Riparian vegetation responses to altered disturbance regimes in the Grand Canyon

Abstract: Flooding is a fundamental source of community organization in riparian zones, and as a disturbance force, it generates both stressors and resources that determine the structure and composition of these systems. Historically, the Grand Canyon corridor experienced frequent, high severity flooding disturbances, but after the completion of the Glen Canyon Dam in 1966, the Colorado River between Lee's Ferry and Lake Mead has experienced less acute, less seasonally variable flows. Due to the alteration of the native disturbance regime, vegetation communities at the old high water line are in decline, while the formerly denuded riverbanks have become occupied by several new vegetation zones, including woody riparian assemblages and marsh patches. These novel assemblages are discussed in the context of their affinity for disturbance, dispersal abilities, and resistance to desiccation. Recent high flow experiments (HFEs) have not approached the historical severity of pre-dam flooding events, and while HFEs may help achieve other management goals, novel riparian vegetation has shown little response to this anthropogenic form of disturbance. The vegetation shifts observed in the Grand Canyon are just one instance of the impacts of altered disturbance regimes. Yet, this case study raises important management questions about the difficulties inherent in conserving ecosystem processes, especially when they conflict with resource use and finer-scale conservation values.

Goals of this paper: This paper will discuss the Grand Canyon riparian corridor's changing disturbance regime after the construction of the Glen Canyon Dam (GCD) and how riparian vegetation has responded to the shifting stressors and resource gradients imposed by new flow patterns. Altered disturbance is just one form of global change, but interacts strongly with other anthropogenic impacts, especially warming temperatures, changing precipitation patterns, fragmentation, species introductions, and human land use. This paper seeks to tie this flooding-focused case study to broader conversations about disturbance ecology and the impacts of novel perturbations on community assembly. The maintenance of native disturbance regimes and landscape-level processes is a topic at the forefront of ecosystem ecology and is increasingly recognized as an essential component of conservation of biodiversity. This paper seeks to highlight the difficulties inherent in managing systems for disturbance, discuss the differences between native and simulated disturbances, and weigh some of the conservation implications of altered flood regimes along the Colorado River within the Grand Canyon.

Literature Synthesis

Flooding as a disturbance force: In an ecological context, disturbance is typically defined as "any relatively discrete event that disrupts the structure of an ecosystem, community, or population, and changes resource availability or the physical environment" (White and Pickett 1985). Disturbance regimes are crucial sources of heterogeneity and influence the structure, function, and composition of communities. Disturbance forces can include a range of ecological processes such as wildfire, herbivory, windfall, disease, and flooding events, but disturbance regimes are typically similarly characterized by the frequency, severity, timing, duration, and spatial extent of perturbations. Across systems, many forces of global change, such as fragmentation, climate change, species invasions, and human land use, have led to the alteration of disturbance regimes and consequent shifts in vegetation dynamics (Turner 2010).

Along the Colorado River within the Grand Canyon, historical flooding regimes strongly structured the composition and local distribution of riparian plant communities (Turner and Karpisciak 1980). Flooding disturbances are both a source of stress and resource availability for plant communities. Historic and contemporary vegetation patterns can both be broadly explained by the opposing gradients of flood damage and desiccation potential with increasing distance from the river. Physical damage from high waters, burial from sediment deposition, or inundation can all cause plant mortality; yet, flooding events are also essential sources of seasonally available water, groundwater recharge, sediment deposition, salinity removal, and propagule dispersal (Schmidt et al. 1998, Nilsson and Berggren 2000). Like other disturbances, flooding regimes can be characterized by their frequency, severity (as described by water flow in cubic feet per second), seasonality, and duration (as described by hydrograph shape and timing).

Historical Flooding Regimes: The 1966 completion of the Glen Canyon Dam (GCD) fundamentally altered the historical flooding regimes experienced by the riparian corridor between Lee's Ferry and Lake Mead. Prior to the 1960s, 80% of annual discharges exceeded 50,000 cfs, and the three-year high flows typically exceeded 100,000 cfs (Webb et al. 2007). These severe, high-frequency disturbance events scoured any vegetation below the 100,000 cfs stage, leaving the riparian corridor mostly devoid of perennial plants, with scattered ephemeral herbaceous species and marsh patches, which only occupied the calmer tributaries and perennial springs (Stevens et al. 1995). The inundation period lasted for weeks, saturating the alluvial banks and providing an essential source of seasonal water availability for plants above the high water line. A paleoflood record that reconstructed the last 4,500 years of flood activity (using radiocarbon dating of organic material in flood deposits) suggested that the historical peak discharge might have even reached 500,000 cfs for certain years between 350-750 ad (O'Connor et al. 1994). The largest flood in the gauging record was in 1921 at 220,000 cfs, and seasonally, pre-dam floods typically peaked between mid-May and early July (Webb et al. 2007).

The construction of the GCD substantially altered the severity, timing, and pattern of this previously high frequency, high severity regime. The dam has homogenized seasonal discharge curves for the Colorado River, reducing both the duration and overall scouring potential of peak flooding events. Currently, only 1% of floods exceed 50,000 cfs, and in the post-dam period, only one flood (in 1983) has approached 100,000 cfs. While seasonal hydrographs have been heavily smoothed, diurnal fluctuations in discharge have increased, generating "tides" due to the operation of the GCD and daily demands for hydroelectric power. Additionally, as high discharge levels have been reduced, low annual discharge levels have increased, making water supply less seasonally variable for plants growing on the banks and simultaneously increasingly scarce for plants still growing at the old high water zone (Webb et al. 2007). Grand Canyon riparian vegetation communities have responded strongly to this more homogeneous, less severe disturbance regime, with the emergence of new vegetation zones below the 100,000 cfs stage and marked decline in the formerly dominant species at the old high water line (Figure 1).

Old High Water Zone: The old high water vegetation zone (OHWZ), delimited by the 100,000 cfs stage, was defined by soil saturation from annual floods, which provided an essential resource for germination and establishment of new individuals (Figure 1) (Webb et al. 1999). OHWZ vegetation consisted primarily of obligate or facultatively riparian small trees and shrubs, such as mesquite (*Prosopis glandulosa),* catclaw acacia (*Acacia greggii)*, netleaf hackberry (*Celtis reticulata*), coyote willow (*Salix exigua),* and Apache plume (*Fallugia paradoxica)* (Turner and Karpisciak 1980). Overall, large-statured riparian vegetation (such as *Populus spp.* or *Salix spp.)* was rare, as recorded by pre-dam river runners, but seasonally plentiful water provided by regular floods meant that small trees and shrubs that would normally be more dispersed in desert settings could occupy the OHWZ in a dense riparian band (Webb et al. 2007).

The density and demography of OHWZ vegetation has shifted following the construction of the GCD, due to reduced seasonal water availability, sediment deposition, and salt removal (Kearsley and Ayers 1999). Saturated substrate now sits 20-50 feet below the OHWZ, and though many of its dominant species are phreatophytes (plants that keep their roots in constant touch with surface or ground water), these plants differ in their ability to survive and reproduce in the OHWZ's increasingly xeric conditions (Webb et al. 1999, 2007). Anderson and Ruffner (1987) recorded reduced recruitment and a scarcity of sub-adult mesquite individuals at the OHWZ, suggesting that high flow events may have been crucial for seedling establishment for this species. Mesquite once dominated the OHWZ, but aerial photo comparisons indicated a reduction in OHWZ densities of this obligately riparian species. Catclaw acacia, a more xerophytic species, is one of the few OHWZ species maintaining its status at the 100,000 cfs stage (Anderson and Ruffner 1987, Webb et al. 2011). However, tree ring analysis in catclaw acacia showed that post-dam flooding regimes have reduced annual growth in adults in the OHWZ, suggesting that even these most xerophytic species may be susceptible to the stressors introduced by new flooding regimes (Anderson and Ruffner 1987).

Prior to the GCD's constuction, xerophytic and phreatophytic plants, including ocotillo (*Fouquieria splendens)*, creosote (*Larrea tridentate)*, Mormon tea (*Ephedra nevadensis)*, and several cactus species, dominated the desert zone above the OHWZ. Despite reduced groundwater recharge and increased annual temperatures, the desert vegetation zone has remained least changed since the construction of the dam, and many desert species have migrated down slope, mixing with the remaining OHWZ vegetation (Webb et al. 2007).

<u>New High Water Zone and New Riparian Vegetation:</u> The new high water line sits near the 40,000 cfs stage, and here, the formerly barren banks host a mix of woody and herbaceous species (Figure 1) (Turner and Karpisciak 1980). These novel assemblages are characterized by the down-slope migration of many OHWZ species, increased recruitment of riparian species, and the introduction of several invasive species, namely the phreatophytic *Tamarix* (Webb et al. 2011). Recruitment of several native species has shifted into this new high water zone (NHWZ) where seedlings experience reduced mortality compared to the OHWZ (Anderson and Ruffner 1987). This zone is rarely inundated, and previously disturbance-limited species such as arrowweed (*Pluchea sericea)*, seep willow (*Baccharis emoryi)*, coyote willow, cottonwood (*Populus fremontii)* and brickelbush (*Brickellia spp.)*, which used to be confined to tributaries, but have expanded into the new riparian zone (Webb et al. 2007). Many of these species have some adaptation to flooding, such as adventitious roots in willows and flood dispersal of poplar seeds, and they are now thriving under these less severe regimes (Kennedy and Ralston 2011).

Nonnative salt cedar (*Tamarix spp.)* has also become a dominant riparian species in the Grand Canyon, often growing in dense monospecifc stands. This species has not been known to extirpate any native species, but it is rapidly spreading; in paired photographs from 1889 and 1990, *Tamarix* appeared in 71% of the post-dam photographs (Johnson 1991). *Tamarix,* a facultative phreatophyte, is thought to have greater salt and drought tolerance compared to native plants, and these traits may allow it to succeed under the current disturbance regime (Johnson 1991, Stromberg 2001, Glenn and Nagler 2005). Native species, such as *Populus fremontii*, are also frequently adapted to time seed release with annual flooding events, to capitalize on newly-scoured substrates for germination, whereas salt cedar produces seeds throughout the summer, and its seedlings establish with higher frequencies under the homogeneous flow conditions imposed by the GCD. Under natural flow regimes, however, many native species (including *Populus* and *Salix spp.)* have shown germination, establishment, and growth rates that are equal to or greater than *Tamarix*, suggesting that restoration of pre-dam regimes could prove to be a valuable invasive species management strategy (Mortenson et al. 2012). Vegetation and invasive species-focused management strategies, however, are often in direct conflict with wildlife-related objectives (discussed below).

Novel Marsh Assemblages: Prior to the construction of the GCD, marsh vegetation was limited to tributaries and perrenial springs, but under altered flow regimes, formerly bare reattachment bar platforms and return current channels have become densely vegetated with novel marsh assemblages between the 15,000-31,000 cfs discharge stages (Figure 1 & 3) (Stephens et al. 1995). The reduction in scouring floods allow marsh plants to colonize these formerly open sites, and diurnal tides keep the banks wetted daily, aiding establishment of these inundation-adapted species. These species frequently reproduce via rhizomes and many have aerenchyma, channels in leaves or stems of plants that allow for oxygen transport to the root system in inundated soils. Four distinct marsh types now occupy the Grand Canyon, and their development and composition varies with soil texture, microsite gradients in inundation, and reach-based geomorphology. Wet fluvial marsh types, comprised by cattail-reed alliances or horseweed-bermuda grass alliances, occupy low velocity, depositional environments with frequent inundation. Dry marsh types, comprised by horsetail-willow and woody phreatophytic (arroweed-tamarisk) alliances, occupy sites that are less frequently inundated, with sandier, well-drained soils (Stephens et al. 1995). Stephens (1995) mapped the associations of these four types and found that, at the system-scale, marsh development typically increased with distance from Lee's Ferry, while at local scales, fluvial marsh density was highest in wide reaches and low-lying geomorphic settings, suggesting that flow is a primary limitation on this vegetation type.

In 1983, unusually high rates of spring snowmelt influx threatened the Glen Canyon Dam, and the Bureau of Reclamation opened the spillways, generating the highest severity flood in the post-dam era, with discharges approaching 90,000 cfs (Webb et al. 1999). The 1983 and 1984 floods scoured the marsh vegetation, reducing fluvial marsh cover by more than 85%; yet, within seven years, marsh vegetation recovered to occupy more than seven times more area than it did in 1983 (Stephens et al. 1995). Many Grand Canyon marsh species are capable of vegetative reproduction via rhizomes, and Stephens et al. attribute rapid marsh recovery to the breaking up and dispersal of marsh vegetative propagules by the flooding events. Marsh vegetation patches are the most susceptible to scouring, but after post-dam proliferation and under current disturbance regimes, they display remarkably high resilience (Stevens et al. 1995).

High Flow Experiments: In the post-dam era, the 1983 flood was the only system perturbation that approached the historical three-year flooding norm. However, the Bureau of Reclamation's high flow experiments (HFEs) have reintroduced moderate severity flooding to the Grand Canyon in order to improve ecological and recreation-related resources downstream of the GCD (Melis et al. 2010, Webb et al. 2010). These HFEs, conducted in March 1996, November 2004, March 2008, 2012, and 2013, have not exceeded 45,000 cfs, but are purported to "mimic natural flooding to some extent" (Glen Canyon Dam Adaptive Management Plan). The Glen Canyon Dam Adaptive Management Program (GCDAMP) established a framework to operate the dam in a way that facilitates scientific research, and in essence, HFEs are studies in system responses to disturbance. The GCDAMP outlines a set of potentially-conflicting goals, including the creation of fish habitat, formation of sandbars and camping beaches, and protection of endangered species, but it also includes vegetation management among its objectives. HFEs aim to set back riparian succession, remove NHWZ individuals that have colonized post-dam, scour fluvial marshes, and aid in invasive species removal, with a specific focus on *Tamarix*.

Vegetation responses to HFEs have been minimal, which is perhaps unsurprising, considering that these manipulated disturbances have only reached about half the severity of the historical flood levels. The 1996 HFE produced an initial 20% reduction in riparian cover, due to both scouring and burial of vegetation; however, 6 months to a year after the flooding event, the change was no longer significant (Kearsley and Ayers 1999). After burial, many woody species were able to grow through deposited sediment, and scoured ephemeral marshes rapidly regenerated, following a pattern of recovery similar to that following the 1983 floods (Kearsley and Ayers 1999). Many marsh species thrived after burial (especially *Typha* and *Phragmites spp*.), and due to their differential capacities for clonal reproduction, there were shifts in marsh composition. The coarsening of sandbars (compared to pre-dam conditions) and recent HFEs seem to be selecting for species adapted to burial, clonality, and sandy soils, namely *Baccharis, Pluchea,* and *Phragmites spp*. Additionally, the HFEs have had little effect in providing water to OHWZ vegetation, which begs the question whether vegetation management goals are worth prioritizing under current low and moderate severity flooding regimes (Melis et al. 2010).

Conlusions:

Management considerations and global change: Kearsley and Ayers (1999) suggest HFE discharges of 77,700 to 88,300 cfs (2,200 to 2,500 m3/s) to accomplish goals of vegetation removal from return-current channel marshes and supply water to the OHWZ. Yet, given the rapid regeneration of marsh vegetation after HFEs, the establishment of many woody, resprouting species in the NHWZ, and reduced densities of OHWZ species, it is uncertain whether the reintroduction of native disturbance regimes would be sufficient to restore historic vegetation patterns. In this context, it is particularly important to remember that our knowledge of pre-dam vegetation dynamics are limited to historical reconstructions of flows and climate, narrative accounts, botanical surveys, and photographic comparisons, none of which include any assessment of densities, demographies, or other ecosystem processes such as nutrient cycling.

In addition, vegetation removal and historically severe flows may directly conflict with sediment deposition and wildlife-related goals (Melis et al. 2010). The new riparian vegetation, including invasive *Tamarix*, has also become a crucial source of habitat for the endangered Southwestern willow flycatcher, the Kanab ambersnail, and a variety of other fauna. R.R. Johnson (1991) claims that the new NHWZ of the Grand Canyon is the only major riverine habitat with increases in riparian animal populations in the desert Southwest. In recent years, there have been increasing calls for the field of conservation to broaden its goals to include larger scale or “coarse-filter” protection of communities, landscapes, and ecosystem processes, including disturbance, rather than traditional fine-filter focuses, such as individual species, genes, or populations (Schwartz 1999). Yet, the Grand Canyon riparian zone is an interesting example in which species-focused conservation and wildlife use of novel habitats are at direct odds with the restoration of a historic ecosystem-level process.

Bengtson et al. (2003) argue that protected areas that fail to incorporate natural disturbance and other ecosystem processes are “social constructs disconnected from ecosystem dynamics.” Changing disturbance regimes in the Grand Canyon are similar to those facing managers in other systems, including fire-suppressed forests across the western US and invaded grassland habitats. Perhaps, given the current anthropogenic water-use in the Colorado River Basin and demands for hydroelectric power, reinstating the Grand Canyon’s historic flooding regimes would be undesirable, if not impossible. Yet, the GCDAMP and HFE’s conflicting management goals and attempts at simulating disturbance highlight the difficulties inherent in managing protected areas for any ecosystem-level process.

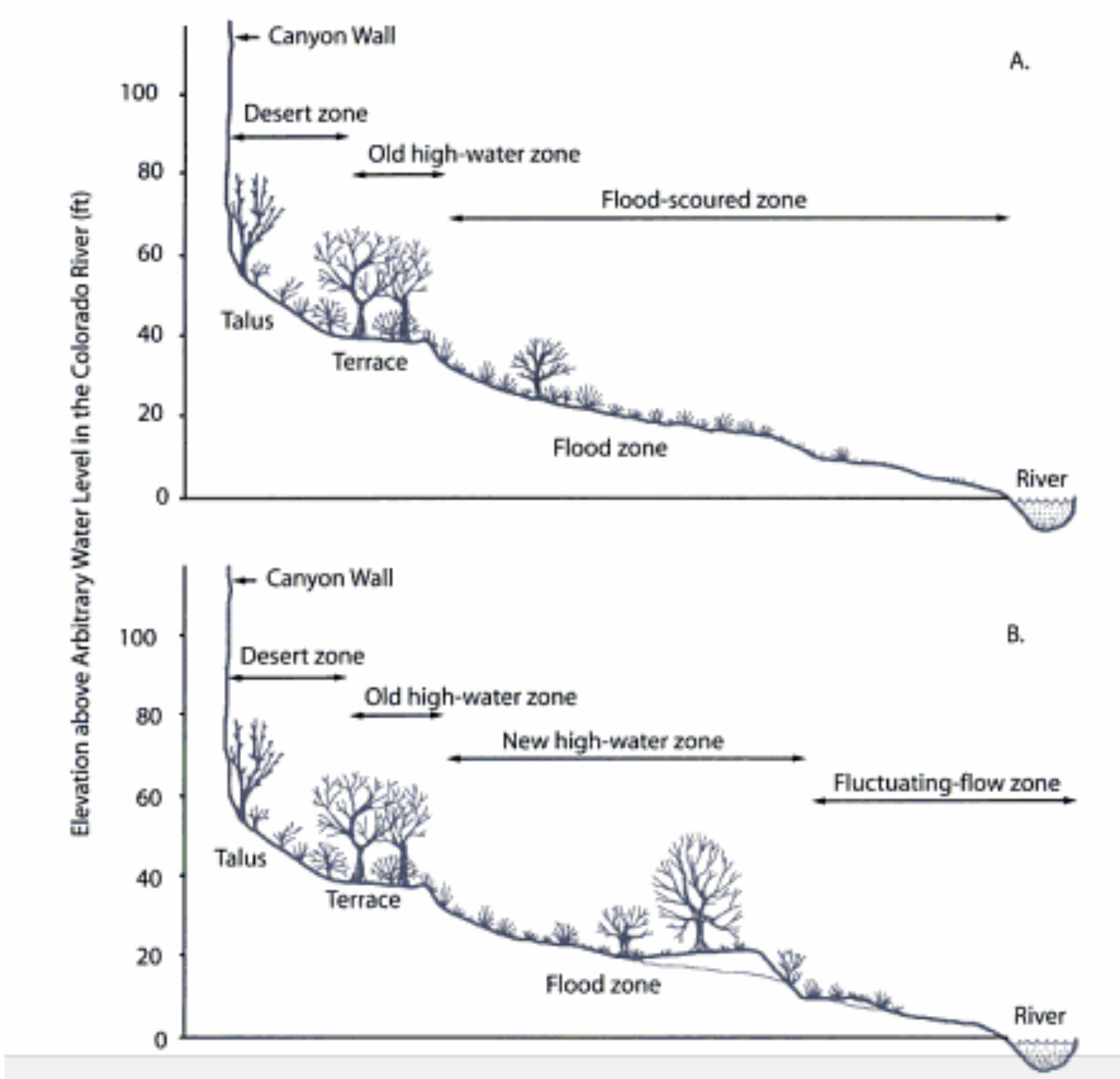

Figure 1. Schematic showing vegetation zone distributions before (top) and after (bottom) the construction of the Glen Canyon Dam. From Webb et al. 2007.

Figure 2. Historical rephotography shows the shifts in riparian and desert vegetation over more than 100 years at Lava Falls Rapid (left photograph was taken in 1890, middle in 1990, and right in 2010). From Webb et al. 2011.

Figure 3. Historical rephotography shows the formation of novel marsh habitat over more than 100 years at the mouth of Cardenas Creek (left photograph was taken in 1890, middle in 1993, and right in 2010). From Webb et al. 2011.

Literature cited

Anderson, L. S., & Ruffner, G. A. 1987. Effects of post-Glen Canyon flow regime on the old high water line plant community along the Colorado River in Grand Canyon. *Glen Canyon Environmental Studies Technical Report*. *Salt Lake City (UT): US Bureau of Reclamation*, 271-286.

Elmqvist, T., Folke, C., Nyström, M., Peterson, G., Bengtsson, J., Walker, B., & Norberg, J. 2003. Response diversity, ecosystem change, and resilience.*Frontiers in Ecology and the Environment*, *1*(9), 488-494.

Clover, E. U., & Jotter, L. 1944. Floristic studies in the canyon of the Colorado and tributaries. *American Midland Naturalist*, 591-642.

Glenn, E. P., & Nagler, P. L. (2005). Comparative ecophysiology of< i> Tamarix ramosissima</i> and native trees in western US riparian zones.*Journal of Arid Environments*, *61*(3), 419-446.

Johnson, R. R. 1991. Historic changes in vegetation along the Colorado River in the Grand Canyon. *Colorado River ecology and dam management. National Academy Press, Washington, DC, USA*, 178-206.

Kennedy, T. A., & Ralston, B. E. 2011. Biological responses to high-flow experiments at Glen Canyon Dam. *US Geological Survey Circular*, *1366*, 93-125.

Melis, T.S., Topping, D.J., Grams, P.E., Rubin, D.M., Wright, S.A., Draut, A.E., Hazel, J.E., Jr., Ralston, B.E., Kennedy, T.A., Rosi-Marshall, Emma, Korman, Josh, Hilwig, K.D., and Schmit, Lara M., 2010. 2008 High-flow experiment at Glen Canyon Dam benefits colorado river resources in Grand Canyon National Park: U.S. Geological Survey Fact Sheet 2010-3009, 4 p.

Merritt, D. M., & Poff, N. L. R. 2010. Shifting dominance of riparian Populus and Tamarix along gradients of flow alteration in western North American rivers. *Ecological Applications*, *20*(1), 135-152.

Mortenson, S. G., Weisberg, P. J., & Stevens, L. E. 2012. The influence of floods and precipitation on Tamarix establishment in Grand Canyon, Arizona: consequences for flow regime restoration. *Biological Invasions*, *14*(5), 1061-1076.

Nilsson, C., & Berggren, K. 2000. Alterations of Riparian Ecosystems Caused by River Regulation Dam operations have caused global-scale ecological changes in riparian ecosystems. How to protect river environments and human needs of rivers remains one of the most important questions of our time.*BioScience*, *50*(9), 783-792.

O'Connor, J. E., Ely, L. L., Wohl, E. E., Stevens, L. E., Melis, T. S., Kale, V. S., & Baker, V. R. 1994. A 4500-year record of large floods on the Colorado River in the Grand Canyon, Arizona. *The Journal of Geology*, 1-9.

Patten, D. T., Harpman, D. A., Voita, M. I., & Randle, T. J. 2001. A managed flood on the Colorado River: background, objectives, design, and implementation. *Ecological Applications*, *11*(3), 635-643.

Powell, J. W. 2012. *The exploration of the Colorado River and its canyons*. Courier Dover Publications.

Schmidt, J. C., Webb, R. H., Valdez, R. A., Marzolf, G. R., & Stevens, L. E. 1998. Science and values in river restoration in the Grand Canyon.*BioScience*, 735-747.

Schwartz, M. W. 1999. Choosing the appropriate scale of reserves for conservation. *Annual review of ecology and systematics*, *30*(1), 83-108.

Stevens, L. E., Schmidt, J. C., Ayers, T. J., & Brown, B. T. 1995. Flow regulation, geomorphology, and Colorado River marsh development in the Grand Canyon, Arizona. *Ecological Applications*, *5*(4), 1025-1039.

Stromberg, J. C. 2001. Restoration of riparian vegetation in the south-western United States: importance of flow regimes and fluvial dynamism. *Journal of Arid Environments*, *49*(1), 17-34.

Turner, R. M., & Karpiscak, M. M. 1980. *Recent vegetation changes along the Colorado River between Glen Canyon Dam and Lake Mead, Arizona*. US Government Printing Office.

Turner, M. G. 2010. Disturbance and landscape dynamics in a changing world. *Ecology*, *91*(10), 2833-2849.

USBR. 2011. Environmental Assessment: Development and implementation of a protocol for high flow experimental releases from Glen Canyon Dam, Arizona, 2011 through 2020. U.S. Department of the Interior, Bureau of Reclamation. Upper Colorado Region, Salt Lake City, Utah. (http://www.nature.nps.gov/ParkScience/index.cfm?ArticleID=519).

Webb, R. H., Wegner, D. L., Andrews, E. D., Valdez, R. A., & Patten, D. T. (1999). Downstream effects of Glen Canyon dam on the Colorado River in Grand Canyon: A review. *Geophysical Monograph Series*, *110*, 1-21.

Webb, R. H., Leake, S. A., & Turner, R. M. (2007). *The ribbon of green: change in riparian vegetation in the southwestern United States*. University of Arizona Press.

Webb, R.H., J. Belnap, M.Scott, and T. Esque (2011) Long term change in perennial vegetation along the Colorado River in Grand Canyon National Park (1889-2010) ParkScience. 28(2):83-87.

White, P. S. & Pickett, S. T. A. 1985. Natural disturbance and patch dynamics: an introduction. - In: Pickett, S. T. A. and White, P. S., (eds), The ecology of natural disturbance and patch dynamics. Academic Press, Orlando, pp. 3-13.