepting the regional aquifer), regulation of flows at dam sites, and discharge of water from agricultural drains and wastewater treatment plants. Stream flows also can be influenced by livestock grazing (Flenniken et al., 2001). Stream flow has been wholly diverted from some rivers in the south-western United States, completely dewatering the channel and aquifer and eliminating riparian vegetation (Figs 3 and 4). Many other rivers are seasonally or partially diverted (Stromberg et al., 2004). Small-scale diversions, such as those for local agricultural use, have minor impacts on the riparian vegetation, particularly where the flow is diverted by small earthen dams that are periodically destroyed by floods; however, cumulative impacts from many small diversions can be great. In contrast, dry-season flow rates have increased (while flood peaks have been dampened) on some rivers that have their flows regulated by dams. Dry-season flows also have increased on some rivers that receive effluent.

Stream diversion and groundwater pumping from riparian and/or regional aquifers have contributed to decreased flow rate, increased flow intermittency and reduced groundwater levels on many rivers in the hot deserts of south-western United States. For example, groundwater pumping along the San Pedro River has converted some perennial segments to intermittent. The depth to saturated soil (averaged across the floodplain) at intermittent sites on the upper San

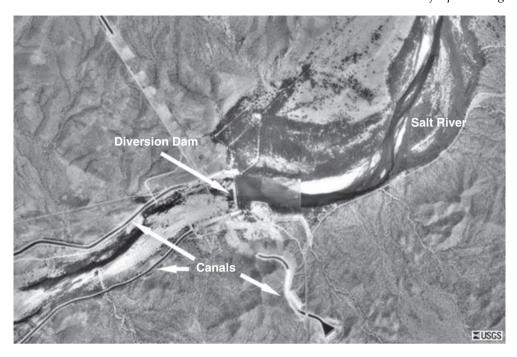


Fig. 3 Granite Reef diversion dam along Arizona's Salt River. Stream flows are diverted from the river into canals for delivery to the Phoenix metropolitan area. Photo source is the United States Geological Survey.

Pedro can be more than 4 m during the summer dry season, with intra-annual variation of >1 m, compared with mean depths of <2 m and intra-annual fluctuation of <0.3 m at some perennial sites (Stromberg *et al.*, 2006). Much greater extremes of water depletion have occurred on other rivers. Along the Gila River, for example, some sites that once supported riparian marshlands (Hendrickson & Minckley, 1984) now have depth to groundwater in excess of 50 m (Judd *et al.*, 1971).

One of the first plant groups to respond to declines in stream flow permanence and groundwater depth are the shallow-rooted wetland herbaceous plants that grow in saturated soils or shallow water. Along the San Pedro River, *Schoenoplectus acutus*, *Juncus torreyi*, smooth horsetail (*Equisetum laevigatum* A. Braun) and various species of spikerush (e.g. *Eleocharis montevidensis* Kunth) were among the plants restricted to reaches with perennial flow or that declined sharply in cover as flows became intermittent (Stromberg *et al.*, 2005). With increasing flow intermittency, these wetland perennial herbs were replaced by mesic species including the introduced bermuda grass [*Cynodon dactylon* (L.) Pers.]. In general, as saturated, marshy conditions along

stream channels have given way to intermittent flow conditions, assemblages of Sonoran riverine marshland species have shifted to those vegetated largely by introduced species including *C. dactylon* and white sweet clover (*Melilotus alba* Medikus). Immigrant species of mesic affinity are abundant in desert river corridors (perhaps reflecting the long historical usage of such areas for irrigated agriculture and livestock grazing) and now contribute to the core south-western riparian flora (McLaughlin, 2004).

Within the floodplain forests, as well, there are shifts in species composition from wetland species to more drought tolerant species as stream flow becomes more intermittent and groundwater level declines (Fig. 5). Whereas *P. fremontii* and *S. gooddingii* decreased in abundance along spatial gradients of stream flow intermittency and groundwater depth and fluctuation along the San Pedro River, *Tamarix ramosissima* Ledeb. (an introduced species) increased in abundance (Lite & Stromberg, 2005). Specific hydrologic thresholds were identified at which this shift in species dominance occurred. Similar patterns for *Tamarix* to be more abundant in drier locations have been documented along other rivers in the arid West (Shafroth *et al.*, 2000; Cooper, Andersen & Chimner, 2003b).



Fig. 4 Vegetation in the dewatered Agua Fria river bed (central Arizona) (top), downstream of New Waddell diversion dam (bottom).

The compositional vegetation shift from Populus and Salix to Tamarix along hydrologic gradients is a result of differences in tolerance ranges and competitive abilities. Tamarix ramosissima has deeper roots and is more of a facultative phreatophyte, and through various morphological and physiological



Fig. 5 Reaches along the San Pedro River with perennial (top) and intermittent (middle and bottom) flow.

adaptations tolerates drought stress and deep and declining water tables (Busch et al., 1992; Busch & Smith, 1995; Horton & Clark, 2001; Horton et al., 2001a,b; Vandersande, Glenn & Walworth, 2001; Glenn & Nagler, 2005). Populus fremontii and other Populus and Salix species throughout western United States, in contrast, are more sensitive to such changes, and have declined in abundance or age-class diversity as stream and groundwater has been diverted and pumped, and streams in general dewatered (Rood et al., 1995; Scott et al., 1999; Amlin & Rood, 2003; Rood, Braatne & Hughes, 2003b). At the wet end of the hydrologic gradient, forest composition appears to be structured by the competitive reduction of *Tamarix* by Populus and Salix (Sher, Marshall & Gilbert, 2000; Sher, Marshall & Taylor, 2002; Sher & Marshall, 2003).

With even greater groundwater decline, deeprooted and facultatively phreatophtic trees such as *Tamarix* spp. are replaced by short, xerophytic shrubs. Over time, along the increasingly dewatered Salt River in Phoenix, *Tamarix* patches initially replaced mixed *Populus* and *Salix* forests but then the *Tamarix* died as water tables declined below about 10 m (Graf, 1982). These dewatered areas now are sparsely vegetated by short (<1 m tall) shrubs such as *Bebbia* sp. *Prosopis velutina* forests died along the Gila River as water tables dropped at a rate of 1 m year⁻¹, from 13 to 33 m (Judd *et al.*, 1971), and today these former riparian sites are sparsely vegetated by small desert shrubs.

Low availability of resources can limit diversity (Grime, 1973; Huston, 1979; Pollock, Naiman & Hanley, 1998), and water frequently is a limiting resource in riparian zones of arid and semi-arid regions (Rood et al., 2003b). Over the length of the San Pedro River, woody species diversity decreased among sites as flows became more intermittent. Herbaceous species diversity in the floodplain, measured during the summer dry season of a dry year, decreased among sites as flows became more intermittent and groundwater deepened; perennial species, in particular, showed strong correlations with hydrological characteristics at the sites (Lite et al., 2005). In the low-flow channel zone, herbaceous plant species diversity during the summer dry season declined along a spatial gradient of flow intermittency, averaging about one species per square meter at sites where stream flow was present <50% of the days of the year compared with about four species per square meter where flow was perennial (Fig. 6; Stromberg *et al.*, 2005). During the summer wet season, herbaceous species diversity in the channel and floodplain remained high even at intermittent sites, because of the uniform presence of summer rains and floods across sites.

Landscape patch structure becomes simplified as streams are dewatered. This phenomenon has not been widely investigated for desert rivers, and of course varies depending upon how one defines a patch; however, studies on the San Pedro indicated that fewer patch types were present in the drier reaches (Fig. 7). At the perennial-flow sites, conditions are suitable for patches dominated by wetland tree species (*Populus, Salix*) and wetland shrubs (*Salix exigua, Baccharis salicifolia*) as well as by more drought-tolerant and deeper-rooted species (*Hymenoclea, Tamarix, Prosopis*), creating a rich mosaic of vegetation

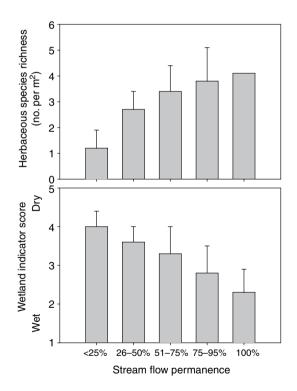


Fig. 6 Species richness and wetland indicator values of herbaceous vegetation on banks and bars of the San Pedro River lowflow channel, as measured during early summer, in relation to annual stream flow permanence (per cent of days in the year in which surface flow is present). The wetland indicator score is a weighted average; a value of 5 indicates predominance of upland species and a value of 1 indicates predominance of obligate wetland species. Values shown are means (plus standard error bars) for five to 29 sites per stream flow class.

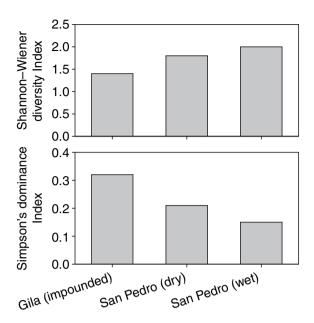


Fig. 7 Patch type diversity and dominance within three river reaches. The two reaches of the San Pedro River are undammed but vary in the degree of stream flow intermittency; dry reaches had <70% flow permanence and wet reaches had >70% flow permanence. The reach of the Gila River is downstream of Coolidge Dam, and just downstream of the confluence with the San Pedro. Values shown are means of six to 10 sites per reach. The diversity and dominance indices were calculated based on the area of the floodplain covered by each of 10 patch types that differed in physiognomy, woody species composition, or age class (open, grassland, dry shrubland, wet shrubland, *Prosopis* shrubland/woodland, young and mature *Tamarix* shrubland/woodland, and young, mature, and old mixed *Populus* and *Salix* forest).

structure types. The wetland forest and shrubland patches become sparse to absent in drier river sections, leaving the floodplains dominated by patches supporting deeper-rooted and drought-tolerant species and resulting in a reduction in the total number of patch types (Fig. 8).

Where anthropogenic actions lead to consistent increases in low flow rates, riparian vegetation can increase in abundance. In some reaches of the flow-regulated but undiverted Bill Williams River (western Arizona), for example, summer dry-season flow rates have increased and intra-annual water table fluctuation has decreased. These changes may be contributing to higher survivorship of *Populus* and *Salix* seedlings on the Bill Williams River (Shafroth *et al.*, 2002a). Summer flows also frequently are increased on the Gila River below Coolidge Dam in central Arizona, because flows are stored in San Carlos Reservoir

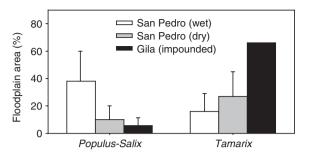


Fig. 8 Relative abundance of patches dominated by mixed *Populus* and *Salix* or *Tamarix* forest within the floodplains of two rivers of central Arizona's Sonoran Desert. The San Pedro River is undammed, but reaches vary in the degree of stream flow intermittency; reaches were classified into wet (>70% flow permanence) and dry (<70% flow permanence) categories. The reach of the Gila River sampled is below Coolidge Dam, just downstream of the confluence with the San Pedro. Values shown are means (and standard errors) of six to 10 sites per reach.

during winter and spring and released for irrigation throughout summer for irrigation by downstream users. However, on this river, survivorship of *Populus* and *Salix* have been low because in some years the growing-season flows have ceased when water users depleted the water upstream and managers held water in San Carlos Reservoir to maintain a minimum pool.

Changes to flood hydrographs

Flood patterns on south-western rivers in the United States are non-stationary, reflecting the highly variable climate. In addition to changing with climate, flood hydrographs also are influenced by land use and vegetation changes throughout catchments and by dam construction and operation. Increasing urbanisation of catchments can lead to increased flood peaks, by increasing the area of impervious surfaces (White & Greer, 2006). Overgrazing, timber harvest, and vegetation shifts in catchments also can result in increased flood magnitude as well as increased sediment transport from the uplands (Cowley, 2006).

Increases in flood magnitude can lead to changes in riparian vegetation area and vegetation type. The area occupied by riparian vegetation doubled along one stream in California, because of urbanisation-linked increases in flood size, in conjunction with increased flow rates from water importation for municipal use (White & Greer, 2006). In the upper reaches of the San Pedro River, the marshlands and grasslands that predominated in the 19th century were replaced in

large part by mixed Populus and Salix woodlands in the 20th century, because of a complex set of changes that appear to have included flood intensification (Hastings, 1959; Hendrickson & Minckley, 1984; Hereford, 1993). Historic overgrazing in the uplands contributed to the replacement of densely vegetated areas (grasslands) by more sparsely vegetated types (desert scrub) that have lower rates of infiltration and higher rates of surface run-off (Miller et al., 2002). These and other changes (e.g. timber harvest), in conjunction with weather extremes, may have contributed to the high flood intensities that caused extreme channel incision in the late 1800s and early 1900s. High scouring forces and sediment loads in the newly incised channel, in conjunction with lowered water tables, favoured the establishment of the pioneer tree species.

Dam operation generally has resulted in reduced flow extremes, although the specific pattern of flood flow alteration varies on many factors including the size and purpose of the dam (e.g. water supply, flood control, hydropower generation, reservoir recreation) (Poff & Hart, 2002). Thus, biological outcomes of river damming vary widely. Biotic changes also vary depending on the geomorphic setting of the impounded river and on interactions with other environmental changes such as flow diversion or groundwater pumping. When discussing river regulation, it is important to note that dams alter many facets of rivers besides the flow regime, including channel morphology and patterns of sediment and nutrient flow, and to note that many dams in western United States are relatively young (many only 50 years old or less; Graf, 1999) with their downstream ecological effects still unfolding (Katz, Friedman & Beatty, 2005).

One product of reduction in flood magnitude or frequency, when not accompanied by flow diversion, is increased density of riparian vegetation. In the narrow, Grand Canyon reach of the Colorado River, marsh plants and woody vegetation have established on sites formerly scoured by the once powerful river flows (Stevens *et al.*, 1995). Density of riparian forests also has increased along the Bill Williams River since closure of Alamo Dam (Shafroth *et al.*, 2002a). Flows at Alamo Dam are managed primarily to reduce the intensity of flood peaks into the Colorado River and secondarily to meet recreational needs in the reservoir while maintaining summer base-flows to sustain riparian forests. Upstream of the dam, the high

magnitude and frequency of flooding maintain a more open floodplain.

Other common effects of flood flow alteration on impounded rivers are changes in composition and age structure of the riparian forests. Reduced frequency of large floods, suppression of spring flooding, and rapid decline of flood waters have contributed to reduced rates of recruitment of *Populus* (and *Salix*) along many dammed western rivers including the Salt in Arizona (Fenner, Brady & Patton, 1985), Rio Grande in New Mexico (Howe & Knopf, 1991), Truckee in Nevada (Rood et al., 2003a), Boulder Creek in Colorado (Auble et al., 1997), and the St Mary and other rivers in Canada's western prairie region (Rood & Heinze-Milne, 1989; Rood & Mahoney, 1990; Rood et al., 1995). Increases in salinity of riparian soils, a byproduct of flood suppression (as well as of irrigated floodplain agriculture), also contributes to stress and mortality of Populus and Salix (Shafroth, Friedman & Ischinger, 1995; Pataki et al., 2005). Changes in channel morphology and dynamics relating to interactions of altered flood and sediment transport patterns, sometimes in conjunction with intentional river channelisation, are implicated with declines of Populus forests in some reaches below dams (Auble et al., 1997; Merritt & Cooper, 2000). On some regulated rivers, Populus has increased in abundance, which may be a short-term response followed by succession to late-seral stages (Johnson, 1994, 1998, 2000; Miller et al., 1995; Friedman et al., 1998).

The degree of change in Populus and Salix abundance and age structure parallels the degree of change in the flood hydrograph, as exemplified by a case study of the Verde River in central Arizona. The two major dams and reservoirs on the Verde are managed to supply water to users in the downstream Phoenix metropolitan area. The total flow volume is not altered, but typical of many rivers (Richter et al., 1996) dam operation has decreased average peak flow rate, flood frequency, and variability of some flow components, and shifted the timing of flow maxima and minima. Compared with some western rivers, the Verde reservoirs have a low storage to runoff ratio. Although small floods are captured in the reservoirs, large floods still occur in very wet years in which the reservoir capacity is exceeded, allowing for periodic channel movement, sediment redistribution, and Populus and Salix regeneration. During the wet winter of 1995, for example, reservoir spills during March and April were largely unmodified (i.e. largely run-of-the-river), and *Populus* and *Salix* established at about equal densities above and below the dam (Beauchamp, 2004). Tree recruitment during wet years also has been observed on other regulated rivers in the region (Zamora-Arroyo *et al.*, 2001). Smaller-scale recruitment events, associated with smaller floods, are likely to be pre-empted along such rivers.

While Populus and Salix have declined in density or age class diversity on some flow-regulated rivers, Tamarix has increased (Shafroth et al., 2002a; Cooper et al., 2003b). Several life-history traits T. ramosissima to thrive in areas where human actions have altered the flood hydrograph. Like P. fremontii and S. gooddingii, T. ramosissima is a pioneer species that produces many small wind- and water-dispersed seeds and requires bare, mineral soils for seedling establishment. It thus establishes in open, disturbed areas and, like Populus and Salix, may have increased on some rivers in response to increased flood disturbance following land use changes. It is more reproductively opportunistic than the two Salicaceae, with viable seeds present over most of the growing season, and thus also can establish in reaches where flood timing deviates from the climatic norm.

The Verde River case study is illustrative of the ways in which changes in the flood hydrograph below dams can lead to increases in T. ramosissima. On this river, subtle alterations to the timing of water flows during potential recruitment years appear to explain the establishment success of T. ramosissima in the reach below the dam (Beauchamp, 2004). Above, the winter floods during one recruitment year were followed by low summer flows, which is the typical pattern for the free-flowing Verde. Tamarix seedlings were sparse above the dam, probably because the earlier seeding Populus and Salix occupied the available germination space. Below the dam, flows were elevated during early summer by in-channel delivery of irrigation water. This release was stopped at the end of June, exposing moist, bare sediment at a time when Tamarix was at its peak seed dispersal. The absence of late-summer monsoon flood peaks below the dam may have further contributed to high Tamarix densities by reducing seedling mortality rates (Levine & Stromberg, 2001).

River impoundment and partial stream diversion, in concert, can lead to near complete dominance of the

floodplain vegetation by *Tamarix*. Along portions of the Gila River below Coolidge Dam, *Tamarix* patches dominate the floodplain and patches of *Populus* and *Salix* are rare (Fig. 8). Here, the shift to *Tamarix* is likely to reflect the combination of altered flood hydrographs, increased water stress associated with seasonal water diversions, and altered channel morphology deriving from steady summer water deliveries during average and wet years (Graf, Stromberg & Valentine, 2002).

Altered flood hydrographs also can change species diversity patterns. This can occur through direct and indirect effects, with both being context-dependent. Reduced flood magnitude associated with river damming can allow for increased plant species diversity in canyon reaches, by reducing scour, but may reduce diversity in less-constrained settings where lack of flooding reduces heterogeneity. The increased tree density and canopy cover that develop in some flood-suppressed reaches may decrease diversity in the ground-cover layer, although such effects may vary depending on season and the degree of heat and drought stress at the site (Schade *et al.*, 2003; Lite *et al.*, 2005).

Even where the flood hydrograph is not altered, dam-related changes in the erosive potential of flood waters can lead to changes in the herbaceous plant community. Sediments on rivers in the desert southwest of the United States typically are coarse, with high sand content (Bagstad et al., 2005), and become more depauperate in silts and clays in reaches below dams. Where sediments are trapped in reservoirs, periodic release of large, clear flood waters can increase the erosion of fine sediments in the reaches below dams (Graf, 2000; Owens et al., 2005). Siltshadows can extend for many kilometres downstream of dams (Phillips, Slattery & Musselman, 2004), with cascading effects on nutrient retention in riparian soils and herbaceous plant growth. Returning to the Verde River, again, there is evidence that the coarse floodplain soils below the dams have insufficient water and nutrient holding capacity to sustain a diverse herbaceous understory (Beauchamp, Stromberg & Stutz, 2007).

Flood waters play an important role in seed dispersal of riparian plants (Merritt & Wohl, 2002; Boedeltje *et al.*, 2004; Jansson *et al.*, 2005). Although many of the riparian plant species in the Sonoran Desert show adaptations for dispersal by wind or

animals, transport in flood waters may be a common secondary dispersal mechanism (Drezner, Fall & Stromberg, 2001). Impeded flood-borne dispersal of seeds by dams thus may alter plant species distribution patterns and species diversity levels as has been observed on some rivers elsewhere (Jansson, Nilsson & Renöfält, 2000; Nilsson *et al.*, 2002), and is a topic in need of study.

Riparian restoration

River and riparian restoration efforts are being undertaken throughout the world for many reasons, among them to counteract the loss of floodplain forests, create habitat for endangered species, improve water quality and increase water supply (Hughes & Rood, 2003; Bernhardt et al., 2005; Galatowitsch & Richardson, 2005; Parkyn et al., 2005; Watanabe et al., 2005). Although water and power supply remain the key drivers of river management in south-western United States, many riparian restoration efforts are underway in this region as well (Goodwin, Hawkins & Kershner, 1997). One impetus for these regional efforts is to create habitat for endangered species, including the south-western willow flycatcher, Empidonax traillii extimus (Phillips), and other birds that depend on riparian habitat (Kus, 1998; Cohn, 2001; Graf, 2001; Boucher et al., 2003). Other projects aim to restore riparian ecosystem functions such as flood flow attenuation and water purification (Cobourn, 2006). Some are undertaken to increase amenities and economic growth by resurrecting degraded riparian corridors in urban areas. Yet other projects have the goal of increasing water supply by reducing abundance of introduced phreatophytic trees (Hart et al., 2005).

In addition to differing widely in goals, riparian restoration projects differ widely in conceptual approaches and costs. Some are based on the premise that restoration of physical river processes is paramount, and that biotic recovery will follow hydrologic and geomorphological restoration (Ward *et al.*, 2001); others involve direct manipulations of the vegetation (planting and weeding) and emphasise restoration of riparian vegetation structure over river flow and geomorphological processes. Implementation costs range from a few thousand dollars per river mile to several million dollars per river mile (Stromberg, 2001).

Restoration of flood flows

Some efforts to restore flood hydrographs of rivers in the desert southwest of the United States to presettlement conditions have addressed hydrologic processes throughout the catchment. To reverse the process of arroyo cutting and rapid run-off of water from the uplands, hundreds of small check-dams have been installed on ephemeral streams of some catchments in Arizona and New Mexico. Some of these efforts have reconnected the channels of these ephemeral streams to alluvial fans and increased the frequency of overbank flow during small floods (Norton et al., 2002). Monitoring of the larger rivers into which the tributaries feed will be necessary to determine whether such actions render flow regimes less 'flashy' by decreasing overland run-off rates and increasing infiltration into and percolation through the aguifer.

While check dams are being installed on tributaries, larger dams are increasingly being considered for removal (Pohl, 2002). Dam removal is an ecological restoration strategy that requires consideration of costs and benefits on a case by case basis. Although dam removal will restore the flood flows that drive riparian patch dynamics, it also can release large slugs of sediment and destroy the biotic communities that have developed in association with the dam site (Johnson, 2002; Shafroth et al., 2002b). Thus, in some cases the decision is made to leave a dam in place or simply to lower it. For example, the Fossil Creek hydroelectric facility, located along a small montane stream in the central mountains of Arizona, was recently decommissioned. In June 2005, the stream diversion ceased, restoring full flows to the river. The diversion dam itself remains in place, but is slated to be lowered by several feet in 2007, at which time researchers will monitor the ecological response to sediment redistribution.

More common than dam removal in the south-western United States is modification of the hydrological regime on dammed rivers to address environmental flow needs (Molles *et al.*, 1998; Patten & Stevens, 2001; Stevens *et al.*, 2001; Rood *et al.*, 2003a). For example, Alamo Dam on the Bill Williams River has been managed for small floods in wet years to meet the recruitment needs of *Populus* in the downstream National Wildlife Refuge (Shafroth *et al.*, 1998). This river is one of several within the

Sustainable Rivers Project, a nationwide collaborative effort of The Nature Conservancy and the U.S. Army Corps of Engineers. Recent discussions and workshops have focused on the complexities of meeting the flow needs of all the 'users'. Although one goal is to restore the flow regime to sustain river biota below the dam, flow needs of other uses, including human recreation by the reservoir, have at times trumped those of the Bill Williams riparian ecosystem. Flood pulses also have been released into the Truckee River in Nevada (Rood et al., 2003a). Here, floods initially were released to restore habitat for an endangered species of fish, which, like some other fish species in the arid Southwest, have high reproductive success in years with large winter floods and high spring flows (Brouder, 2001). The floods also triggered establishment of Populus, providing an example of a multispecies response to a hydrological approach to river restoration. Experimental floods have inundated riparian forests along the Rio Grande, in New Mexico, revealing the importance of such events to ecosystem processes such as organic matter decomposition (Molles et al., 1998). Some of these regional flood restoration efforts have been short-term and experimental; others, such as those on the Grand Canyon reach of the Colorado River (Meretsky, Wegner & Stevens, 2000), represent legally mandated, long-term adaptive management efforts.

Also becoming common are attempts to simulate high-flow events on fallow farm fields or cleared land parcels that have been disconnected from the river as a result of channelisation or river regulation. For example, taking advantage of agricultural infrastructure, water has been transported through delivery channels to restoration sites at the appropriate times of the year to trigger seedling establishment of Populus, Salix and other woody riparian plants (Taylor & McDaniel, 1998). Many efforts have been successful at establishing the target species, but research is on-going to fine-tune knowledge of issues such as the effect of water drawdown rate on seedling survivorship (Sprenger, Smith & Taylor, 2002). Actions also have been undertaken along impounded and channelised urban streams to simulate conditions for *Populus* establishment by first creating physical disturbance (i.e. mimicking some of the geomorphic effects of a large flood) followed by irrigation (i.e. mimicking some of the hydrologic effects of a flood). Given such conditions, Friedman, Scott & Lewis (1995) concluded that Populus could establish by natural seed-fall, which would serve to conserve the genetic structure of the local population.

Most flood-related efforts to restore riparian vegetation in the south-western United States have focused on increasing population size of pioneer trees; fewer have focused on the herbaceous vegetation or on community-level attributes such as plant species diversity. It would be worthwhile to determine experimentally whether herbaceous cover and species diversity could be increased by restoring the high-frequency flood events (i.e. annual summer floods) that routinely are captured by reservoir storage. It also would be worthwhile to experiment with the restoration of sediment transport (as sediments now accumulate in reservoirs) in conjunction with flood pulses to below-dam reaches of sedimentdepleted rivers, as has been attempted in some wetland ecosystems (Mendelssohn & Kuhn, 2003). Such measures may have cascading effects on consumers, if, for example, bird populations increase following the herbaceous vegetation increase (Krueper, Bart & Rich, 2003).

Restoration of low flows

Although water supplies are in short supply in much of western United States, a few riparian restoration projects have focussed on the low-flow period of the hydrological regime. On some rivers, riparian vegetation has been accidentally restored by the release of municipal effluent to dewatered river channels (Stromberg et al., 2004). However, there is no guarantee that the effluent will remain in the channel and not be diverted for other uses in the future. Questions also persist about the degree to which nutrient-enriched water facilitates the formation of biofilms that impede water flow from the stream channel to the aquifer (Commission on Geosciences, Environment and Resources, 1994), thereby preventing the stream flow from supporting riparian vegetation that depends on shallow groundwater in the riparian aquifer. Additionally, although effluent discharge may increase biological diversity and productivity along the channel, it may not result in long-term survivorship of phreatophytes in the floodplain if the riparian aquifer has been disconnected from surface flow as a result of severe, long-term dewatering.

In other cases, land and water have been purchased (or water rights reclaimed) specifically for conserva-

tion efforts. Notable examples include the return of stream flows to Rush Creek and other dewatered rivers in California, based on Public Trust Doctrine (Hill & Platts, 1998; Policansky, 1998). Another example can be found on Arizona's San Pedro River, where an active conservation community is working to restore riparian ecosystems by managing the hydrologic regime. The Arizona Nature Conservancy, U.S. Bureau of Reclamation (a federal water supply and hydropower generation agency), and Salt River Project (a local water supply and power generation entity) have purchased floodplain and terrace land along the river, and reduced agricultural water use, partly as mitigation for loss of south-western willow flycatcher habitat on other rivers (Haney, 2005). Revegetation is expected to occur naturally on this unimpounded river. Populus, Salix, Baccharis and other pioneer species will establish following floods, and should survive in formerly dry reaches given the higher stream flows and shallower groundwater. Many herbaceous species also will re-establish, with some being dispersed in flood waters and others emerging from persistent soil seed banks that are present even in dry reaches (Boudell, 2004). Costs are low because active measures such as tree planting, earth moving, and irrigation are not necessary. Longterm monitoring has been initiated, and will provide critical feedback on rates and patterns of change.

Opportunities exist on many other rivers to simultaneously restore riparian habitat and provide goods and services to humans. On the Colorado River, for example, water to restore base flows to the delta could be purchased at relatively small cost; by one estimate, the delta could be rewatered by redistributing only one percent of the water allocated in the Colorado River and thus retaining most agricultural and municipal uses of the river water (Pitt, 2001). A feasibility study on Arizona's Agua Fria River showed that restoration of riparian habitat and recharge of groundwater for subsequent municipal use do not have to be mutually exclusive exercises; rather than being stored in a reservoir, water could be released into the natural river bed and thus transported to downstream groundwater recharge sites without any net increase in evaporative water loss (Springer et al., 1999). Opportunities also exist to combine riparian habitat restoration with agricultural uses of water and land. For example, the practice of establishing hedgerows could be resurrected by allowing riparian trees and shrubs to establish and survive along unlined irrigation canals.

Tree planting

For many years, riparian restoration in the south-west of the Unites States was synonymous with tree planting. Some of the early efforts to establish riparian forests by planting 'pole cuttings' were met with failure, because of inappropriate physical conditions (e.g. deep water tables, high salinity) to sustain the plants (Anderson & Ohmart, 1985; Anderson, 1989). Monitoring of tree planting projects revealed that survivorship was high only where the root causes of the low tree density at the outset were addressed or where stream flows and geomorphology had not been altered (Briggs, Roundy & Shaw, 1994). A recent example of a successful tree-planting project is one that was implemented along the Gila River in New Mexico. To reverse environmental changes caused by overgrazing, the river banks were excavated to the level of the river and planted with riparian trees. Together with cessation of livestock grazing, these actions created, for example, nesting habitat for willow flycatcher (Boucher et al., 2003).

Planting of pole cuttings and nursery stock of Populus and Salix and other tree and shrub species remains a key element of many restoration projects, particularly those implemented along rivers that are heavily modified for urban or agricultural purposes, which is where societal conflicts over restoration of flow regimes often arise (Alpert, Griggs & Peterson, 1999). By planting the disturbance-dependent species that historically occurred in the riparian corridor, one can bypass the need to restore the fluvial processes that would create the seed beds, and by maintaining trees on irrigation one can bypass the need to recharge the aguifers to levels that will moisten the rhizospheres. An example can be found along the Salt River in the Phoenix metropolitan area, Arizona, the site of several federally funded urban riparian restoration projects. Here, the occasional surface flows released from the upstream diversion dam are no longer hydraulically connected to the deepened (and contaminated) groundwater table in all reaches. Upstream diversion and flow-regulating dams create barriers to the flow of fine sediments, seeds and other materials; channelisation has disconnected the river from most of its historic floodplain; and many

tributary-mainstem connections have been severed (Graf, 1982, 2000). Actions are not being undertaken to reverse these changes. Rather, localised oases of wetland and riparian habitat are being created by transporting pumped groundwater via delivery channels to sustain trees planted at the termini of irrigation lines, and by re-shaping the land surface to create ponds and perched aquifers. Another example is the multi-million dollar Lower Colorado Multi-Species Conservation Plan. Among other tasks, this plan calls for planting and 50-year maintenance of >2800 ha of riparian forest (mixed Populus and Salix or Prosopis) on the highly regulated Colorado River from Lake Mead (below Hoover Dam) to the international border with Mexico, to create breeding habitat for rare and endangered bird species that depend on riparian habitat (USBR, 2005).

Although tree-planting actions may restore a small number of plant species and age classes to highly regulated rivers, they do not address long-term vegetation dynamics and may not restore species diversity or landscape heterogeneity to preimpact levels. Re-vegetated sites along the Lower Colorado River, for example, did not have sufficient plant species diversity to sustain diverse butterfly assemblages (Nelson & Andersen, 1999). Bird species such as the south-western willow flycatcher, that depend on continuing formation of young riparian forest patches to provide nesting habitat, will not be favoured by such projects unless tree planting is staggered over time (Paradzick & Woodward, 2003). Such projects also do not restore other functions that are carried out by flood pulses on natural river courses. This includes decomposition of organic matter, removal of the woody debris that can increase fire-risk, and flushing of salts that concentrate in arid landscapes.

Tree removal

Another common practice undertaken putatively to restore riparian ecosystems in south-western United States is removal of *Tamarix*. *Tamarix ramosissima* (or the closely related *T. chinensis* Lour. or a hybrid thereof; Gaskin & Schaal, 2002) has been present in south-western United States for over a century (Horton, 1964), having been introduced for soil erosion control and landscaping purposes. *Tamarix* has naturalised, and is now one of the most wide-

spread and abundant woody species in riparian zones (Robinson, 1965; Harris, 1966; Friedman *et al.*, 2005). Aerial and ground herbicide spraying, bulldozing, root-ploughing, burning and biocontrol insects all have been used to control its spread and dominance (Taylor & McDaniel, 1998; McDaniel & Taylor, 2003; Quimby *et al.*, 2003; Dudley & DeLoach, 2004; Hart *et al.*, 2005; Shafroth *et al.*, 2005). Recently, federal legislation was enacted (Salt Cedar and Russian Olive Control Demonstration Act) that could intensify these efforts.

These projects have been undertaken based on the assumption that *Tamarix* is a prime cause of riparian ecosystem degradation. Many review articles have stated that Tamarix alters physical processes (e.g. reducing stream flows and increasing soil salinities) and adversely affects biota (e.g. reducing species diversity or displacing local species) (Brock, 1994; Walker & Smith, 1997; di Tomaso, 1998; Zavaleta, 2000). However, some of these conclusions about Tamarix's role in the ecosystem were based on early studies with suspect methodologies (in the case of evapotranspiration rates and stream dewatering) or on propogation in the literature of poorly documented statements (in the case of soil salinisation and biodiversity change). Some arose from confusion over cause and effect (with respect to species and site conditions). Recent studies suggest that Tamarix does not differ greatly from local riparian trees and shrubs with respect to evapotranspiration (Glenn & Nagler, 2005; Nagler et al., 2005) and soil salinisation (Stromberg, 1998; Bagstad, Lite & Stromberg, 2006; Ladenburger et al., 2006). Biotic changes attributed to Tamarix, including reduced diversity or growth of herbaceous understory, were not apparent on an unimpounded river (Stromberg, 1998; Bagstad et al., 2006) or in a greenhouse experiment (Lesica & DeLuca, 2004), suggesting that some underlying factor may be driving the changes in both the diversity decline and Tamarix increase. The shift from mixed Populus and Salix forests to Tamarisk that has occurred along some river reaches is not so much a displacement of one set of species by another as a replacement in response to shifting environmental conditions (Anderson, 1996; Sher et al., 2000; Horton et al., 2001a,b; Lesica & Miles, 2001; Sher et al., 2002; Sher & Marshall, 2003; Lite & Stromberg, 2005).

Within some river types and regions, *Tamarix* dominance appears to be a symptom, rather than a

prime cause, of riparian ecosystem degradation (MacDougall & Turkington, 2005). Apparently it is not simply the presence of the *Tamarix* that causes change in the plant and animal biota (e.g. Fleishman et al., 2003), rather it is the loss of tall, productive tree species such as Populus and Salix and loss of the habitat heterogeneity that can follow from flood suppression, stream dewatering and other physical changes. Apparently it is not the presence of Tamarix that causes inordinate drops in stream water level or increase in floodplain soil salinity, rather it is the tendency for Tamarix to dominate at sites that have become dry or salty as a result of water abstraction or flood suppression. Interactions between site and species may occur, with, for example, Tamarix potentially increasing surface soil salinities at sites with saline groundwater, or evapotranspiration rates being high in the very dense Tamarix stands that can develop on impounded rivers, but the situation is not as clear-cut as many once suspected.

In addition to removing plant species labelled as 'invasive exotics' [i.e. recently introduced species that spread rapidly and are perceived as causing undesirable change (Richardson et al., 2000)], some restoration plans call for removing all species, native and exotic alike, that were not present in the ecosystem at some designated point in time. Approaches that constrain one to an approved selection of species ignore the intrinsically open nature of ecosystems, in which species immigration and emigration are ongoing processes (Odum, 1971; Tredici, 2004). Restoration efforts that emphasise plant species removal run two risks: first, because the 'target' species may be less well adapted to the current conditions than the introduced species, they may be less likely to sustain themselves over the long term. Reductions in the species pool can reduce the resistance of the ecosystem to future environmental changes, as outlined in the 'insurance hypothesis' (Allison, 2004). Secondly, if the root causes of the riparian vegetation change are not addressed, restoration goals may not be met. For example, riparian management efforts that focus strictly on *Tamarix* eradication may destroy nesting habitat for birds while failing to replace it with equivalent habitat (Taylor & McDaniel, 2004; Harms & Hiebert, 2006). In some cases, the root cause of the vegetation change may have been some historic land or water use that has since ceased (e.g. Everitt, 1998), thereby increasing the likelihood that the species-removal approach will achieve the restoration goals.

Flow restoration and modelling

Quantitative models that link plant species establishment requirements and tolerance ranges with site hydrology are useful for planning restoration projects, because they allow one to simulate the effects of stream flow and groundwater alterations on riparian vegetation dynamics. The 'recruitment box model' (Mahoney & Rood, 1998), which emphasises the importance of flood timing and rate of flow recession on Populus establishment, has proven to be a useful tool for developing flow prescriptions that favour Populus establishment along rivers in the western United States (Rood, Kalischuk & Mahoney, 1998; Rood et al., 2003a). Building on these relationships, hydraulic models have been used to explore how the flood flows that trigger Populus recruitment can be released without compromising other river services such as power generation (Bovee & Scott, 2002). The recruitment box concept can be broadened to simulate dynamics of multiple species that differ in dispersal phenology and other demographic and life-history characteristics (Shafroth et al., 1998; Horton & Clark, 2001; Amlin & Rood, 2002). Recruitment box models also can be expanded to take into account site-specific differences in groundwater dynamics (i.e. minimum groundwater levels and annual fluctuation) and effects of floods on sapling mortality, and used to simulate the effects of flood and groundwater restoration scenarios on riparian tree recruitment and survivorship.

Models that link groundwater and vegetation across larger spatial scales have been used to predict landscape-level vegetation response to hydrological changes such as reservoir operation scenarios (Rains, Mount & Larsen, 2004). Such linked groundwatervegetation models can be refined to take into account interactive effects of the newly established vegetation on groundwater levels, recognising that hydrologyvegetation interactions are bi-directional, with vegetation influencing groundwater levels through evapotranspiration (Baird, Stromberg & Maddock, 2005). Models that link vegetation, hydrology and geomorphology will further improve ability to predict restoration outcomes, by including the influence of sediment flows on riparian vegetation dynamics (Hauer & Lorang, 2004).

Conclusion

Restoration of riparian ecosystems along rivers of the semi-arid south-western United States, in the strict sense, will require restoration of longitudinal river connectivity (e.g. to allow for unimpeded flows of water, including flood pulses), lateral connectivity (e.g. to allow for overbank flooding) and vertical connectivity (e.g. to reconnect the regional aquifer with the riparian aquifer and thus restore surface water to the channel) (Boon, 1998). Some restoration projects in the south-western United States are restoring flow regimes and hydrologic connectivity, but many others still focus on planting desired trees (such as Populus) or removing those viewed as invasive (such as Tamarix). From a restoration perspective, dominance of a riparian corridor by patches of deeprooted, salt-tolerant species such as Tamarix can be viewed as an indicator of the need to restore flood regimes and increase water availability and thereby increase patch heterogeneity and species diversity and shift species composition from drought-tolerant, salt-tolerant and reproductively opportunistic species such as Tamarix towards wetland pioneer trees such as Populus and Salix. Both planting and plant-removal approaches are likely to be most effective when conducted in conjunction with efforts to restore river flow regimes and to address other regional factors that modify riparian ecosystems as livestock grazing and channel modification.

Acknowledgments

Research summarised in this paper was funded, in part, by the NSF Center for the Sustainability of semi-Arid Hydrology and Riparian Areas.

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(Manuscript accepted 8 May 2006)

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