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Influence of Hydrologic Connectivity on Plant Species Diversity Along Southwestern Rivers: Implications for Restoration

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PURPOSE: This technical note is a product of the Ecosystem Management and Restoration Research Program (EMRRP) work unit titled "Improving Restoration and Management of Stream and Riparian Ecosystems using a Multi-function Approach." The objectives of this study are to improve the Corps' ability to successfully restore structure, function, and dynamics of stream and riparian ecosystems that more closely resemble pre-disturbance conditions. Objectives to reach this goal include providing a suite of timely guidelines, principles, criteria, and design tools, and making them readily available to the field. This technical note discusses a collaborative investigation designed by Arizona State University in cooperation with the U.S. Army Engineer Research and Development Center, Vicksburg, MS.

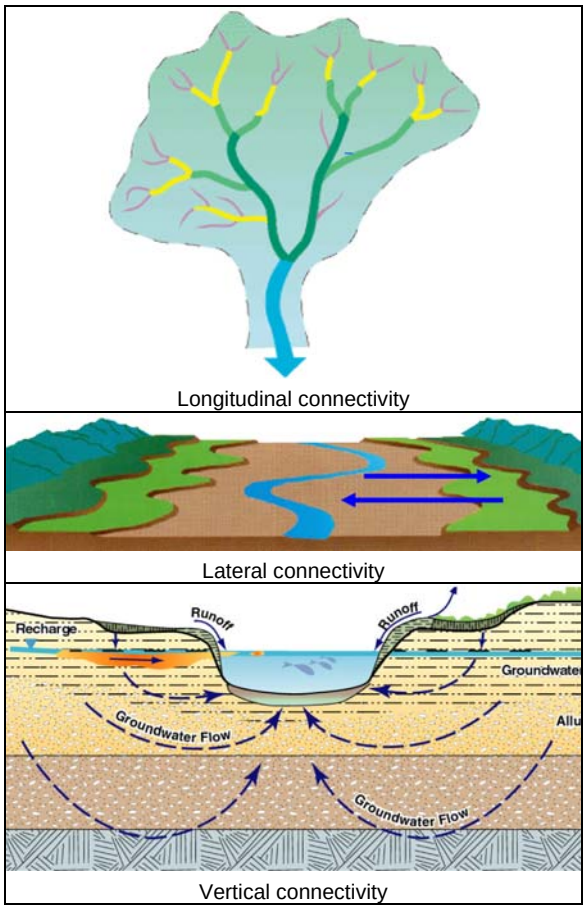

Figure 1. Examples of connectivity.

BACKGROUND: Ecosystem restoration is among the most extensive (and expensive) conservation actions practiced worldwide (Holl et al. 2003). Riparian restoration efforts, in particular, have vast spatial and economic extent (Bernhardt et al. 2005). Many of these efforts, however, have typically focused narrowly on a given piece of land or waterway, with less consideration for the landscape setting or river-wide processes (Wissmar and Beschta 1998). However, the long-term success of

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restoration efforts does depend on the landscape matrix in which a project is embedded, and on a high degree of longitudinal, lateral, and vertical connectivity between landscape elements (Boon 1998) (Figure 1). Where connectivity is high, and key fluvial processes can be restored, restoration goals are more likely to be met (Ward at el. 2001; Rood et al. 2003; Rhode et al. 2005).

The goals of riparian restoration projects vary widely, as do the approaches taken to achieve these goals. In the southwestern United States, the recovery of riparian habitat often is approached through the restoration of the historically dominant trees and shrubs. One method is to artificially recreate the vegetation structure. For example, cuttings or container-grown saplings of cottonwood (*Populus* sp.) and willow (*Salix* sp.) have been planted to re-establish populations of riparian tree species on dewatered and flow-regulated rivers. These plantings are often maintained by drip irrigation (Anderson and Ohmart 1985; Alpert et al. 1999). Other projects have made greater attempts to simulate fluvial processes (Friedman et al. 1995; Palmer et al. 2005). For example, flows have been released onto cleared fields during spring, to mimic the pattern of flood-triggered seedling establishment of pioneer tree species (Taylor and McDaniel 1998), and elevated riverbanks have been excavated to the water table level to create suitable seedbeds (Boucher et al. 2003). Still other projects have focused more directly on riverine processes and connectivity: flood pulses have been released from regulating dams in a fashion that allows the pioneer trees to establish, and groundwater flows in the stream alluvium have been increased to allow for high survivorship of obligate phreatophytic trees (Haney 2002; Rood et al. 2003). These different approaches vary in the degree to which they restore vegetation dynamics, landscape heterogeneity, and species diversity (e.g., Nelson and Andersen 1999) (Figure 2).

Figure 2. Two different approaches to riparian restoration: Tree planting and irrigation along the Salt River (left) and flood pulsing along the Bill Williams River (right). Right photo courtesy of Andrew Hautzinger.

Species diversity is an ecosystem attribute that is both a product of, and an influence on, the environment. Diversity of plant species and of functional types influences primary productivity and trophic interactions (Schmid and Hector 2004; Lecerf et al. 2005; Duffy et al. 2007). High diversity in one trophic level does not guarantee high diversity in another, but where riparian plant species are diverse, there often are high numbers of butterflies and other invertebrates that form the food base for many riparian birds and mammals (Hawkins and Porter 2003). Diversity also can influence resilience of an ecosystem (Chapin et al. 1997) in that the number and types of species present will influence how the plant community responds to press disturbances such as drought or climate change and pulse disturbances such as floods. Although some riparian and wetland restoration projects are implemented with the goal of increasing plant species diversity (Rhode et al. 2005), restored sites can remain species-poor compared to natural sites (Seabloom and van der Valk 2003).

A multi-year study was initiated in 2005 to address the role of hydrologic connectivity and landscape-scale processes on diversity of riparian plant species diversity in riparian ecosystems of the desert Southwest, and thereby provide information that can be used to improve restoration success. Differences in the landscape setting of Sonoran Desert rivers are being used to answer research questions that relate to effects on plant diversity (inclusive of that in soil seed banks) of natural variations in stream flow regimes and of cultural alterations to flow regimes. The first set of experiments involves comparisons between wet and dry reaches and between dry reaches located at varying distances from wet reaches (Figure 3). This publication presents background information on research questions and some preliminary results.

What processes maintain diversity of plant species in riparian corridors?

Although a small number of tree and shrub species provide much of the biomass structure in desert riparian zones of the American West, several hundred vascular plant species and many different plant community types can be present along the rivers (Wolden et al. 1994; Stohlgren et al. 1997; Rundel and Sturmer 1998; Makings 2006). Each river maintains its own unique set of species (Zimmerman et al. 1999), and the degree of hydrologic connectivity is one factor that influences the diversity at a given site (Bornette et al. 1998; Ward et al. 2002). Connectivity of the river to its watershed allows for inflow of seeds from riverine headwater and upland communities and also allows for runoff of water from the watershed to the river. The subsequent disturbance from river flooding creates temporal and spatial heterogeneity in the riparian corridor, which in turn allows for co-existence of species with a variety of life-history strategies and tolerance ranges. Below ground, a high degree of hydraulic connectivity allows for inflow of water from regional aquifers. This helps to sustain the high levels of resources that allow for high species diversity despite frequent and intense disturbance (Pollock et al. 1998; Bagstad et al. 2005; Sarr et al. 2005; Stromberg 2007).

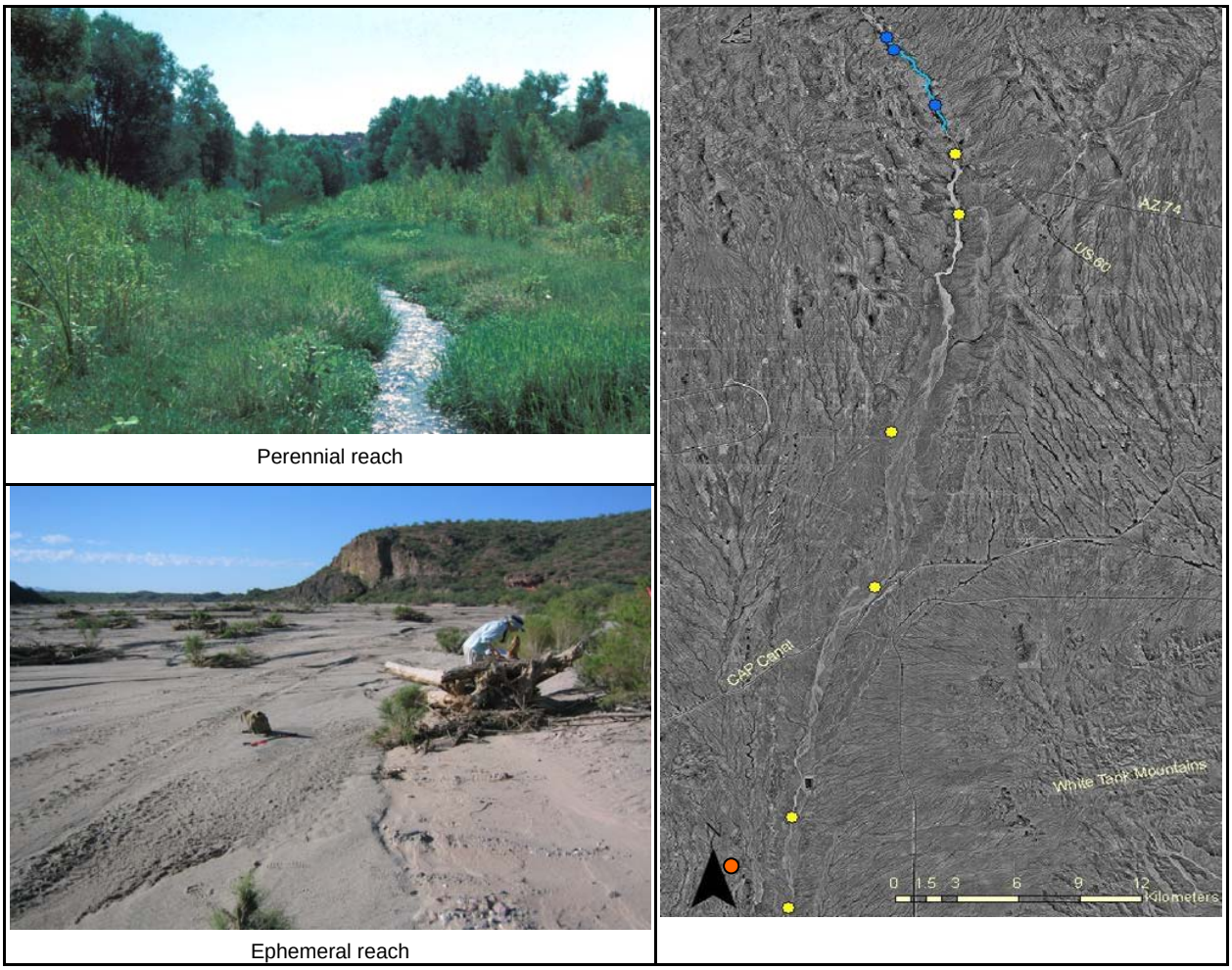

Figure 3. Location of study sites along one southwestern river, the Hassayampa. Blue line indicates perennial flow and blue dots indicate sites in the perennial reach. Yellow dots indicate sites in the downstream ephemeral reach; orange dot indicates study site on ephemeral tributary.

What factors influence seed pools in riparian zones?

Vegetation diversity is in part a product of diversity in the seed pool. Seed pools at a riparian site fluctuate over time and space depending on many processes, which can be grouped into four categories: (1) in situ production of seeds, (2) in situ storage of seeds, (3) seed dispersal within the riparian site, and (4) immigration and emigration of seeds from off-site sources. The relative importance of local seed rain, seed storage, and dispersal processes to species diversity and revegetation patterns following riparian ecosystem disturbance is an area in need of study.

(1) *In situ seed production: local seed rain*. Trees, shrubs, and some of the herbaceous perennials that grow in riparian zones have long life spans and annually contribute to the local seed rain once they reach sexual maturity. Seeds of some pioneer trees, including *Populus* and *Salix*, are viable for only a few weeks, while those of later successional species, such as mesquite (*Prosopis*

spp.), can remain viable for decades but are often eaten by animals. Other plants have a different reproductive strategy. The majority of plant species in the riparian corridors of Southwestern rivers are annuals or short-lived perennials, and many of these establish opportunistically during years when rainfall or floods create suitable conditions. Their seed set can be more episodic.

(2) *In situ seed storage: soil seed banks*. Many of these annual and short-lived perennial plants produce persistent seeds that remain dormant in the soil as a seed bank until suitable germination conditions are met. Sediment flows and animal activity can cause the seeds to be shallowly buried. These stored seeds are important as a regeneration strategy at sites with frequent disturbance and fluctuating resource levels (Finlayson et al. 1990; Hanlon et al. 1998; Abernethy and Willby 1999; Goodson et al. 2001, 2002; Richter and Stromberg 2005; Capon and Brock 2006).

(3) *Immigration of seeds:Long-distance seed dispersal*. Many plants in riparian corridors adapt for seed dispersal by water, wind, and animals (Drezner et al. 2001, Lamb and Mallik 2003). These vectors can disperse seeds to the riparian zone from the uplands and from upstream and downstream reaches and tributaries (Johansson et al. 1996; Andersson et al. 2000; Merritt and Wohl 2002; Boedeltje et al. 2003, 2004; Mouw and Alaback 2003; Renofalt et al. 2005; Tabacchi et al. 2005).

(4) *Within-site seed dispersal: Landscape heterogeneity*. Riparian landscapes consist of spatially structured plant communities, with each occupying different geomorphic surfaces. Flood waters not only transport seeds downstream (longitudinal transport) but also can disperse seeds broadly within a reach (lateral transport) to internally connect the riparian communities via a common seed bank (Boudell and Stromberg 2008). Environmental conditions in a patch can change substantially after flood scour and the presence of a diverse pool of seeds may increase the rapidity of plant community redevelopment. A high degree of topographic heterogeneity also may be important for post-disturbance recolonization. High surfaces that lie above the zone of frequent flood scour can function as spatial refugia for riparian animals (Wijnhoven et al. 2005) and may do the same for plants by providing loci for tree survivorship, ongoing seed rain, and seed storage.

How does diversity change in response to changes in stream flow regime and hydrologic connectivity?

Stream flow permanence. Many rivers in the southwestern United States are spatially intermittent, with ephemeral or intermittent flow reaches alternating with perennial flow reaches. The extent of perennial reaches has increased on some dammed and flow-regulated rivers, in association with dampening of the low-flow and high-flow extremes. On some other rivers, the extent of the seasonally dry reaches has increased as a result of diversion of stream flow, pumping of groundwater from the

stream aquifer, and basin-wide pumping that reduces connectivity between the regional and stream aquifer (Stromberg et al. 2004). Additionally, the location of perennial reaches has changed on some rivers following urbanization and associated effluent discharge.

Because diversity is in part a function of resource availability, changes in stream flow permanence of a dryland river can change plant species diversity. Along the San Pedro River in southern Arizona, for example, groundwater pumping, in concert with underlying variation in hydrogeologic conditions, has produced a spectrum from dry to wet reaches. Plant cover and species diversity on channel bars and banks were found to decrease along a spatial gradient of increasing stream flow intermittency (Stromberg et al. 2005). Composition at the drier sites shifted from hydric species to those of more xeric affinity. Diversity also was low in the floodplain of sites characterized by high stream intermittency and deep groundwater levels, but only when measured during the summer dry season (Lite et al. 2005).

Preliminary results for this study also suggest that species diversity is higher in perennial than ephemeral reaches of southwestern riparian zones, when measured during dry seasons. This pattern reflects the scarcity of hydric species at the ephemeral sites. However, this study also suggests that several hydric species are abundant in the soil seed bank of perennial and ephemeral reaches alike. Rivers of the southwestern United States, like those of other dry regions, have highly variable flood regimes characterized by cycles of drought and intense flooding. This has been colloquially termed a ‘boom and bust’ phenomenon (Bunn et al. 2006) wherein dense vegetation develops during periods of moderate water availability and flood intensity, but declines after intense drought or floods. A strategy of long-term seed persistence, with seeds lying dormant in the soil for long periods, is adaptive under such conditions.

Flood flows and river damming. Floods are destructive forces that remove vegetation, but also are regenerative forces that create opportunities for establishment of pioneer plants. They also increase riparian zone water availability on short- to long-term scales. Plant species diversity along unconstrained desert rivers typically increases after moderate river flooding but can decline if flood intensities are very high (Stromberg et al. 1993). If floods are of sufficient size and duration to wet soils and elevate surface and groundwater levels for several weeks, hydric riparian plants increase in abundance and diversity, and replenish the soil seed banks (Bagstad et al. 2005).

Preliminary results of this study indicate that large winter floods with sustained runoff create pulses of plant species diversity along channels and floodplains, with effects most pronounced in typically dry reaches. High abundance of species (of hydric to xeric affinity) in both ephemeral and perennial stream reaches of spatially intermittent rivers was observed when sampled during a season with large winter floods and a wet spring. Hydric plants growing in the ephemeral reaches may have originated from the local seed bank or may have been dispersed to the site via

floodwaters from an upstream perennial reach.

In the arid Southwest, all of the major rivers and many of the smaller ones are influenced by flow-regulating or flow-diverting dams (Graf 1999). Often this results in floods becoming less frequent and less intense and occurring at times of the year that are out of synch with rainfall seasons. Dam-reservoir systems serve as longitudinal barriers to the flow of many materials, and can inhibit downstream transport of seeds and fine sediments (Jansson et al. 2000). With reduced flooding and sediment inflow, the fluvial landscape can become simplified. All of these changes can influence plant species diversity, with effects varying with dam age, the specific nature of the flood alteration, and the hydrogeomorphic setting of the river. Thus, low levels of plant species diversity levels have been observed along some regulated rivers in the western United States (Uowolo et al. 2005; Beauchamp et al. 2007) while high levels occur on others (Stevens et al. 1995). This project investigated diversity differences between above-dam and below-dam reaches, and results for this portion of the effort will be made available in a future publication.

RESTORATION IMPLICATIONS

Restoring diversity by restoring hydrologic connectivity

Seeds are often purchased and dispersed at a restoration site using broadcast seeding or hydroseeding methods (i.e., anthropochory) (e.g., Baird 1989; Kus 1998). The number of species introduced in this fashion typically is a small fraction of the potential flora, and seeds often are released only once. The efficacy of this and other approaches in increasing diversity is poorly understood, as monitoring studies often are neglected in river and riparian restoration projects (Bernhardt et al. 2005). Results of seed bank studies such as the one undertaken in this investigation can facilitate riparian re-seeding efforts by indicating which types of plants are likely to be present in the soil seed banks and which require active introduction to a site.

As an alternative or supplementary approach to increasing plant species diversity at a restoration site, efforts can focus on restoring the processes by which plant propagules arrive on site and are produced and stored on site, and the processes that allow for coexistence of a wide range of species. To this end, several specific actions could be considered, and implemented on an experimental basis. First, groundwater pumping or flow diversion can be reduced to restore hydraulic connectivity and raise water tables in the riparian corridor, thereby increasing growth and survivorship of hydroriparian plants (Haney 2002; Lite and Stromberg 2005). Second, seasonal flood pulses can be restored to regulated rivers and their floodplains (Rood et al. 2003; Bhattacharjee et al. 2006). Third, levees can be removed or set back to widen a channelized river, thereby creating spatial refugia from flood scour and internally reconnecting landscape patches (Rhode et al. 2005; Ahn et al. 2006). Fourth, road overpasses or underpasses can be built to reconnect tributaries to mainstem rivers. Fifth, buffer strips of upland vegetation can be created adjacent to the riparian corridor to

restore lateral connectivity between different habitat types.

Landscape context and selection of restoration sites

Many factors come into play when selecting sites for riparian restoration activities (Landers 1997). Sometimes highly degraded sites are selected, but restoration challenges can be great in such areas. In other cases sites with the greatest restoration potential are selected. The hydrologic attributes and landscape context of a site will influence its potential for natural revegetation and thus for restoration success.

Preliminary results on soil seed banks and plant diversity patterns indicate that regeneration potential varies spatially within a watershed. Ephemeral reaches that occur along spatially intermittent rivers, and that are near perennial reaches, have a high diversity of dormant riparian seeds in the soil. This indicates a high potential for natural revegetation of riparian plant species in such reaches should the river be re-watered as a part of restoration activities. In contrast, ephemeral reaches of rivers that are dry over their entire length do not have buried hydroriparian seeds, and would require more active intervention in terms of re-seeding efforts.

SUMMARY: The success of riparian revegetation efforts in the southwestern United States depends on a broad suite of factors, including such things as hydrogeomorphic setting, and timing and duration of water delivery via hydrologic regime or artificial water delivery. Few studies have investigated the efficacy of exploiting the natural seed bank as a means of revegetation. As such, there is little information about soil seed banks in the variety of stream/riparian conditions that exist in the southwestern United States. This technical note describes research being conducted by Arizona State University, in coordination with the U.S. Army Engineer Research and Development Center, to investigate the influence of soil seed banks on plant diversity patterns in river systems. This research addresses processes that influence seed pools and plant diversity in riparian corridors, the influence of varying hydrologic regimes (and associated hydrologic connectivity) in these systems, and the influence that restoring hydrologic connectivity may have on plant diversity. One key finding is that along spatially intermittent rivers, persistent riparian seed banks develop in soils of ephemeral to perennial reaches alike. The diversity of the seed bank in the dry reaches varies with proximity to a wet reach, with implications for selection of suitable sites for hydrologic restoration. Another key finding is that although riparian plant species diversity is typically low in dry reaches, dry and wet reaches alike show pulses of diversity following large winter floods with sustained seasonal runoff; this finding has potential implications for management of flood pulses on regulated rivers.

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