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A large-scale environmental flow experiment for riparian restoration in the Colorado River Delta

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A B S T R A C T

Managing streamflow is a widely-advocated approach to provide conditions necessary for seed germination and seedling establishment of trees in the willow family (Salicaceae). Experimental flow releases to the Colorado River delta in 2014 had a primary objective of promoting seedling establishment of Fremont cottonwood (*Populus fremontii*) and Goodding's willow (*Salix gooddingii*). We assessed seed germination and seedling establishment of these taxa as well as the non-native tamarisk (*Tamarix* spp.) and native seepwillow shrubs (*Baccharis* spp.) in the context of seedling requirements and active land management (land grading, vegetation removal) at 23 study sites along 87 river km. In the absence of associated active land management, experimental flows to the Colorado River delta were minimally successful at promoting establishment of new woody riparian seedlings, except for non-native *Tamarix*. Our results suggest that the primary factors contributing to low seedling establishment varied across space, but included low or no seed availability in some locations for some taxa, insufficient soil moisture availability during the growing season indicated by deep groundwater tables, and competition from adjacent vegetation (and, conversely, availability of bare ground). Active land management to create bare ground and favorable land grades contributed to significantly higher rates of Salicaceae seedling establishment in a river reach with high groundwater tables. Our results provide insights that can inform future environmental flow deliveries to the Colorado River delta and its ecosystems and other similar efforts to restore Salicaceae taxa around the world.

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1. Introduction

River and floodplain environments include some of the most highly valued but also severely degraded ecosystems globally. They are subject to a variety of anthropogenic perturbations, including dam construction, flow diversions, and channelization, and are heavily used for agriculture, transportation, and municipal and industrial development (Gregory, 2006). In particular, regulation of flow and sediment regimes by dams has led to profound changes to associated physical and biological systems in and along rivers (Nilsson et al., 2005; Poff et al., 2007; Wohl et al., 2015). River-dependent ecosystems frequently support high levels of biodiversity and threatened taxa relative to adjacent uplands (Soykan et al., 2012), and conservation of this diversity is a common driver of efforts to restore degraded river and riparian ecosystems (Gonzalez et al., 2015).

In many regions around the world, native floodplain forests historically dominated by trees and shrubs in the Salicaceae family (willows (*Salix* spp.)) and cottonwoods (poplars; (*Populus* spp.)) have high conservation value (Gonzalez et al., 2015; Karrenberg et al., 2002). Decline of *Populus* spp. forests has been noted on rivers in Europe (Gonzalez et al., 2010), Asia (Liu et al., 2005), and North

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America (Johnson et al., 2012; Rood and Mahoney, 1990) and often has been attributed to adverse effects of dams and flow regulation on seedling recruitment.

A strong understanding of the biophysical requirements for successful seed germination and seedling establishment of *Populus* and *Salix* spp. has emerged from results of numerous field (Cooper et al., 2003; Scott et al., 1996), laboratory (Mahoney and Rood, 1991; Segelquist et al., 1993; Stella et al., 2010), and modeling (Dixon and Turner, 2006; Harper et al., 2011) studies. Here, we define seedling establishment as the result of successful germination, survival and growth for one growing season. The full set of requirements for these pioneer taxa (i.e., early colonizers of bare soil following disturbance) includes conditions necessary for seed germination and subsequent conditions necessary for survival and growth of germinants to the seedling stage, or, conversely, conditions that are likely to decrease seedling survival or growth (Bloodworth et al., 2016; Harper et al., 2011; Shafroth et al., 1998). Pioneer woody riparian plants other than *Populus* and *Salix* (such as *Tamarix* and *Baccharis* in western North America) have some overlapping seedling establishment requirements (Horton and Clark, 2001; Shafroth et al., 1998).

Many of these required conditions are produced by processes typically associated with streamflow (Cooper et al., 1999; Mahoney and Rood, 1998; Scott et al., 1996; Stromberg et al., 2007a). Bare, moist mineral substrate are required for germination (Cooper and Andersen, 2012), and high flows can create these ideal seed beds through channel change, bar creation, and inundation. Natural timing of floods is often coincident with seed dispersal periods of riparian pioneer species. For subsequent seedling survival and growth, seedlings require access to moist soil throughout the growing season (Cooper et al., 1999; Mahoney and Rood, 1998). Following a flood peak, flow recession exposes substrate and, if gradual enough, maintains sufficient soil moisture as seedling roots elongate. Later in the growing season, alluvial groundwater tables are often maintained at relatively shallow levels by low or base flows, again supplying moisture to new seedlings' roots. Additional requirements include protection from significant flooding while plants are still small (Auble and Scott, 1998; Cooper et al., 1999), relatively low soil salinity (Glenn and Nagler, 2005), low competition from adjacent vegetation (Stromberg et al., 1991; Cooper et al., 1999), and low herbivory (Cooper and Andersen, 2012).

Reducing the abundance of the non-native *Tamarix* relative to *Populus* and *Salix* is a very common riparian management objective in western North America (Shafroth and Briggs, 2008). Although *Tamarix*-dominated riparian vegetation is a component of suitable habitat for various wildlife (Bateman and Paxton, 2010; Sogge et al., 2008; Van Riper et al., 2008), habitat dominated by *Populus* and *Salix* is superior for some wildlife taxa (Hinojosa-Huerta et al., 2013). High levels of flow regulation have been shown to disfavor *Populus* and *Salix* but have little or even a positive effect on *Tamarix* (Merritt and Poff, 2010; Mortenson and Weisberg, 2010; Stromberg et al., 2007b).

Given the strong understanding of the linkages between streamflow and Salicaceae seedling establishment, and the effects of flow regulation on the relative abundance of *Tamarix* vs. Salicaceae taxa, efforts to increase *Populus* and/or *Salix* recruitment in a restoration context often include management of streamflow and associated fluvial processes (Gonzalez et al., 2015; Rood et al., 2005). In western USA, several case studies have demonstrated the efficacy of this approach (Rood et al., 2003, 2005; Wilcox and Shafroth, 2013) both to achieve restoration objectives and to help clarify flow–ecological response relationships through large-scale flow experiments (Konrad et al., 2011; Olden et al., 2014).

However, managed flows (or "environmental flows" in this context, *sensu* Acreman and Dunbar, 2004) can be limited by factors such as water availability, dam outlet works capacity, or human infrastructure within the river bottomland, and therefore may not always be of sufficient quality or quantity to produce the desired functions and fulfill establishment requirements. In these cases, it is possible to combine active land management with flow releases to produce conditions conducive to seedling establishment. For example, mechanically clearing vegetation to create bare substrate, in addition to providing suitable hydrologic conditions, can lead to successful Salicaceae seedling establishment (Cooper and Andersen, 2012; Taylor et al., 1999).

Here, we report results of experimental flow releases conducted in spring and summer 2014 on the lower Colorado River and its delta in Mexico and the U.S. that were part of Minute 319, a historic bi-national Colorado River water management agreement between Mexico and the United States (Flessa et al., 2013; International Boundary and Water Commission (IBWC), 2012; Pitt and Kendy, 2017). Although Minute 319 did not specify environmental goals or flow patterns, working groups of scientists and water managers recommended a set of high and low flow releases that had a primary objective of promoting germination and establishment of two Salicaceae species: *Populus fremontii*, and *Salix gooddingii* (Pitt and Kendy, 2017). For an 87 km-long stretch of the river, we report patterns of germination and first-year establishment of these species plus two other woody riparian taxa common in the study area (the non-native *Tamarix* spp., and native *Baccharis* spp.; hereafter *Tamarix* and *Baccharis*) and assess the extent to which experimental flows as well as active land management helped to provide the conditions that promote pioneer woody riparian seedling establishment. We base our analysis of the effects of the experimental flows and active land management on riparian plant recruitment on a conceptual model of conditions or processes that fulfill requirements for seed germination and seedling establishment of Salicaceae species (Fig. 1), aspects of which also apply to *Tamarix* and *Baccharis*.

Our work also examined several specific hypotheses:

- High flow releases will create significant areas of bare, moist sediment.
- Woody riparian seed germination will occur where there is available seed and exposure of bare, moist sediment.
- The rate of flow and associated alluvial groundwater recession following the peak of the experimental flow hydrograph will be gradual enough to allow survival and growth following germination.
- Seedling establishment will be (1) highest where low flow releases continue throughout the growing season and shallow alluvial groundwater tables are maintained, and (2) lowest where low flow releases are not sustained throughout the growing season, and where alluvial groundwater tables are deepest.
- High flows will lead to a reduction of soil salinity where inundation occurs.
- Seedling establishment will be lower where there is higher cover of other riparian vegetation.
- Active land management to create bare ground and reduce competition will be associated with higher rates of seedling establishment compared to unmanaged areas.

2. Materials and methods

2.1. Study area

The study area was within the most downstream reaches of the Colorado River, the master drainage of interior western North America, which supplies water to seven states in the U.S. and two in Mexico. The study area included much of the Colorado River delta riparian corridor, beginning at Morelos Dam at the U.S.–Mexico
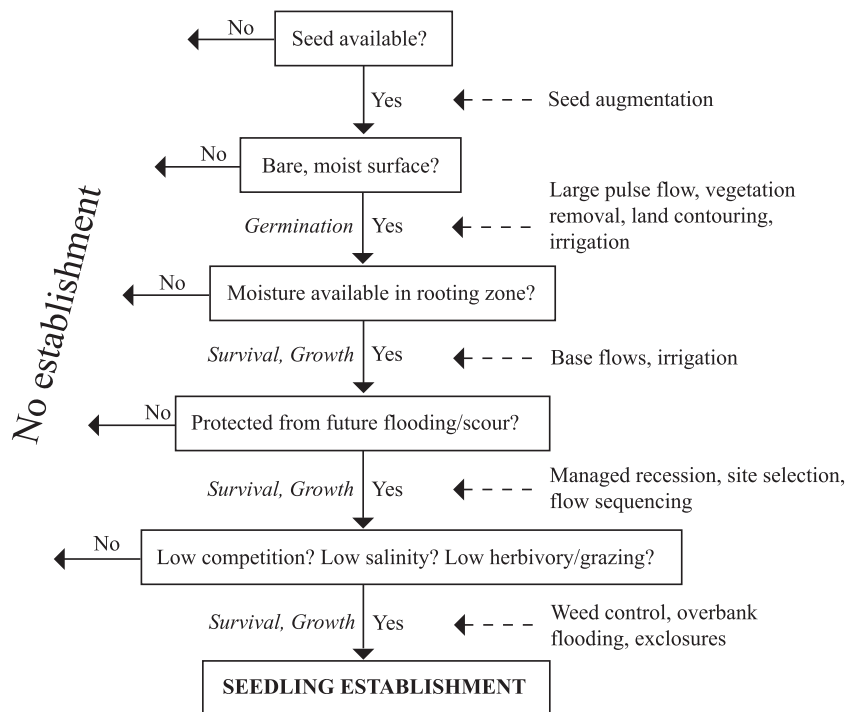
Fig. 1. Key requirements for germination and establishment of pioneer riparian trees and shrubs in the Salicaceae family. Requirements are described inside the boxes in the form of questions and are presented sequentially. If a requirement is met ("yes"), then germination, survival, or growth occurs and the next requirement is examined (downward facing arrows). If a requirement is not met ("no"), then no establishment is likely (solid arrows facing left). Management actions that might enable a requirement to be met are indicated on the right side of the figure, with dashed arrows pointing to the condition or requirement addressed by the management action.

border and extending downstream approximately 87 km (Fig. 2). Study sites were in bottomland areas with natural vegetation and channels, confined between levees that protect adjacent agricultural land or municipalities. Bottomland width between the levees ranged between 500 and 3000 m. The Colorado River channel continues another 70 km downstream of the study area to its terminus in the Gulf of California. The study area is in the most arid subdivision of the Sonoran Desert (Shreve and Wiggins, 1964): mean annual temperature recorded at a nearby weather station during the last 20 years ranged from 21.9 to 23.7 °C, average maximum temperatures in July ranged from 38.8 to 43.3 °C, and mean annual precipitation was 60.4 mm (Yuma Valley station, 1995–2015, The Arizona Meteorological Network, http://ag.arizona.edu/azmet/). Evapotranspiration rates in the study area are estimated to be 1.1–1.2 m/year (Nagler et al., 2008).

The streamflow regime in the study area has been dramatically altered by the construction of numerous dams upstream and diversions of water for agricultural and municipal uses (Mueller et al., 2017). In particular, after completion of Hoover Dam in 1934 and Glenn Canyon Dam in 1964 the historical annual water volume flowing to the delta (~18 billion m^3) and sediment transport declined significantly (Woodhouse et al., 2006; Zamora et al., 2013). Flows large enough to result in overbank flooding and channel change have only occurred a few times in recent decades (in particularly wet years with high discharges in the Colorado and Gila rivers upstream of Morelos Dam; Mueller et al., 2017). In most years, all flow is diverted for agricultural, municipal, and industrial use prior to reaching the historic delta, resulting in channel and floodplain desiccation.

The study area included four reaches of the river, distinguished by differences in surface and groundwater hydrology, distance downstream from Morelos Dam, and existing riparian vegetation at the beginning of our study (Fig. 2). The first reach, "Perennial Limitrophe" (PL), extended approximately 20.7 river km downstream from Morelos Dam and was characterized by perennial

surface water flow and a high alluvial groundwater table due to seepage from Morelos Dam and seepage from agricultural irrigation (Ramírez-Hernández et al., 2013). This reach supported stands of mixed riparian vegetation including native trees (*P. fremontii* and *S. gooddingii*), the non-native shrub *Tamarix*, and native shrubs (*Pluchea sericea*, *Baccharis salicina*, *B. salicifolia*) (Zamora-Arroyo et al., 2001). Along much of this reach, channel banks were lined with dense stands of giant cane (*Arundo donax*) and common reed (*Phragmites australis*).

The next reach downstream, "Ephemeral Limitrophe" (EL), extended for approximately 13 river km to slightly south of the Southerly International Boundary, where the km 27 spillway enters the river channel. This reach was characterized by strongly influent or "losing" flow conditions where surface flow rapidly infiltrates the subsurface alluvium. This condition was exacerbated by significant groundwater pumping in the area and a notable groundwater cone of depression (Ramírez-Hernández et al., 2015). As a result, water tables were deep (4.38–11.95 m maximum in 2014), and the channel was typically dry, relatively wide, and sandy. However, there was some longitudinal variation in this reach, with presence of occasional, remnant native trees in the upstream section. Farther downstream, floodplains were dominated by *Tamarix*, which can tolerate deeper groundwater, with almost no Salicaceae trees present (Zamora-Arroyo et al., 2001).

The third reach, "Ephemeral Delta" (ED), extended from the km 27 spillway downstream 29.5 km. This reach was similar to the downstream sections of the "Ephemeral Limitrophe" reach, with deep alluvial groundwater tables (5.07–16.96 m maximum in 2014) and sparse, *Tamarix*-dominated riparian vegetation. A distinguishing feature of this reach was that some experimental low flows were delivered into the channel at km 27 during the study period (Fig. 2).

The next reach, "Perennial Delta" (PD) extended 26.4 km and was characterized by high water tables and surface water in the channel throughout most of its length for most of the year. In this
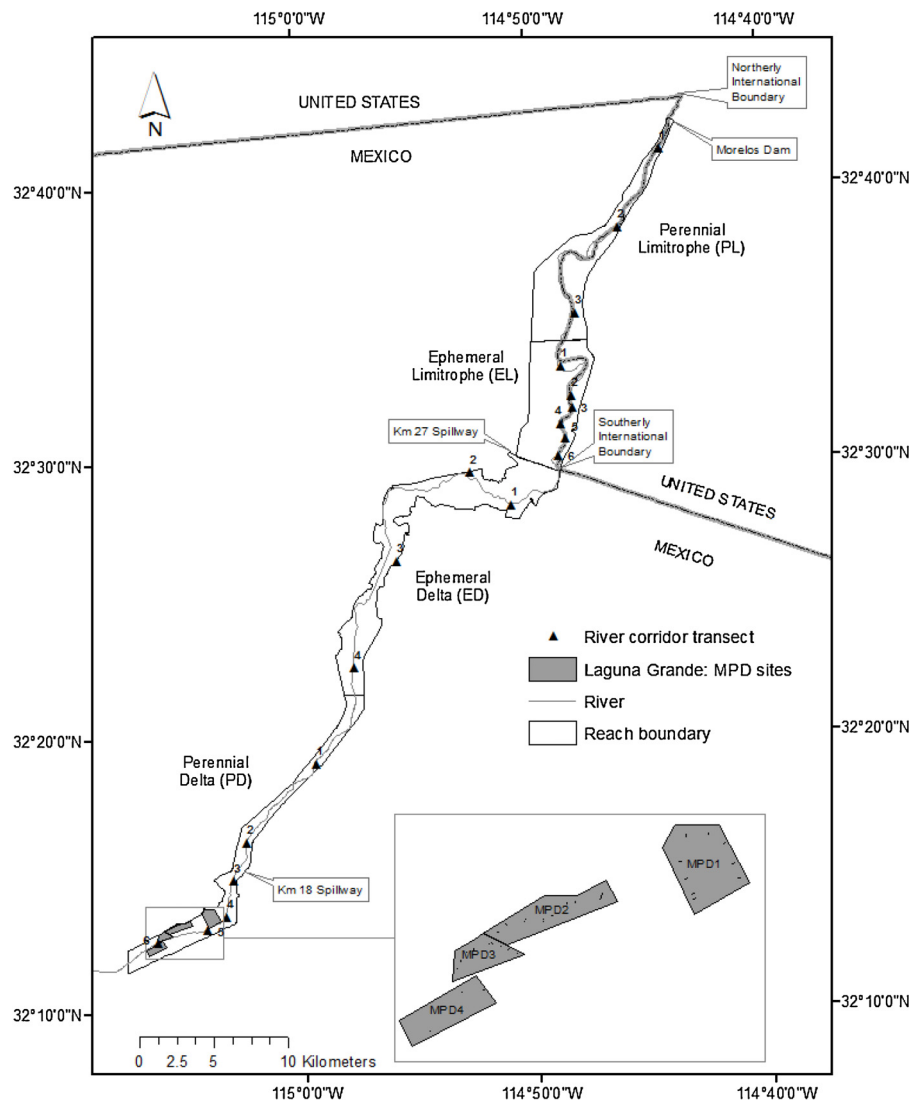
Fig. 2. Study site locations, including unmanaged river corridor transects and actively managed areas (Laguna Grande: MPD sites).

reach surface and groundwater dynamics were typically driven by irrigation return flows (Ramírez-Hernández et al., 2015). The high water table supported stands of native trees and shrubs (Zamora-Arroyo et al., 2001; Nagler et al., 2005; Nagler et al., 2009). During 2014, the PD received surface water from experimental flow releases at Morelos Dam, km 27 spillway, and another spill-way, km 18, which enters the channel 15.3 km downstream of the ED/PD reach boundary. Several large-scale, actively managed ripar-ian restoration sites were located within the Perennial Delta reach in an area known as Laguna Grande. We treated the Laguna Grande area as a distinct reach, the "Managed Perennial Delta" (MPD).

Note that the reach boundaries for our Perennial Limitrophe, Ephemeral Limitrophe, and Ephemeral Delta reach differ slightly from those described by others (Jarchow et al., 2017a,b; Nelson et al., 2017) as Reach 1, Reach 2, and Reach 3. Our boundaries for Perennial Delta are the same as Reach 4 as described by these other authors.

2.2. Experimental flow releases

Experimental flows were released from March 23 to April 18, 2014 through Morelos Dam, April 13 to May 2 through the km 27 spillway, and from May 3 to the end of October through the km 18

spillway (Fig. 3). High flows were released through Morelos Dam, with a peak discharge of 119 m^3/s on March 29, and a flow recession until April 18 when releases stopped. Releases from km 27 had a peak discharge of 23.8 m^3/s on April 27, and additional releases from km 18 spillway had a peak of 9.7 m^3/s on May 9 (Fig. 3). A total flow volume of 5.1 Mm^3 was delivered through Morelos Dam from September 5 to September 10, 2014. An additional 6.7 Mm^3 was delivered via km 18 spillway as low flows between May 18 and the end of October 2014 (exact dates and flow rates not available). Finally, some additional low flow releases were made from various delivery points within the Laguna Grande area after May 18, 2014 (exact dates, volumes, and flow rates not available).

The timing and maximum extent of inundation from the exper-imental flow releases were estimated by Nelson et al. (2017). The high flow release from Morelos Dam that started on March 23 inun-dated the PL reach the same day. In the following days from March 24 to March 26 the water front moved through the EL, and through the ED from March 27 to April 1. From April 2 to April 7 the water front moved through the PD reach. The km 18 flow releases in May inundated portions of the Laguna Grande sites (MPD reach) and some areas along the unmanaged river corridor in the PD reach. Releases from delivery points within the MPD also inundated some areas after May 18.
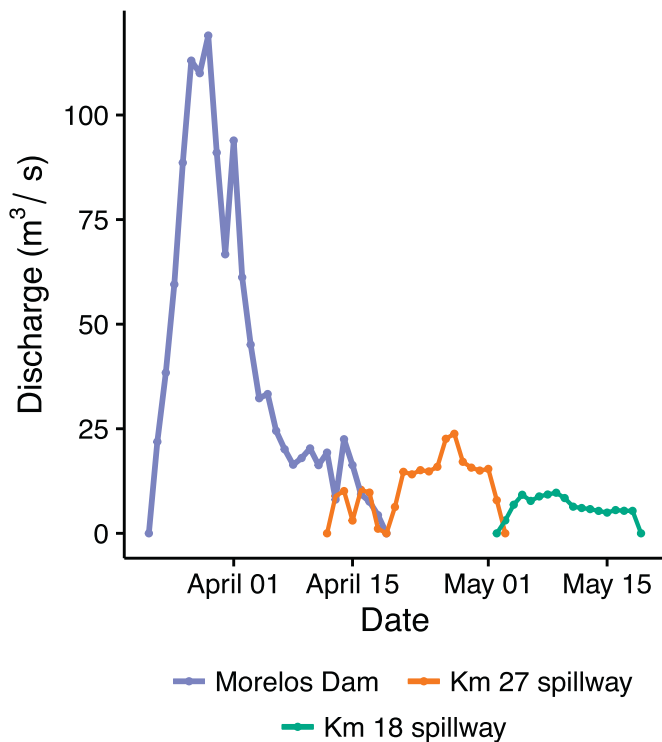
Fig. 3. Experimental flow release hydrographs during 2014. Flows were released from three distinct delivery points (see text and Fig. 2).

The maximum inundation in reaches PL, EL and ED occurred during the week of March 31 in response to deliveries from Morelos Dam. A second peak in the extent of inundation was observed during the week of May 2 in ED, likely in response to deliveries from km 27. In the PD reach the maximum inundation also occurred during the week of May 2. By the end of May, surface water returned to close to pre-flow conditions in the ephemeral reaches but was still 50% and 100% higher than pre-flow conditions in PL and PD, respectively.

During the high flow release, the alluvial groundwater table rose several meters mostly in the PL, EL, and ED reaches; however, groundwater levels returned to pre-release levels by the fall of 2014 (Kennedy et al., 2017). In the PD reach, where water tables are consistently high, groundwater levels were not strongly affected by the March–May releases (Rodríguez-Burgueño et al., 2017). The flow release from Morelos Dam in September resulted in surface water flow in the first two reaches downstream of the dam (PL and EL) and a small rise in groundwater levels for a short duration (Rodríguez-Burgueño et al., 2017).

2.3. Field and statistical methods

2.3.1. Study sites
2.3.1.1. *Unmanaged river corridor transects.* We assessed riparian seedling recruitment and several conditions related to seed germination and seedling establishment along 19 river corridor transects in the four study reaches, spanning river km 2–87. Three, six, four and six transects were in the PL, EL, ED, and PD reaches, respectively. To relate vegetation responses to experimental flow hydrology, we co-located transects with pre-existing groundwater monitoring sites and frequently with river stage monitoring sites. Transect locations were in areas without active vegetation or channel management. Transects were oriented perpendicular to the direction of flow in the main channel, crossed the primary natural flow channels, and extended above estimates of the highest stage associated

with the peak of the experimental flow release. Transect length varied depending on channel and floodplain morphology, ranging from 60 to 417 m.

2.3.1.2. *Actively managed sites.* To help increase the availability of bare, moist surfaces with little competition from existing vegetation, sites in the Laguna Grande area within the Perennial Delta reach (MPD) were actively managed prior to the experimental flow releases. Site preparation occurred in places that were predicted to be inundated by experimental flows based on a one-dimensional hydraulic model (HEC-RAS; Hydrologic Engineering Center, Davis, CA, USA). Management actions included: (1) mechanical removal of *Tamarix* and *P. sericea* from 129 hectares (ha) using heavy equipment; (2) excavation to reconnect three former channel meanders (hereafter, "meanders") with the Colorado River main stem; (3) excavation to connect portions of six former channel meanders with each other; and (4) land grading and contouring to maximize the extent of inundation.

We established vegetation transects within four sites along historic river meanders, distinguished from each other based on differences in site hydrology. Site MPD1 is a historic river meander and is farthest upstream. This site received incidental flows from the river channel due to experimental flows, but no experimental flows were delivered directly to the site. Site MPD2 is mostly disconnected hydraulically from the main channel and therefore received relatively little incidental flow from the river. However, the site received direct experimental low flow inputs from a local delivery point. Site MPD3 is highly connected to the main river channel and also received significant experimental low flow inputs from the MPD2 delivery location. MPD4 is also highly connected to the river channel, and was affected by experimental flows entering from the main channel, MPD3 deliveries, and lower-volume, on-site flow deliveries. Specific information on the dates, volume, and flow rates for these local flow deliveries was not available.

Within each site, we established between five and nine belt transects (nested 1 m and 4 m wide) oriented perpendicular to meander channels (MPD1: *n* = 9 transects; MPD2: *n* = 9; MPD3: *n* = 9; MPD4: *n* = 5). Transects started at the water's edge where surface water was present, or at the bottom of the meander channel if surface water was no longer present, and extended to just above the area that was inundated by high flow releases. Within a site, transects were spaced approximately every 400 m. We treat transects as sub-samples and report and analyze data at the site level.

2.3.2. Seedling and vegetation responses
To assess vegetation change and seedling recruitment along the river corridor transects, we strung a measuring tape along each transect and recorded the length along the line intersected by all vascular plants, litter, and water (line-intercept method; Canfield, 1941). We refer to woody plants that germinated following the experimental flow releases as "seedlings". Line-intercept sampling occurred in March, May, and October 2014. Several rebar stakes were placed along transects to enable precise relocation.

We conducted more extensive surveys for the presence of seedlings of several target species (*Baccharis* spp. – seepwillow or willow baccharis; *P. fremontii* – Fremont cottonwood; *S. gooddingii* – Goodding's willow; *Tamarix* spp. – tamarisk, saltcedar) within 1 m – (March, May, and October) and 20 m –wide belt transects (October only). Similar to the line-intercept measurements (above), we noted the length along transects containing seedlings within these belts. We calculated "transect occupancy" for seedlings, by species, defined as the percent of the transect length with seedlings.

In the MPD, we recorded the number and length interval of woody seedlings in both a 1 m- and 4 m-wide transect. We recorded cover of woody seedlings, new herbaceous, and pre-existing woody vegetation within the 4 m-wide transect. Transects were moni-

tored once in August 2014 for the presence of native tree and shrub seedlings. Detailed surveys were conducted in October 2014, and additional observations of germination and early establishment were noted during several site visits made in May–August.

2.3.3. Conditions required for seedling recruitment

For the 19 river corridor transects and 4 actively managed sites, we estimated to what extent conditions associated with successful seed germination and subsequent seedling survival and growth (Fig. 1) were met using field measurements whenever possible, and hydrologic models in some cases. For germination, requirements are the coincident availability of viable seed and bare, moist substrate. For subsequent establishment, requirements include availability of moist soil in the rooting zone, protection from future flooding, and low levels of competition, soil salinity, and herbivory.

2.3.3.1. Germination: seed availability.
Seed dispersal of the 4 target taxa was observed at all river corridor transects and actively managed restoration areas using two methods between February 26 and June 18, 2014. At most sites, 1 or 2 seed traps were placed above the expected maximum inundation point. Seeds landing on the traps were identified to species and counted approximately every 2 weeks. Traps consisted of a 0.6 m × 0.6 m (2 ft × 2 ft) plywood board coated with Tree Tanglefoot (Tanglefoot®, Contech Enterprises, Inc., Grand Rapids, MI) insect trapping material. Following each sampling event, seeds and Tanglefoot were scraped from the plywood board and a new coat of Tanglefoot was applied. The second method was an estimate of the number of individuals of each of the four target taxa that were dispersing seed and the relative abundance of seed dispersal within a ca. 200 m-wide belt centered on each transect. Because of differences in the timing and frequency of site visits, personnel, and numbers of seed traps per transect, we used a conservative measure of seed dispersal for our analysis here – simply a weekly presence or absence of dispersing seed by species (for *Populus*, *Salix*, *Tamarix*, and *Baccharis*) between February 26 and June 18, 2014, and an overall seasonal, relative abundance (four levels: zero, low, medium, high). Additionally, we made anecdotal observations of seed dispersal throughout the growing season in the MPD.

2.3.3.2. Germination: availability of bare, moist substrate during seed dispersal period.
Assessing the availability of bare, moist substrate during the seed dispersal period required combining information from a continuous estimate of surface water elevation (river stage) along each transect, an estimate of bare ground along each transect, and the seed dispersal timing information described above. Detailed topographic surveys along each river corridor transect were critical for integrating river stage data with transect topography and locations of bare ground. Surveying was completed using a Real Time Kinematic Global Positioning System (RTK-GPS) with estimated horizontal (x–y) and vertical (z) resolution of <3 cm. These surveys were conducted in March, prior to the high flow releases, and in May, after the releases.

For river corridor transects, the length intervals along the transect consisting of bare ground were derived from the line intercept data, and the horizontal position and elevation of these bare areas were tied to the RTK-GPS topographic surveys. We converted these values at each transect to the percentage of the inundated area that was bare. To evaluate our hypothesis that the pulse flow would create significant areas of new bare ground, we conducted paired one-sided t-tests for reaches PL, EL, ED, and PD on the arcsine square root transformed difference between March and May percent bare ground (R package 'stats', version 3.2.4).

Availability of moist substrate was estimated by identifying the portions of each transect that were inundated and then exposed by receding flow. Daily river stage data were collected between March

23 and May 22 at 25 sites along the river channel between river km 1 and 88. To estimate inundated areas between the 25 sites, we created a continuous water surface elevation grid, based on a linear interpolation of water surface elevations between measuring stations. Stage hydrographs were generated at the 19 river corridor transect locations by overlaying the daily stage data on the RTK-GPS topographic profiles of each transect.

We combined these estimates into a simple model to predict on which river corridor transects germination should occur for each of the four target plant taxa. The availability of bare, moist substrate was reconstructed at each river corridor transect at weekly intervals between March 23 and May 22, beginning 1 week after the peak of the experimental flow release at each site. This information was compared to the timing of seed dispersal observations (above), by species. If all three conditions were met (bare substrate, moist substrate, and seed available), the requirements for germination were assumed to have been met. To assess the strength of this germination model, we created a 2 × 2 contingency table for each species, with predictions from the model comprising one set of values in the table, and observed germination in May (from the 1 m belt transects) comprising the others. We conducted an unconditional two-tailed Boschloo's exact test on each contingency table (R package 'Exact', version 1.6).

Along the managed transects in the Laguna Grande area, vegetative cover was recorded in October 2014. Percent bare substrate was calculated by subtracting the visually estimated existing vegetation percent cover (excluding seedlings established in 2014) observed in October 2014 from 100. Surface flow volumes in Laguna Grande were not great enough to cause vegetation scour or sediment erosion and deposition; thus, we assumed that environmental flows did not create new bare surfaces and that existing vegetation and bare soil cover in October 2014 were approximately representative of cover in March 2014. River stage data were not available for MPD1–MPD4; therefore, we could only determine that moist substrate conditions were present at various times during periods of seed dispersal but not the exact timing of the presence of moist substrate.

2.3.3.3. Establishment: available soil moisture.
We estimated two indirect measures of available soil moisture in the rooting zone at the transect scale: (1) the maximum 2-week average groundwater recession rate that followed period(s) when seed germination was possible (cm/d, when moist, bare soil and seed were available); and (2) maximum 1-week average depth to groundwater (m) during the growing season following the high experimental flow release (May–October). To estimate both of these measures of soil moisture for the river corridor transects, we used depth to the water table measurements from piezometers located 50–200 m from transects. Some piezometers were equipped with transducers that recorded daily data; others were manually measured approximately every 2 weeks. Depth to groundwater was related to the ground surface elevation along transects by linking topographic survey data from transects and elevation data of each piezometer. Recession rate was calculated as the weekly average change in water table level during the growing season. Maximum depth to groundwater was calculated as the deepest weekly average below the topographic mid-point of the transect (the average of the lowest point in the channel (thalweg) and the high water mark of the experimental flow release).

For MPD transects, we estimated groundwater recession rates using piezometers equipped with pressure transducers. For MPD1, we used a piezometer located approximately 300 m from the site. For MPD2 and MPD3, we used piezometers within each site. For MPD4, we used the mean of two piezometers approximately 100 m from the site. Elevation of each piezometer and groundwater depth from the surface was determined from a digital elevation

model created from Light Detection and Ranging (LiDAR) remote-sensing data (collected in March 2014; average point densities of 10.7 points/m^2 first-return and 5.8 points/m^2 ground classified). The groundwater recession rate was determined as above for the river corridor transects. Maximum depth to groundwater at the mid-point of each transect was estimated from an interpolated groundwater surface produced from data collected between July 1 and October 31, 2014. Due to weaker connectivity of the MPD1 site to the mainstem and a lack of direct baseflow deliveries to the site, we would expect groundwater levels to respond more slowly and at lower magnitude compared to the other MPD sites that were near base flow delivery points and had strong connections to the river. We therefore expect that recession rates calculated from the piezometer located 300 m from the site are sufficiently representative, especially given the high conductivity of the sandy subsurface sediments.

We also obtained soil texture data, which can influence soil moisture and water availability due to different water-holding capacities of soils with different grain-size distributions. For both river corridor transects and the MPD sites, samples were analyzed by the Soils and Water Laboratory of the Universidad Autónoma de Baja California, Institute of Agricultural Sciences (Mexicali, Baja California, Mexico) for grain size distribution using the Bouyoucos hydrometer method (Bouyoucos, 1962). Although we initially collected 4–6 soil samples per river corridor transect, the majority of samples were compromised while in storage prior to laboratory analysis. As a result, our ability to assess soil texture at the transect level was too limited and instead we provide a reach-scale value. Sample sizes varied among reaches: PL = 11; EL = 19; ED = 1; PD = 4. Each sample was a composite of four subsamples.

For the MPD sites, composite soil samples were collected from MPD1–MPD4 in March ($n = 11$) and October ($n = 15$) 2014 (MPD1 = 4 in March and 6 in October; MPD2 = 3 in March and 5 in October; MPD3 = 3 in March and October; MPD4 = 1 in March and October) between 0 and 60 cm below ground surface. Most samples were not resampled from the same locations between March to October, were not in areas that were inundated from experimental flows, and were not collected at random locations within sites; sampling was designed to capture the full range of salinity values across the site to calibrate electromagnetic induction equipment that was being used to map soil salinity for a separate study. Therefore, our data represent an estimate of the range of soil conditions at the site scale.

2.3.3.4. Establishment: protection from secondary flooding. High flows that occur after the main flow recession (secondary floods) have the potential to cause seedling mortality or damage through scour or prolonged inundation of established seedlings (Auble and Scott, 1998; Friedman and Auble, 1999; Polzin and Rood, 2006; Wilcox and Shafroth, 2013). The September releases of 5.1 Mm^3 from Morelos Dam, growing season releases of 6.7 Mm^3 from the km 18 spillway, and additional releases in the MPD re-inundated some areas. We conducted field surveys following secondary flooding events to observe effects on seedlings, and for the MPD we also consulted the continuous ground water level data to estimate the frequency and duration of secondary flooding. We assigned one of three levels of secondary flooding to each transect or actively managed site: no secondary flooding; low frequency and/or duration of secondary flooding; high frequency and/or duration of secondary flooding.

2.3.3.5. Establishment: competition from adjacent vegetation. We estimated competition from two sources of adjacent vegetation: inter-specific competition between tree and shrub seedlings that established in 2014, and competition of seedlings with all other vegetation (comprised of herbaceous plants and older woody veg-etation). At the river corridor sites, we summed the percentage of the line intercept transect with vegetation cover in October 2014 within the area that was inundated by the peak flow release. For MPD transects, we used vegetation cover values from 4 m × 5 m belt sections where seedlings were present in October 2014 to estimate the level of competition.

2.3.3.6. Establishment: soil salinity. In the laboratory, saturated paste extract electrical conductivity (dS/m) was determined for the same sediment samples described above (see Section 2.3.3.3). To test the hypothesis that the high experimental flow release would reduce soil salinity, we conducted paired one-sided *t*-tests on log-transformed EC values (March minus May). Sample sizes were only large enough to run these tests for PL and EL. These two reaches are nearest to Morelos Dam, and, therefore are also where flows were highest, prior to downstream attenuation of the peak.

2.3.3.7. Establishment: statistical methods. All data were tested for normality using qqPlots (R package 'car', version 2.1-3) and for equal variance, using Bartlett's tests (R package 'stats', version 3.3.1). If data could not be successfully transformed, an appropriate nonparametric test was applied.

We tested for differences in October competition, maximum depth to groundwater, and maximum recession rate between all five reaches with three successive one-way Kruskal–Wallis non-parametric ANOVAs (chi-square test statistic), followed by Kruskal post hoc tests to differentiate groups (R package 'agricolae', version 1.2-3).

We then conducted regression analyses to assess the importance of variables hypothesized to influence survival and growth of germinants of the four target taxa within the PL, EL, ED, and PD reaches. We analyzed a binary dependent variable, presence or absence of seedlings at the end of the growing season, using nonparametric logit regression (R package 'glm2', version 1.1.2). Because native taxa became established at very few sites (i.e., zero-inflated data), the associated small sample sizes for individual taxa required us to lump all native taxa (*Populus, Salix, Baccharis*) for analysis. For all models, we used three independent variables: the two indirect measures of soil moisture availability (maximum 2-week ground water recession rate; maximum 1-week depth to groundwater) and one measure of competition from surrounding vegetation (October plant cover). Data for other potentially important independent variables (secondary flooding, soil salinity) were inadequate to include in these models. We evaluated our independent variables for collinearity by verifying that their variance inflation factors (VIFs) were less than five (R package 'usdm', version 1.1-15).

Next, we used a model selection framework based on the Akaike Information Criterion, corrected to avoid overfitting with small sample sizes (AICc; R package 'glmulti', version 1.0.7) to determine the most parsimonious combination of independent variables and interaction terms and to assess the relative importance of variables, which was of interest in cases without statistical significance. We also performed a general linear model regression on the arcsin square root transformed percent of transect with seedlings from the 4 m (MPD) or 20 m (river corridor transects) belts (R package 'glm2', version 1.1.2). This analysis was only possible for *Tamarix* alone and all four taxa combined, given the zero-inflated nature of the native taxa data.

To test the hypothesis that active land management in the MPD sites would increase seedling establishment compared to unmanaged PD sites, we conducted successive one-tailed nonparametric Wilcoxon signed rank tests on all taxa, native taxa, *Tamarix*, and Salicaceae only (R package 'exactRankTests', version 0.8-28).
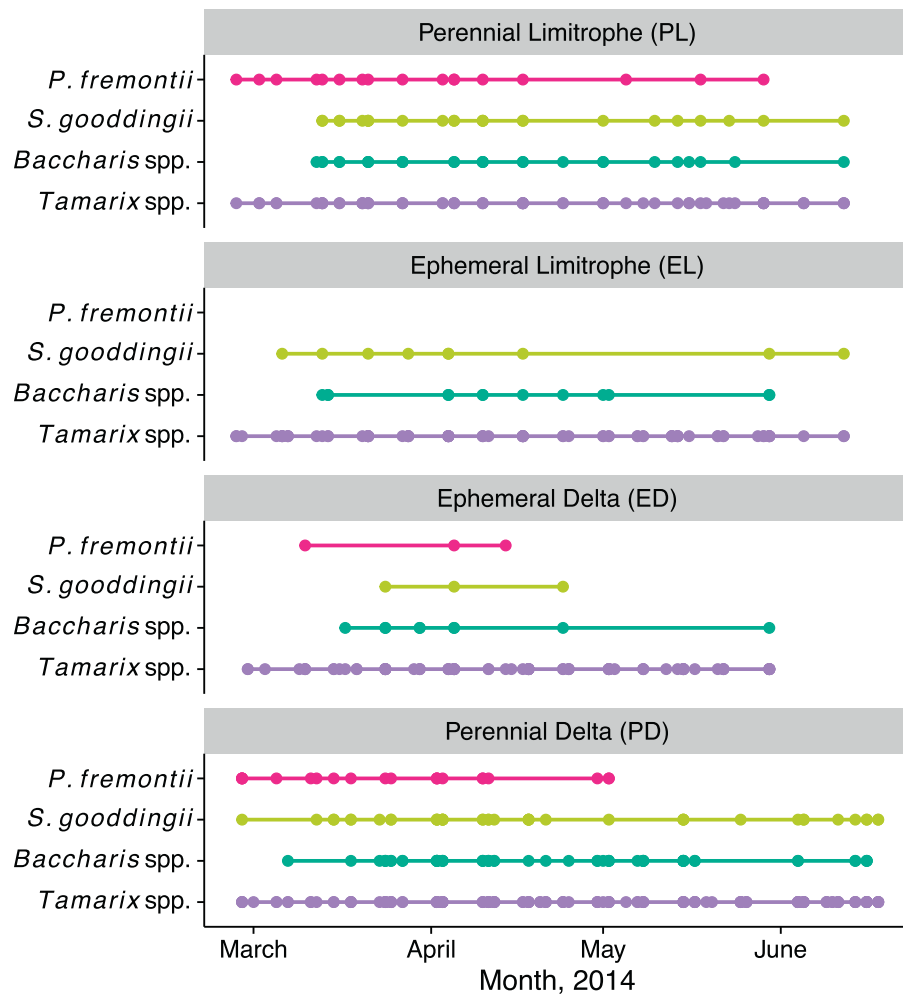
Fig. 4. Seed dispersal timing by species and reach between February 26 and June 18, 2014. Dots indicate observation dates. Dispersal was assumed to be continuous between observations, as reflected by the lines connecting the dots.

3. Results

3.1. Germination requirements

3.1.1. Seed availability

The timing of seed availability varied by species and across space in the study area (Fig. 4). At the scale of the entire study area, all four of our target taxa released seed for most of the February 26–June 18 monitoring period: March 5–May 29 for *P. fremontii*; March 5–June 18 for *S. gooddingii*; February 26–June 16 for *Baccharis*; and February 26–June 18 for *Tamarix*. Anecdotal observations in the MPD revealed some *Salix* dispersal occurring into August and some *Baccharis* and *Tamarix* dispersal into October.

The four taxa differed considerably with respect to the spatial distribution and relative abundance of seed availability (Fig. 5). *Tamarix* occurred at the most sites (all 23), followed by *Baccharis* (18 sites), *S. gooddingii* (13 sites), and *P. fremontii* (9 sites). *Tamarix* seed was available at high abundance at all sites, but seed availability of other taxa was frequently low or moderate (Fig. 5).

3.1.2. Bare substrate

The ephemeral river corridor reaches (EL and ED), which are characterized by wide, dry, sandy channels, had the highest percentage of bare substrate along transects before and after the pulse flow. Bare ground within the two perennial reaches was lower than the ephemeral reaches, particularly in the PD (Fig. 6). The average percent of bare substrate along the MPD sites ranged from 88 to 99% due to vegetation removal (Fig. 6). The average percent of transect length with bare substrate was not significantly greater after the pulse flow than before in any of the four reaches (PL ($t_2 = 0.05$, $p = 0.95$), EL ($t_5 = -0.54$, $p = 0.62$), ED ($t_3 = 0.78$, $p = 0.75$), or PD ($t_5 = -0.63$, $p = 0.28$)).

3.1.3. Germination predictions and May 2014 observations, river corridor transects

The germination model predicted *Populus* germination would occur at only five of 19 river corridor transects; *Salix* at seven transects; *Baccharis* at 13 transects; and *Tamarix* at all 19 river corridor transects. In most cases for *Populus* (12 of 14 transects) and *Salix* (8 of 11 transects), lack of available seed was the reason for a prediction of germination failure, but there were also some instances where bare, moist soil was not available, often because a secondary peak in the hydrograph re-inundated areas where germination otherwise would have been predicted to occur (Fig. 7).

In May 2014, we observed germination and early survival of seedlings along 16 of 19 river corridor transects. *Tamarix* germination was common, occurring on 16 of the 19 transects (Fig. 7). Native taxa germination was infrequent: we only observed *Populus* germinants on two of the 1-m belt transects, one each in PL and PD; *Salix* germinants on three transects, one each in PL, EL, and PD; and *Baccharis* germinants on four transects, two each in the PL and PD (Fig. 7). The germination model was a significant predictor of ger-

mination success or failure for *Populus* and *Salix* ($p = 0.034$, $p = 0.030$, respectively, two-tailed Boschloo's exact test) but not for *Baccharis* or *Tamarix* ($p = 1$). Despite this lack of statistical significance for *Tamarix*, the model did predict its occurrence at 16 of 19 sites, but incorrectly predicted it would occur at three sites where it did not.

3.2. Establishment requirements

3.2.1. Available moisture: groundwater recession rate, maximum depth to groundwater, and sediment texture

Within the two perennial flow reaches (PL and PD) the maximum 2-week average recession rate was less than 4 cm/d in all but one case (Fig. 8a). Within the two ephemeral reaches, recession rates were highly variable, ranging from <3 cm/d at three sites, >4 and <8 at 4 sites, and >15 cm/d at 2 sites (Fig. 8a). There was no significant difference in maximum recession rate between reaches (Chisq = 6.16, $p = 0.19$).

Significant differences in maximum depth to groundwater were found between reaches (Chisq = 18.58, $p = 0.001$), with reaches ED and EL significantly different than MPD and PL, and with PL and PD significantly different than the rest. All of the perennial sites had a maximum depth to groundwater <2.5 m, whereas the maximum at all of the ephemeral sites was >5 m (Fig. 8b).

Sediments were generally very sandy along all of the river corridor transects and variable at the actively managed sites (MPD). Sand comprised 78% of the sediment sampled in both the PL and EL, 84% in the ED, and 71% in the PD. Within the MPD, two sites had relatively low sand composition (MPD1 = 38%, MPD2 = 26%) and two sites had high sand composition (MPD3 = 79%, MPD4 = 89%).

3.2.2. Protection from secondary flooding

We did not observe mortality of or damage to 2014 season seedlings along the river corridor transects following the September flow release from Morelos Dam. Areas within the main channel in the PL and EL reaches were inundated, but to shallow depths and for short duration. Transects and actively managed sites in the ED and PD reaches were not inundated by the September release from Morelos Dam.

Flows delivered from the km 18 canal to the PD were of shallow depth and short duration, and we did not observe associated seedling mortality. Along the Laguna Grande transects we did not observe vegetative scour caused by secondary flooding events, but did observe mortality in some sites due to frequent and/or long duration secondary flooding events due to releases from km 18 and other delivery points.

3.2.3. Competition

At the end of the 2014 growing season (October), total plant cover (a proxy for combined inter- and intra-specific competition) was highest in the two perennial river corridor reaches (mean ± std dev; PL = 65.5 ± 24.8; PD = 86.4 ± 29.4), and lowest in the ephemeral reaches and the actively managed perennial reach (EL = 28.2 ± 8.1; ED = 28.6 ± 9.1; MPD = 25.9 ± 11.3; Fig. 8c). Differences between reaches were statistically significant (Chisq = 11.53, $p = 0.021$), and post hoc comparisons revealed the greatest differences between the high competition PD and a low competition group (MPD and EL).

3.2.4. Soil salinity

The average salinity by reach was <2.5 dS/m in all four river corridor reaches (May 2014), but >11 in the MPD (October 2014). Note, however, that sample sites within the MPD were not entirely within the inundated zone, whereas all river corridor samples were inundated.

For the two reaches nearest Morelos Dam (hypothesized to be most affected by the high flow release) salinity was not sig-
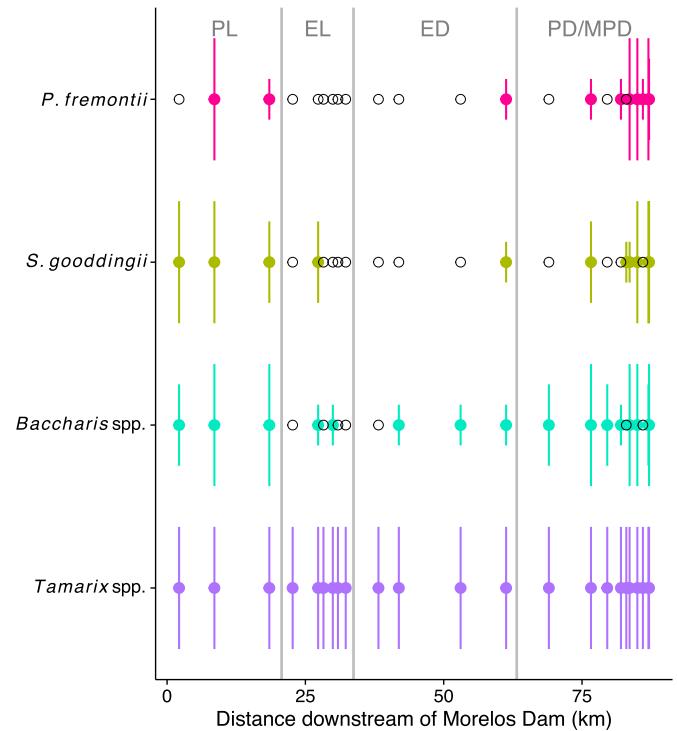

Fig. 5. Longitudinal variation in seasonal seed availability, by species, at 23 study sites. Bar height indicates the relative abundance of seed: short bar = low availability; medium bar = medium availability; tall bar = high availability. Empty black circles indicate no observed seed dispersal. PL = Perennial Limitrohphe; EL = Ephemeral Limitrophe; ED = Ephemeral Delta; PD = Perennial Delta; MPD = Managed Perennial Delta.
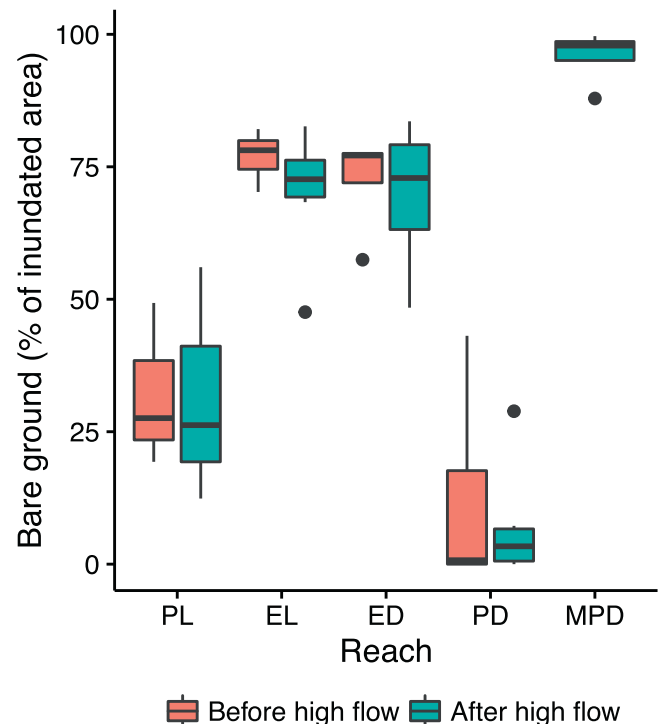

Fig. 6. Box plots of bare ground, as the average percentage of the transect that was inundated by the experimental flow peak, before (March) and after (May) the peak. For the MPD sites, data were only available for October 2014 (see text for details). PL = Perennial Limitrophe; EL = Ephemeral Limitrophe; ED = Ephemeral Delta; PD = Perennial Delta; MPD = Managed Perennial Delta.

nificantly lower in May than March 2014 (PL: $t_9 = 0.805$, $p = 0.22$; EL: $t_{35.318} = -4.547$, $p = 1$). Salinity actually increased notably in EL (March mean = 0.70 dS/m; May mean = 1.40 dS/m), which is the opposite of what we hypothesized. Soil salinity decreased from an average of 5.18 dS/m to 2.36 dS/m in reach PD, although this reduction was not statistically significant due to small sample size and high variability ($t_{4.23} = 0.560$, $p = 0.30$).

3.3. End of season seedling establishment

3.3.1. River corridor transects

In October 2014 within the 1-m belt transect, *Tamarix* seedlings established at 10 of 19 river corridor transects, *Baccharis* at two transects, and *Populus* and *Salix* at only one transect each. The native taxa only established at perennial transects, whereas *Tamarix* seedlings were present at both perennial and ephemeral transects. Within the 20 m belt, *Tamarix* seedlings were present at 14 transects, *Baccharis* at three transects, and *Populus* and *Salix* at one transect each (Fig. 7). Where seedlings were present, transect occupancy (percent of length interval with seedlings) within the area inundated by the peak was 6.8% for *Tamarix*, 4% for *Baccharis*, 2% for *Salix*, and 1.4% for *Populus*.

For all four taxa combined, model selection including three fixed effects (maximum depth to groundwater, recession, and competition) and their interaction terms determined that maximum depth to groundwater was the only significant predictor of seedling establishment (variable importance = 0.49; $t_{21} = 2.54$, $p = 0.020$).

The most parsimonious model to predict only *Tamarix* establishment included maximum depth to groundwater, and the interaction of recession rate with October competition (AICc = 46.21, $w = 0.09$). However, neither of the interaction terms alone was significant in the analysis of this model. Likelihood ratio tests indicated that dropping all terms except maximum depth to groundwater had no significant effect on model accuracy, and the resulting model with only maximum depth to groundwater was significant ($t_{21} = 2.22$, $p = 0.037$).

Four rounds of model selection were conducted on the binary logistic response of the three native seedling taxa to the hypothesized predictor variables. Three rounds were necessary because of convergence in the model, resulting from low occurrences of seedlings relative to the number of parameters. When all three predictor variables were included, October competition and maximum depth to groundwater were preserved in the best model (AICc = 25.49, $w = 0.45$), of which depth to groundwater had a significant effect on seedling establishment (October competition: $t_{17} = -1.86$, $p = 0.062$, DTW: $t_{17} = -2.17$, $p = 0.030$). Model selection on October competition and depth to groundwater, including their interaction, produced a best model which included all terms (AICc = 23.01, $w = 0.64$), but lacked significance. Model selection on recession rate, October competition, and their interaction found that the best model included only the model intercept (AICc = 29.14,
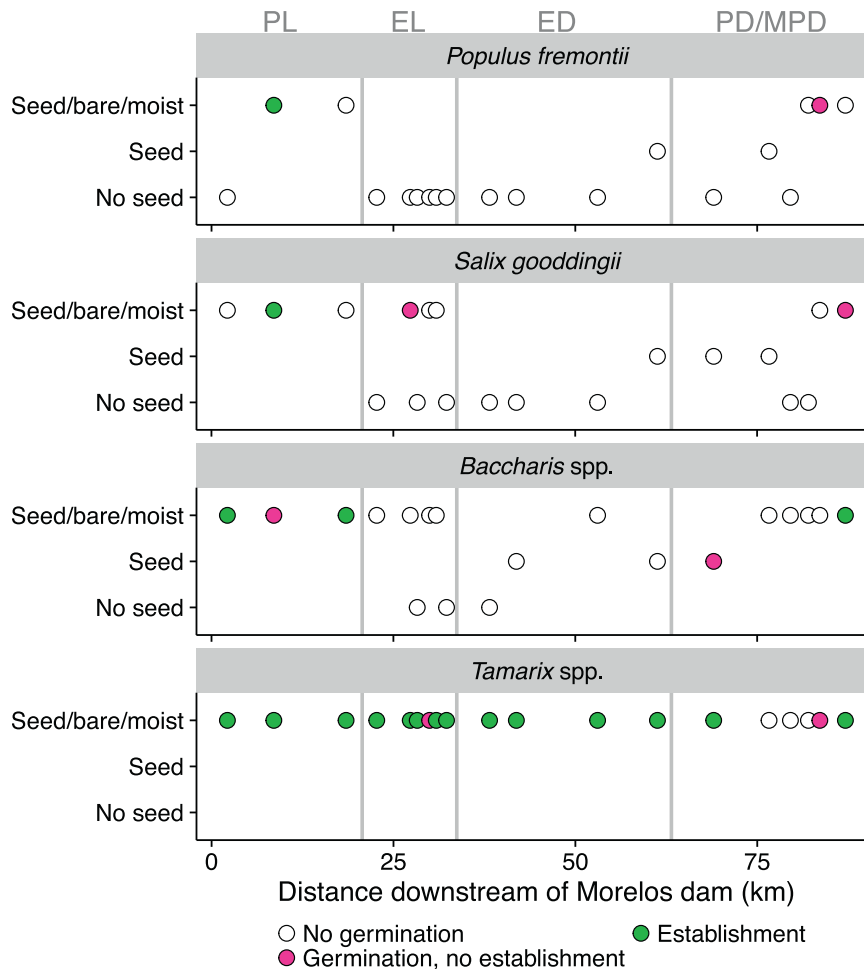

Fig. 7. Germination and establishment along the 19 river corridor transects. Hollow circles indicate sites where germination did not occur. Pink circles indicate sites where germination occurred but not establishment. Green circles indicate germination and establishment. Y-axis categories indicate presence or absence of germination requirements: bare/moist/seed = presence of bare, moist substrate and seed; seed = seed only; no seed = absence of all germination requirements.
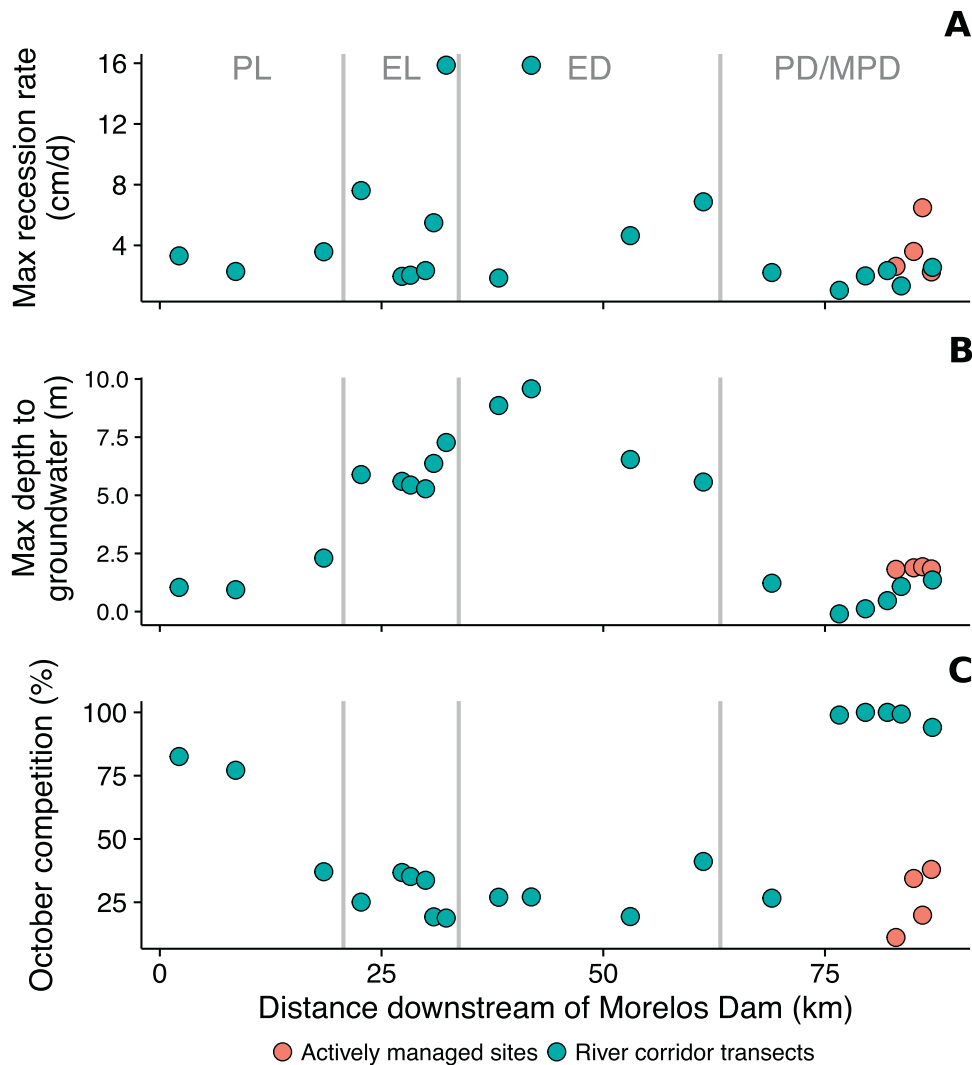
Fig. 8. Longitudinal variation in key variables that can influence seedling establishment at 23 study sites. PL= Perennial Limitrohphe; EL=Ephemeral Limitrophe; ED=Ephemeral Delta; PD=Perennial Delta.

$w = 0.41$), and none of the predictor variables or their interactions. The final round of model selection on recession rate and depth to groundwater eliminated recession rate (importance = 0.31) from the final most parsimonious model (AICc = 27.33, w = 0.49), and retained depth to groundwater (importance = 0.72). This model was marginally significant ($t_{18} = −1.78$, $p = 0.080$).

Raw data illustrate the importance of maximum depth to groundwater, the apparent interaction with competition, and the lack of pattern associated with maximum 2-week average recession rate. In particular, no seedling establishment of native taxa occurred at sites where the maximum depth to groundwater was >2.3 m, or where competition approached 100% (Fig. 9).

Although comparable statistical analyses were not possible for Salicaceae taxa, the pattern in the raw data indicate no establishment where the maximum depth to groundwater was >2 m, and an apparent interaction with October competition, with no establishment where competition was >77% (Fig. 9).

By contrast, *Tamarix* seedling establishment was not limited at all by deep groundwater, and was primarily limited by October competition values that approached 100% (Fig. 9).

3.3.2. Managed perennial delta sites

In October 2014 within the 1 m belt transect, *Tamarix* and *Salix* occurred at all four MPD sites, *Populus* at three of four sites, and

Baccharis at two of four sites. Within the 4 m belt, *Tamarix*, *Salix*, and *Populus* were present at all four sites; *Baccharis* was present at three of four sites.

Seedling establishment varied greatly among the MPD sites. In particular, native species establishment was very low in MPD1, with *Populus*, *Salix*, and *Baccharis* detected in 1, 2, and 0 of the 9, 4 m belt transects, respectively. *Populus* establishment was highest in MPD2 (7 of 9, 4 m belt transects) whereas *Salix* and *Baccharis* establishment was highest in MPD4 (5 of 5 and 4 of 5, 4 m belt transects, respectively).

Woody seedling transect occupancy for all taxa combined was higher in managed sites (MPD = 43.1%) than in the unmanaged river corridor transects (PD = 4.4%; w = 0, p = 0.009). Similarly, occupancy was higher for the component taxa including *Tamarix* (seedling cover in MPD = 30.4%, PD = 3.1%; w = 2, p = 0.009), native taxa combined (MPD = 12.8%, PD = 1.3%; w = 2, p = 0.038) and Salicaceae (MPD = 6.2%, PD = 0, w = 0, p = 0.057).

4. Discussion

4.1. Germination and establishment requirements

In the absence of associated active land management, experimental flows to the Colorado River delta were minimally successful

at promoting establishment of new woody riparian seedlings, except for non-native *Tamarix*. Our results suggest that the primary factors contributing to low seedling establishment varied across space, but included low or no seed availability in some locations for some taxa, insufficient soil moisture availability throughout the growing season indicated by deep groundwater tables, and competition from adjacent vegetation (and, conversely, availability of bare ground). Active land management to create bare ground and favorable land grades contributed to significantly higher rates of Salicaceae seedling establishment in a river reach with high groundwater tables. Other factors that can limit seedling establishment, such as soil salinity, may have been important in some local contexts (Schlatter et al., 2017) but overall were not of great importance in this study. Our results are consistent with and generally match expectations based on previous studies of Salicaceae seedling establishment.

Our measures of the simultaneous availability of seed and bare, moist substrate (germination model) were generally good predictors of where we observed germination. This model was strongest for *Salix* and *Populus*, the taxa for which it was primarily developed. Possible differences in germination requirements could explain poorer suitability of the model for *Baccharis*, which has been much less studied, and *Tamarix*, which has generally broader environmental tolerances (Glenn and Nagler, 2005; Schlatter et al., 2017).

The absence of *Salix* and *Populus* seed was likely an important factor at some of the perennial sites (Fig. 5), and augmenting seed supply at these sites when hydrologic conditions are suitable could increase germination (Figs. 1 and 7; Friedman et al., 1995; Grabau et al., 2011; Schlatter et al., 2017). At the ephemeral sites, seed augmentation could overcome germination limitations, but would not likely lead to seedling establishment and eventual growth to sexual maturity and a sustainable seed source. The lack of available moisture at ephemeral sites is likely the reason for the absence of mature trees and associated seed source.

We hypothesized that the peak of the experimental flow would create significant new areas of bare ground, suitable for seed germination and early establishment. However, even at our PL and EL sites where the peak flow magnitude was highest, we did not observe a significant increase in bare ground. Some small, local areas between transects with notable erosion and deposition were observed in the PL and EL in another study (Mueller et al., 2017). Extensive *Populus* recruitment generally occurs where flood events create large areas of bare ground through channel change (Scott et al., 1996; Polzin and Rood, 2006) vs. small, local areas of sediment turnover. This reflects a limitation of flows up to 119 m^3/s in the Colorado River delta, which is not surprising given that high flows commonly exceeded 3000 m^3/s in the pre-dam era (Mueller et al., 2017). Flood control releases from the early 1980s through late 1990s exceeded 300 m^3/s on several occasions (Mueller et al., 2017) and were associated with widespread Salicaceae seedling establishment in some years (Nagler et al., 2005; Zamora-Arroyo et al., 2001). The creation of bare ground in the MPD was one of the primary outcomes of active management and allowed for a strong contrast between MPD and PD sites, and also has been shown to be an effective management tool in other studies where hydrologic conditions were also suitable (Cooper and Andersen, 2012; Sprenger et al., 2002; Taylor et al., 1999).

The rate of alluvial ground water recession following peak flows was apparently not limiting seedling establishment at most of our study sites. Previous work has shown decreasing rates of *Populus* seedling survival between 1 and 8 cm per day (Amlin and Rood, 2002; Mahoney and Rood, 1991, 1998; Segelquist et al., 1993; Stella et al., 2010). Seedlings of most *Salix* spp. can only tolerate water table decline rates <4 cm/day, and some less than 2 cm/day (Amlin and Rood, 2002; Horton and Clark, 2001). These results are largely from controlled laboratory experiments, in which the recession
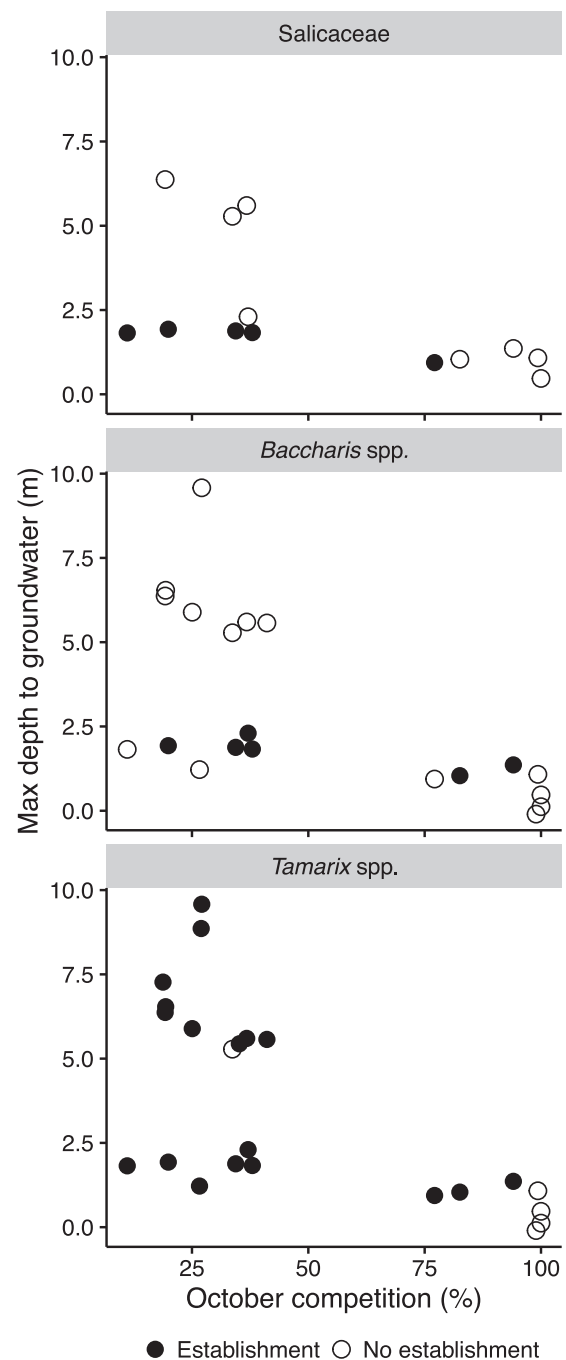

Fig. 9. Relationships between variables hypothesized to influence seedling establishment, and observed establishment of native taxa. Points included are river corridor transects where germination was predicted to occur, as well as the four MPD sites.

rate is constant over the study period. In field situations, recession rates are almost never constant, because flows fluctuate to various extents and the recession rate is also dependent on channel and floodplain geometry, which is spatially variable (Shafroth et al., 1998). We analyzed the maximum recession rate over a 2-week period (running average), which was <4 cm/d at 16 of 23 sites, between 4 and 8 cm/d at four sites and >8 cm/d at two sites. Thus, the recession rate during the experimental flow release period (March 23 to May 18) was likely acceptable for our target taxa at most of our sites, although recession rate was quite high at some of the EL and ED sites (Fig. 8). Controlling the flow recession rate

was an intentional part of the experimental flows in this study, and managing streamflows to provide a gradual recession rate for Salicaceae seedlings has been implemented in several river systems in western North America (Rood et al., 2005). Surprisingly, the cessation of flow releases from Morelos Dam did not result in an abrupt increase in recession rate at all transects downstream. Some of this was likely due to continued low flows in the PL from dam seepage and groundwater inflows.

The maximum depth to groundwater during the growing season was the strongest predictor of seedling establishment in our study. No new establishment of *Baccharis* occurred where the maximum depth to groundwater exceeded 2.3 m, and *Salix* and *Populus* only established where the maximum depth to groundwater was less than 2 m. This value is consistent with several other studies of Salicaceae seedling establishment in western North America where establishment was noted to occur most often at elevations of 0.6–1.5 m above base flow, but up to 2.6 m (Mahoney and Rood, 1998). We suggest that a maximum depth to groundwater of 2 m is a potentially useful threshold for riparian managers to be aware of when selecting and managing areas for new seedling recruitment and longer term forest persistence in arid settings like our study area (Lite and Stromberg, 2005). Unlike the native taxa, *Tamarix* seedlings became established at almost all of our sites, reflecting its much greater tolerance of low soil moisture conditions (Glenn and Nagler, 2005). Groundwater depths were different in different river reaches, and consideration of this spatial variability is key to planning future restoration efforts and management strategies (Shafroth et al., 2000). Managing flow releases to maintain shallow groundwater for establishment and maintenance of *Populus euphratica* has been central to the environmental flow program along the Tarim River, China (Zhang et al., 2013), and also implemented in Australia for the maintenance of river red gum (*Eucalyptus camaldulensis*) along the lower River Murray, Australia (Souter et al., 2014). However, other studies have shown early woody riparian seedling establishment to be tied more to vadose zone soil moisture and not linked directly to water table elevation (Cooper et al., 1999).

Secondary inundation occurred in our study, but the depth and duration were not severe enough to result in significant mortality. Some mortality, however, was observed in the MPD due to secondary inundation. Future managed flow efforts should consider the possible negative effects of secondary flow releases on new seedlings (Cooper et al., 1999), although it is also possible that secondary flows could have more detrimental effects on *Tamarix* than native taxa (Wilcox and Shafroth, 2013).

Growth and survival of new seedlings can be hindered by competition for light, water, and nutrients by surrounding vegetation (Cooper et al., 1999; Sher et al., 2002; Stromberg, 1997; Stromberg et al., 1991), and this was likely an important factor at some of our sites. The most obvious, significant competition in our study appeared to be from dense stands of two, large emergent grasses, giant reed (*A. donax*) and common reed (*P. australis*) in both the PL and PD. These taxa grew in dense thickets along banks and up to the water's edge and were typically not removed by the peak of the experimental flows. The efficacy of future flow events could be increased by removing or otherwise controlling these taxa prior to flow releases, although their root systems are dense, resilient, and the source of copious resprouts.

Soil electrical conductivity above 4 dS/m can limit germination and growth of some mesic riparian species (including *Populus* and *Salix*), and most mesic and many xeric riparian species are negatively affected by levels above 8 dS/m (Beauchamp et al., 2009; Shafroth et al., 2008). All of the post-experimental flow soil samples from the river corridor transects had salinity values below 8 dS/m, and almost all were below 4 dS/m. Soil salinity was higher in parts of the MPD, but results were highly spatially variable.

Site MPD1 appears to have the highest surface soil salinity of the MPD sites, which may have inhibited seed germination. However, we observed both native and nonnative seedling establishment in areas that had surface soil salinity >8 dS/m prior to the pulse and base flow deliveries (salt visible on surface), and many existing (remnant) cottonwood and willow trees in the MPD currently survive in areas with high surface salinity, which has been observed elsewhere on the Lower Colorado River (Merritt and Shafroth, 2012). This suggests a need for greater understanding of salinity tolerances as well as the potential importance of variability in soil salinity vertically in the soil profile.

Although we hypothesized that the high flow release would reduce soil salinity values, our data were inconsistent in this regard and, in fact, salinity increased in one of our reaches. Results from another study in the MPD (Schlatter et al., 2017) suggest that in most areas soil salinity decreased from March to October 2014, consistent with flushing of salts that could have resulted from pulse and base flow deliveries to the restoration areas.

Although herbivory can significantly reduce seedling establishment in some contexts (Cooper and Andersen, 2012; Stromberg, 1997), we did not observe significant effects on first-year seedlings in our study. However, anecdotal observations of second-year seedlings in the study area have revealed some herbivory by rabbits in the MPD, and also some by beaver in the PL.

4.2. Summary of seedling requirements

Based on comparisons of our results to values in the literature (above), we generated a simplified assessment of how well seed germination and seedling establishment requirements were met within the different study reaches (Table 1). We suggest that this sort of summary table could be a useful management tool for highlighting river reaches that are likely to be most suitable for target species establishment, and also for identifying particular management actions that might be implemented to help better meet requirements. Understanding which functions or seedling requirements can or cannot be fulfilled through environmental flow deliveries within a given reach can suggest what functions management actions should seek to fulfill (Fig. 1). For example, if peak flows are not likely to create significant areas of new bare ground, but can moisten sediments and provide continued moisture, then management actions could focus on vegetation removal and perhaps land grading prior to flow releases (Schlatter et al., 2017; Fig. 1). This approach was used in the MPD in our study with considerable success and could likely be applied strategically to the PL in the future. Table 1 clearly indicates that the most favorable areas for native recruitment were the MPD sites, where seedling establishment requirements were met in the majority of sites due to management actions implemented before, during, and after the pulse flow (including the provision of base flows). These results should be considered in combination with assessment of past flow events that resulted in successful seedling establishment (Nagler et al., 2005; Zamora-Arroyo et al., 2001).

4.3. Implications for future flow management

The considerable spatial variation in our study area in terms of flow conveyance and surrounding land and water use highlights common challenges of environmental flow experiments (Konrad et al., 2011). The two perennial reaches have the highest potential for seedling establishment, but they are separated by the two ephemeral reaches, which extend for 42 km. This complicates delivering flow from Morelos Dam to the PD reach, as much of this water is "lost" to the alluvium in the EL and ED reaches (Rodríguez-Burgueño et al., 2017). Smaller deliveries were made via the km 27 and km 18 canals, but the maximum possible dis-

Table 1
Qualitative estimates based on comparisons to values in the literature of how well requirements for recruitment of *Populus* and *Salix* were met by the experimental flows in each reach and with the combination of flow and management actions in the MPD.

Component	Reach PL	Reach EL	Reach ED	Reach PD	Reach MPD
Seed availability	Good	Fair	Poor	Good	Good
Bare substrate	Fair	Good	Good	Poor	Excellent
Continued moisture (recession rate)	Good	Poor	Poor	Good	Good
Continued moisture (max depth to groundwater)	Good	Poor	Poor	Good	Good
Low competition	Fair	Good	Good	Poor	Good
Low soil salinity	Good	Good	N/A	Fair	Fair-poor
Lack of herbivory/grazing	Good	Good	Good	Good	Good

N/A indicates insufficient data to assess. PL = Perennial Limitrophe; EL = Ephemeral Limitrophe; ED = Ephemeral Delta; PD = Perennial Delta; MPD = Managed Perennial Delta.

charge rate is relatively small. Further, flow attenuation in the downstream direction was significant: the peak discharge in the PL was ~119 m^3/s but only 9 m^3/s in the PD (Rodríguez-Burgueño et al., 2017). Groundwater levels are also spatially variable in the absence of surface flow deliveries; perennial surface water in the PD is typically sustained from agricultural return flows and shallow groundwater inputs from adjacent irrigated agricultural areas (Ramírez-Hernández et al., 2015), whereas the EL and ED reaches have deep alluvial water tables due in part to groundwater pumping.

Experimental flows are invariably linked to interactions between social context and hydroclimatology, which drive complex water management systems such as the Colorado River with its myriad water users up- and downstream of Morelos Dam (Konrad et al., 2011; National Research Council, 2007). Social context also relates to the expectations associated with environmental flows, which sometimes can be unrealistically high given that constraints on flow releases by a fixed available water volume, limitations of dam outlet works, or downstream flood control concerns may limit the functional capacity of flow releases. In the case of the Minute 319 experimental flows, the magnitude of the peak discharge was insufficient to create significant channel change and associated areas of new bare sediment to promote *Populus* and *Salix* germination and establishment, even in the reach closest to the dam. By the time the peak reached the PD, its magnitude was further diminished, rendering impossible significant geomorphic work. By clarifying these sorts of limitations, results from studies of the 2014 experimental flows can help to articulate realistic expectations for future flow releases. In some cases, limited on environmental flow releases may only be able to support a sub-set of desired functions in a down-sized area (Hall et al., 2011).

While our results provide a basis for assessing the outcome of the 2014 experimental flows and planning future flow releases, efforts to plan future flow releases to the Colorado River Delta would also benefit from quantitative modeling approaches that link seedling requirements and surface and groundwater hydrology in a spatially explicit and extensive format. Surface and groundwater models have been developed for the delta study area since 2014, and these have the potential to be combined with key seedling establishment parameters to facilitate simulation of different flow scenarios and associated seedling response. A variety of such approaches have been developed for Salicaceae and other riparian taxa on other North American rivers to evaluate likely effects of different water management scenarios (Benjankar et al., 2014; Dixon and Turner, 2006; Harper et al., 2011; Hickey et al., 2015; Morrison and Stone, 2014). These models do not typically integrate scenarios with different land management actions, which would be important to include in the case of the Colorado River delta.

5. Conclusions

Riparian *Populus* spp. (cottonwood, poplar) forests are globally iconic, often threatened, and their restoration is a priority throughout the Northern Hemisphere, including Europe (Gonzalez et al., 2010; Hughes and Rood, 2003), Asia (Zhang et al., 2013), and North America (Rood et al., 1995; Stromberg et al., 2007a), and was a high priority for the experimental streamflow releases described in this paper. However, the volume, peak magnitude, and duration of flow released to the Colorado River delta in 2014 were insufficient to drive a significant recruitment event for *P. fremontii* and *S. goodingii*, constituent trees of a globally-rare riparian forest type. Where combined with active land management such as vegetation removal and land grading, the experimental flows contributed to successful *P. fremontii* and *S. gooddingii* seedling establishment.

Evaluating establishment success and failure in the context of key conditions associated with pioneer woody seedling establishment helped clarify requirements that were not provided by the experimental flows, but were or could be provided by active land management. Quantifying these conditions through rigorous monitoring of key physical and biological metrics and interpreting the effects on seedling establishment should provide insights that can inform future environmental flow deliveries to the Colorado River delta and its ecosystems, and provide insights for efforts to manage flow for riparian restoration around the world. Beneficial future work could include spatially-explicit modeling that links ecological response parameters with surface and groundwater models and different active land management and flow delivery scenarios.

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