PATTERNS IN SHORELINE VEGETATION AND SOILS AROUND LAKE MOHAVE, NEVADA AND ARIZONA: IMPLICATIONS FOR MANAGEMENT

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ABSTRACT.—Lake Mohave, on the lower Colorado River in Nevada and Arizona, was created by the construction of Davis Dam for power generation, flood control, and water supply. Management has led to the periodic lowering of the water level of the reservoir (drawdown), such that it reveals a gradient of zones around the margins of the reservoir that range from frequently inundated to frequently dry. The initial filling of Lake Mohave flooded the preexisting native riparian woodlands of *Populus-Salix* (cottonwood-willow), creating a new shoreline and plant community. We analyzed the spatial distribution of the plant species that dominate the plant community (i.e., native *Salix gooddingii* C.R. Ball [Goodding's willow] and nonindigenous *Tamarix ramosissima* Ledeb. [saltcedar]) and the soil components to discern patterns. Data analyses and modeling indicate that there are 3 emergent patterns in the distribution and composition of vegetation and soils. First, even though both *S. gooddingii* and *T. ramosissima* were present in the inundated zones, there were more mature *S. gooddingii* individuals in the frequently inundated reaches, while *T. ramosissima* presence and cover increased with distance from the water's edge. *Salix gooddingii* seedlings were not observed, but *T. ramosissima* seedlings were present in all zones. The only regeneration of *S. gooddingii* was vegetative. Naturally occurring *Populus fremontii* S. Watson (Fremont cottonwood) was completely absent in the drawdown and upland plant communities. Second, soil salinity and pH values range from 49.4 to 0 dS · m⁻¹ and 6.4 to 9.4, respectively, and varied significantly with landform type and geographic location along the reservoir. Patterns in soil chemistry may be related to shore geomorphology that either shelters or exposes soils to wave action, which mechanically agitates, aerates, and flushes soils. Presence of *Salix gooddingii* in the frequently inundated zones and the co-occurrence of *T. ramosissima* and relatively high soil salinity concentration reflect patterns among plant flood tolerance and soil responses to periodic inundation. While reasons for the absence of *P. fremontii* are unknown, the absence of *S. gooddingii* seedlings may be related to the fact that seed release coincides with the period when the reservoir is at its highest, thereby limiting recruitment. Third, the only regeneration of *S. gooddingii* appeared to have occurred following herbivory (*Castor canadensis* Kuhl [North American beaver]) and wind damage. We conclude with suggestions for the conservation of novel riparian ecosystems as surrogates for lost native ecosystems. These suggestions include manipulating reservoir water levels to simulate natural fluvial processes so that nonnative plant establishment is inhibited, excessive soil salts are flushed from the system, and native transplants can be established.

RESUMEN.—El Lago Mohave, en la parte baja del Río Colorado en Nevada y Arizona, E.U.A., fue creado por la construcción de la presa Davis para la generación de electricidad, control de inundaciones y abastecimiento de agua. Su manejo ha causado el descenso periódico del nivel del agua del embalse (reducción) de modo que revela un gradiente de zonas alrededor de la orilla del embalse que varían desde las frecuentemente inundadas hasta las frecuentemente secas. Al llenar por primera vez el Lago Mohave, se inundó el bosque preexistente nativo y ribereño de *Populus-Salix* (álamos y sauces), creando nuevas riberas y nuevas comunidades de plantas en sus orillas. Analizamos la distribución espacial de las especies que dominan la comunidad de plantas (i.e., la especie nativa *Salix gooddingii* C.R. Ball [el sauce de Goodding] y la invasora *Tamarix ramosissima* Ledeb. [tamarisco]) así como los componentes del suelo para discernir patrones entre la vegetación y los suelos. El análisis de datos y la modelación indican que hay tres patrones emergentes en la distribución y composición de la vegetación y los suelos. Primero, a pesar de que tanto *S. gooddingii* como *T. ramosissima* estuvieron presentes en las zonas inundadas, hubo más individuos maduros de *S. gooddingii* en las zonas frecuentemente inundadas; en cambio, la presencia y cobertura de *T. ramosissima* aumentó a medida que aumentaba la distancia de la orilla. No se observaron plántulas de *S. gooddingii*, mientras que plántulas de *T. ramosissima* estuvieron presentes en todas las zonas. La única regeneración de *S. gooddingii* fue vegetativa. *Populus fremontii* S. Watson [álamo], que ocurre de manera natural, estuvo totalmente ausente en las comunidades de plantas que habitan las zonas donde se ha reducido el nivel del agua y en tierras altas. Segundo, la salinidad y los valores de pH del suelo variaron de 49.4 a 0 dS · m⁻¹ y de 6.4 a 9.4, respectivamente, y variaron substancialmente en distintos tipos de formación geológica y en distintas ubicaciones geográficas alrededor del embalse. Los patrones en la composición química del suelo podrían estar relacionados con la geomorfología de la ribera, la cual puede proteger los suelos o exponerlos a la acción de las olas que mecánicamente agitan, airean y humedecen los suelos. La presencia de *Salix gooddingii* en las zonas frecuentemente inundadas y la

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coincidencia de *T. ramosissima* y una concentración de sales en el suelo relativamente alta reflejan patrones de la resistencia a inundaciones por parte de las plantas y los efectos en los suelos de las inundaciones periódicas. Aunque se desconocen las causas de la ausencia de *P. fremontii*, la ausencia de plántulas de *S. gooddingii* podría estar relacionada con el hecho de que la dispersión de semillas coincide con el periodo en que el embalse alcanza su nivel máximo, limitando de esta manera el reclutamiento. Tercero, la única regeneración de *S. gooddingii* parece haber ocurrido después de la herbivoría (*Castor canadensis* Kuhl [castor americano]) y de los daños ocasionados por el viento. Concluimos con sugerencias para la conservación de los ecosistemas ribereños nuevos como reemplazos de los ecosistemas originales perdidos. Éstas incluyen el manipular el nivel del agua en los embalses para simular procesos fluviales naturales y así impedir que se establezcan las plantas invasoras, limpiar del sistema las sales excesivas en el suelo y permitir que se establezcan plantas nativas que hayan sido transplantadas.

Lake Mohave, an aridland reservoir on the border of Nevada and Arizona in the southwestern United States (Fig. 1), was formed following the construction of Davis Dam in 1953 on the lower Colorado River. Davis Dam was constructed to generate power, control floods, and supply water for downstream urban, industrial, and agricultural use (Bureau of Reclamation 2011). Construction of the Davis Dam altered the natural flow of the Colorado River downstream of the Hoover Dam. Management of the river has led to periodic lowering of the reservoir water level (drawdown), such that a gradient of zones has developed around the margins of the reservoir. The zones range from frequently inundated to frequently dry (Fig. 2).

The filling of Lake Mohave flooded the preexisting native woodlands dominated by *Populus fremontii* (Fremont cottonwood) and *Salix gooddingii* (Goodding's willow) and created a new shoreline around reservoir margins at higher elevations previously dominated by the desert shrub *Larrea tridentata* (DC.) Colville (creosote bush). The plant communities of the new shoreline are comprised of native *S. gooddingii* and nonindigenous *Tamarix ramosissima* (saltcedar). However, there is a complete absence of *P. fremontii* (C. Deuser and J. Haley, Lake Mead National Recreation Area, Nevada, personal communication, 1996), the pioneer tree species that co-occurred with *S. gooddingii* along the Colorado River prior to regulation by dams (Braatne et al. 1996). In this paper, a riparian ecosystem is the terrestrial environ adjacent to the reservoir whose freshwaters provide soil moisture sufficient to support the growth of phreatophytic vegetation (modified from Warner and Hendrix 1984). *Salix gooddingii* and *P. fremontii* are obligate phreatophytes (i.e., a deep-rooted, "water-loving" plant that obtains its water from permanent ground supply or capillary fringe [hyporheic zone] of streams, rivers, lakes, and reservoirs; Braatne et al. 1996, Smith et al.

1997, 1998). *Tamarix ramosissima* is a facultative phreatophyte and, thus, can obtain water at lower soil water potential than native riparian trees (Smith et al. 1997).

Notably, the plant communities currently occurring around Lake Mohave are perceived by the public and land managers as valuable systems that provide habitat for native plant species and wildlife as well as scenic landscapes that are as culturally pleasing as they are unique to arid environments. Throughout arid regions worldwide, there are novel riparian ecosystems that have species compositions and relative abundances that have not occurred previously within a given biome (Hobbs et al. 2006). Many of these ecosystems have arisen along human-generated water-bodies and waterways, such as stockpounds in Oklahoma (Keltling and Penfound 1950, Penfound 1953) and Kentucky (Hall and Smith 1955), Colorado gravel pits and diversion canals (Mahoney and Rood 1998, Roelle and Gladwin 1999, Roelle et al. 2001, Crifasi 2005), reservoirs and rivers in Montana (Johnson 2002), Australian lakes (Williams 2000), and the lower Colorado River reservoir Lake Mohave on the border of Nevada and Arizona (Tallent-Halsell 1998). Direct (e.g., dam construction) and indirect human interventions (e.g., construction of dispersal barriers) have resulted either in major changes to the abiotic environment or a decrease in the original propagule species pool, both of which can prevent the reestablishment of preexisting species assemblages and alter the biogeochemistry of the system (Nilsson and Berggren 2000, Johnson 2002, Crifasi 2005).

Efforts to introduce native *S. gooddingii* and *P. fremontii* around the lower Colorado River reservoir Lake Mohave, in an attempt to expand and sustain novel but aging woodlands, have not been successful (<1% establishment of introduced saplings, C. Deuser and J. Haley, Lake Mead National Recreation Area, Nevada, personal communication, 1996). The

Fig. 1. Locations of 34 study sites at Lake Mohave in the Lake Mead National Recreation Area in Nevada and Arizona. Descriptions of numbered sites are provided in the Appendix.

transplants' failure to establish was due, in part, to the fact that native *S. gooddingii* experiences high mortality and reduced biomass under flood conditions (Tallent-Halsell and Walker 2002). In addition, revegetation efforts may have been further compromised by a suite of factors that affect riparian ecosystems throughout the Southwest, such as the rapid colonization by *T. ramosissima* (Anderson 1996) and riparian soil salinization (Vandersande et al. 2001). Foraging on *S. gooddingii* and *P. fremontii* transplants by *Castor canadensis* (North American beaver; Rosell et al. 2005) may also have limited the survival of transplants (C. Deuser and J. Haley, Lake Mead National Recreation Area, Nevada, personal communication, 1996).

Little is known about the ecology of novel riparian ecosystems; therefore, we designed a study to better understand the resulting plant distributions and factors affecting these distributions in the riparian zone along Lake Mohave. Our 3 main objectives were to (1)

describe the pattern of *S. gooddingii* and *T. ramosissima* cover; (2) describe the pattern of soil salinity, nutrients, and texture; and (3) relate these patterns to a suite of variables, including landform (beaches in sheltered coves or line beaches that were exposed), geographic location (eastern or western bank, northern or southern basin), herbivory, presence of native vegetation, and location of plants from the water's edge. Our study contributes information about the ecology of riparian ecosystems on reservoirs in deserts and the environmental factors that shape them.

METHODS

Study Area

Lake Mohave is a long (108 km) and narrow (average 6.4 km) reservoir with a total surface area of 114 km² (Bureau of Reclamation 2011). The release of water through Davis Dam (draw-down) creates a distinct gradient of zones that

Fig. 2. Hydrograph characterizing the hydrologic regime of Lake Mohave (1950–2007) and illustrating that water level drops approximately 3 m beginning in September and rises again in January. The y-axis is the mean water level, and error bars depict one standard deviation around the mean.

TABLE 1. Characteristics of groupings of sites at Lake Mohave, Nevada and Arizona, USA. Sample sizes are in parentheses.

Characteristic	Grouping 1 (n)	Grouping 2 (n)
Bank ^a	West (21)	East (13)
<i>Salix</i> ^b	Present (18)	Absent (16)
Landform ^c	Exposed (13)	Cove (21)
Herbivory ^d	Present (20)	Absent (14)
Basin ^e	Upper (21)	Lower (13)
Location in the drawdown ^f	Band A ^g	Band B ^g

^aBank = western or eastern side of river.

^b*Salix* = presence of *Salix gooddingii*.

^cLandform = either exposed (line beaches) or (sheltered) coves; see text for further explanation.

^dHerbivory = presence or absence of herbivory

^eBasin = located in the upper northern or lower southern basin.

^fLocation in the drawdown = group based on the distance from waters at maximum drawdown; see text for further explanation.

^gSee Figs. 4 and 5 for sample size.

is approximately 25 m in width from minimum to maximum water level, depending on the slope of the shoreline. These zones range from frequently inundated to frequently dry. The maximum and minimum lake elevations for Lake Mohave are 197 m and 193 m, respectively (Fig. 2). This study was conducted in the 2 widest basins and interconnecting area where the gradient of zones is most evident and where the largest stands of native, woody vegetation occur (Appendix; Fig. 1).

Our sites were grouped by side of the lake (east or west), location in the basin (upper [northern] or lower [southern]), and landform type (Fig. 1). The landform types were defined as sheltered coves and exposed line beaches. Sheltered coves were defined as inlets that were sheltered from the wind on 3 sides by upland hills and that had shorelines at least 50 m away from the mouth of the inlet. Exposed line beaches were characterized as unbroken, linear stretches of shore with full exposure to wind from all sides. In addition, we grouped the sites by whether we observed *S. gooddingii*, as well as evidence of beaver foraging and activity (henceforth referred to as herbivory).

Additionally, we divided the data into 2 groups based upon whether the sampling point was located 0–25 m (band A) or 26–50 m (band B) from the water's edge at maximum drawdown (Table 1). Band A was characterized by having been frequently inundated (i.e., approximately 9 months prior to the sample period), whereas band B was characterized by having been frequently dry throughout the year.

To select study sites we divided the shoreline of the 2 widest basins and interconnecting area into 264 segments, each 1 km long. From these segments, 20% ($n = 53$) were randomly selected as potential locations from

Fig. 3. Schematic representing the field sampling design at Lake Mohave.

within which to randomly establish 50×50 -m (2500-m^2) study sites along the shoreline (henceforth referred to as “sites”). When sites with steep slopes ($>10\%$), rock walls, compacted soils, or extensive cobble ($>80\%$ cover of cobble >6 cm in diameter) were excluded, 34 sites remained (Appendix 1; Fig. 1).

The sites were located on loamy sand alluvium derived from basalt (Hoffman and Jones 1972), and soils were shallow, hyperthermic aridisols (Natural Resource Conservation Service 1993) that had been intermittently inundated for at least 60 years. The climate is typical of the southern Mojave Desert, with hot summers and cool winters (MacMahon and Wagner 1985). The yearly mean precipitation, though highly variable, is 109 mm; the majority of the precipitation falls in winter, with rare rainfall events occurring during the summer. The mean monthly high and low temperatures range from 18°C and 1°C in January to 44°C and 27°C in July (National Park Service 2011).

Field Measurements

At each of the 34 sites, a 50-m-long baseline was placed parallel to the shoreline at 193 m above sea level (asl), which was the minimum water level during our study period (Fig. 3).

Five transects (2×50 m) were placed perpendicular to the plot baseline at intervals of 10 m, moving up from the wetter (band A) to the drier zones (band B) around the reservoir margins (henceforth referred to as “shoreline”). The slope from the shoreline to the upland was determined by using a clinometer (Compton 1985). Latitude and longitude of the center of each plot were recorded using a global positioning system (Trimble GeoExplorer I, Trimble Navigation Limited, Sunnyvale, CA). Vegetation and soil were sampled in each plot during the December 1997 drawdown (Fig. 2).

Total vegetative canopy cover (%), canopy cover by species (%), extent of bare ground (%), and litter cover (%) were estimated using a modified Daubenmire method within each of twenty-five $2 \times 1\text{-m}^2$ quadrats, which were placed at 2-m intervals along the 50-m transect, beginning at the 1-m mark (Daubenmire 1959; Fig. 3). We also noted when there was evidence of herbivory or foraging (e.g., presence or absence of pointed stumps, downed trees, piles of shavings, and dens).

Surface soil samples (100 g) were collected from 30-cm-deep cores at regular 5-m intervals along each transect, beginning at the 0 mark (Fig. 3). Soil samples were air-dried

before analysis of soil salinity (Rhoades 1982). They were then dried in an oven at 105 °C for 48 hours and passed through a 2-mm sieve before analysis of soil pH (Tan 1996) and particle size (hydrometer method; Tan 1996). Total soil N, C, and S were determined on 0.2-g oven-dried soil samples using a Leco-2000 CNS analyzer (LECO Corporation, St. Joseph, MN).

Data Analysis

We used χ^2 and likelihood-ratio statistics (G^2 test; Zar 2010) for categorical data to test differences in categorical vegetation measurements, and we used binary logistic regression (Hosmer and Lemeshow 2000) to determine the suite of independent, continuous variables (i.e., soil measurements) that best differentiated between the groupings described in Table 1. Because our response variables were dichotomous (i.e., the presence or absence of vegetation or cover by *S. gooddingii* and *T. ramosissima*), multiple logistic regression was used to model patterns of shoreline vegetation and soils around the reservoir as a function of the groupings (Table 1).

Initially, we examined the magnitude of the collinearity of the vegetation and soil measurements. If 2 variables in the model had a pairwise correlation coefficient (r) of ≥ 0.8 , one of the variables was removed from the model sequentially and the most significant variable was retained in the final model (Tabachnick and Fidell 2007). We used the Wald χ^2 (Allison 1999, Tabachnick and Fidell 2007) in logistic regression analysis, which is analogous to a standard regression analysis where the model F value is used to test the null hypothesis (H_0 : all coefficients are equal to zero). Wald χ^2 and its probability can be used in rejecting the null hypothesis that states that all coefficients are zero. Concordance and discordance values derived from the logistic regression analysis were used to measure the association between the predicted probabilities and to check the model's ability to predict the presence of certain vegetation cover groupings. Higher concordance corresponds to greater predictive ability of a model. We also used the standardized coefficient estimates to rank the relative importance of each of the independent variables.

Stepwise selection in SAS was used to identify independent variables for the logistic multiple regression analysis (Allison 1999, Hosmer and Lemeshow 2000). Based on iterative

steps in model development, we selected the P values for variable entry and elimination as 0.3 and 0.1, respectively (Hosmer and Lemeshow 2000). The significance level $\alpha \leq 0.1$ was used to identify which soil and cover variables were retained in the final models (Nash and Bradford 2001). In some cases, transformation of predictors was carried on to improve prediction.

All data were analyzed using SAS version 9.1 (SAS Institute, Cary, NC), and variables not conforming to normality were appropriately transformed prior to analysis.

RESULTS

Vegetation

The field survey of vegetative cover revealed several interesting patterns. *Salix gooddingii* and *T. ramosissima* were the 2 dominant species at Lake Mohave (Fig. 4). *Salix gooddingii* was present in the plant community in both linear, monospecific stands (circa 25-m-wide strips parallel to the water's edge) and as scattered, mature individuals (ranging in height from 4 m to >8 m). Although *S. gooddingii* was distributed throughout bands A and B, *S. gooddingii* cover ($\bar{x} = 9.36\%$, $SE = 0.34$) was greatest (Fig. 4) between 6 m and 21 m (band A) from the waterline (193.4 m and 195.1 m asl). There were more individual mature *S. gooddingii* present in band A than in band B. *Salix gooddingii* cover in band B was attributed to individual trees scattered within the *T. ramosissima* thickets. Indicators of herbivory, including 5 beaver lodges, were evident at all sites where *S. gooddingii* was present. There was a significant (positive) relationship between herbivory and *S. gooddingii* cover ($G = 30.23$, $df = 5$, $P < 0.001$).

There was *T. ramosissima* in both bands; however, *T. ramosissima* cover increased with distance from the water's edge. *Tamarix ramosissima* cover was greatest in band B, starting at 26 m (195.5 m asl; Fig. 4), which was attributed to the presence of dense thickets (4 m tall and 25–100 m wide). *Tamarix ramosissima* seedlings and saplings were present in both bands; however, *T. ramosissima* cover between 4 m and 13 m (band B) from the waterline (193.4 m and 194.3 m asl) was the result of several stunted, scattered individuals.

Two other native species, *Prosopis pubescens* Benth. (screwbean mesquite) and *Pluchea*

Fig. 4. Mean percent cover of the distribution of *Salix gooddingii*, *Tamarix ramosissima*, and other vegetation in 2-m intervals from the Lake Mohave shoreline (the water's edge at maximum drawdown). Other vegetation comprises *Prosopis pubescens*, *Pluchea sericea*, and *Larrea tridentata*. Means and standard errors are represented. Counts per meter interval are as follows:

Interval	Count	Interval	Count	Interval	Count	Interval	Count	Interval	Count
1 m	163	11 m	155	21 m	124	31 m	115	41 m	106
3 m	163	13 m	149	23 m	122	33 m	113	43 m	105
5 m	163	15 m	142	25 m	121	35 m	111	45 m	102
7 m	160	17 m	136	27 m	118	37 m	110	47 m	102
9 m	159	19 m	130	29 m	116	39 m	107	49 m	100

sericea (Nutt.) Coville (arrowweed), were established in band B although they had a limited presence (cover < 20%) in band A. Neither *S. gooddingii* seedlings nor naturally occurring *P. fremontii* was present in either band. (Although not on the study sites, 5 *P. fremontii* individuals planted by the Lake Mead National Recreation Area National Park Service were observed during the study.)

Soils

The average soil salinity at Lake Mohave was $4.7 \text{ dS} \cdot \text{m}^{-1}$ (SE = 0.1, range $49.5\text{--}0.3 \text{ dS} \cdot \text{m}^{-1}$; 75% of the samples were $<5.7 \text{ dS} \cdot \text{m}^{-1}$). Based on the binary logistic regression of site

groupings, soil salinity was significantly greater on the western bank than on the eastern bank, in sheltered coves than on exposed line beaches, and along the northern basin than along the southern basin ($P < 0.001$ for all). Soil salinity was also significantly greater in band B than below ($P < 0.001$; Fig. 5). Soil pH was significantly greater on the western bank, lower at sites with evidence of herbivory and sites with *S. gooddingii*, greater on exposed line beaches and along the southern basin, and lower in value moving upland from the water's edge (Table 2; $\bar{x} = 7.9$, SE = 0.01, range 6.3–9.4). In contrast to salinity and pH measurements, nutrient levels remained uniform in both bands.

Fig. 5. Mean electrical conductivity ($\text{dS} \cdot \text{m}^{-1}$) of soils from Lake Mohave in 5-m intervals from the shoreline or water's edge at maximum drawdown. Means and standard errors are represented. Counts per meter interval are as follows:

Interval	Count	Interval	Count	Interval	Count	Interval	Count	Interval	Count
0 m	170	10 m	143	20 m	116	30 m	101	40 m	95
5 m	154	15 m	133	25 m	110	35 m	98	45 m	90

TABLE 2. Results of binary logistic regressions of site groupings (Table 1) as a function of soils variables. Analyses with $P > 0.1$ are not shown. Values in bold are significant ($P \leq 0.05$).

Site grouping variable	State with greater value	Measurement	P value
Bank	West	Soil salinity	≤ 0.001
	West	pH	≤ 0.001
	East	C	≤ 0.001
	West	N	≤ 0.001
Salix	Absent	pH	≤ 0.001
	Present	N	≤ 0.001
Landform	Cove	Soil salinity	≤ 0.001
	Exposed	pH	0.025
	Exposed	N	0.043
	Exposed	Clay	0.060
Herbivory	Absent	pH	0.002
	Present	C	0.033
	Present	N	≤ 0.001
Basin	North	Soil salinity	0.002
	South	pH	≤ 0.001
	North	C	0.054
Location in the drawdown	Band A	pH	≤ 0.001
	Band B	Soil salinity	≤ 0.001
	Band A	S	0.057

TABLE 3. Variables from the stepwise logistic regression models that relate to the presence of *Salix gooddingii* (>5%), *Tamarix ramosissima* (>10%), and total vegetation cover (>10%; includes cover estimate of *S. gooddingii*, *T. ramosissima*, and all other vegetation). Columns containing rank values show the ranking of the relative importance of each contributing variable as measured by the standardized estimate[†] of that variable.

Response variables	<i>S. gooddingii</i> cover (n = 301)		<i>T. ramosissima</i> cover (n = 302)		Total cover (n = 303)	
	Coefficient	Rank	Coefficient	Rank	Coefficient	Rank
Cover by <i>S. gooddingii</i>			-0.0957**	1		
Cover by <i>T. ramosissima</i>	-0.0678**	2				
Cover by litter	0.0611**	3	0.0498**	2		
Cover of sqrt (litter)					0.9746**	2
Location in the drawdown zone			0.0699**	3	0.0930**	3
Soil salinity			0.3061**	4		
Carbon	-0.7925**	4	-0.3185*	5		
Sulfur	231.0000**	1			227.0000**	1
Herbivory			0.3880**		0.6528**	
Clay	0.3311**	5	-0.2100*	5		
Soil pH					2.6185**	4

* $P < 0.1$
** $P < 0.05$
[†]Standardized estimate = (coefficient (B) × standard deviation of independent variable) / standard deviation of dependent variable). Herbivory is a categorical variable (presence or absence of herbivory at a site); therefore, there is no standardized estimate value.

Total soil N content ($\bar{x}$ = 0.12%, SE = 0.01, range 0.0009–1.26) was significantly greater on the west bank, on exposed beaches, and at sites with evidence of herbivory and presence of *Salix* (Table 2). Total soil C was greater on the east bank and at sites with evidence of herbivory ($\bar{x}$ = 2.0%, SE = 0.1, range 0.04–12.37). There were no discernible patterns for soil S content ($\bar{x}$ = 0.010%, SE = 0.001, range 0.00006–0.89) based on the site groupings. Nitrogen and sulfur levels were below instrument detection limits in 27% and <1% of the total number of soil samples analyzed, respectively.

Patterns among Vegetation, Soil,
and Environmental Variables

The multiple logistic regression model revealed a positive relationship among *S. gooddingii*, soil S, litter, and measurable clay content in the soil and a negative relationship between the presence of *T. ramosissima* and soil C (Table 3; Wald χ^2 = 55.4, $P < 0.0001$). However, there was not a model in which *S. gooddingii* presence corresponded with distance from the shoreline. The model correctly classified sampling points with the presence of *S. gooddingii* at 87.6% of the sites (i.e., concordance = 87.6). The absolute values of the standardized estimates (StEst) indicated the relative importance of a variable in predicting presence of *S. gooddingii* (Table 3).
The multiple logistic regression model predicting *T. ramosissima* cover revealed a nega-

tive relationship between the presence of *T. ramosissima* and the presence of *S. gooddingii*, and positive relationships among *T. ramosissima* and litter, location on the shore, soil salinity, clay content, and herbivory (Table 3; Wald χ^2 = 64.3, $P < 0.0001$). *Tamarix ramosissima* cover was greater in band B; that is, as the distance from the shoreline increased, the probability of finding *T. ramosissima* cover also increased (Fig. 4). Soil salinity increased with distance from shoreline. The model of *T. ramosissima* cover correctly classified sampling points with *T. ramosissima* cover at 87.5% of the points. The model of vegetative cover (by all plant species—*S. gooddingii*, *T. ramosissima*, *Prosopis pubescens*, and *Pluchea sericea*) consisted of a positive relationship among herbivory, soil S, litter (square-root transformation), location, and herbivory (Table 3). The model correctly classified sampling points with vegetative cover (>10%) at 93.7% of the points.

DISCUSSION

Data analyses and modeling indicate that there are 3 discernible patterns in the distribution and composition of vegetation and soils around Lake Mohave. First, although *S. gooddingii* and *T. ramosissima* were both found in the more frequently inundated reaches of the drawdown (Fig. 4), they rarely co-occurred, and there were significantly more mature *S. gooddingii* individuals established than *T. ramosissima*.

This may be attributed to the specific difference in tolerance to long-term inundation between *S. gooddingii* and *T. ramosissima* (Vandersande et al. 2001, Tallent-Halsell and Walker 2002, Glenn and Nagler 2005).

Despite the presence of mature *S. gooddingii* in the inundated zones, there were no *S. gooddingii* seedlings in the riparian plant community along the reservoir margins, perhaps because *S. gooddingii* seed release coincides with the period when the reservoir is at its highest. Released seeds fall into the water rather than on moist soil (i.e., beaches, sandbars) suitable for germination. Observations of organic debris on the shoreline indicate that seed capsules can move from tree to water to soil. Nevertheless, the *S. gooddingii* seeds that wash up onto beaches already vegetated with *S. gooddingii* or *T. ramosissima* probably would not germinate because they are shade-intolerant, and germinate poorly in plant litter (Sedgwick and Knopf 1989, Scott et al. 1996). In addition, *S. gooddingii* expansion by seeds into areas above the inundated zones also may be prohibited by inhibiting salt crusts under *T. ramosissima* thickets (Jackson et al. 1990).

Secondly, patterns in soil salinity and pH were associated with the location around the reservoir, landform type, and distance from water's edge. Geomorphic processes influence the flow of wind and water, which greatly influences the distribution of soil particles and the chemical composition of soils along the shoreline of water bodies (Gerrard 1992). Considering that the northern and southern basins differ in size, shape, and orientation, we speculate that these factors might account for differing localized wind and wave patterns, leading to stirring and mixing of soils that could account for the relatively lower concentrations of salt and nutrients in some areas along the shoreline than in others. A decrease in soil salinity on the east banks of the reservoir, along the exposed line beaches, and on shores of the southern basin may be due to strong winds, which generate waves that mechanically agitate, aerate (Whitlow and Harris 1979, Petts 1996), and flush soils. In general, the slopes on the western bank of Lake Mohave are steeper than those on the eastern bank, which may account for greater runoff velocities and flushing of soils.

Co-occurrences of vegetation and attributes of soil chemistry may reveal patterns of plant

flood tolerance and soil responses to periodic inundation (Bagstad et al. 2006). However, these patterns may not reflect associations among vegetation and soils; instead, they may be an artifact of processes that occur in soils that are periodically inundated through water management. Soil salinity levels in the "dry" band B, where soils are exposed to minimal wave action, exceeded the threshold level at which vigor of *P. fremontii* and *S. gooddingii* starts to decline ($3 \text{ dS} \cdot \text{m}^{-1}$; Anderson 1996). Thus, these soils may be too toxic for seeds of native trees to germinate (Jackson et al. 1990). Soil rehabilitation efforts may be necessary when native vegetation is introduced above the zone of frequent inundation (Swenson and Mullins 1985, Egan et al. 1993). Frequent flushing and the periodic removal of litter and woody debris may account for the low concentrations of soil N and P in the inundated zones of the drawdown.

Finally, the significant relationship between beaver herbivory and presence of *S. gooddingii* suggests that beavers are attracted to sites where *S. gooddingii* is present. Finding beaver at Lake Mohave is noteworthy because it is a keystone riparian species that can considerably alter the ecosystem (Collen and Gibson 2001, Mortenson et al. 2008). Five well-developed beaver lodges were found hidden within dense *S. gooddingii* stands not visible during high water. These lodges were mostly constructed with *S. gooddingii* branches in a matrix of mud, which suggests that beaver selectively forage for *S. gooddingii* over *T. ramosissima* when constructing bank-dwellings. Even though the beaver is a natural component of southwestern riparian ecosystems and contributes to revegetation, an imbalance may result if beaver populations are allowed to increase unchecked (Collen and Gibson 2001, Rosell et al. 2005, Mortenson et al. 2008). The damage incurred by beaver foraging appears to have promoted vegetative coppicing that, in turn, increased total cover by *S. gooddingii* within the drawdown zone. In many cases, felled trees and stems had resprouted, creating dense, woody stands. In fact, the herbivory appeared to contribute both to stand regeneration and to stand destruction. During our study period, beaver felled and removed 3 mature *S. gooddingii* trees, the total number of native trees present within an isolated cove, in one day.

These results, when placed in the context of reservoir management, provide a basis for

making general suggestions for management practices that may favor the conservation and expansion of the shoreline riparian ecosystem around Lake Mohave. Altering reservoir downstream flows through dams has a significant effect on riparian vegetation dynamics within both reservoirs and downstream reaches (Poff et al. 1997, Hauer and Lorang 2004, Rood et al. 2005). Within-year and among-year water-level variations can potentially be tools to manage shoreline plant community composition (Hill et al. 1998). Simulated flow regimes (Schmidt et al. 1998, Stromberg et al. 2007a, 2007b) meant to mimic the ecological needs of riparian taxa have been successful in the Colorado River (Zamora-Arroyo et al. 2001). Yet the timing, intensity, and duration of simulated floods are complex and, therefore, must be customized to the species being managed. Above a certain recruitment box (Mahoney and Rood 1998), native seedlings may not recruit because of drought. Below a certain recruitment box, recruitment is prevented by flooding or stream scouring. Rates of water drawdown are also critical for seedling survival. Bhattacharjee et al. (2006) suggested an optimal rate of $2 \text{ cm} \cdot \text{day}^{-1}$ drawdown for restoring *Populus deltoides* seedlings on the Rio Grande in New Mexico. Unfortunately, *Tamarix chinensis* has similar requirements, making it difficult to orchestrate recovery of native species while removing nonindigenous species. Furthermore, although raising the water level in reservoirs may remove *T. chinensis*, it may also negatively impact native vegetation, as Sprenger et al. (2001, 2002) found for *P. deltoides* in the Rio Grande floodplain of central New Mexico.

At Lake Mohave, one option might be to maintain high water levels from mid-May to early November over several years when *T. ramosissima* plants are releasing seed to prevent *T. ramosissima* colonization and to remove individuals already present. Flooding may reduce the abundance, distribution, and size of established *T. ramosissima*, while a drawdown may facilitate native seedling establishment. Drawdown starting in March (i.e., timed to match seed dispersal of indigenous species of *S. gooddingii* and *P. fremontii*) and continuing until saplings are tall enough to survive when water levels are at maximum could lead to the colonization of native riparian tree species (Levine and Stromberg 2001, Stromberg et al. 2007a, 2007b). However, manual seeding may

be needed in areas where native species are no longer present or setting seeds. This approach may present difficulties because a prolonged drawdown may reduce the groundwater supporting present mature native phreatophytes (Schmidt et al. 1998).

Best management practices, which include manipulating reservoir water levels to simulate natural fluvial processes so that nonnative plant establishment is inhibited, may also flush excessive soil salts from the shoreline soils, enabling native transplants to survive (Briggs 1996). However, our suggestion to manipulate water levels and flows have been based on only the physiological needs of riparian vegetation, without consideration of the tightly regulated water storage and release cycles that are bound by Colorado River water law (Hobbs 1997). Before managers can realistically entertain alternative flow scenarios that might lead to the reestablishment of native riparian vegetation along the Colorado River and associated reservoirs, they need to investigate the legal and political ramifications of reallocating Colorado River water or rescheduling water release and storage cycles (and in doing so, impacting hydroelectric power delivery schedules).

Our objectives were to discern patterns in the existing vegetation and soils and link those patterns to environmental factors characteristic of the created (novel) ecosystem. We realize that “fixing the system back to some preexisting condition” (Hobbs et al. 2006) is unlikely. Rather, we present this information to further the common goal to enhance, augment, and restore southwestern riparian and reservoir shoreline woodlands, which may prove to be suitable surrogates for the native riparian systems that have been lost.

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APPENDIX. Code, name, coordinates, and descriptions of the 34 sites at Lake Mohave, Nevada and Arizona, USA. Locations of sites are numbered on Fig. 1.

Code	Name	Latitude (N), Longitude (W)	Bank ^a	<i>Salix</i> ^b	Landform ^c	Herbivory ^d
1	Middle Arizona Bay	35° 30'48", 114° 39'52"	E	P	C	P
2	Painted Canyon Cove	35° 30'50", 114° 40'58"	W	A	C	A
3	Klondike Cove	35° 31'08", 114° 40'49"	W	A	C	A
4	Cove North of South Basin Cove	35° 22'46", 114° 36'28"	E	A	C	A
5	North Glory Hole Area	35° 25'18", 114° 36'43"	E	A	C	A
6	Carp Cove	35° 28'41", 114° 39'38"	E	P	C	P
7	Three Mile Flat	36° 26'51", 114° 37'26"	E	P	E	P
8	Across from Castle Cliff Light	35° 33'22", 114° 39'58"	W	P	E	P
9	2nd Cove N of Two Dollar Cove	35° 33'17", 114° 40'10"	W	P	C	P
10	Owl Cove	35° 34'34", 114° 39'30"	E	A	C	A
11	Twin Cove	35° 34'46", 114° 39'47"	E	P	C	P
12	Opel Cove (North)	35° 35'28", 114° 39'51"	W	P	C	P
13	Open Cove (South)	35° 35'25", 114° 40'04"	W	A	E	A
14	Nevada Bay	35° 34'38", 114° 41'18"	W	P	C	P
15	Nevada Bay Beach	35° 35'02", 114° 40'41"	W	A	E	P
16	Basalt Cove	35° 35'19", 114° 40'16"	W	P	C	P
17	North Arizona Bay	35° 31'07", 114° 39'25"	E	P	E	P
18	South Arizona Bay	35° 31'03", 114° 39'27"	E	A	E	P
19	Jeff Davis Cove	35° 32'15", 114° 38'56"	E	A	C	A
20	Perkins Cove	35° 34'21", 114° 39'28"	E	A	C	A
21	Golden Door Cove	35° 32'47", 114° 39'17"	E	A	C	A
22	1st Cove North of Two Dollar Cove	35° 33'06", 114° 40'14"	W	P	C	P
23	Rockefeller Cove	35° 32'37", 114° 40'29"	W	P	C	P
24	Beach North of Rockefeller Cove	35° 32'45", 114° 40'17"	W	P	E	P
25	Box Cove	35° 30'12", 114° 41'06"	W	A	E	A
26	Beach North of Three Mile Flat	35° 27'29", 114° 37'52"	E	P	E	P
27	Sandy Cove	35° 28'15", 114° 40'48"	W	P	C	P
28	Cottontail Cove	35° 29'10", 114° 41'03"	W	P	C	P
29	Gremlin Cove	35° 23'40", 114° 38'54"	W	A	C	A
30	Dead Cove	35° 23'51", 114° 39'10"	W	A	C	A
31	Beach S of Nine Mile Cove	35° 24'45", 114° 40'13"	W	A	E	A
32	Beach N of Nine Mile Cove	35° 25'05", 114° 40'34"	W	A	E	A
33	Beach N of Six Mile Cove	35° 27'18", 114° 40'36"	W	P	E	P
34	Bill Gayes Cove	35° 27'26", 114° 40'41"	W	P	E	P

^aBank = east (E) or west (W).
^b*Salix* = presence (P) or absence (A) of *Salix gooddingii* at site.
^cType = exposed (E) line or sheltered cove beach (C).
^dHerbivory = presence (P) or absence (A) of herbivory at site.