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PROPAGULE BANKS: POTENTIAL CONTRIBUTION TO RESTORATION OF AN IMPOUNDED AND DEWATERED RIPARIAN ECOSYSTEM

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Abstract: The Agua Fria River in Arizona's Sonoran Desert was impounded and diverted more than 70 years ago. Immediately below New Waddell dam there are semi-permanent pools, but water has been released into the channel only during rare wet years. To determine whether a propagule bank exists below the dam, and whether it could contribute to the revegetation of the Agua Fria riparian ecosystem should flow be restored to the dewatered reach, we collected 45 soil cores from four plant associations. We examined species in the samples in a growth chamber using the seedling emergence method. A total of 74 species (mostly herbaceous) and an abundance of individuals were present in propagule banks. The propagule banks were similar to those of a free-flowing reference river despite considerable differences in extant vegetation. Riparian species were present in propagule banks of all four associations and were the dominant type in three (*Tamarix* forests, *Tamarix*-*Salix* forests, and *Baccharis*-*Bebbia* shrublands). Propagule distribution varied with soil depth in three of the associations (*Tamarix* forests and the two xerophytic shrublands) with riparian species more prevalent in deep sediment and upland species more prevalent in surface soil and litter. Collectively these patterns suggest that a riparian legacy is present in Agua Fria propagule banks. However, riparian propagule density was low in the *Hymenoclea*-*Bebbia* shrublands, reflecting xerification of the riparian corridor. Given the physical barrier of the dam, continued diversion of stream flow, and rare flood releases, local inputs from xerophytes will dominate propagule bank dynamics in the future. Although propagule banks could contribute to redevelopment of the herbaceous component of the vegetation should stream flows be restored to this river reach, the riparian legacy likely will decline over time as riparian propagules reach the end of their lifespan while propagules of xerophytes continue to be replenished.

Key Words: arid region, floodplain, seed bank, vegetation

INTRODUCTION

Riparian plant associations are strongly influenced by stream flow regime (Poff et al. 1997). In rivers of the Sonoran Desert, powerful floods sculpt riparian plant associations by scouring vegetation, eroding and depositing sediment across the floodplain, and maintaining metacommunity dynamics via flood-pulse dispersal (Boudell and Stromberg 2008). Plant species that persist in these ecosystems either avoid flood disturbances by occupying high surfaces, resist flooding without undergoing mortality, or invade flood-scoured sites (Naiman and Decamps 1997, Nilsson and Svedmark 2002). For ruderal species that depend on flood disturbance to create sites for establishment, adaptations such as persistent seeds or vegetative remnants capable of resprouting (both hereafter referred to as propagules) allow for survival during periods in which growing conditions are unsuitable (Boudell 2004, Capon and Brock 2006, Stromberg et al. 2008).

Many riparian ecosystems in arid regions throughout the world have been altered by stream flow impoundment and diversion, and groundwater pumpage for agricultural, municipal, and industrial use. Where flood regimes are arrested or altered, flows often become unsynchronized with the phenological stages and life cycles of local plant species (Patten 1998, Shafroth et al. 1998, Shafroth et al. 2002). Where streamflow has been reduced or eliminated or where groundwater tables have been lowered, plant associations have shifted from hydrophytes towards more drought tolerant species (Judd et al. 1971, Elmore et al. 2003, Lite and Stromberg 2005, Stromberg et al. 2005).

The past few decades have seen a groundswell of interest across the globe in restoring, or at least rehabilitating, degraded riparian ecosystems (Molles et al. 1998, Middleton 1999, Hughes and Rood 2003). Many early restoration efforts focused exclusively on tree planting and hydroseeding. Because life history characteristics of many riparian plant species are tied to local hydroregimes, and many have high water needs, recent efforts have focused on mimicking the local flow regimes with respect to timing and amount of flow. These efforts are undertaken in hopes of restoring a more natural structure and function to regulated rivers (Nilsson et al. 1997, Poff et al. 1997, Rood et al. 2003). Indeed, without restoring naturalizing flow regimes on regulated rivers, the restoration of riparian ecosystems (*sensu stricto*) may be an unachievable goal. However, if the flow regime is restored, and if local seed sources are available, riparian vegetation may establish of its own accord.

Relict riparian ecosystems such as floodplain fragments located below reservoirs may have an ecological legacy that can contribute to the reestablishment of pre-disturbance plant associations (Stevens et al. 2001, Johnson 2002). Propagule banks of degraded floodplain forests and other wetland ecosystems in humid regions often contain remnant species typical of pre-disturbance plant associations (McDonald et al. 1996, Wetzel et al. 2001, Combroux et al. 2002, Matus et al. 2003, Middleton 2003), although the number of viable propagules may decline as time since drainage or dewatering increases (Wienhold and van der Valk 1989). The role of remnant propagule banks in contributing to the revegetation of rewatered floodplains and channel bars of dryland rivers of the American Southwest remains unknown.

The goal of our investigation was to assess the potential contribution of remnant floodplain propagule banks to revegetation of a dewatered dryland riparian corridor should stream flows be restored. Our objective was to determine the distribution pattern of riparian and upland propagules in remnant floodplain forest and shrubland propagule banks of a regulated river. To better understand the potential of the remnant propagule banks, we tested the hypothesis that propagule banks of remnant floodplain forests and shrublands would be similar to those of comparable forests and shrublands of a nearby free-flowing river reach in number of riparian species, density of riparian propagules, and mean wetland indicator scores.

STUDY AREA

Climate of the Study Sites

The climate of the Sonoran Desert is arid and hot. Precipitation falls in a bimodal pattern with gentle rains falling in the winter and "monsoon" thunder storms occurring in the summer (Dimmitt 2000). Total precipitation near the study areas in 1998 was 39 cm at Wickenburg (630 msl), above the average annual rainfall of 29 cm (for the period 1908–2006), and 33 cm at Castle Hot Springs (607 msl), below the annual average of 39 cm (for the period 1959–2006). The average maximum and minimum temperature during the study period was 28.7°C and 13.3°C, respectively (Castle Hot Springs Station, Western Regional Climate Center, Historical Climate Summaries).

The Agua Fria River

The 193 km Agua Fria River is an allogenic desert river with headwaters in the Bradshaw Mountains of Arizona's Basin and Range physiographic province. Its low-elevation reaches course through the Sonoran Desert in central Arizona. The Agua Fria was impounded in 1927 by Waddell Dam, which formed Lake Pleasant. The dam was replaced in 1985 by New Waddell Dam. Water from Lake Pleasant is diverted via a diversion dam into canals to sustain municipal and agricultural uses. Immediately below the diversion dam, semi-permanent pools are supported by dam seepage and occasional spring flow from Morgan City Wash (Springer et al. 1999). Two kilometers downstream from the dam, the channel is completely dry. Water has flowed in the below-dam Agua Fria channel only during scheduled releases in wet years, which have occurred during nine of the 73 years since impoundment to the end of the study period (1927–2000). These releases ranged in size from 0.03 $m^3 s^{-1}$ in 1966 to 1,094 $m^3 s^{-1}$ in 1980, and typically lasted from one to three months (Maricopa Water District records). Releases did not occur during the study period (1998).

The study area was selected along a 4-km stretch of the Agua Fria below the diversion dam in northwest Maricopa County (112°15′) (Figure 1). The elevation of the study reach is approximately 425 msl and the gradient is 6 m km^{-1}. The substrate is comprised of alluvial sediments including sand, gravel, and pebbles. Boulders and rock outcropping also occur on the floodplain. Land in the study area is undeveloped and is periodically grazed by trespass cattle and feral burro. Vegetation in the study area included a mix of hydroriparian, mesoriparian, and xeric plant species.

Study sites were selected in each of the four dominant plant associations present: *Tamarix*-*Salix* forest, *Baccharis*-*Bebbia* shrubland, *Tamarix* forest, and *Hymenoclea*-*Bebbia* shrubland (Figure 1). The

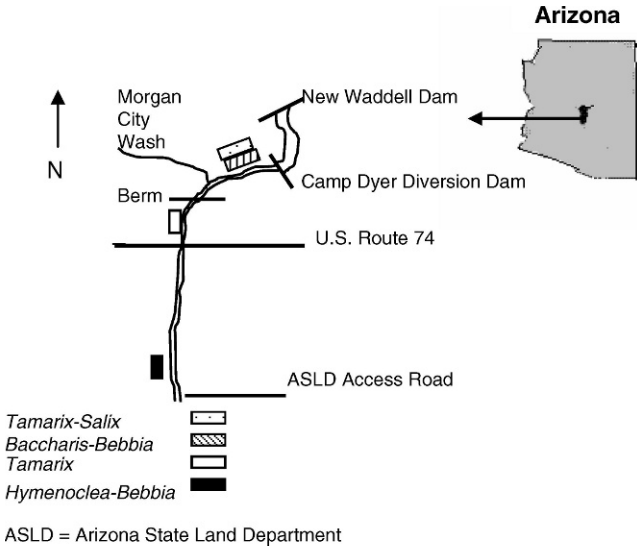

Figure 1. Schematic of study sites in relation to Agua Fria River below New Waddell Dam (Maricopa County, Arizona, USA). Map is not to scale.

small but dense *Tamarix ramossissima* Ledeb. (salt cedar) and *Salix gooddingii* Ball (Goodding willow) forest, both hydromesic riparian species, is located immediately below the diversion dam closest to the seep pools. Lateral to the *Tamarix-Salix* forest is a low-density *Baccharis sarothroides* A. Gray (desert broom) and *Bebbia juncea* (Benthe.) Greene (sweet bush) shrubland, both of which are xeroriparian species. A dense *Tamarix* forest is located in an ephemeral reach farther downstream and is immediately below a berm. A *Hymenoclea monogyra* Torr. & A. Gray (burro brush) and *Bebbia juncea* shrubland, both xeroriparian species, is located approximately 4 km downstream of the dam located near a completely dewatered channel.

The Hassayampa River

The Hassayampa River, in central Arizona, was the reference stream for the Agua Fria. It drains the same mountain range (Bradshaws) and is the nearest free-flowing Sonoran Desert river with similar elevation and historically similar flow regime to the Agua Fria. A 1-km free-flowing perennial reach located on the Hassayampa River Preserve, was selected for study. The preserve is located within 33 km of the Agua Fria study area (112°37′30″) at an elevation of approximately 610 msl. The gradient of the study reach is 6 m km^{-1}. The soil is comprised of mostly alluvial sediments.

The Hassayampa River Preserve is populated by plant associations that typify low-elevation riparian ecosystems of the Sonoran Desert (Stromberg et al. 2007) and has a high level of floristic diversity (Wolden et al. 1994). The mixed *Populus fremontii* S. Watson (Fremont cottonwood) and *Salix gooddingii* forests, both hydromesic riparian species, are located adjacent to the channel bar on aggraded floodplains, and occupy extensive areas of the floodplain. *Hymenoclea* shrublands are interspersed in the floodplain mosaic, on aggraded surfaces with very dry soils (Stromberg et al. 1997, Bagstad et al. 2006).

METHODS

Vegetation Surveys

Woody and herbaceous vegetation were surveyed May–June and September–October of 1998. Three 100 m^2 sites were located within each plant association. Within each site, five 1 m^2 plots were randomly selected for study. Percent cover of woody and herbaceous vegetation (by species) was visually estimated within each plot, and species richness was determined. Species were identified according to Kearney and Peebles (1960) and recent treatises. Voucher specimens were deposited in the Arizona State University herbarium.

Propagule Bank Soil Core Collection

Propagule bank samples were collected during October–November, 1998 within the same plots in which vegetation was surveyed. Samples collected at that time captured recently dispersed seeds of cool and warm season species, as well as older propagules (Baskin and Baskin 1998). Three soil samples were collected within each plot. Litter was collected from each core location; samples were then collected using a 5 cm diameter split-core soil sampler. Each core was divided into depths of 0–2, 2–5, and 5–8 cm. The three samples collected within plots were combined by depth for a total of 45 soil cores per plant association.

Seed Germination and Plant Identification

The seedling emergence method was used to estimate propagule bank composition. This method often underestimates seed bank composition (Thompson et al. 1997). To address this shortcoming, we designed a method to enhance seed germination.

Samples were processed and maintained in the growth chamber for two years under conditions that mimicked local weather conditions. Litter and soil samples were spread evenly to a maximum depth of 3 cm on top of pasteurized soil substrate and placed in the growth chamber following a random block design. Containers filled with only soil substrate were placed between blocks of samples to test for seed contamination. Temperature regimes of the growth chamber were based on six years of data from Wickenburg, Arizona. Average maximum and minimum monthly temperatures were used to establish temperature ranges. The temperature changed approximately 10 times a day to mimic gradual diurnal temperature fluctuations (Schmidli 1993). Average day length data collected from 33°58′ N, 112°44′ W was used to program the growth chamber light timers. Average PAR (photosynthetically active radiation) measurements ranged from 118–221 μmol m^{-2} s^{-1}.

Several actions were taken to maximize germination. Containers were bottom-watered and sprayed with distilled water when needed to prevent water stress. With each seasonal change in the growth chamber, the sample soil, as opposed to soil substrate, was gently stirred to bring any seeds at the bottom of the sample close to the surface (Roberts 1981, Thompson et al. 1997). Competition was reduced by removing plants from trays when they could be identified (Thompson and Grime 1979, Thompson et al. 1997). At the end of two years, any remaining mature plants that had not flowered were placed in a greenhouse. Plants were identified according to Kearney and Peebles (1960) and recent treatises. Voucher specimens were deposited in the Arizona State University herbarium.

Data Reduction

As a measure of a riparian legacy presence, species were categorized by moisture affinity (riparian or upland) and weighted-average wetland indicator scores (WISs) were calculated. Species were considered riparian if classified as obligate wetland, facultative wetland, facultative, or facultative upland according to (Reed 1997). Upland species were those classified as such by Reed (1997). Weighted-average WISs were calculated by multiplying the relative abundance of plants (cover for extant vegetation and density for propagule banks) within each of five wetland indicator classes by class weights from 1 (obligate wetland) through 5 (obligate upland) (Wentworth et al. 1988). Species cover and density values were summed across sampling seasons. Only one season of woody species values was used in data analyses.

Data Analyses

Differences in mean number of individuals per m^2 (total and by category) between Agua Fria plant associations and between depths within associations were analyzed at the $\alpha = 0.05$ level using analysis of variance (ANOVA) or Kruskal-Wallis tests. A posteriori comparisons were completed using Tukey's method (Sokal and Rohlf 1995) or a Nemenyi test (Zar 1999). To further assess patterns by depth in the soil, Spearman rank order correlation analysis was conducted on depth vs. mean WIS data ($\alpha = 0.05$). When $n < 12$, a table of critical values for Spearman's correlation was consulted (Ramsey 1989, Sokal and Rohlf 1995).

Differences between propagule banks of the Agua Fria and the Hassayampa River were analyzed using Welch's separate variance t-tests ($\alpha = 0.05$) (Welch 1937). Comparisons were made between similar vegetation structure types between rivers; that is, the mean number of individuals and species (total and by category) were compared between Agua Fria *Tamarix-Salix* and *Tamarix* forests and Hassayampa River *Populus-Salix* forests, and between Agua Fria *Baccharis-Bebbia* and *Hymenoclea-Bebbia* shrublands and Hassayampa *Hymenoclea* shrublands. Sorenson's similarity coefficient (Krebs 1999) was used to determine the degree of similarity in species composition between the Agua Fria and Hassayampa plant associations.

Scatter and probability plots were used to test the assumptions of homoscedasticity and normality (Sokal and Rohlf 1995). Heteroscedastic and nonnormal data were transformed using square root or log transformations. Transformed data were not analyzed if problems with heteroscedasticity could not be corrected. SYSTAT Version 8.0 was used to analyze the data (SPSS Inc. 1998).

RESULTS

Agua Fria Plant Associations

The riparian legacy was most evident in the deeper soil depths, particularly in *Tamarix* ($F_{3,8} = 7.24$, $P = 0.011$) and *Hymenoclea-Bebbia* ($F_{3,6} = 10.98$, $P = 0.008$) associations (Figure 2). There was a negative correlation between soil depth and WISs in *Tamarix* ($r_s = -0.80$, $P = 0.002$) and *Hymenoclea-Bebbia* ($r_s = -0.67$, $P < 0.05$) propagule banks, with the scores being lower in the lower soil depths. The correlation was also present in *Baccharis-Bebbia* ($r_s = -0.45$, $P = 0.138$) and *Tamarix-Salix* ($r_s = -0.26$, $P > 0.05$) propagule banks.

The distribution of propagules between remnant forest and shrubland propagule banks varied

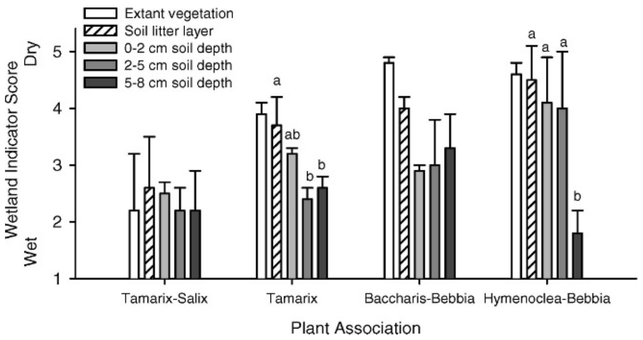

Figure 2. Mean ± SD weighted-average wetland indicator scores (WIS) per m^2 among soil depths, within *Tamarix-Salix*, *Tamarix*, *Baccharis-Bebbia*, and *Hymenoclea-Bebbia* propagule banks. Lower scores indicate greater relative contribution from wetland species. Different letters indicate significant differences by depth within associations ($P < 0.05$, ANOVA/Kruskal-Wallis). Also shown is the mean ± SD WIS per m^2 for extant vegetation.

(Table 1). Propagule density differed between associations ($F_{3,8} = 13.27$, $P = 0.002$), which was a pattern mirrored by riparian propagules ($F_{3,8} = 24.42$, $P = 0.000$). Mean WIS also varied between associations ($H_3 = 10.39$, $P = 0.016$).

Riparian species were present in propagule banks of all four plant associations, and were most abundant in *Tamarix-Salix* forests (Table 1). The majority of species (68%) and individuals (87%) in *Tamarix-Salix* propagule banks were riparian. *Tamarix-Salix* propagule banks had a lower mean WIS than shrublands (Nemenyi test, $P < 0.05$) and extant vegetation also had the lowest average WIS of all associations.

The propagule banks of *Baccharis-Bebbia* shrublands, located higher up on the floodplain and adjacent to *Tamarix-Salix* forests, contained both upland and riparian species (Table 1). Slightly more than half of the species (57%) and slightly less than half of individuals (48%) in propagule banks were riparian. In comparison to the xerophytic extant vegetation, the propagule bank was reflective of wetter conditions.

The *Tamarix* forests located farther downstream and below a berm had WISs that were somewhat drier (propagule bank and extant vegetation) than *Tamarix-Salix* forests, although the majority of species (67%) and individuals (93%) in propagule banks were riparian (Table 1). There were more propagules (for all comparisons $P \leq 0.005$), and especially riparian propagules (for all comparisons $P \leq 0.001$), in *Tamarix* propagule banks than in all other associations. *Tamarix* propagule banks had a lower mean WIS than *Hymenoclea-Bebbia* propagule banks (Nemenyi test, $P < 0.05$).

The *Hymenoclea-Bebbia* shrubland propagule banks, located farthest downstream in the dewatered floodplain, were dominated by upland species (Table 1). The propagule bank had a greater WIS than Agua Fria forests (Nemenyi test, $P < 0.05$) and *Baccharis-Bebbia* shrublands. Almost half (49%) of the species but only 21% of individuals in *Hymenoclea-Bebbia* propagule banks were riparian. The density of upland propagules was greater than other

Table 1. Species richness, mean ± SD wetland indicator score (WIS), and mean ± SD density (total and by moisture affinity) within propagule banks of *Tamarix-Salix*, *Baccharis-Bebbia*, *Tamarix*, and *Hymenoclea-Bebbia* associations at the Agua Fria River during 1998. Different superscript letters indicate significant differences among associations ($P < 0.05$, ANOVA/Kruskal-Wallis). Density and species values summed across riparian affinity categories differ from total density because some individuals could not be identified to species and grouped into categories.

	Tamarix-Salix	*Baccharis-Bebbia*	*Tamarix*	*Hymenoclea-Bebbia*
Vegetation	(species per 15 m^2)			
	7	17	14	12
Propagule bank	(species per 884 cm^2)			
Total	38	48	48	46
Riparian	26	27	32	22
Upland	12	20	16	23
Vegetation	WIS[1] (per m^2)			
	1.8 ± 1.0	4.8 ± 0.2	3.8 ± 0.4	4.9 ± 0.1
Propagule	WIS (per m^2)			
	2.1 ± 0.6^{c}	3.6 ± 0.1^{ab}	3.1 ± 0.1^{bc}	4.5 ± 0.1^{a}
Density	(individuals per m^2)			
Total	2,739 ± $1{,}139^{b}$	3,859 ± $2{,}906^{b}$	26,335 ± $11{,}222^{a}$	3,803 ± $2{,}903^{b}$
Riparian	2,388 ± $1{,}093^{b}$	1,867 ± $1{,}135^{b}$	24,491 ± $10{,}244^{a}$	781 ± 946^{b}
Upland	181 ± 257^{a}	1,245 ± $1{,}492^{a}$	1,268 ± $1{,}036^{a}$	3,350 ± $2{,}141^{a}$

[1] Data were too heteroscedastic for analysis.

Table 2. Sorenson's similarity scores between Agua Fria River and Hassayampa River forest and shrubland associations, for extant vegetation (species per 15 m^2) and propagule banks (species per 884 cm^2) during 1998. The closer Sorenson's coefficient is to 1.0, the greater the similarity.

	Extant Vegetation	Propagule Bank
Tamarix-Salix vs. *Populus-Salix* forests	0.25	0.44
Tamarix vs. *Populus-Salix* forests	0.19	0.48
Baccharis-Bebbia vs. *Hymenoclea* shrublands	0.29	0.47
Hymenoclea-Bebbia vs. *Hymenoclea* shrublands	0.21	0.48

associations, but not significantly so ($F_{3,8} = 3.09$, $P = 0.090$).

Comparisons between the Agua Fria and Hassayampa Rivers

There was relatively high similarity (Sorenson's 0.44–0.48) in species composition between propagule banks of regulated and reference forests and between regulated and reference shrublands, but lower similarity (Sorenson's 0.19–0.29) in species composition of extant vegetation for these same comparisons (Table 2). The mean species richness of propagule banks did not differ between regulated and reference forests (*Tamarix-Salix* vs. *Populus-Salix*: $t_{3.7} = 0.89$, $P = 0.426$; *Tamarix* vs. *Populus-Salix*: $t_{3.7} = -0.20$, $P = 0.853$) and between regulated and reference shrublands (*Baccharis-Bebbia* vs. *Hymenoclea*: $t_{2.0} = -0.78$, $P = 0.519$; *Hymenoclea-Bebbia* vs. *Hymenoclea*: $t_{2.0} = -0.19$, $P = 0.868$) (Table 3). The cumulative numbers of species in the propagule banks also were generally similar at the two rivers. In contrast, consistently fewer species were sampled in extant vegetation at the Agua Fria River than at the Hassayampa (Table 3).

Overall, the types of species and mean number of propagules by moisture affinity and class between reference and regulated associations were similar, but some differences existed (Tables 3, 4). Mean density of individuals in propagule banks generally did not differ between regulated and reference forests (*Tamarix-Salix* vs. *Populus-Salix*: $t_{2.4} = 0.70$, $P = 0.545$; *Tamarix* vs. *Populus-Salix*: $t_{2.4} = -3.26$, $P = 0.065$) and shrublands (*Baccharis-Bebbia* vs. *Hymenoclea*: $t_{2.9} = 1.78$, $P = 0.178$; *Hymenoclea-Bebbia* vs. *Hymenoclea*: $t_{2.9} = 1.81$, $P = 0.172$) (Table 4). *Tamarix* forest propagule banks at the Agua Fria contained more riparian species ($t_{3.5} = -3.13$, $P = 0.043$) and had more riparian individuals than the Hassayampa River *Populus-Salix* forest (Tables 3, 4). *Baccharis-Bebbia* shrublands had fewer upland propagules than the Hassayampa River *Hymenoclea* shrublands ($t_{3.7} = 3.01$, $P = 0.043$) (Table 4).

For comparisons between matched plant associations, WISs for the propagule banks and vegetation were generally similar (Table 4). Agua Fria *Tamarix-Salix* forest propagule bank WISs were lower than for the Hassayampa River *Populus-Salix* forests ($t_{3.5} = 3.18$, $P = 0.040$). Regulated shrubland WISs were similar to reference shrubland WISs; however, the mean WIS of *Baccharis-Bebbia* propagule banks was lower than that of *Hymenoclea* propagule banks ($t_{4.0} = 11.84$, $P < 0.001$).

DISCUSSION

The presence of riparian species in Agua Fria propagule banks and the similarity between Agua Fria and Hassayampa River Preserve propagule banks indicate that a riparian legacy is present at the flow-regulated and diverted Agua Fria riparian ecosystem. Many characteristics, such as species richness, propagule density, and distribution of species and individuals by moisture affinity, were similar between forest and shrubland propagule banks on the regulated and free-flowing rivers. This suggests to us that the remnant forest and shrubland propagule banks can contribute to redevelopment of a floristically and functionally diverse plant assemblage should perennial flow and flood pulses be restored to the Agua Fria River.

Riparian Legacies

A relatively rich riparian legacy has been preserved in propagule banks of Agua Fria floodplain forests. Both forest propagule banks were species-rich, but vegetation in these associations was species-poor. It is unlikely that ongoing seed production and storage can explain the high number of riparian species in these propagule banks. Many environmental factors can be altered in river reaches downstream of flow-regulating dams, and many of these changes can lead to reduced plant species diversity. For example, soil salinity is probably higher than in free flowing riparian ecosystems as the infrequent flooding allows for the build up of ions in the soil profile (Busch and Smith 1995).

Table 3. Extant vegetation and propagule bank species richness of floodplain forests and shrublands at the Agua Fria and Hassayampa Rivers during 1998. Different superscript letters indicate significant differences in mean ± SD species richness between paired Agua Fria and Hassayampa River forests and shrublands, within rows ($P < 0.05$, t-test).

	Forest Associations			Shrubland Associations		
	Agua Fria River		Hassayampa River	Agua Fria River		Hassayampa River
	Tamarix-Salix	*Tamarix*	*Populus-Salix*	*Baccharis-Bebbia*	*Hymenoclea-Bebbia*	*Hymenoclea*
Vegetation (species per 15 m^{2})	7	14	17	17	12	25
Propagule bank (species per 884 cm^{2})	38	48	53	48	46	38
Propagule bank (mean species per 295 cm^{2})						
All species	21 ± 12^{a}	30 ± 7^{a}	29 ± 9^{a}	26 ± 16^{a}	21 ± 18^{a}	19 ± 1^{a}
Riparian species	15 ± 7^{a}	21 ± 2^{b}	16 ± 2^{a}	13 ± 7^{a}	9 ± 10^{a}	12 ± 1^{a}
Upland species	4 ± 6^{a}	7 ± 5^{a}	14 ± 7^{a}	10 ± 8^{a}	10 ± 6^{a}	9 ± 3^{a}

While *Tamarix* and various herbaceous halophytes can successfully germinate and establish in saline soils, many other riparian species cannot and thus species richness can be low in saline floodplains (Shafroth et al. 1995, Salinas et al. 2000, Vandersande et al. 2001). Additionally, the deep shade and dense litter layer that has developed in the *Tamarix-Salix* forests likely contribute to low species richness by precluding establishment in the understory (Xiong and Nilsson 1999).

The presence of riparian species in the Agua Fria xerophytic shrublands also appears to be a legacy of pre-dam conditions. Current abiotic conditions of the Agua Fria shrublands are not conducive to the establishment and seed set of riparian species as they need moist soils during the majority of the growing season (Penfound 1952), thus riparian species present in propagule banks are not from ongoing seed input from the current flora. The riparian species were most abundant in the deeper soil layers of the shrublands suggesting that they are older than the seeds in the litter and shallow soil. Some of the deeply buried riparian species, which were not found in extant vegetation of any Agua Fria association, are from genera such as *Cyperus* and *Nicotiana* that are known to remain viable for over a century (Leck and Schutz 2005). They may have been present in the associations for relatively long time periods (Espinar et al. 2005).

Stream Flow Management

It is possible that some propagules in the shrublands and forests emigrated from above-dam reaches

Table 4. Mean ± SD extant vegetation and propagule bank WIS, and mean ± SD propagule density (total and by moisture affinity) between paired Agua Fria and Hassayampa River floodplain forests and shrublands during 1998. Different superscript letters indicate significant differences between paired Agua Fria and Hassayampa River forests and shrublands, within rows ($P < 0.05$, t-test).

	Forest Associations			Shrubland Associations		
	Agua Fria River		Hassayampa River	Agua Fria River		Hassayampa River
	Tamarix-Salix	*Tamarix*	*Populus-Salix*	*Baccharis-Bebbia*	*Hymenoclea-Bebbia*	*Hymenoclea*
Vegetation WIS (per m^{2})	1.8 ± 1.0^{a}	3.8 ± 0.2^{a}	3.1 ± 0.9^{a}	4.8 ± 0.2^{a}	4.9 ± 0.1^{a}	4.8 ± 0.2^{a}
Propagule WIS (per m^{2})	2.1 ± 0.6^{b}	3.1 ± 0.1^{a}	3.5 ± 0.4^{a}	3.6 ± 0.1^{b}	4.5 ± 0.5^{a}	4.5 ± 0.1^{a}
Density (individuals per m^{2})						
Total	2,739 ± 1,139^{a}	26,335 ± 11,222^{a}	4,229 ± 3,507^{a}	3,859 ± 2,906^{a}	3,803 ± 2,903^{a}	7,164 ± 1,395^{a}
Riparian	2,388 ± 1,093^{a}	24,491 ± 10,244^{a}	2,101 ± 1,209^{a}	1,867 ± 1,135^{a}	781 ± 946^{a}	1,596 ± 530^{a}
Upland	181 ± 257^{a}	1,268 ± 1,036^{a}	2,082 ± 1,188^{a}	1,245 ± 1,492^{b}	3,350 ± 2,141^{a}	5,544 ± 1,971^{a}

via hydrochory during the rare water releases into the Agua Fria channel but the magnitude of such replenishment likely is small. Storage reservoirs can become depauperate in species and dams can impede seed movement (Nilsson and Jansson 1995, Nilsson et al. 1997, Middleton 1999, Dynesius et al. 2004). Merritt and Wohl (2006) reported that seed concentration in water downstream from dams was reduced by 70%–94% compared to that in free-flowing reaches.

Dam releases may also stimulate germination of some riparian species and allow some replenishment of the riparian propagule bank. However, at distances of several kilometers downstream from the dam, it is likely that the zone of wetted soils was restricted to a narrow band along the low-flow channel. If so, such releases would not have replenished riparian propagule banks across the floodplain.

Potential for Vegetation Development: Role of the Propagule Bank

The remnant propagule banks of the Agua Fria forests and shrublands can contribute to restoration or reclamation of the herbaceous component of riparian plant associations. The banks contain propagules of a subset of species, mainly herbaceous species that produce persistent propagules. Consequently, while remnant propagule banks can contribute to herbaceous restoration as suggested by other studies on wetlands (Brown 1998, Wetzel et al. 2001, Combroux et al. 2002, Smith et al. 2002), they may not contribute to the restoration of many of the woody and herbaceous species that produce transient propagules. A restoration approach that combines the introduction of species that produce transient propagules via introduced seed sources and/or transplantation, as well as including the contribution of propagule banks, could result in a more successful restoration.

The capacity of the Agua Fria propagule banks to contribute to re-establishment of herbaceous riparian vegetation varies spatially, with some associations harboring more riparian species than others, and some harboring the propagules more deeply in the soil. Should the flow regime be naturalized, flood-pulse metacommunity dynamics would mobilize sediment, expose buried riparian propagules, and redistribute the propagules from various plant associations widely across the floodplain (Boudell and Stromberg 2008). Collectively, the range of species present across the floodplain would allow for high resilience, by allowing for 'matching' of species to the new environmental conditions created by the return of the naturalized flow regime.

The riparian legacy preserved in Agua Fria propagule banks that could contribute to the restoration of the floodplain may be declining, particularly in the shrublands. Most of the below-dam Agua Fria floodplain now supports shrublands vegetated by xeroriparian species typical of dry (emphemeral-flow) streambeds and the propagule banks of these areas reflects the conversion of hydromesic riparian vegetation to xerophytic species. In these shrublands, individuals capable of surviving the dry conditions are driving propagule bank dynamics through local seed input. The decline in riparian propagules is most evident in *Hymenoclea-Bebbia* shrublands, which are located the farthest downstream of the dam and furthest from dam seepage and input from Morgan City Wash. The number of riparian propagules, which were found in the deepest soil layer sampled, is low in comparison to *Hymenoclea* shrublands of the Hassayampa River. As found in other remnant wetlands, the legacy will diminish overtime as propagules lose viability (Wienhold and van der Valk 1989), with few, if any, riparian species in extant vegetation left to replenish propagule banks, and with no guarantee of future flood pulses that may supplement propagule banks.

CONCLUSIONS

In the below-dam, partially dewatered Agua Fria riparian ecosystem, the forest and shrubland propagule banks contain a riparian legacy. If perennial flow is restored, a hydromesic riparian ecosystem will develop, which will be a reflection of the former free-flowing river condition, current impounded river conditions, and any revegetation efforts undertaken. With increasing passage of time without water, however, the riparian legacy will diminish. Along the Agua Fria, the conversion of hydromesic forest to xerophytic shrubland, ongoing loss of viability of remnant riparian propagules, and reduced input of new riparian propagules will lead to the decline in the ability of the propagule banks to contribute to the re-establishment of riparian herbaceous vegetation should river flows be restored.

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