Regeneration of Native Trees in the Presence of Invasive Saltcedar in the Colorado River Delta, Mexico

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Abstract: *Many riparian zones in the Sonoran Desert have been altered by elimination of the normal flood regime; such changes to the flow regime have contributed to the spread of saltcedar (* Tamarix ramosissma *Ledeb.), an exotic, salt-tolerant shrub. It has been proposed that reestablishment of a natural flow regime on these rivers might permit passive restoration of native trees, without the need for aggressive saltcedar clearing programs. We tested this proposition in the Colorado River delta in Mexico, which has received a series of large-volume water releases from U.S. dams over the past 20 years. We mapped the vegetation of the delta riparian corridor through ground and aerial surveys (1999–2002) and satellite imagery (1992–2002) and related vegetation changes to river flood flows and fire events. Although saltcedar is still the dominant plant in the delta, native cottonwood (* Populus fremontii *S. Wats.) and willow (* Salix gooddingii *C. Ball) trees have regenerated multiple times because of frequent flood releases from U.S. dams since 1981. Tree populations are young and dynamic (ages 5–10 years). The primary cause of tree mortality between floods is fire. Biomass in the floodplain, as measured by the normalized difference vegetation index on satellite images, responds positively even to low-volume (but long-duration) flood events. Our results support the hypothesis that restoration of a pulse flood regime will regenerate native riparian vegetation despite the presence of a dominant invasive species, but fire management will be necessary to allow mature tree stands to develop.*

Key Words: fire, flood flows, invasive species, *Populus*, riparian, *Salix*, *Tamarix,* wetlands

Regeneración de Árboles Nativos en Presencia de la Invasora *Tamarix ramosissma* en el Delta del Río Colorado, México

Resumen: *Muchas zonas ribereñas en el Desierto de Sonora han sido alteradas por la eliminación del régimen normal de inundación; tales cambios en el régimen de flujos han contribuido a la diseminación de* Tamarix ramosissma *Ledeb., un arbusto exótico tolerante a la salinidad. Se ha propuesto que el restablecimiento de un régimen de flujo natural en estos ríos podría permitir la restauración pasiva de árboles nativos, sin la necesidad de agresivos programas de eliminación de* T. ramosissma*. Probamos esta propuesta en el delta del Río Colorado en México, que ha recibido una serie descargas de agua de gran volumen desde presas en E.U.A. durante los últimos 20 años. Trazamos un mapa de la vegetación del corredor ribereño del delta a partir de recorridos terrestres y aéreos (1999–2002) e imágenes de satélite (1992–2002) y relacionamos los cambios en la vegetación con eventos de inundación y fuego. Debido a las frecuentes descargas de presas*

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en E. U. A. desde 1981 se han regenerado árboles de las especies nativas Populus fremontii *S. Wats. y* Salix gooddingii *C. Ball, aunque* T. ramosissma *aun es la planta dominante en el delta. Las poblaciones de árboles son jóvenes y dinámicas (edades entre 5 y 10 años). El fuego es la principal causa de mortalidad de árboles en períodos entre inundaciones. La biomasa de la llanura de inundación, medida con el índice normalizado de diferencia de vegetación en imágenes de satélite, responde positivamente incluso a eventos de inundación de bajo volumen (pero larga duración). Nuestros resultados sustentan la hipótesis de que la restauración del régimen de inundación regenerará a la vegetación ribereña nativa a pesar de la presencia de una especie invasora dominante, pero será necesario manejar el fuego para permitir que los árboles lleguen al estado adulto.*

Palabras Clave: especie invasora, flujo de inundación, fuego, humedales, *Populus*, ribereño, *Salix*, *Tamarix*

Introduction

Many dryland riparian zones have been altered by human changes of the flow regime and many have experienced spread of invasive species. Alterations include water diversion, groundwater decline, flow regulation, channelization, and dams that reduce flows and eliminate the normal pulse flood regime of dry-region rivers (Poff et al. 1997; Graf 1999). Native species that depend on timed, seasonal flooding for germination show reduced recruitment and, as a result, are replaced by more opportunistic species. Interacting problems of human disturbance and invasive species have been documented for rivers in arid and semiarid areas in South Africa (Dye et al. 2001), Australia (Cowie & Werner 1993), Asia (Dudgeon 1992), and North America (Stromberg & Chew 2002*a*, 2002*b*; Katz & Shafroth 2003).

In the southwestern United States, the native riparian forests of cottonwood (*Populus* spp.) and willow (*Salix* spp.) have declined on most major rivers over the last 100 years, whereas an invasive, exotic shrub, saltcedar (*Tamarix ramosissima* Lebed.), has spread at rates of up to 20 km/year along some river systems (Cleverly et al. 1997; DiTomosa 1998; Everitt 1998). Today, saltcedar in monoculture or in association with other salt-tolerant shrubs dominates the lower Colorado River (Busch & Smith 1993). Wildlife has been affected by the linked changes in hydrology and vegetation. In particular, birds that use rivers as migration routes and nesting sites in a desert environment have declined in abundance (Rice et al. 1980; Ohmart et al. 1988).

Resource managers are engaged in a running debate about the best way to restore arid-zone riparian ecosystems in the southwestern United States (Anderson 1998; Barrow 1998). On one side are those who argue for an aggressive campaign to eradicate saltcedar wherever possible with mechanical, chemical, and biological control agents (Barrow 1998). On the other side are those who believe intermittent water releases will improve riparian ecological conditions; and thus, the first priority is to restore a semblance of the natural flow regime to encourage the regeneration of native trees (Anderson 1998; Stromberg & Chew 2002*a*, 2000*b*; Sher & Marshall 2003).

The comparative ecophysiology of saltcedar and native trees is reviewed in Glenn and Nagler (2005). Saltcedar is capable of producing seeds and germinating throughout spring and summer under a wide range of environmental conditions, whereas cottonwood and willow trees require spring floods timed to their shorter window of seed production and germination (Stromberg & Chew 2002*a*, 2000*b*). After germination, cottonwood and willow seedlings must have access to moist soil or a water table within 2 m of the surface during the first season (Mahoney & Rood 1998) and a water table no deeper than 3–4 m for continued growth thereafter (Horton et al. 2003). Saltcedar can grow as a facultative phreatophyte, can access groundwater as deep as 6 m, and has greater salt and drought tolerance than cottonwood or willow (DiTomosa 1998). On the other hand, the native trees can withstand inundation longer than saltcedar (Vandersandae et al. 2001).

A key question is whether restoration of a pulse-flow regime would permit native trees to regenerate in the presence of saltcedar (Stromberg & Chew 2002*a*, 2000*b*). Native trees regenerate under favorable hydrological conditions on undammed rivers such as the Hassayampa and San Pedro in Arizona (U.S.A.) (Stromberg et al. 1993; Stromberg 1997, 1998). Hydrologic conditions differ, however, for large, highly altered rivers such as the Colorado. The lower Colorado River has undergone extensive change over the past century (Ohmart et al. 1988). After Hoover Dam was completed in 1937, excess water in wet years was stored in the reservoirs, and little water reached the river delta for nearly 50 years. Since the last large reservoir (Lake Powell behind Glen Canyon Dam) filled, however, flood releases to Mexico and the Gulf of California have resumed (Glenn et al. 1996). Since 1981, there were eight major releases of water (50–800 m^3/second), with these occurring in 1983 through 1988, 1993, and 1997 through 2000 (Fig. 1) during major El Niño events. In addition to the large releases, smaller flows in the range of 1–5 m^3/second (mean = 2 m^3/second) frequently enter the river as a result of “administrative spills” (water ordered by irrigators but not used).

These large and small releases constitute an unplanned, 20-year experiment on the effects of pulse floods on the

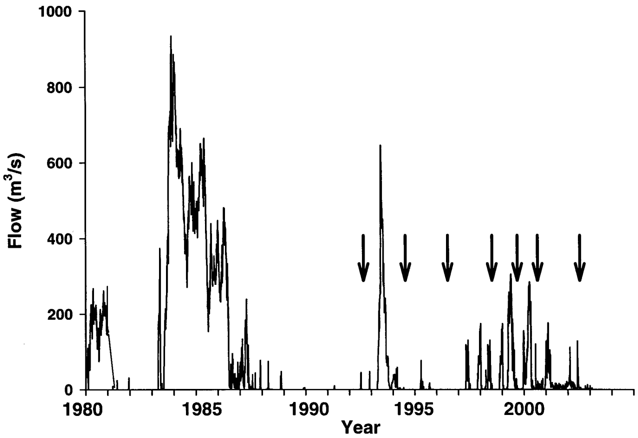

Figure 1. Instantaneous flows in the Colorado River at the southerly international boundary, 1980–2004. Arrows show years in which summer thematic mapper satellite images were obtained to compare vegetation intensity with previous years of flow.

regeneration of native trees in the presence of saltcedar on a highly altered arid-region river system. We studied the regeneration of native willow (*Salix gooddingii* C. Ball) and cottonwood (*Populus fremontii* S. Wats.) trees in the floodplain of the river in response to these releases with satellite imagery from 1992 to 2002 and ground and aerial surveys. Our objectives were to document the current status of the vegetation, determine the rate of turnover of native trees on the floodplain, and identify the factors that influenced recruitment and mortality. We asked several questions: (1) How frequently do cohorts of cottonwood and willow establish? (2) Do the cohorts establish in response to each large flood, or are there threshold values that trigger establishment? (3) What factors (e.g., fire, depth to groundwater, salinity) account for the mortality of trees? (4) Does recruitment match mortality over multiple flood cycles? (5) How does vegetation biomass change between years in response to differing annual flow conditions?

Methods

Study Area

The ecology of the Colorado River delta is described in Glenn et al. (1996, 2001). We concentrated on the stretch of river between Morelos Dam, the last diversion point for water on the river, and the junction with Rio Hardy, a distance of approximately 110 km. Flow through this stretch is intermittent, depending on releases of water into the channel from the United States and Mexico (Fig. 1). The riparian corridor is confined between levees in this stretch. The floodplain between the levees is as narrow as 1–2 km in the north but increases to over 35 km in the south. We defined a 24,000-ha area that contained most of the native tree growth as our study area. Soils in this zone are generally not saline (Zamora-Arroyo et al. 2001). South of the junction with the Rio Hardy, the Colorado River is influenced by tides and disposal of irrigation return flows and is too saline for native trees (Glenn et al. 1996, 2001).

Aerial Surveys and Vegetation Mapping

Vegetation was mapped from high-resolution aerial photographs. Aerial surveys were conducted in June of 1999, 2000, and 2002 from a light aircraft equipped with a belly-mounted camera pod (Nagler et al. 2001, 2004). In 1999 photographs were acquired with a multiband (blue, red, and near infrared) digital camera (DyCam, Chatsworth, California) flown at 150 m above ground level (AGL) over the riparian corridor. The camera acquired a string of seven photographs at 2-second intervals. It took several minutes between strings to process images before the next string could be acquired. Each image covered approximately 100 × 67 m of ground area with a resolution of 0.5 m. Each string covered approximately 1 km of river length. Individual photographs in a string were separated by approximately 40 m. Seven strings were acquired over the study area. Four strings, spaced approximately evenly along the river, contained populations of native trees and were used to track changes in cohorts of native trees over time by comparison with 2000 and 2002 photographs. The sites of the photographs were ground truthed in 1999 to confirm our interpretation of vegetation types (Nagler et al. 2001; Zamora-Arroyo et al. 2001).

In 2000 and 2002 we acquired high- (3000 m AGL) and low-level (1000 m AGL) aerial photographs (20% overlap) with a visible-band, panchromatic digital camera (Nikon, Melville, New York). Resolution was approximately 1.5 m for high-elevation and 0.5 m for low-elevation photographs. The 2002 set of images was more complete than the 2000 set and was used to map the vegetation on the floodplain. The 2002 low-level photographs covered the central portion of the riparian corridor, whereas the high levels covered the floodplain from levee to levee and adjacent agricultural land. For the high-elevation imagery, we made a photomosaic of 333 jpg images, and for the low-elevation imagery, we made a mosaic of 562 jpg images with a computer-assisted rubbersheeting method (Adobe Photoshop, San Jose, California). These images were split into nine sections of the river and georectified to an enhanced thematic mapper (ETM+) image (acquired from the MODIS satellite on 3 June 2002) with ERDAS Imagine 8.0 software (Leica Geosystems GIS & Mapping, Atlanta, Georgia). To determine the accuracy of matching the aerials to the ETM+ image, we used compared positions of three objects (road intersections, trees, etc.) on the ETM+ and on each of the nine images and thus obtained 27 data points over the entire riparian-area aerial mosaic. The mean position accuracy error for these points was 25.5 m, about the same magnitude as the resolution of the ETM+ image (28.5 m/pixel).

Vegetation and landscape features were digitized manually in ERDAS from the aerial photomosaics. The land-cover classes that could be unambiguously separated on the photomosaics were areas of recent fire scars; roads and levees; open water; emergent marsh vegetation; shrub vegetation (saltcedar and other midstory species); willow or cottonwood trees 6 m or taller; and dead trees. Fire scars quickly regreened. We scored only fresh burns (1–2 years old) dominated by blackened soil as fire scars. Willow and cottonwood were distinguished from other vegetation by the area and color of their canopies and by the fact that they were taller than surrounding vegetation and cast characteristic shadows (Nagler et al. 2001, 2004; Zamora-Arroyo et al. 2001). This identification was aided by the fact that the aerial photographs were taken in the morning (0700 to 1000 hours), when shadow lengths are maximal. Dead willow and cottonwood were identified by their white, skeleton-like crown of leafless branches. We could not distinguish between willow and cottonwood trees on the photographs, and the generalized shrub layer was a mixture of species up to 5 m tall that could not be separated into species on aerials (Nagler et al. 2001).

The digitized coverages were converted into shape file layers using ArcInfo, ArcView, and ArcMapper software (ESRI, Redlands, California). They were overlaid on the classified ETM+ layer that formed the base map. Hence, the final vegetation map had a generalized background layer (the ETM+) showing riparian shrubs and surrounding agricultural fields overlaid with detailed depictions of the features of major interest in the riparian zone: roads, levees, fire scars, dead trees, live trees, open water, and marsh vegetation. We were able to determine areas of each class and to layer coverages on top of each other to determine their extent of spatial overlap with geographic information science (GIS) techniques. Using GIS software, we divided the floodplain into a series of strips 50 wide, covering the floodplain for 1 km on the left and right banks of the river. We scored the coverage of both live and dead trees as functions of distance from the active channel.

Ground Surveys

We estimated land-cover classes in 2002 from the ground, along 30, 2000-m, perpendicular-to-the-river transects distributed within the study area. Each transect included eight circular survey stations (50-m radius, 0.785 ha) located 200 m apart, for a total of 240 survey stations. The study area extended from San Luis Rio Colorado, south to Ayala Drain on the left margin of the floodplain and to the Hardy River on the right margin of the floodplain. The transects were set starting from the levee and running perpendicular to the river. Our method for recording habitat measurements followed Ralph et al. (1996). At each station we estimated the percent cover and the minimum, maximum, and average height of each plant species encountered in the plot. The center of each plot was recorded using an eTrex, a ground positioning system (GPS) device (Garmin, Olathe, Kansas). We used tapes to mark off four 50-m radii in each cardinal direction. The cover of plants and other land features along each of these transects was then measured with a tape measure and by pacing. Cover classes were bare soil, water, or vegetation; vegetation was further recorded by species. We measured the diameter at breast height (dbh) and height of five individuals for cottonwood and willow in each plot. Trees were randomly selected from those encountered along the four transects. For open water, we recorded type (primary or secondary stream, drain, irrigation canal, or lagoon), depth, and width.

We compared results of this survey with previous ground surveys conducted in 1999 (Zamora-Arroyo et al. 2001). Those surveys were conducted along 10 transects evenly spaced along the riparian corridor. Cottonwood and willow trees were measured for height and canopy width at three stations (approximately 100 trees per station) in that survey.

Comparison of Ground and Aerial Surveys

We compared ground survey results with interpretations of the aerials at 36 randomly chosen field plots. Because there was positional error in both the photomosaic and the GPS field readings, we did the final placement of the field plot boundaries on the photomosaic visually based on referencing known features within the plot (e.g., large trees, the riverbank). The ERDAS software was used to place a fine grid containing 200 intersections over the plot area on the photomosaic, and we determined the land-cover class at each intersection. Each intersection was scored as shrub, native tree (willow or cottonwood), marsh, bare soil, or open water. Then we compared these aerial assessments with the ground assessments and recorded the correspondence, either correct or incorrect, between the aerial classes and the field plots. Ground and aerial surveys produced similar estimates of percent cover (within 3%) of shrub, soil, marsh, and water land cover classes. Willow and cottonwood cover was underestimated by 40%, however, on aerial compared to ground surveys. This discrepancy occurred because differentiation between tree and shrub categories on the aerial photographs was based on height (6 m or above for trees), but many of the trees in ground surveys were juveniles (under 5 m tall). We used the aerial and satellite images to spatially depict the distribution of trees, shrubs, marsh, fire scars, and other land cover classes. We used the ground surveys to quantify the vegetation components of the landscape in detail.

Estimating Tree Age

To assess changes in native tree populations over time, we compared 1999 survey data (264 trees) with 2002 survey data (750 trees). We previously found a significant linear relationship between number of tree rings and basal tree diameter (Zamora-Arroyo et al. 2001). The equation for willow and cottonwood combined was $y = 0.287x$ ($r^2 = 0.94$, $n = 29$, SE of estimate = 1.7 years), where x is diameter in centimeters and y is tree age in years. We estimated the age of uncored trees based on the regression equation. Tree diameters were determined at breast height in the 2002 surveys, so we transformed the 2002 diameter data by multiplying by 1.11 based on a subsample of trees measured at both ground level and breast height. The tree age estimates are only approximate because only a subsample of trees were actually cored and the trees did not necessarily all grow at the same rate. We conducted a two-way analysis of variance (ANOVA) of the estimated tree ages, with year of sampling and plant species as categorical variables.

Comparison of Tree Cohorts on 1999 and 2002 Aerial Photographs

We compared the fate of individual trees on 20 matched pairs of 1999 and 2002 aerial photographs taken at four sites along the river. Each 1999 photograph, covering 670 m^2 of ground area, was georeferenced to a 2002 image by matching three or more common features on each photograph (roads, river feature, common vegetation features). Only photographs that could be unambiguously matched were used in the analysis ($n = 4$–7 photographs/site, total image pairs = 20 over four sites). We marked all individual trees with canopy diameter >3 m separately on each photograph of the matched pairs. We then compared photographs and placed each tree into one of three categories: present in both 1999 and 2002, present in 1999 but absent or dead in 2002, or not present (or not large enough to be scored as a tree) in 1999 but present in 2002. The photographs were also scored for the presence or absence of recent fire scars. This analysis allowed us to estimate percent survivorship, percent recruitment of new trees, and percent attrition of trees between 1999 and 2002 and to evaluate the effect of fire on tree populations.

Tree-density data were log transformed to normalize the distributions and subjected to two-way ANOVA in which year (1999 or 2002) and location (sites along river, $n = 4$) were the independent variables and tree density per hectare was the dependent variable. Log-transformed tree density data from 2002 were further subjected to one-way ANOVA in which condition (burned or unburned) was the independent variable. Differences between burned and unburned sites in percent survivorship, percent recruitment, and percent total trees in 2002 compared with 1999 were tested by the nonparametric Kruskall-Wallis one-way ANOVA because histograms of the percentage data showed that they were not normally distributed, and we were unable to normalize the data through transformation.

Groundwater Data

In 1999 well points (5-cm-diameter steel tubes with a perforated "sand point" at the tip to admit water into the tube) were installed into the water table to a depth of 4 m at five sites along the river. Two well points were installed at each site, one near the bank of the active channel and one 100 m away from the channel. Depth to groundwater and electrical conductivity were sampled in November 1999 and January and February 2000 (Zamora-Arroyo et al. 2001). In 2003 measurements were resumed at three of the sets of well points (tubes at the other two sites were removed by local residents). Depth to water and electrical conductivity were measured in July, October, and December 2003 and January, March, and April 2004. Water depth was determined after pumping three or more volumes of water from the casing and then allowing the well to recharge to a constant depth (Zamora-Arroyo et al. 2001). Electrical conductivity on each sample was measured in the laboratory with an electrical conductivity meter (Markson, Chicago, Illinois). Salinity in milligrams per liter was equal to electrical conductivity in decisiemens per meter times 620, based on a KCl calibration solution.

Correlation of Vegetation Intensity with Water Flows

Flow data at the Southerly International Boundary (SIB), near San Luis, Mexico, was supplied by the International Boundary and Water Commission (U.S. Department of State, El Paso, Texas) (Fig. 1). We acquired thematic mapper 5 or ETM+ images for early summer scenes of the delta for 1992, 1994, 1996, 1997, 1998, 1999, and 2002, corresponding to years before and after major water releases. Pixels were converted to exo-atmospheric reflectance values by EarthSat (Beltsville, Maryland), then into normalized difference vegetation index (NDVI) values. The NDVI transforms the red and NIR wavelength reflectances to a ratio to discriminate degrees of foliage density (green leaves absorb red and reflect NIR radiation) (Nagler et al. 2001). We could not correct for atmospheric effects, but when the NDVI values for different pure target types (water, sand, agricultural fields) were compared, values were similar across images (Zamora-Arroyo et al. 2001), attributed to the generally clear, dry air over this region. Hence mean values of NDVI across the riparian corridor could be compared across years as a measure of foliage density (Nagler et al. 2001, 2004). We correlated summer biomass in the study area either with the volume of the previous winter's river flow or with the number of preceding years in which peak river flows were >50 m^3/second.

Table 1. Land cover at 240 sample stations (0.785 ha each) in the Colorado River delta, Mexico.*

Land cover class	*Mean cover (%) (SEM)*	*Mean height (m) (SEM)*
Saltcedar	34.7 (1.6)	2.76 (0.06)
Arrowweed	11.2 (1.1)	1.44 (0.04)
Willow	6.2 (0.7)	4.32 (0.16)
Seepwillow	4.8 (0.6)	1.72 (0.05)
Cottonwood	1.7 (0.3)	5.80 (0.31)
Quailbush	1.3 (0.5)	1.34 (0.04)
Screwbean mesquite	0.8 (0.3)	3.46 (0.14)
Honey mesquite	0.3 (0.2)	3.81 (0.21)
Cattail	2.1 (0.3)	2.04 (0.07)
Common reed	2.0 (0.4)	2.30 (0.09)
Bulrushes	0.4 (0.1)	1.14 (0.07)
Bare soil	24.0 (1.3)	n.a.
Open water	5.7 (0.6)	n.a.

**Data are means and standard errors; n.a., not applicable.*

Results

Species Composition of the Floodplain

Saltcedar (mean height 3 m) was the most common plant on the floodplain, with 35% cover (Table 1). Arrowweed (*Pluchea sericea* [Nutt.] Coville [ca. 2 m tall]), a native salt-tolerant shrub, was next in abundance. It grew in large, single-species patches up to several hectares on the floodplain or in mixed stands with saltcedar. Willow and cottonwood trees accounted for 6.2% and 1.7% of ground cover, respectively, and were the tallest plants in the floodplain at 4–6 m or greater. The mesophytic native shrub seepwillow (*Baccharis salicifolia* [Ruiz & Pavor] Pers.) made up nearly 5% of the ground cover. The salt-tolerant shrub quailbush (*Atriplex lentiformis* [Torr.] S.Wats.) was abundant at some locations, especially in drier, saline benches away from the main channel. The two native mesquite trees—honey mesquite (*Prosopis glandulosa* Torrey) and screwbean mesquite (*P. pubescens* Benth.)—together accounted for only 1% of cover.

Bare soil accounted for 24% of ground cover. At the time of the survey, the river was running at only 2 m/second at the gauging station at the Southerly International Boundary, but there was still a continuous run of water in the main channel from Morelos Dam to the junction with the Rio Hardy and in some backwaters along the river. Open water accounted for about 6% of ground cover, whereas the emergent plants cattail (*Typha domengensis* Crantz), common reed (*Phragmites australis* [Car.] Trin. ex Steud), and bulrush (*Scirpus americanus* Pers. and *S. maritime* L.) accounted for nearly 5% cover. Thus, more than 10% of the floodplain was aquatic or semiaquatic habitat even in the relatively dry year of 2002.

Age and Height Distribution of Trees

The frequency distribution of tree ages clearly reflects the effect of recent floods on the establishment of cottonwood and willow trees (Fig. 2). In both the 1999 and 2002 surveys, willow trees were more numerous than cottonwood trees (3:1 ratio). In the 1999 survey, the majority of the trees appeared to have established during the 1993 water release (Fig. 1), but numerous, larger trees, apparently started from the releases of the 1980s, were present on the floodplain. The floods of 1983–1988 kept most of the floodplain continuously inundated, and the trees corresponding to the 1988 cohort probably germinated when water finally receded from the benches above the main channel. There was also a cohort of 2-year-old trees in 1999, started by the 1997 release.

By 2002 the tree populations had changed considerably. The largest age class of trees was 2 years old, started by the 2000 (ca. 100 m^2/second) flood release. The 1997 age class was still present for both species as a secondary peak. The 1993 age class was present as a minor peak for cottonwood but was not present for willow, and the 1980s age classes had nearly disappeared from the floodplain.

A two-way ANOVA showed that the cottonwood and willow populations average significantly older ($F = 114$, $p < 0.001$) in the 1999 survey than in the 2002 survey. Mean tree ages in 1999 were 9.8 years (SEM = 0.5), whereas in 2002 mean tree age was 4.1 years (SEM = 0.3). Tree heights differed by year ($F = 147$, $p < 0.001$) and species ($F = 7.8$, $p < 0.01$), and the interaction term (year × species) was also significant. Tree heights were similar for cottonwood and willow in 1999 ($p > 0.05$), (mean = 8.2 m, SEM = 0.2), whereas in 2002 their mean heights were 6.0 m (SEM = 0.3) and 4.8 m (SEM = 0.2), ($p < 0.05$), respectively, because they were younger trees. These data suggest a rapid turnover of tree populations on the floodplain.

Spatial Distribution of Live and Dead Trees

The floodplain was analyzed as a series of lateral strips going out from the channel. Live willow and cottonwood trees accounted for approximately 20% of land cover along the first 50 m of the river bank on either side of the channel, forming a nearly continuous strand of trees from the Northerly International Border (NIB) to the junction with the Rio Hardy, a length of more than 100 km (Fig. 3). Smaller numbers of trees were distributed across the floodplain as far as 1 km from the channel. Dead trees were also concentrated along the current channel but were proportionately more abundant farther out on the floodplain than were live trees. The ratio of dead to live trees over the whole floodplain was 1:2.2.

Fresh fire scars covered 2896 ha (12%) of the floodplain in 2002 and were scattered across the floodplain along the entire length of the study area. Eighty-two percent of the dead trees occurred in the fire scar areas. Hence fire appears to be the major cause of tree mortality.

The high proportion of dead trees in 2002 supports the age-class data that suggest a rapid turnover of trees on the floodplain between 1999 and 2002. The ground data,

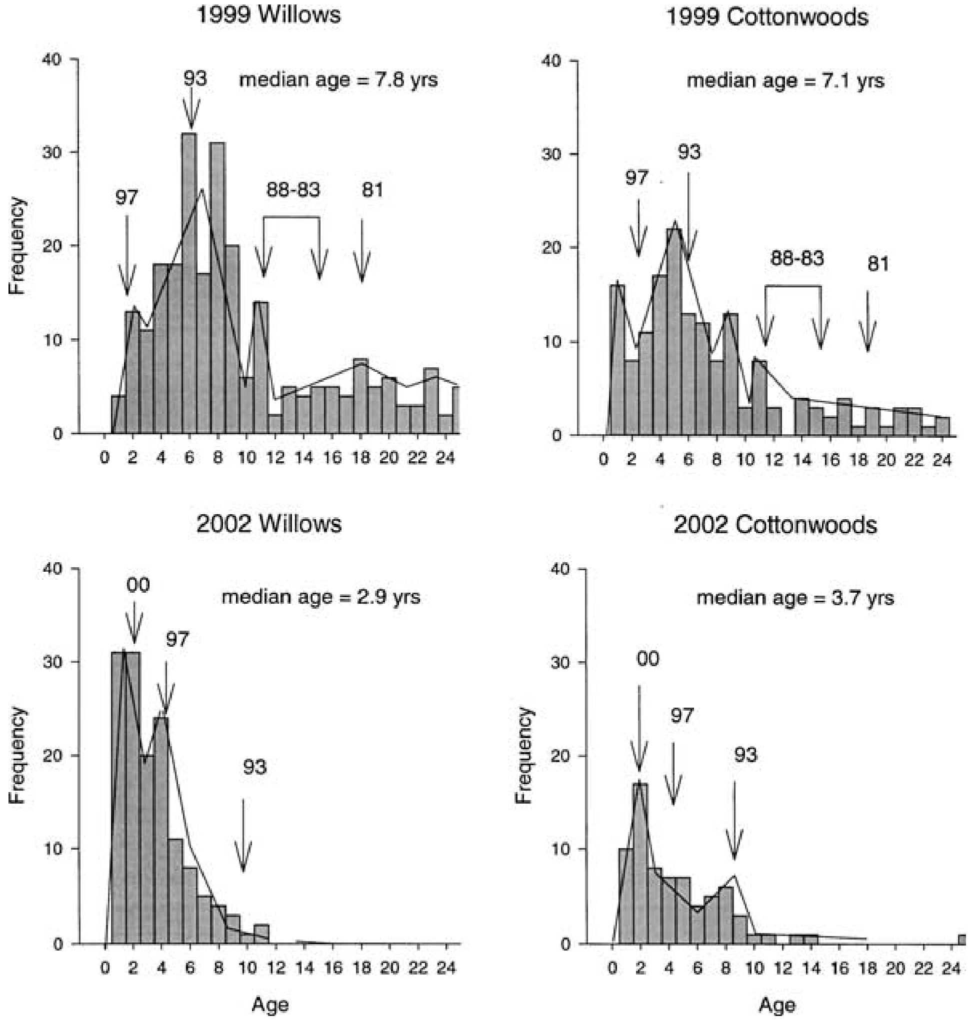

Figure 2. Estimated ages (years) of willow and cottonwood trees in the Colorado River delta riparian corridor in 1999 and 2002. Arrows show years in which major flood events occurred. Because the age distribution was skewed toward younger trees, the median age rather than mean age is the estimator of central tendency.

however, were collected on relatively few trees surveyed at different sites in 1999 and 2002. We analyzed aerial photographs to track the fate of individual trees over time and to quantify the effects of fire on tree turnover (Fig. 4). Of the 20 paired images included in the analysis, 8 exhibited burn scars in 2002 that were not present in 1999. One-way ANOVA on data from 2002 images showed that burning had a significant effect ($F = 13.1$, $p < 0.01$) on tree density. Unburned plots had 59.4 trees/ha (SEM = 11.6) compared with 20.0 trees/ha (SEM = 11.3) on plots that had burn scars. Both burned and unburned plots had a high turnover of trees between 1999 and 2002. Expressed as a percentage of total trees present in 1999, in 2002 the unburned plots had 131% of the 1999 value, of which 52% were new trees and 79% were survivors from 1999. By contrast, the burned plots had only 49% of the amount of trees they had in 1999, of which 35% were new recruits and only 15% were survivors from 1999.

Groundwater Data

In 1999, following large floods in 1998, groundwater in the riparian corridor ranged from 1 to 2 m below the soil surface at all five stations measured. The mean electrical conductivity at the first four stations was 2.0 dS/m (range = 1.4–2.7 dS/m, $n = 30$) compared with 1.2 dS/m for river water (840 mg/L) (Zamora-Arroyo et al. 2001). The southernmost station was placed at the end of the native tree zone and was influenced by agricultural drainage water from the Mexicali Valley. The electrical conductivity there was much higher, 9.1 dS/m (range = 9.0–9.2 dS/m). In 2003–2004 mean depth to groundwater at the three stations that were still measurable was 2.0 m (range = 0.8–3.1 m, $n = 24$). Electrical conductivity at the first two stations was 3.6 dS/m (range = 1.2–6.6 dS/m), nearly twice as high as values in 1999 ($p < 0.5$ by t test). On the other hand, in 2003 the mean electrical conductivity at site 3, the same as the southernmost station in 1999, was 3.7 dS/m (range = 1.4–9.3 dS/m), lower than in 1999. The water table at this site was influenced by the amount and salinity of agricultural drain water in the Rio Hardy and is highly variable.

Correlation of Vegetation Intensity with Water Flows

Biomass intensity in the riparian corridor, as measured by summer NDVI values on TM images, responded positively

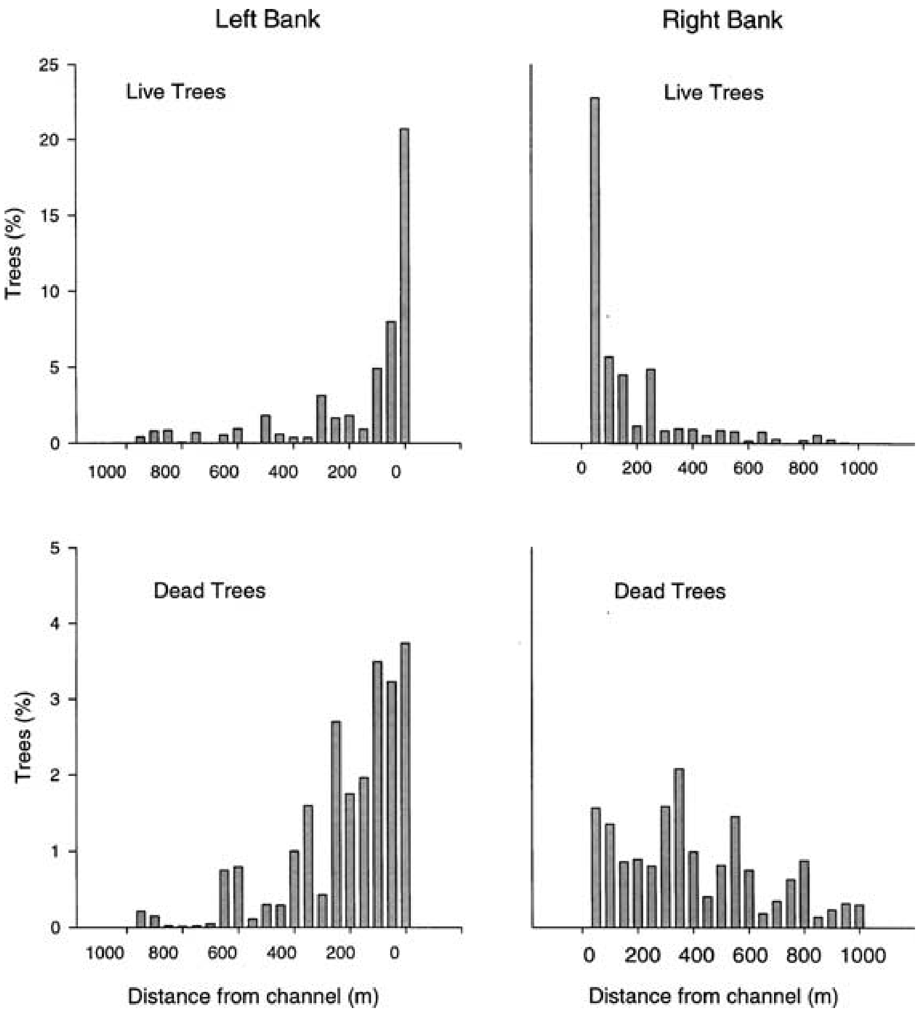

Figure 3. Distribution of willow and cottonwood trees along the banks of the active river channel of the Colorado River in Mexico in 2002. Values are the percent ground cover occupied by live or dead trees in 50-m strips progressively distant from the river channel, based on GIS analysis of the vegetation map. Top panels show live trees and lower panels show dead trees (y-axis scales are different).

to river flows from 1992 to 2002 (Fig. 5). As in a previous analysis (Zamora-Arroyo et al. 2001), the volume of flows was not as important as the number of years of flow in stimulating vegetation growth. The lowest summer NDVI values were recorded for years that did not have preceding winter floods (1992, 1996, 2002). The NDVI values increased proportionally in years that were preceded by 1 (1994, 1998), 2 (1999), or 3 (2000) years of winter flow.

Discussion

Regeneration Potential of Native Trees in Response to Pulse Floods

The hypothesis that native hydromesic trees would regenerate in response to pulse floods despite the presence of an invasive dominant species was supported for the species cottonwood and willow in this study. In both 1999 and 2002 surveys, cottonwood and willow trees made up about 10% of the total vegetation, much higher than on the lower Colorado River above the NIB, which has regulated flow (see Zamora-Arroyo et al. 2001 for a comparison of tree density in the U.S. and Mexico portions of the river). Seepwillow, a mesic native shrub that has become rare on the U.S. stretch of river, made up 5% of the ground cover in the delta.

Mahoney and Rood (1998) defined a "recruitment box" for the germination and establishment of *Populus* spp. Successful establishment required spring floods and a water table within 2 m of the surface so that seedling roots could grow fast enough to remain within the capillary fringe of the water table as it declined over the first summer. In the Colorado River riparian corridor, which has a similar sandy soil to the river system studied by Mahoney and Rood (1998), February to April floods ranging from 50 to 500 m^3/second brought the river out of its channel and germinated cottonwood and willow seedlings on the floodplain in 1993, 1997–1998, and 2000. The river receded to its channel by May of each flood year, but the vadose zone retained sufficient moisture to carry the seedlings through summer. The water table was within 2 m of the surface even between floods. The riparian groundwater is recharged by underflow from the United

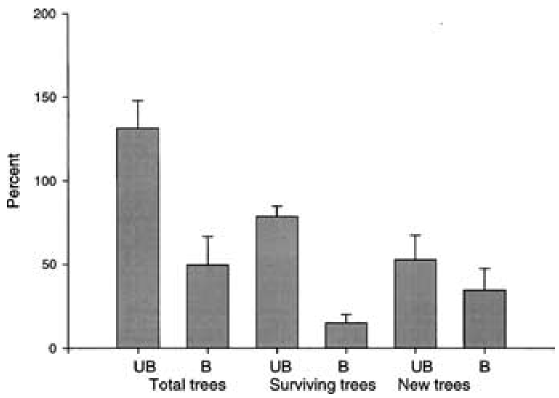

Figure 4. Turnover of willow and cottonwood trees in the Colorado River delta, Mexico. Results are mean values from four sites along the river, with four to six plots per site. Bars show mean and standard errors of percentage of trees present in 2002 relative to the number present in 1999 (total trees); the percentage of trees that survived between 1999 and 2002 (surviving trees); and the percentage of new trees in 2002 relative to the number of trees in 1999 (new trees). Results are shown for burned (B) and unburned (UB) plots, based on the presence of burn scars in 2002 images. Mean values between burned and unburned plots were different for total and survival but not recruitment classes at $p < 0.05$ *by Kruskal-Wallis tests.*

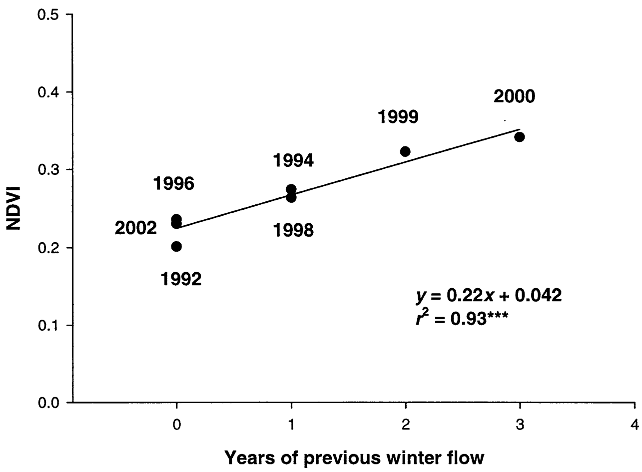

Figure 5. Dependence of vegetation intensity on number of years of river flow in the Colorado River delta riparian corridor, Mexico. Vegetation intensity was measured by the normalized difference vegetation index (NDVI) on summer satellite scenes of the riparian corridor, 1992-2002. The NDVI of bare soil was 0.08 (SEM = 0.005) and of dense vegetation (cropland) was 0.56 (SEM = 0.04) among years ($n = 7$*) (*** $p < 0.001$).*

States and discharge from surrounding agricultural fields (Cohen et al. 2001).

Floods play several roles in the establishment of hydromesic species (Poff et al. 1997). They flush salts from the soil surface, creating suitable soil salinity conditions for germination (Busch & Smith 1995). They create bare, moist sites for seed germination and establishment (Sher et al. 2002; Sher & Marshall 2003), scour out vegetation and deposit new sediment (Stromberg et al. 1993; Stromberg 1997), and stimulate decomposition of litter to release nutrients and reduce the fuel load (Molles et al. 1998).

Native trees tended to dominate the banks of the active river channel, forming an overstory that partially excluded saltcedar. On the other hand, saltcedar and arrowweed tended to dominate the large areas of floodplain away from the river. In many locations, however, the plants grew together in mixed stands. These results support other studies showing that native trees can establish and coexist with saltcedar under favorable hydrological conditions (Stromberg et al. 1993; also reviewed in Stromberg & Chew 2002*a*, 2002*b*). Although the larger flow events were responsible for germinating native tree seeds, the small flows of 1–5 m^3/second maintained an active channel containing valuable marsh vegetation from the NIB to the junction with the Rio Hardy. Hence the habitat value of the riparian corridor depends on occasional large pulse-flood events and on smaller maintenance flows.

The native tree populations were unexpectedly dynamic, with a turnover rate of approximately 5 years. By contrast, those portions of southwestern U.S. rivers that still maintain significant populations of native trees tend to be dominated by older cohorts and show limited recruitment of new trees (Howe & Knopf 1991; Stromberg et al. 1993; Stromberg 1997, 1998; Shafroth et al. 1998; Shafroth et al. 2002).

The most important cause of tree mortality was fire. Eighty-two percent of the dead trees occurred in fresh fire scars, which covered 12% of the floodplain in 2002. Based on the analysis of aerial photographs, about 30% of the trees within a fire scar survived burning. Many of the older trees on the floodplain exhibited burn scars from past fires. Busch (1995) examined fire records for the lower Colorado River in the United States and calculated that 37% of the floodplain had been burned over a 12-year period. Saltcedar spreads fire readily and resprouts rapidly following fires. Over time it can replace native trees when fires are frequent and there is no pulse-flood regime to establish new trees (Busch & Smith 1993, 1995). In the delta, however, recruitment of new trees appeared to keep pace with attrition due to fire. Many of the fires are deliberately set because the local residents burn trash in the floodplain. Other fires are started accidentally from the burning of wheat straw in the surrounding agricultural fields (authors' observations).

Salinity of the water table also increased between floods and may have contributed to tree mortality because values greater than 6 dS/m are inhibitory to cottonwood and willow growth rates (Glenn et al. 1998). Large trees from the floods in the 1980s were sometimes logged by local residents for lumber (authors' observations). Given the high turnover rate of trees, any management practices that reduced the frequency of flood events would rapidly reduce the tree populations in the delta.

Conservation Status of the Colorado River Delta

The southern part of the delta is protected in the Biosphere Reserve of the Upper Gulf of California and Delta of the Colorado River (Glenn et al. 1996). The riparian corridor, however, is currently unprotected and its future is uncertain. The International Boundary and Water Commission has proposed clearing vegetation and digging a pilot channel in the part of the river that forms the border between the United States and Mexico, and Mexico's National Water Commission has proposed extending that work to the junction of the Rio Hardy (Cornelius et al. 2003). On the other hand, the riparian corridor is now recognized as an important link for Neotropical terrestrial birds on the Pacific Flyway and has been proposed for protected status (Garcia-Hernandez et al. 2001; Hinojosa-Huerta et al. 2002). Our results show that the habitat value of the riparian corridor would be improved by fire management (Busch 1995), which could allow older trees to develop and might increase the overall cover of trees compared to shrubs.

Feasibility of Restoring Pulse Floods to Arid Rivers

The pulse floods we studied were not initiated to produce environmental benefits. Experimental floods in the Grand Canyon of the Colorado River (Patten et al. 2001), the Truckee River (Rood et al. 2003), and the Rio Grande (Molles et al. 1998), however, show the feasibility of incorporating variable flow regimes into river management. Natural resource managers and river operations specialists should examine the potential for providing beneficial floods on arid-zone rivers as a means of reestablishing native vegetation.

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