

# Edaphic, salinity, and stand structural trends in chronosequences of native and non-native dominated riparian forests along the Colorado River, USA

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**Abstract** *Tamarix* spp. are introduced shrubs that have become among the most abundant woody plants growing along western North American rivers. We sought to empirically test the long-held belief that *Tamarix* actively displaces native species through elevating soil salinity via salt exudation. We measured chemical and physical attributes of soils (e.g., salinity, major cations and anions, texture), litter cover and depth, and stand structure along chronosequences dominated by *Tamarix* and those dominated by native riparian species (*Populus* or *Salix*) along the upper and lower Colorado River in Colorado and Arizona/California, USA. We tested four hypotheses: (1) the rate of salt accumulation in soils is faster in *Tamarix*-dominated stands than stands dominated by native species, (2) the concentration of salts in the soil is higher in mature stands dominated by *Tamarix* compared to native stands, (3) soil salinity is a function of *Tamarix* abundance, and (4) available nutrients are more concentrated in native-dominated

stands compared to *Tamarix*-dominated stands. We found that salt concentration increases at a faster rate in *Tamarix*-dominated stands along the relatively free-flowing upper Colorado but not along the heavily-regulated lower Colorado. Concentrations of ions that are known to be preferentially exuded by *Tamarix* (e.g., B, Na, and Cl) were higher in *Tamarix* stands than in native stands. Soil salt concentrations in older *Tamarix* stands along the upper Colorado were sufficiently high to inhibit germination, establishment, or growth of some native species. On the lower Colorado, salinity was very high in all stands and is likely due to factors associated with floodplain development and the hydrologic effects of river regulation, such as reduced overbank flooding, evaporation of shallow ground water, higher salt concentrations in surface and ground water due to agricultural practices, and higher salt concentrations in fine-textured sediments derived from naturally saline parent material.

**Keywords** *Tamarix* · *Populus* · Soil salinity · Colorado River · Flow regime · Dams

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## Introduction

Floodplain ecosystems are characterized by dynamic fluvial environments as well as strong feedbacks between vegetation, fluvial landforms, and soil properties. Along free-flowing alluvial rivers, floodplain development occurs through vertical and lateral accretion of fluvial

surfaces, which are associated with and facilitated by channel migration and increased hydraulic resistance caused by floodplain vegetation (Merritt and Cooper 2000; Nanson and Beach 1977). Plant species composition changes in predictable ways along such gradients, transitioning from more flood and fluvial disturbance-adapted taxa on bars and low floodplains to more drought tolerant communities on high floodplains and terraces (Auble et al. 2005; Merritt and Cooper 2000; Pockman and Sperry 2000). Increases in the elevation of fluvial surfaces above the channel due to sediment deposition are accompanied by directional changes in many abiotic factors. These factors include decreases in the frequency and duration of flooding, increases in the depth to groundwater, fining of sediment particle size (Adair et al. 2004; Menges 1986), increases in available and total nitrogen (Adair et al. 2004; Boggs and Weaver 1994), and increases in salinity (Busch and Smith 1993; Jolly et al. 1993). Anthropogenic factors such as flow regulation and agricultural irrigation can strongly influence floodplain vegetation dynamics (Busch and Smith 1995; Cooper and Merritt 2012) as well as the chemical properties of floodplain soils (Glenn et al. 2012).

Floodplain vegetation can influence soil properties in various ways. Sediment particle size tends to become finer as the relative elevation of fluvial surfaces increases over time due to the dissipation of energy and settling of particles associated with hydraulic resistance of plant stems (Nepf 1999). Furthermore, litter inputs increase organic matter and soil nutrient pools in floodplain soils (Adair et al. 2004; Boggs and Weaver 1994; Xiong et al. 2001). In addition, particular plant species can directly influence soil chemistry through deposition of leaf litter high in nutrients or salts, high litter decomposition rates, leachates, and root exudates (Weidenhamer and Callaway 2010). With respect to leaf litter, a number of studies have revealed an increase in soil nutrients associated with leaf litter deposition and relatively rapid decomposition of nitrogen-fixing plants (reviewed in Weidenhamer and Callaway 2010). Secondary compounds exuded from roots can have allelopathic effects on soil micro- and macrobiota as well as on surrounding plants (Bertin et al. 2003). Studies of the effects of individual plant species on soil chemistry has focused largely on invasive plants and the hypothesis that non-native species may exclude or disadvantage native taxa by altering soil

chemistry (Weidenhamer and Callaway 2010). For example, along western North American rivers, shrubs and small trees in the Eurasian genus *Tamarix* (which occupy several hundred thousand acres of low elevation riparian vegetation; Nagler et al. 2011) have been hypothesized to increase soil salinity to the detriment of native taxa by concentrating and exuding salts from their deciduous leaves, which are then deposited on the soil surface (Di Tomaso 1998).

Water soluble salts on *Tamarix* foliage may enter the soil via direct exudation drip, rinsing and mobilization of salts off of foliage by rainwater, and/or litter inputs. Salts and minerals observed in *Tamarix* leaf exudates include Al, B, Ca, Cl, Cu, HCO<sub>3</sub>, K, Mg, Mn, Mo, Na, NO<sub>3</sub>, P, Si, SO<sub>4</sub>, and Zn (Berry 1970; Bosabalidis and Thomson 1984; Dressen and Wangen 1981; Kleinkopf and Wallace 1974; Storey and Thomson 1994; Thomson et al. 1969). Eight ions (Na, K, Ca, NO<sub>3</sub>, Mg, SO<sub>4</sub>, HCO<sub>3</sub>, and Cl) account for more than 99 % of the total ions secreted by *Tamarix* (Thomson, 1975). As discussed below, these ions have differential effects on growth and fitness of other riparian species.

Most *Tamarix* species shed some leaves throughout the season and lose all foliage in the winter. Foliage and salts crystallized on its surfaces can accumulate on the soil surface. Sites dominated by *Tamarix* can generate 299–970 g m<sup>-2</sup> year<sup>-1</sup> of leaf litter along rivers in the western USA (Ellis et al. 1998; Kennedy and Hobbie 2004). *Populus-Salix*-dominated stands with dense *Tamarix* understory may have as much as 33.7 mg ha<sup>-1</sup> of woody debris and 1,056 g m<sup>-2</sup> of forest floor litter along rivers in the western USA (Ellis 2001). In addition to accumulating on the surface, minerals may be incorporated in leaf and branch tissue. *T. ramosissima* litter may contain 18 % mineral content, 4.3 % lignin, and 0.7 % sodium (Kennedy and Hobbie 2004). The persistence of litter, and the rate of release of minerals, is a function of the rate of removal by flooding, microbial activity-decomposition, and incineration.

Few published studies have examined changes to floodplain soils that occur beneath stands of *Tamarix* over time (Busch and Smith 1995; Stromberg 1998b), or effects of *Tamarix* on soil salinity (but see Ladenburger et al. 2006; Lesica and DeLuca 2004). Despite the paucity of published data, it is commonly reported that *Tamarix* litter increases salinity of

floodplain soils (Brock 1994; Di Tomaso 1998; Walker and Smith 1997). Lesica and DeLuca (2004) found that electrical conductivity (EC) was significantly higher in soils beneath mature *Tamarix* canopies in Montana, USA compared to adjacent areas supporting native-dominated grassland, and attributed this to higher EC and organic N and P concentrations and decreasing K concentrations, pH, and  $\text{NH}_4/\text{NO}_3$  ratio. Ladenburger et al. (2006) found higher EC and lower pH in soils beneath mature *Tamarix* stands compared to soils beneath vegetation that did not include any *Tamarix* along the Bighorn River, Wyoming, USA. High soil salinities associated with but not necessarily caused by *Tamarix*, have been reported by Busch and Smith (1995), Anderson (1995), Sher et al. (2002), Ladenburger et al. (2006), and Glenn et al. (1998). In such studies, other causes of high soil salinity have included unintended consequences of irrigation, interactions between soil texture and salinity, and capillary rise and evaporative concentration (Glenn et al. 2012). The presence of *Tamarix* is likely associated with its tolerance of salinity, rather than the cause of it.

Our objective is to investigate changes through time in soil properties in stands of riparian vegetation dominated by *Tamarix* and those dominated by native forest species using a space-for-time substitution approach along two reaches of the Colorado River in western USA. Given the potentially important effect of flow regulation on soil salinity, we studied both a heavily regulated reach that is no longer subjected to soil-flushing overbank flows (lower Colorado) and a reach along the upper Colorado River that still experiences occasional overbank flows. We characterized changes in stand structure (e.g., basal area, stem density, and cover) through time. In addition, we tested the following hypotheses: (1) the rate of salt accumulation in soils is higher in *Tamarix*-dominated stands compared to stands dominated by native species, (2) the concentration of salts in the soil in mature *Tamarix*-dominated stands is higher than in stands dominated by native species, (3) soil salinity is a function of *Tamarix* abundance (e.g., cover, density, and basal area), and (4) nutrients are more concentrated in native-dominated stands compared to *Tamarix*-dominated stands. We also sought to understand how changes in soil properties could influence the suitability of western floodplains for other plant species.

## Materials and methods

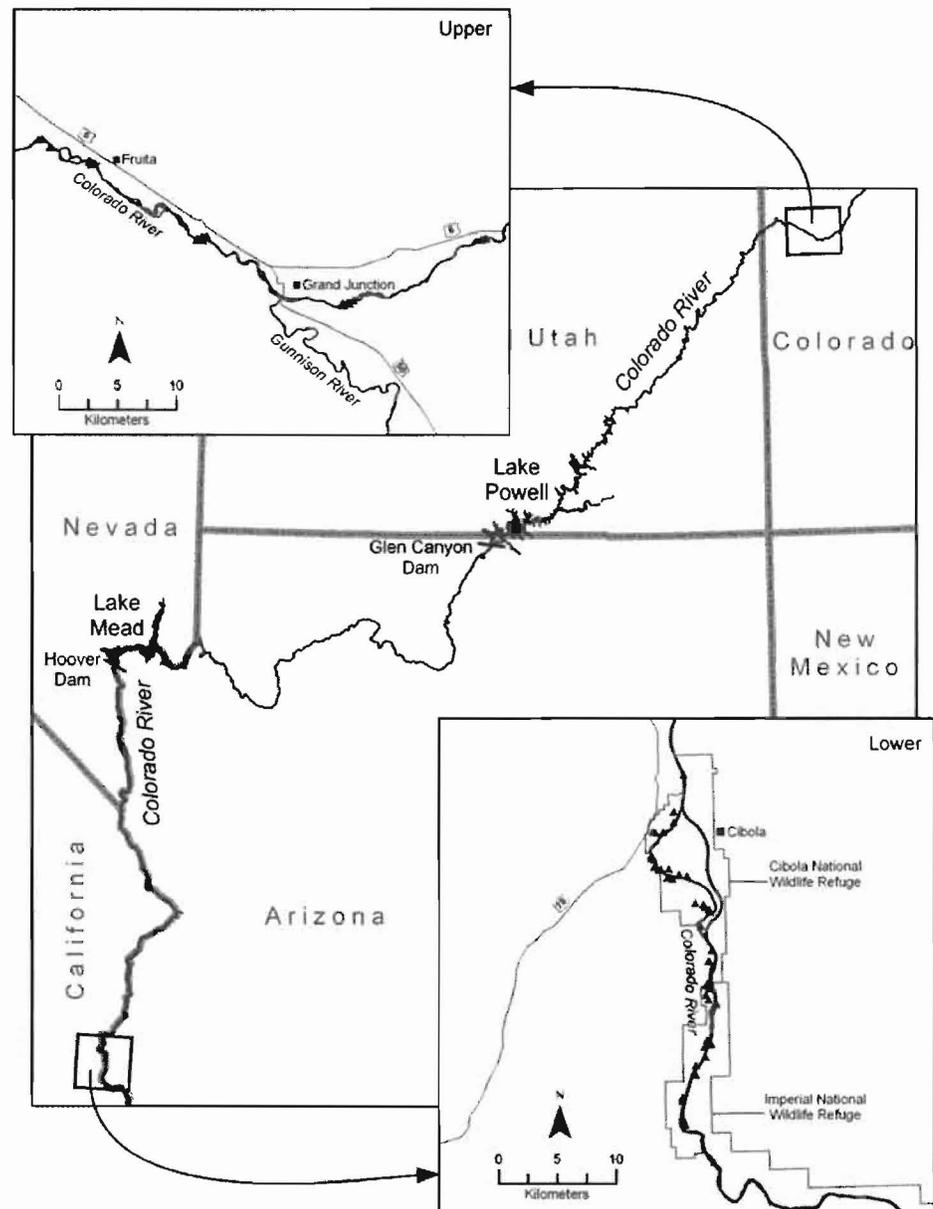
### Study sites

The Colorado River is the master drainage of the intermountain western USA, flowing 2,300 km from its headwaters at 3,200 m above mean sea level in the Rocky Mountains of western Colorado and Wyoming to its terminus in the Gulf of California. We conducted our study within two stream segments, one along the upper Colorado River in western Colorado in the intermountain desert ecoregional province and the second along the lower Colorado River on the Arizona-California border in the American desert ecoregional province (Bailey 1995). The two reaches were chosen to contrast effects of *Tamarix* on a relatively free-flowing and a completely regulated river segment in the arid western USA.

The upper Colorado River study reach was located in the Grand Valley near the city of Grand Junction, Colorado. Our sites were distributed along ca. 30 km of the river within state or federally managed wildlife areas. Climate is semi-arid, with an average of 278 mm of annual precipitation (NOAA 2010). Land use in the Grand Valley consists of a mix of agriculture, urban development, and undeveloped riparian areas. Riparian forests along the river are dominated by trees, primarily *Populus fremontii* (syn. *P. deltoides* var. *wislizeni*), *Tamarix* spp. (Gaskin and Schaal 2002), and *Elaeagnus angustifolia*. Common riparian shrubs included *Salix exigua* which occurs on young surfaces near the active river channel, and *Chrysothamnus nauseosus* (syn. *Ericameria nauseosa*) and *Rhus trilobata* on older, drier surfaces. Common herbaceous species include *Bassia hyssopifolia*, *Distichlis spicata*, *Sporobolus airoides*, and *Sporobolus cryptandrus*.

The lower Colorado River study reach was north of the USA—Mexico border between the cities of Blythe, California and Yuma, Arizona (Fig. 1). Our sites were distributed along 40 km of the river within the Cibola and Imperial National Wildlife Refuges. The climate is arid, with an average of 100 mm of annual precipitation (at Cibola National Wildlife Refuge; Nagler et al. 2009). Streamflow is highly regulated in this reach with several large dams along the mainstem and tributaries upstream from the study reach. Riparian vegetation along this reach is dominated by shrubs and small trees including *Tamarix*

**Fig. 1** Map of upper and lower Colorado River with study sites indicated



spp., *Pluchea sericea*, *Prosopis glandulosa*, *Prosopis pubescens*, *Atriplex lentiformis*, and occasional, small patches of *P. fremontii*, *S. goodingii* and *S. exigua*. Herbaceous vegetation is uncommon except patches of hydrophytic plants (e.g., *Arundo donax*, *Typha latifolia*, *Phragmites australis*, *Scirpus americana*, *Schoenoplectus pungens*, and *Scirpus maritimus*) immediately adjacent to the channel. On drier sites, *Cynodon dactylon* and *D. spicata* occur in the understory, and various desert annuals may be present following rain events.

#### Vegetation sampling

We sampled 38 *Tamarix*-dominated stands along the upper Colorado River and 41 along the lower Colorado River. We used recent vegetation maps and aerial photography to identify stands that had at least 60 % relative cover of *Tamarix* and had some reasonable point of access, which we defined as within 200 m of a road, foot trail, or channel bank. Candidate stands were delineated on aerial photographs, and the specific locations for vegetation sampling were randomly

selected within stands. We deliberately selected stands that represented a range of ages, which we initially based on tree size and bark characteristics.

Within each stand, we estimated canopy cover of all woody species and measured stem density and diameter (20 cm above ground) of all woody stems (dead and alive, by species) in rectangular plots that ranged in size from 10 to 50 m<sup>2</sup>, depending on our assessment of the scale of stand homogeneity. For 2–3 of the largest trees in a stand, we estimated the date of last disturbance (such as wildfire) by aging a stem cross-section taken from the ground surface. We also estimated tree establishment date by excavating the primary buried stem down to the root crown, cutting cross-sections along the length of buried stem, sanding the cross-sections in the laboratory, and counting and cross-dating annual rings under a microscope using methods described in Friedman et al. (2005).

To provide a comparison of soil characteristics beneath native-dominated vegetation versus *Tamarix*-dominated stands, we collected age and soil data from stands dominated by either cottonwood (*P. fremontii*) or (tree) willow (*S. gooddingii*) (see below for soil sampling methods). These stands were particularly uncommon along the lower Colorado River study reach; thus, our criteria for dominance required simply that a minimum of three trees were clustered and that the relative canopy cover was at least 60 % cottonwood and/or willow. Fifteen and 10 cottonwood/willow stands meeting our criteria were selected on the upper and lower Colorado River, respectively. Ages of stands dominated by native vegetation (*Populus* or *Salix*) were estimated by collecting increment cores <50 cm above the ground surface, mounting and sanding the cores in the laboratory, and counting the rings under a microscope (Schweingruber 1993). Rings were digitized on a Velmex TA Unislide measuring system with ACU-Rite linear encoder and QC1100 digital readout device (Velmex, Inc., Bloomfield, New York). The ring-reading software was Measure J2X, Version 3.1 (Project J2X, Voortech Consulting, Holderness, NH).

#### Soil sampling and laboratory analysis

At every *Tamarix* plot and at every site where we aged *Populus* or *Salix*, we collected two soil samples: one from the ground surface (after removing organic litter) to 2 cm below the ground surface (1.21), and the other

from 2 to 17 cm below the surface (1.2 l). Within each *Tamarix* plot we estimated the percent cover of organic litter and calculated litter depth by averaging five measured litter depths within each plot (four corners and the center of the plot). Soil samples were air dried and processed at the Soil, Water and Plant Testing Laboratory at Colorado State University, Fort Collins, Colorado for grain size and chemical analyses. Percent of sand, silt, and clay in each soil sample was determined by the hydrometer method (Klute 1986). Percent saturation, pH, EC, and calcium (Ca<sup>+</sup>), magnesium (Mg<sup>+</sup>), sodium (Na<sup>+</sup>), potassium (K<sup>+</sup>), boron (B<sup>+</sup>), carbonate (CO<sub>3</sub><sup>-</sup>), bicarbonate (HCO<sub>3</sub><sup>-</sup>), chloride (Cl<sup>-</sup>), sulfate (SO<sub>4</sub><sup>-</sup>), nitrate (NO<sub>3</sub><sup>-</sup>), ammonium (NH<sub>4</sub><sup>+</sup>), and orthophosphate (PO<sub>4</sub><sup>3-</sup>) concentrations were determined for all soil samples. Percent saturation was determined by weighing 100 g of soil, adding water until soil was saturated, reweighing the soil and calculating the weight over 100 g (Richards 1954). pH was measured from a saturation paste extract (Spark 1996) with a Corning combination electrode. EC was measured from a saturation paste extract (Spark 1996) with a Yellow Springs Instruments electrode (YSI 3417). Cations (Ca<sup>+</sup>, Mg<sup>+</sup>, Na<sup>+</sup>, K<sup>+</sup>, and B<sup>+</sup>) were measured by inductively coupled plasma (Thermo Jarrell Ash IRIS Advantage Dual View High Resolution ICP; Spark 1996). CO<sub>3</sub><sup>-</sup> and HCO<sub>3</sub><sup>-</sup> were determined using a titration with 0.01 NH<sub>2</sub>SO<sub>4</sub> (USEPA Method 310.1). Cl<sup>-</sup> and SO<sub>4</sub><sup>-</sup> were analyzed by ion chromatography (USEPA method 300.0) with a Dionex 2000 i/sp with AS4A Separator column P/N 37041. NO<sub>3</sub> was analyzed by flow injection analysis (Spark 1996) with cadmium reduction using an OI Analytical Flow Solution 3000. NH<sub>4</sub> was analyzed by flow injection analysis (Spark 1996) using an OI Analytical Flow Solution 3000, automated phenate method. Orthophosphate was determined using the Molybdate Blue method (EPA 1983).

We also examined composite variables such as salinity (sum of milli-equivalents), sodium absorption ratio ( $\text{Na}^+ / [0.5(\text{Ca}^{2+} + \text{Mg}^{2+})]^{0.5}$ ; see Harron et al. 1983), total inorganic nitrogen (sum of NH<sub>4</sub> and NO<sub>3</sub>), and NH<sub>4</sub>/NO<sub>3</sub> ratio.

#### Determination of plot locations and height above river level

Plot elevations and adjacent river water surface elevations were measured using a Trimble 4800

survey grade global positioning system (GPS). Plot elevations are expressed as height above the adjacent water surface. Measurements had an estimated precision of  $\pm 2$  cm. A minimum of three replicate GPS observations was made for each surveyed location.

### Statistical analyses

After accounting for stand age, there were no significant differences in average soil EC or salinity between upper and lower soil horizons within *Tamarix*-dominated stands along the upper and lower Colorado River ( $P > 0.05$ ). This pattern held in *Populus-Salix*-dominated stands as well ( $P > 0.05$ ). Therefore, we analyzed only the lower horizon (2–17 cm depth) for the remainder of temporal trends in soil chemistry.

We first tested for differences in soil chemical attributes (pH, EC,  $\text{Ca}^+$ ,  $\text{Mg}^+$ ,  $\text{Na}^+$ ,  $\text{K}^+$ ,  $\text{B}^+$ ,  $\text{CO}_3^-$ ,  $\text{HCO}_3^-$ ,  $\text{Cl}^-$ ,  $\text{SO}_4^-$ ,  $\text{NO}_3^-$ ,  $\text{N}^-$ ,  $\text{NH}_4\text{-N}^+$ , and ortho  $\text{P}^-$ ) between the upper and lower Colorado River study sites using multivariate analysis of variance (MANOVA). Soil chemical attributes were found to be significantly different between sites; therefore, we conducted further analysis to examine soil chemical attributes through successional time in stands of *Populus* and *Tamarix* at each site separately. We also tested for differences in the rates of change in salinity and ion concentration (e.g., slopes of the linear models) between *Populus* and *Tamarix*-dominated stands. We performed contrasts as a part of analysis of covariance with stand age as a covariate to test for differences in least squares means at 5, 30, and 60 year old stands for the upper Colorado River and 5, 15, and 30 year old stands for the lower Colorado River. Differences in the age comparison were due to the younger maximum age of *Populus* on the lower Colorado River (24 years compared to 118 years on the upper Colorado River). We were interested in testing for differences in soil attributes in young, intermediate and old stands to determine when these differences are most pronounced. In addition to soil chemical and textural attributes, we tested for trends in stand structure and composition through time. We examined trends in total basal area, basal area of native species, and basal area of non-native species in *Tamarix*-dominated stands. All data, with the exception of pH and salinity, were natural logarithm transformed to more closely comply with the assumptions of normally distributed residuals.

We used a smearing technique (sensu Duan 1983) to plot the expected response on the untransformed scale of the variables after fitting a linear regression model on a transformed scale. The smearing estimate is a nonparametric bias correction term used for back-transforming the predicted response to the original observation scale (Duan 1983). The coefficient of determination,  $r^2$ , and  $P$  values are presented for linear regression.

### Results

#### Upper and lower Colorado River stand structure and cover

*Populus* stand ages ranged from 2 to 118 years along the upper Colorado River and 8 to 24 years along the lower Colorado River. *Tamarix* stand ages ranged from 3 to 70 years along the upper Colorado River and 9 to 60 years along the lower Colorado River.

Stem density of all woody species ( $S$ ) was highest in young *Tamarix*-dominated stands (<20 years old) along both the upper and lower Colorado (averaging 102,000 and 127,000 stems  $\text{ha}^{-1}$ , respectively). Stands older than 50 years had average stem densities of 12,300 and 16,800 stems  $\text{ha}^{-1}$  along the upper and lower Colorado River, respectively. Stem density decreased significantly as a function of stand age ( $P < 0.005$ ). Stem thinning rate averaged 2,317 ( $\pm 394$ ) stems  $\text{ha}^{-1} \text{ year}^{-1}$  along the upper Colorado River and 3,257 ( $\pm 937$ ) stems  $\text{ha}^{-1} \text{ year}^{-1}$  along the lower Colorado River. Equations for thinning are:

$$\text{Upper Colorado River } S = 130,790 - 2,317 (\text{age}) \\ (r^2 = 0.47; P < 0.005)$$

$$\text{Lower Colorado River } S = 167,781 - 3,257 (\text{age}) \\ (r^2 = 0.24; P < 0.005)$$

There was no significant difference in the thinning rate between the upper and lower Colorado River ( $P = 0.1$ ), and the overall thinning rate of *Tamarix* was  $2,455 \pm 312$  stems  $\text{ha}^{-1} \text{ year}^{-1}$  over the 70 years modeled. The relationship between stand age and *Tamarix* stem density ( $S_T$ ) along both upper and lower Colorado River sites is  $S_T = 135,478 - 2,455 (\text{age})$  ( $r^2 = 0.27$ ;  $P < 0.0001$ ). On average, there were 82,633 ( $\pm 1,201$ ) and 252,290 ( $\pm 54,606$ ) dead stems  $\text{ha}^{-1}$  in *Tamarix*-dominated stands along the upper and lower Colorado rivers, respectively.

Basal area of woody vegetation in *Tamarix* stands ranged from 0.8 to 75.3 m<sup>2</sup> ha<sup>-1</sup> along the upper Colorado River and from <0.1 to 77.7 m<sup>2</sup> ha<sup>-1</sup> along the lower Colorado River. Basal area of woody vegetation ( $BA_w$  in m<sup>2</sup> ha<sup>-1</sup> year<sup>-1</sup>) increased significantly as a function of stand age along the upper Colorado River ( $BA_w = 5.6 + 0.53(\text{age})$ ;  $r = 0.68$ ,  $P < 0.0001$ ), but not along the lower Colorado River ( $r = 0.08$ ,  $P = 0.08$ ). Basal area of dead stems of all species was 7.9 ( $\pm 1.0$ ) and 20.4 ( $\pm 2.1$ ) m<sup>2</sup> ha<sup>-1</sup> in *Tamarix*-dominated stands along the upper and lower Colorado River, respectively.

Only two other woody species occurred in *Tamarix*-dominated stands along the lower Colorado River, native *Pluchea sericea* and *Atriplex lentiformis*. Cover of *P. sericea* ranged from <1 to 60 %. *Atriplex lentiformis* occurred in only one stand, in which it was relatively abundant (40 % cover). The number of woody species co-occurring with *Tamarix* in *Tamarix*-dominated stands was higher along the upper Colorado River (6 species): *P. deltoides* (in 17 % of stands sampled), *E. angustifolia* and *S. exigua* (each in 10 % of stands), *C. nauseosus* and *Rhus trilobata* (each in 5 % of stands), and *Ulmus pumila* (in 2 % of stands). With the exception of *E. angustifolia* and *Ulmus pumila*, all species listed above are native to Colorado, California and Arizona. Total cover of woody species was generally low in *Tamarix*-dominated stands where other woody species occurred (2–20 %).

We recorded litter depths in *Tamarix* stands as high as 5 cm along the upper Colorado River and 15 cm along the lower Colorado River and found average litter biomass of 264 g m<sup>-2</sup> (maximum 1,000 g m<sup>-2</sup>) and 910 g m<sup>-2</sup> (maximum 3,000 g m<sup>-2</sup>), respectively. Litter was not measured in *Populus-Salix*-dominated stands.

#### Soil physical and chemical attributes: upper Colorado River

Soil texture varied across the chronosequence of both *Tamarix*- and *Populus-Salix*-dominated stands along the upper Colorado River. Percent silt ( $r^2 = 0.11$ ,  $P = 0.04$ ) and clay ( $r^2 = 0.13$ ,  $P = 0.02$ ) increased and sand decreased as a function of age in *Tamarix* stands ( $r^2 = 0.42$ ,  $P = 0.009$ ). Similarly, in *Populus*-dominated stands, silt and clay increased strongly as a function of stand age ( $r^2 = 0.73$ ,  $P < 0.0001$  and  $r^2 = 0.42$ ,  $P = 0.01$ , respectively) and sand fraction

decreased significantly ( $r^2 = 0.71$ ,  $P = 0.0002$ ). Percent fines increased at a rate of 0.5 % per year in *Populus* stands ( $r^2 = 0.71$ ,  $P = 0.0002$ ), compared to 0.4 % per year in *Tamarix*-dominated stands ( $r^2 = 0.13$ ,  $P = 0.02$ ).

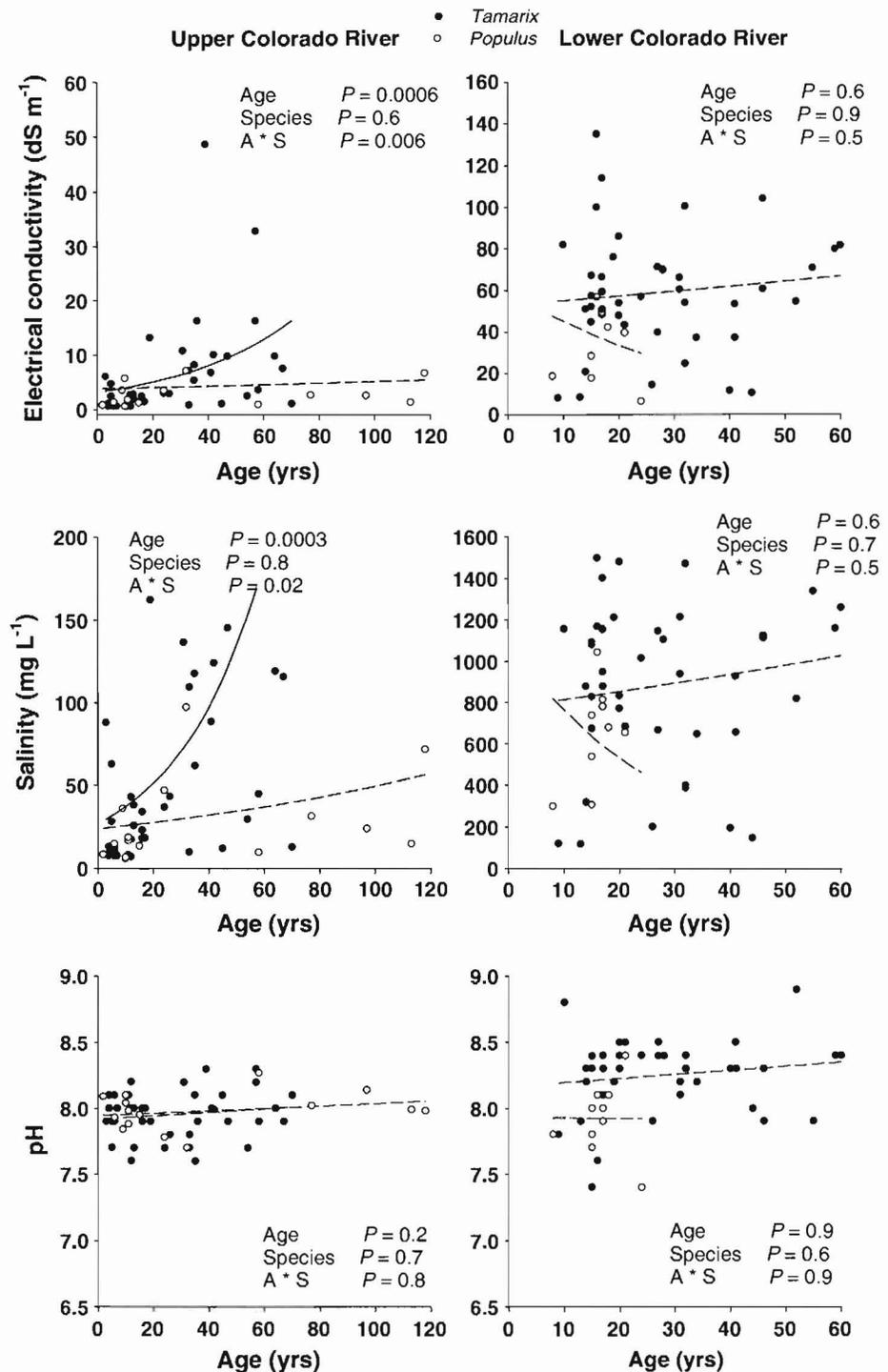
With regard to Hypothesis 1, soil EC and salinity increased as a function of age in *Tamarix* ( $P = 0.0003$  and  $P = 0.0004$ , respectively) but not *Populus* stands ( $P = 0.40$  and  $P = 0.19$ , respectively; Fig. 2). The interaction between stand age and species was significant, indicating differences in the rate of change in EC ( $P = 0.006$ ) and salinity ( $P = 0.02$ ) through time in *Tamarix*- versus *Populus-Salix*-dominated stands. pH did not vary significantly as a function of stand age ( $P = 0.19$ ) nor did the rate of change in pH differ between *Tamarix* and *Populus-Salix*-dominated stands ( $P = 0.79$ ).

B, Na, HCO<sub>3</sub>, and K concentrations all increased significantly as a function of stand age in both *Tamarix* and *Populus-Salix*-dominated stands (Figs. 3, 4). The rate of increase (e.g., the interaction between species and stand age) in B and Na concentration through time was significantly higher in *Tamarix* stands ( $P < 0.02$ ); the rate of increase did not differ significantly between *Tamarix* and *Populus-Salix*-dominated stands for HCO<sub>3</sub> or K ( $P = 0.33$  and  $P = 0.15$ , respectively). Cl increased significantly in *Tamarix*, but not *Populus-Salix*-dominated stands (Fig. 3).

In 60 year-old stands EC, salinity, sodium absorption ratio and concentrations of B, NH<sub>4</sub>, P, SO<sub>4</sub>, Na, Mg, Ca, CO<sub>3</sub>, and Cl were all significantly higher ( $P < 0.01$ ) in *Tamarix* compared to *Populus-Salix*-dominated stands, providing support for hypothesis 2. Total inorganic N and NO<sub>3</sub> concentrations were four times higher in *Populus*-dominated stands compared to *Tamarix*-dominated stands on the upper Colorado River (respectively;  $P < 0.05$ ), whereas NH<sub>4</sub> concentrations were thirty times higher in older *Tamarix*-dominated stands than in *Populus*-dominated stands ( $P < 0.05$ ), pH and concentrations of HCO<sub>3</sub> and K did not differ ( $P > 0.1$ ) between 60 year old *Tamarix* versus *Populus* (Table 1).

Regarding Hypothesis 3, *Tamarix* abundance was associated with increased salinity levels and soil EC. EC level decreased as a function of *Tamarix* stems ha<sup>-1</sup> ( $r^2 = 0.21$ ,  $P = 0.002$ ), and increased as a function of *Tamarix* basal area ( $r^2 = 0.41$ ,  $P < 0.0001$ ), but did not vary as a function of *Tamarix* cover ( $r^2 = 0.08$ ,  $P = 0.07$ ). Salinity was positively associated with *Tamarix* basal area ( $r^2 = 0.38$ ,  $P <$

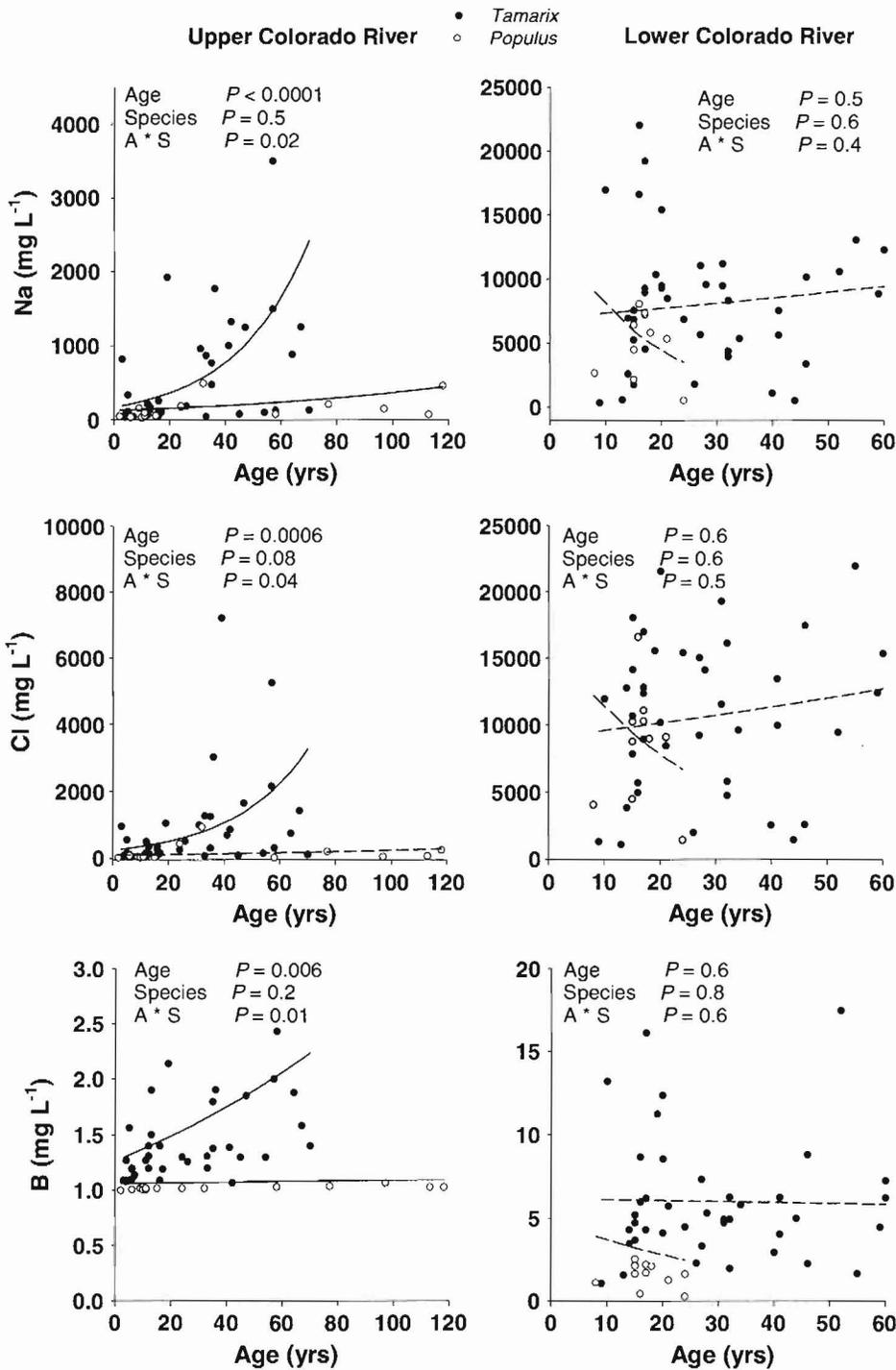
**Fig. 2** Soil electrical conductivity, salinity, and pH as a function of *Tamarix* and *Populus* stand age along the upper and lower Colorado River. Electrical conductivity and salinity models were fitted with natural log transformed data. Models were then plotted in the non-transformed scale using the smearing technique described in the text. *Solid lines* indicate significant relationship between age and soil attribute at  $P < 0.05$ ; *dotted lines* indicate non-significance



0.0001) and *Tamarix* cover ( $r^2 = 0.10$ ,  $P = 0.047$ ), and negatively associated with *Tamarix* stems ha<sup>-1</sup> ( $r^2 = 0.22$ ,  $P = 0.001$ ). Elevation of plots was positively associated with EC in both *Tamarix* ( $r^2 = 0.41$ ,  $P < 0.05$ ) and *Populus* stands ( $r^2 = 0.35$ ,  $P < 0.05$ ). Elevation of plots was also positively associated with

salinity in both *Tamarix* ( $r^2 = 0.47$ ,  $P < 0.05$ ) and *Populus* stands ( $r^2 = 0.38$ ,  $P < 0.05$ ).

There were several differences between *Tamarix* and *Populus*-*Salix*-dominated stands in the concentrations of macronutrients through time (Hypothesis 4). NH<sub>4</sub> concentrations increased in *Tamarix* stands



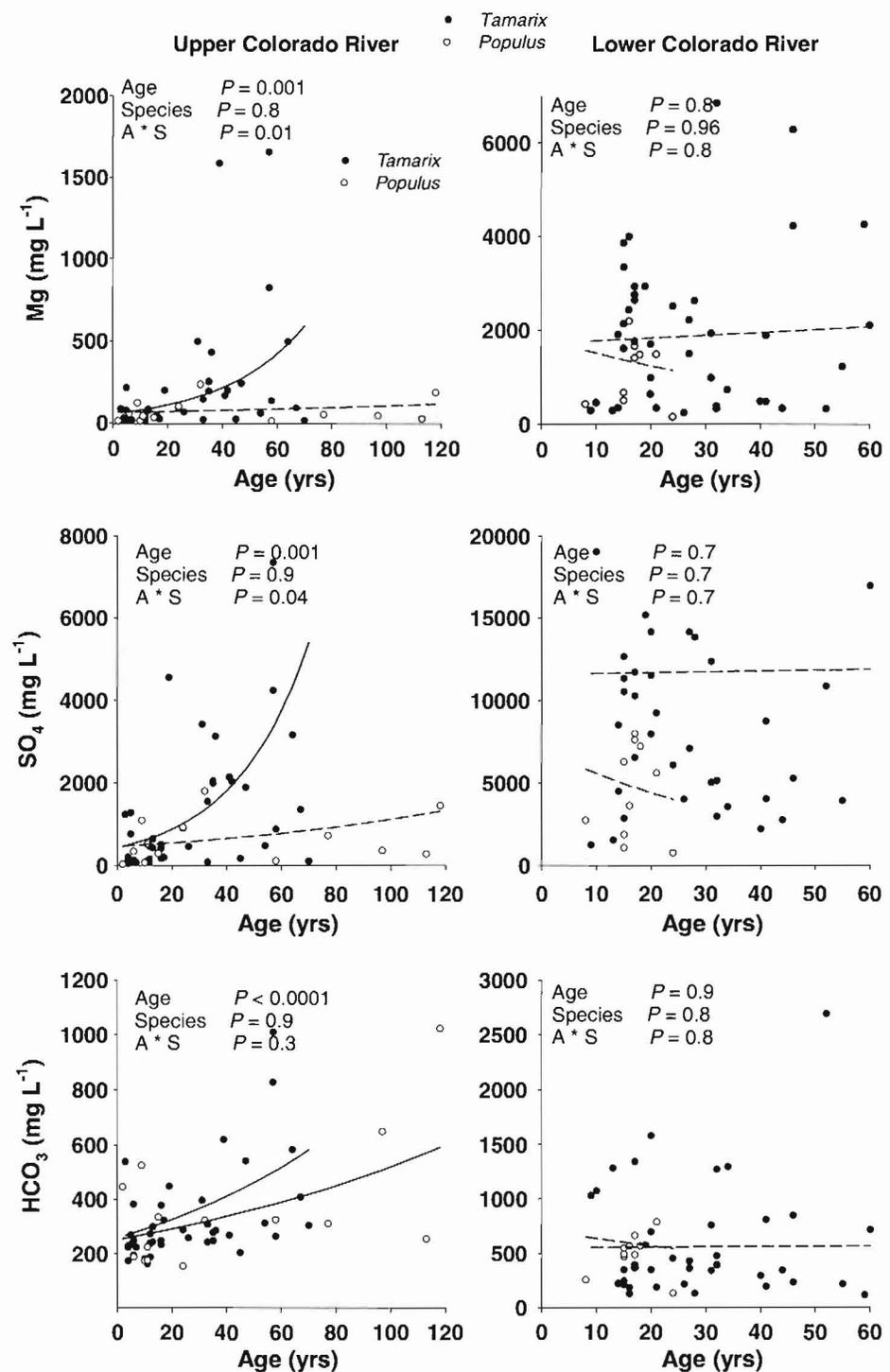
**Fig. 3** Concentrations of Na, Cl, B, Mg, SO<sub>4</sub>, and HCO<sub>3</sub> as a function of *Tamarix* and *Populus* stand age along the upper and lower Colorado River. Models were fitted with natural log transformed data. Models were then plotted in the non-

through time, but did not increase significantly in *Populus-Salix*-dominated stands along the upper Colorado River (Fig. 4). Total inorganic N concentrations

transformed scale using the smearing technique described in the text. *Solid lines* indicate significant relationship between age and soil attribute at  $P < 0.05$ ; *dotted lines* indicate non-significance

increased significantly in *Populus-Salix*-dominated stands, but not in *Tamarix*-dominated stands. NO<sub>3</sub> concentrations did not increase significantly as a

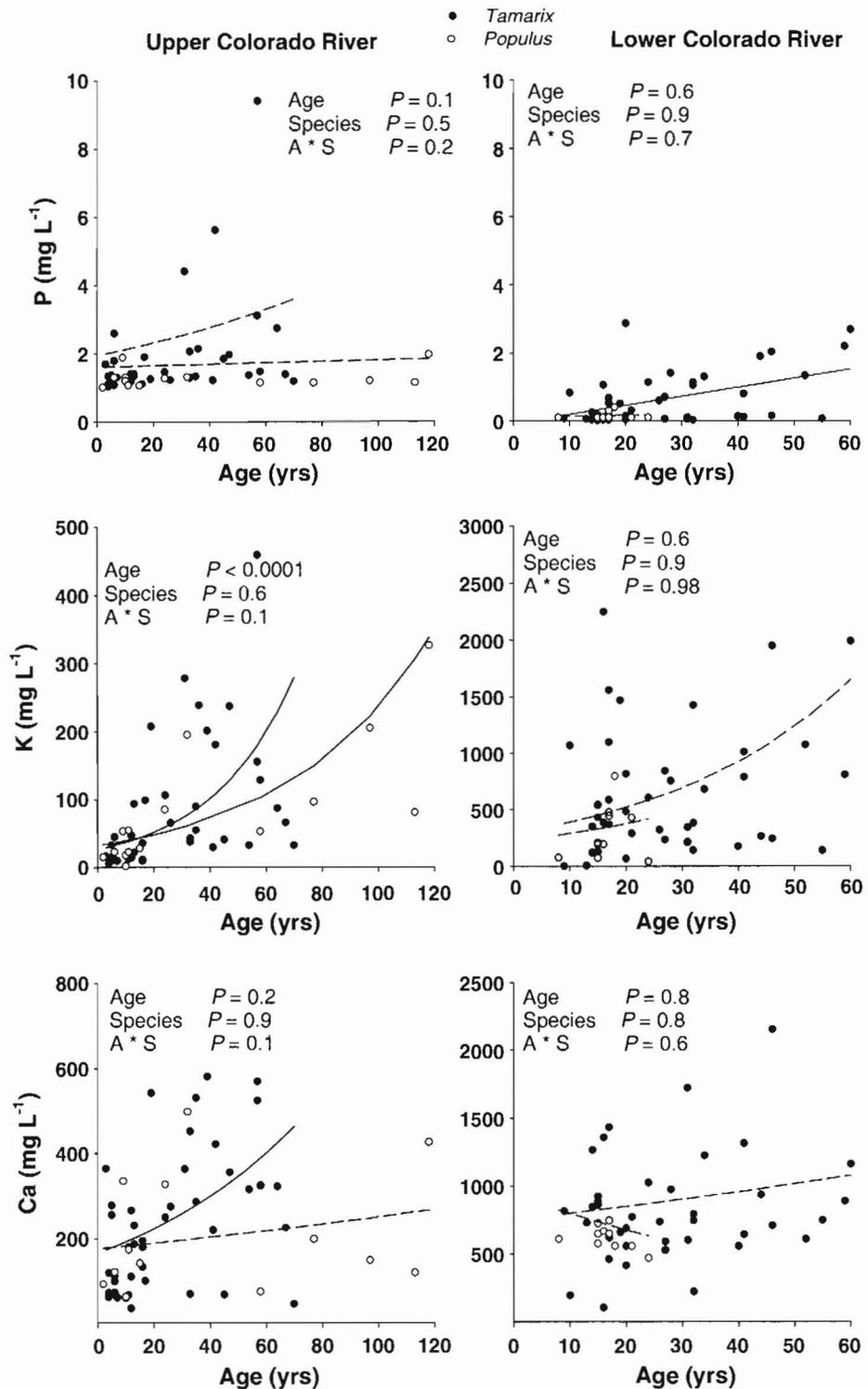
Fig. 3 continued



function of stand age in either *Tamarix* or *Populus*. Mg, SO<sub>4</sub>, and Ca concentrations increased significantly in *Tamarix*, but not *Populus-Salix*-dominated stands (Fig. 4). K concentrations increased in both

*Populus* and *Tamarix*-dominated stands with stand age, but the rate of increase did not differ between stand types (Fig. 4). P concentrations did not vary as a function of stand age in either stand type (Fig. 4).

**Fig. 4** Soil macronutrient concentrations (P, K, Ca,  $\text{NO}_3$ ,  $\text{NH}_4$ , and inorganic N) as a function of *Tamarix* and *Populus* stand age along the upper and lower Colorado River. Models were fitted with natural log transformed data. Models were then plotted in the non-transformed scale using the smearing technique described in the text. *Solid lines* indicate significant relationship between age and soil attribute at  $P < 0.05$ ; *dotted lines* indicate non-significance

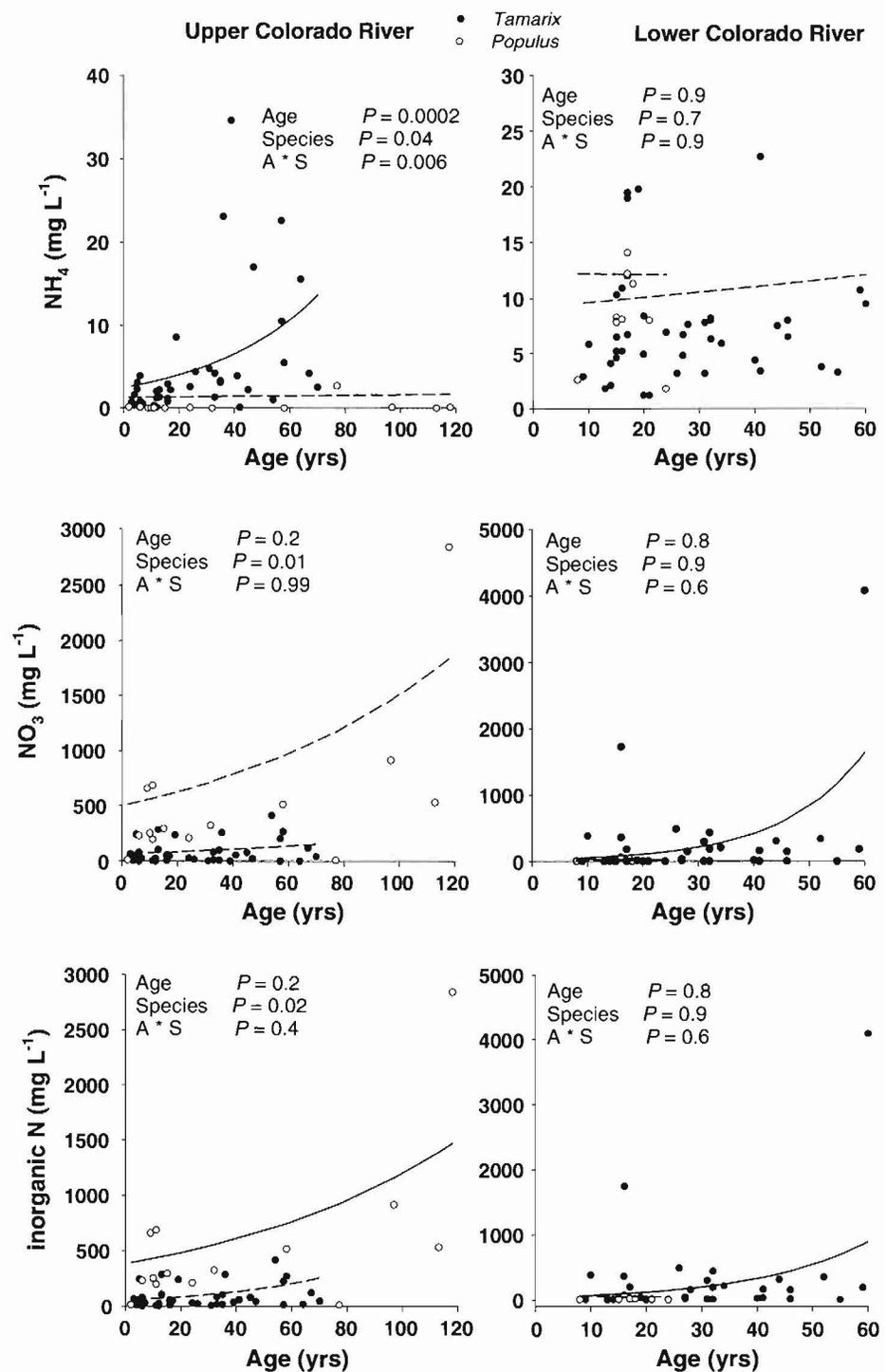


Soil physical and chemical attributes: lower Colorado River

On the lower Colorado River, clay decreased significantly as a linear function of stand age ( $r^2 = 0.32$ ,

$P = 0.05$ ) and sand increased marginally significantly as function of time ( $r^2 = 0.30$ ,  $P = 0.06$ ). There were no significant linear trends in silt through time in *Tamarix*-dominated stands along the lower Colorado River ( $r^2 = 0.26$ ,  $P = 0.1$ ). Nor were there significant

Fig. 4 continued



trends in soil texture in *Populus-Salix*-dominated stands along the lower Colorado River ( $P > 0.05$ ).

After accounting for the variability in stand age (which was not significant in any models for the lower Colorado River) differences in mean soil chemical

attributes were tested between stand types (ANCOVA). None of the measurements of salinity, salts, minerals or macronutrients were significantly different in *Tamarix* versus *Populus-Salix*-dominated stands (Figs. 3, 4;  $P > 0.05$ ).

**Table 1** Comparisons between mean ( $\pm$ SE) soil chemical characteristics of 5, 30 and 60 year old *Tamarix* and *Populus-Salix*-dominated stands on the upper Colorado River and 5, 15 and 30 year old stands along the lower Colorado River

	Upper Colorado River					
	<i>Tamarix</i>			<i>Populus</i>		
	5	30	60	5	30	60
Electrical conductivity (dS m <sup>-1</sup> )	2.2 $\pm$ 1.7	6.7 $\pm$ 1.2	<b>12.2 <math>\pm</math> 2.2</b>	2.3 $\pm$ 2.5	2.6 $\pm$ 2.0	3.0 $\pm$ 2.1
Salinity (mg l <sup>-1</sup> )	19.6 $\pm$ 1.3	<b>93.6 <math>\pm</math> 1.2</b>	<b>171.1 <math>\pm</math> 32.3</b>	21.6 $\pm$ 36.6	26.0 $\pm$ 28.0	31.4 $\pm$ 31.1
pH	7.92 $\pm$ 0.04	7.96 $\pm$ 0.03	8.0 $\pm$ 0.05	7.95 $\pm$ 0.06	7.97 $\pm$ 0.04	8.0 $\pm$ 0.05
SAR	<b>15.5 <math>\pm</math> 7.8</b>	<b>37.7 <math>\pm</math> 5.3</b>	<b>64.5 <math>\pm</math> 10.2</b>	7.8 $\pm$ 11.5	10.3 $\pm$ 9.0	13.4 $\pm$ 9.8
NH <sub>4</sub> (mg l <sup>-1</sup> )	<b>1.4 <math>\pm</math> 1.3</b>	<b>5.5 <math>\pm</math> 0.9</b>	<b>10.3 <math>\pm</math> 1.7</b>	0.06 $\pm$ 2.0	0.17 $\pm$ 1.5	0.3 $\pm$ 1.7
NO <sub>3</sub> (mg l <sup>-1</sup> )	58.3 $\pm$ 85.3	124.9 $\pm$ 58.9	204.7 $\pm$ 112.0	<b>182.1 <math>\pm</math> 126.7</b>	<b>431.8 <math>\pm</math> 98.8</b>	<b>731.4 <math>\pm</math> 107.9</b>
P (mg l <sup>-1</sup> )	1.3 $\pm$ 0.9	<b>1.8 <math>\pm</math> 0.6</b>	<b>2.3 <math>\pm</math> 1.1</b>	0.2 $\pm$ 1.3	0.3 $\pm$ 1.0	0.3 $\pm$ 1.1
Mg (mg l <sup>-1</sup> )	37.3 $\pm$ 67.5	<b>225.7 <math>\pm</math> 46.3</b>	<b>451.8 <math>\pm</math> 88.1</b>	53.8 $\pm$ 99.6	61.9 $\pm$ 77.7	71.6 $\pm$ 84.8
Na (mg l <sup>-1</sup> )	217.9 $\pm$ 246.1	<b>766.2 <math>\pm</math> 168.7</b>	<b>1424.2 <math>\pm</math> 321.2</b>	90.7 $\pm$ 363.0	128.7 $\pm$ 283.2	174.2 $\pm$ 309.1
K (mg l <sup>-1</sup> )	31.9 $\pm$ 18.7	87.1 $\pm$ 12.8	153.4 $\pm$ 24.4	28.5 $\pm$ 27.5	68.4 $\pm$ 21.5	116.1 $\pm$ 23.5
SO <sub>4</sub> (mg l <sup>-1</sup> )	534.3 $\pm$ 453.3	1653.6 $\pm$ 311.0	<b>2996.7 <math>\pm</math> 592.0</b>	466.9 $\pm$ 669.0	539.2 $\pm$ 522.0	625.9 $\pm$ 569.7
Cl (mg l <sup>-1</sup> )	<b>229.7 <math>\pm</math> 266.7</b>	<b>895.3 <math>\pm</math> 182.8</b>	<b>1694.1 <math>\pm</math> 348.1</b>	126.7 $\pm$ 393.4	138.2 $\pm$ 306.9	152.2 $\pm$ 335.0
B (mg l <sup>-1</sup> )	0.3 $\pm$ 0.2	<b>0.7 <math>\pm</math> 0.1</b>	<b>1.3 <math>\pm</math> 0.2</b>	0.1 $\pm$ 0.2	0.02 $\pm$ 0.2	0.03 $\pm$ 0.2
Ca (mg l <sup>-1</sup> )	179.5 $\pm$ 38.6	271.2 $\pm$ 26.4	<b>381.2 <math>\pm</math> 50.4</b>	175.5 $\pm$ 56.9	191.5 $\pm$ 44.4	210.7 $\pm$ 48.5
CO <sub>3</sub> (mg l <sup>-1</sup> )	0.0 $\pm$ 8.3	<b>25.0 <math>\pm</math> 5.7</b>	<b>55.3 <math>\pm</math> 10.8</b>	0.0 $\pm$ 12.2	0.0 $\pm$ 9.6	0.0 $\pm$ 10.4
HCO <sub>3</sub> (mg l <sup>-1</sup> )	250.9 $\pm$ 54.7	384.6 $\pm$ 37.5	545.0 $\pm$ 71.3	239.9 $\pm$ 80.6	321.7 $\pm$ 62.9	420.0 $\pm$ 68.7
Sand (%)	69.7 $\pm$ 4.1	59.7 $\pm$ 3.1	47.7 $\pm$ 6.2	75.4 $\pm$ 6.4	63.0 $\pm$ 5.0	48.2 $\pm$ 6.2
Silt (%)	19 $\pm$ 3.7	26.6 $\pm$ 2.6	35.8 $\pm$ 5.2	15.4 $\pm$ 5.5	25.7 $\pm$ 4.3	38.0 $\pm$ 5.3
Clay (%)	11.4 $\pm$ 1.0	13.7 $\pm$ 0.7	16.5 $\pm$ 1.4	9.2 $\pm$ 1.5	11.3 $\pm$ 1.2	13.8 $\pm$ 1.4
	Lower Colorado River					
	<i>Tamarix</i>			<i>Populus/Salix</i>		
	5	15	30	5	15	30
Electrical conductivity (dS m <sup>-1</sup> )	56.0 $\pm$ 8.2	56.9 $\pm$ 5.9	58.4 $\pm$ 4.4	36.5 $\pm$ 27.1	35.3 $\pm$ 9.4	33.6 $\pm$ 30.9
Salinity (mg l <sup>-1</sup> )	830.7 $\pm$ 114.7	854.1 $\pm$ 81.0	889.2 $\pm$ 61.0	632.3 $\pm$ 374.9	600.8 $\pm$ 131.1	553.6 $\pm$ 427.3
pH	8.2 $\pm$ 0.1	8.2 $\pm$ 0.1	8.3 $\pm$ 0.05	7.9 $\pm$ 0.3	7.9 $\pm$ 0.1	7.9 $\pm$ 0.3
SAR	260.5 $\pm$ 48.5	251.1 $\pm$ 34.2	236.9 $\pm$ 25.8	194.4 $\pm$ 158.5	164.8 $\pm$ 55.4	120.3 $\pm$ 180.6
NH <sub>4</sub> (mg l <sup>-1</sup> )	9.1 $\pm$ 1.9	9.3 $\pm$ 1.4	9.6 $\pm$ 1.0	9.7 $\pm$ 6.2	10.6 $\pm$ 2.2	11.7 $\pm$ 7.2
NO <sub>3</sub> (mg l <sup>-1</sup> )	0.0 $\pm$ 176.3	32.3 $\pm$ 124.5	2767.0 $\pm$ 93.8	9.6 $\pm$ 576.3	7.1 $\pm$ 201.6	3.4 $\pm$ 656.9
P (mg l <sup>-1</sup> )	0.06 $\pm$ 0.06	0.3 $\pm$ 0.1	0.7 $\pm$ 0.1	0.1 $\pm$ 0.6	0.1 $\pm$ 0.2	0.2 $\pm$ 0.7
Mg (mg l <sup>-1</sup> )	1638.6 $\pm$ 448.3	1770.3 $\pm$ 316.6	1967.8 $\pm$ 238.6	1044.4 $\pm$ 1465.5	1143.3 $\pm$ 512.5	1291.7 $\pm$ 1670.4
Na (mg l <sup>-1</sup> )	8398.2 $\pm$ 1439.6	8275.2 $\pm$ 1016.5	8090.7 $\pm$ 766.3	5516.2 $\pm$ 4705.9	5069.0 $\pm$ 1646.0	4398.2 $\pm$ 5363.9

Table 1 continued

	Lower Colorado River	
	<i>Tamarix</i>	<i>Populus/Salix</i>
K (mg l <sup>-1</sup> )	468.7 ± 155.8	551.9 ± 110.0
SO <sub>4</sub> (mg l <sup>-1</sup> )	11816.0 ± 2924.5	<b>11844.0 ± 2065.1</b>
Cl (mg l <sup>-1</sup> )	9498.9 ± 1639.5	10039.0 ± 1157.7
B (mg l <sup>-1</sup> )	5.6 ± 1.2	<b>5.5 ± 0.9</b>
Ca (mg l <sup>-1</sup> )	900.6 ± 180.7	905.7 ± 127.6
CO <sub>3</sub> (mg l <sup>-1</sup> )	17.3 ± 22.9	24.0 ± 16.1
HCO <sub>3</sub> (mg l <sup>-1</sup> )	496.2 ± 143.9	533.0 ± 101.6
Sand (%)	35.4 ± 5.4	38.6 ± 3.8
Silt (%)	42.3 ± 4.2	41.2 ± 3.0
Clay (%)	22.3 ± 3.2	20.2 ± 2.2
		17.0 ± 1.7
		6.3 ± 10.4
		30.7 ± 13.7
		63.0 ± 17.7
		440.4 ± 470.6
		<b>259.3 ± 74.8</b>
		727.6 ± 590.7
		2.3 ± 4.0
		9290.6 ± 5359.6
		4021.5 ± 9560.1
		131.5 ± 509.5
		268.0 ± 178.2
		4403.6 ± 3343.9
		8622.5 ± 1874.6
		1.7 ± 1.4
		0.9 ± 4.5
		634.6 ± 206.6
		495.1 ± 673.4
		<b>198.2 ± 26.2</b>
		487.5 ± 164.6
		34.7 ± 6.2
		47.3 ± 4.8
		<b>72.3 ± 15.6</b>
		0.0 ± 20.2
		17.9 ± 3.6
		35.4 ± 11.9

Bold indicates significantly higher levels, concentrations, or percentages between species for an age class

Regarding Hypothesis 3, *Tamarix* abundance was not associated with increased salinity levels and soil EC. EC level was not associated with *Tamarix* stem density ( $r^2 = 0.0001$ ,  $P = 0.95$ ), basal area ( $r^2 = 0.05$ ,  $P = 0.2$ ), or *Tamarix* cover ( $r^2 = 0.003$ ,  $P = 0.7$ ). Similarly, salinity was not associated with *Tamarix* stem density ( $r^2 = 0.003$ ,  $P = 0.9$ ), basal area ( $r^2 = 0.06$ ,  $P = 0.1$ ), or cover ( $r^2 = 0.003$ ,  $P = 0.7$ ). *Populus* cover was not associated with salinity ( $r^2 < 0.001$ ,  $P = 0.99$ ) or EC ( $r^2 = 0.002$ ,  $P = 0.93$ ).

In analyses considering both stand types together, there was no linear association between time since fire and EC ( $r^2 = 0.0005$ ,  $P = 0.9$ ) or salinity ( $r^2 = 0.003$ ,  $P = 0.7$ ). Elevation was not associated with EC ( $r^2 = 0.0001$ ,  $P = 0.96$ ) or salinity ( $r^2 = 0.004$ ,  $P = 0.7$ ). There were only a few stands with fire scars on the upper Colorado River, so time since fire was not included in the analyses.

## Discussion

We found no significant trends in soil salinity (or EC) through *Tamarix* and *Populus-Salix*-dominated chronosequences along the lower Colorado River. However, we did find significant trends in salt concentration (both salinity and EC) in *Tamarix*-dominated stands along the upper Colorado River. B, Na, HCO<sub>3</sub>, and K concentrations all increased at significant rates in both *Tamarix*- and *Populus-Salix*-dominated stands, and each of these (with the exception of HCO<sub>3</sub>) concentrated at faster rates in *Tamarix*-dominated stands. As discussed in detail below, our findings provide empirical support for the long-held contention that *Tamarix* can contribute to soil salinity, but our regional-scale study illustrates distinctions concerning the degree and direction of this effect between unregulated and heavily regulated river segments (Fig. 1). In some cases, like along the lower Colorado River, the influence of *Tamarix* on soil chemistry is inconsequential relative to other natural and human influenced factors that contribute to soil salinity.

Changes in soil texture through time in the upper Colorado River study segment were similar to other riparian chronosequence studies from the arid and semi-arid western USA (Adair et al. 2004; Ohrtman 2009; Stromberg 1998b; Uowolo et al. 2005) and on alluvial rivers elsewhere (Balian and Naiman 2005;

Boggs and Weaver 1994; Fierke and Kauffman 2005). Percent fines increased with stand age in both *Populus* and *Tamarix*-dominated stands. Along the major streams in the upper Colorado River basin (Green and Yampa Rivers) (Uowolo et al. 2005), the Missouri River (Wilson 1970), the Snake River (Merigliano 2005), and the San Pedro River (Stromberg 1998a), soil clay fraction increases as a function of increasing stand age in *Populus*-dominated riparian forests, while sand fraction decreases (Stromberg 1998b). Sodicity may occur in clay-dominated soils through the binding of Na to negatively charged clay particles. Na may remain in such fine-textured soils even when other water soluble salts are flushed through infiltration or flooding.

#### Influence of *Tamarix* on soil chemistry

Our results indicate that *Tamarix* may contribute to elevated soil salinity in some settings. By translocating salts to the surface from groundwater and the vadose zone and depositing salt from leaf exudates and in litter (Bertin et al. 2003; Smith et al. 1998; Sookbirsingh et al. 2010), *Tamarix* concentrated salts in soils at significantly higher rates compared to chronosequences dominated by *Populus* on the upper Colorado River. Ohrman (2009) also found that soil surface salinity levels were higher in monotypic *Tamarix* stands along the heavily regulated middle Rio Grande, New Mexico, USA and that salts concentrated as a function of stand age and *Tamarix* density, particularly in sites that no longer flooded. On the lower Colorado River, any effect of *Tamarix* on soil salinity was overwhelmed by extremely high salinities in all soils sampled.

One factor that may distinguish mechanisms of *Tamarix* contribution to soil salinity from other salt-contributing factors such as those from ash following fires and from evaporation and concentration from groundwater, is preferential uptake and exudation of specific ions by *Tamarix*. Though it is known that the chemical composition of *Tamarix* exudates reflects site soil and groundwater chemistry (Di Tomaso 1998) in terms of the anions and cations present in exudates, *Tamarix* may preferentially exude certain ions. Higher concentrations of B ions in mature *Tamarix* stands compared to *Populus*-dominated stands along our upper Colorado River reach, suggest that *Tamarix* may have some ability to preferentially exude B. B can

have negative effects on other floodplain species, even in small concentrations (Nable et al. 1997).

#### Interactions with floodplain hydrology and geomorphology

Along the upper Colorado, where flows are only moderately altered from historic conditions, natural patterns of flooding and fluvial disturbance have maintained stand dynamics typical of active alluvial riverine systems, and patterns of stand structural and edaphic change essentially matched our expectations. Flows through the upper Colorado River study reaches still experience occasional high spring snowmelt peaks and fluvial processes reflecting historic conditions (Richter et al. 1998; Van Steeter and Pitlick 1998). Our study reach included a gradient ranging from frequently flooded, high turnover, non saline, coarse grained sediment in and near the channel to infrequently flooded, finer-grained soils with higher levels of both salts and macro-nutrients far from the channel. A continuum of young to old stands of native-dominated forest (*P. fremontii*) occurred with locally abundant patches of *Tamarix*. Clearly defined fluvial features along the upper Colorado River range from scoured active channel to active channel shelves, sparsely vegetated channel margins, low, intermediate and high floodplains and abandoned terraces, channel side arms and backwaters.

In contrast, along the lower Colorado River, flow regulation and channelization have dramatically altered natural processes, and riparian forests there exhibited less uniform and directional changes as a function of stand age. Reduced magnitude and frequency of flooding and hydrologic isolation of riparian areas from the channel have facilitated the development of extremely saline soils (EC as high as  $162 \text{ dS m}^{-2}$  and salinity exceeding  $2,920 \text{ mg l}^{-1}$ ). Flooding functions to flush salts from the soil column (Anderson 1995; Jolly et al. 1993; Tiegs et al. 2005). A number of studies have demonstrated that the lower Colorado River is less fluvially dynamic and experiences significantly less frequent and lower magnitude flooding than prior to flow regulation (Graf 2006; Schmidt and Wilcock 2008). In addition, a large segment of the lower Colorado River has been channelized and leveed, further isolating the river from its former floodplain. Under such circumstances, floods rarely inundate the floodplain, but rather elevate

the water table (along with dissolved salts) in former-floodplain areas outside of levees.

In conjunction with channelization and termination of flows sufficient to flood and periodically flush salts and nutrients from floodplain soils along the lower Colorado River, the very fine texture of the bottom-land soils facilitate capillary rise of saline groundwater and evaporative concentration of salts on soil surfaces. Soils contained 56 % fines along the lower Colorado River, with some stands having as high as 84 % clay and silt. In fine-textured soils, evaporative concentration of salts on the surface may occur even where the water table is several meters deep (Hillel 1980). Such “sub-irrigation” by brackish groundwater is the most significant contributor to soil salinity along the lower Colorado River (Glenn and Nagler 2005). Soil EC was positively correlated with percent clay and silt on the nearby Bill Williams River (Shafroth et al. 1998).

#### Interactions with riparian wildfire

The pattern of increasing basal area and decreasing stem density (self thinning) over time, such as we observed, is common in forest succession, and driven externally by increasing size of (and thus competition with) neighbors and driven intrinsically by aging (Zeide 2010). The increase in biomass of dead stems as stands age has implications for fuel loading and fire intensity in *Tamarix*-dominated stands.

Fire intensity and frequency have been altered from historic conditions along the lower Colorado River (Busch 1995), as well as throughout many arid-land rivers in western USA (Conway et al. 2010; Ellis 2001). Fire influences soil chemistry, nutrient processing, and stand dynamics. Through volatilizing nutrients and increasing salinity, frequent or high temperature fire may result in major shifts in plant community structure by favoring fire-, drought- and salinity-tolerant species over other riparian plants. On the Bill Williams and lower Colorado rivers, post-fire soils exhibited a fourfold increase in EC, and communities often became dominated by *Tamarix* and *Pluchea*, taxa that are ecophysiologicaly tolerant of the higher salinity and lower water availability characteristic of burned sites (Busch and Smith 1993). Some of the increase in EC was likely driven by significant increases in Na (increased 3.5 fold), Cl (increased fourfold), and Mg (increased threefold) concentrations as a result of fire. Busch and Smith

(1993) also noted increases in macronutrients such as  $\text{NH}_4$  (increased threefold),  $\text{NO}_3$  (increased 283 fold), and Ca (increased 2.7 fold) due to volatilization from fire.

The fuels provided by *Tamarix* may have an important influence on fire frequency and intensity (Ellis et al. 1998). On our lower Colorado River sites, there were an average of 252,290 dead stems  $\text{ha}^{-1}$  and 20  $\text{m}^2 \text{ha}^{-1}$  of dead basal area in *Tamarix*-dominated stands. *Tamarix* accounted for 95 % of all dead stems on average and 97 % of the total basal area of these stands. The historical significance of fire in riparian areas is not well-understood for the upper Colorado River; however, average basal area of dead stems ( $7.9 \text{ m}^2 \text{ha}^{-1}$ ) was less than half of that measured along the lower Colorado River, as was dead stem density ( $82,201 \text{ dead stems ha}^{-1}$ ). Though there was evidence of past fire, fire scars and scorched stems were not as common along the upper compared to the lower Colorado River. Higher fire frequency and severity, and associated contributions of fire to soil salinity, along the lower Colorado River are likely interrelated with decreased flooding of the floodplain due to channelization. Decreased flooding and subsequent reduced microbial activity and decomposition of organic material contribute to fuel accumulation, which in turn amplifies fire and fire-related contributions to salinity (Busch and Smith 1995; Molles et al. 1998). Higher flood frequency along the upper Colorado River not only serves to flush salts from floodplain sediments periodically, but also to promote microbial activity, decomposition, nutrient cycling, reduced fire intensity when fires do occur, and lower contributions of ash to soil salinity.

#### Phytotoxicity effects and tolerances of riparian species

Because of the potential effects of *Tamarix* and flow regulation on floodplain soil salinity, we reviewed the literature to better understand the likely effects of specific ions as well as salinity in general on common floodplain species in the North American Southwest. Soil salinity may affect fitness (e.g., growth rates, fecundity, survival) of salt-intolerant species, for example by causing osmotic stress, increasing concentrations of salts in tissue (which can damage cells), decreasing the concentration and availability of essential nutrients, and hindering water uptake,

exacerbating water stress (Yeo 1998). In greenhouse studies aimed at determining relative salinity tolerance of several Sonoran desert riparian species based on growth rates, Glenn et al. (1998) ranked *Allenrolfea occidentalis*, *T. ramosissima*, *Pluchea sericea*, *Baccharis salicifolia*, *P. fremontii*, and *S. gooddingii* as most to least salt tolerant. In laboratory experiments, *Tamarix* and *Pluchea* were much better able to extract water from saline soils than *Salix*, *Populus*, and *Baccharis* (Vandersande et al. 2001). Other studies have examined salinity tolerance of dozens of additional herbaceous and woody riparian plants in greenhouse (Beauchamp et al. 2009) and field settings (Beauchamp and Shafroth 2011; Shafroth et al. 2008). These studies suggest which western USA riparian species and communities are more or less likely to be adversely affected by increases in soil salinity.

Considerable research has elucidated effects of salinity on dominant native riparian trees in the *Populus* and *Salix* genera, which are the most common native analogs to *Tamarix*. *P. fremontii* is intolerant of high salinity, showing reductions in transpiration and relative growth rate of seedlings when salt concentrations exceed approximately  $3.4 \text{ dS cm}^{-1}$  (Glenn et al. 1998; Vandersande et al. 2001). Root and shoot growth of *P. fremontii* and *S. gooddingii* seedlings was inhibited by soil salinity greater than  $2.6 \text{ dS m}^{-1}$  in greenhouse experiments (Jackson et al. 1990; Wiesenborn 1996). One hundred percent *Populus fremontii* mortality was recorded after 30 days of exposure to  $61.2$  and  $102 \text{ dS m}^{-1}$ , and no seedlings lived beyond 60 days of exposure to  $30.6 \text{ dS m}^{-1}$  (Jackson et al. 1990). In greenhouse experiments, *Populus* and *Salix* growth was reduced by 7–9 % for every  $\text{g l}^{-1}$  of NaCl added to irrigation water (Glenn et al. 1998). Neuman et al. (1996) reported some of the physiological effects of high soil salinity on *Populus* such as ion imbalance affecting osmosis and water stress. Higher concentrations of ions (such as Na, Cl, Mg and K) in *Tamarix* stands could affect germination, water balance, salt uptake and growth rates of colonizing *Populus*, though *Populus* colonization of existing *Tamarix* stands is uncommon (Glenn et al. 1998; Vandersande et al. 2001). Salinity may inhibit *Populus* growth by suppressing stomatal conductance, photosynthesis, and carbohydrate production (Singh et al. 1999).

In contrast to the relatively low salinity tolerance of *Populus* and *Salix*, *Tamarix* typically occurs on sites with soil salinities ranging from  $\text{dS } 1.2$  to  $25.5 \text{ dS m}^{-1}$ ,

but may tolerate soils with salinities as high as  $34 \text{ dS m}^{-1}$  or higher (Carman and Brotherson 1982; Glenn et al. 1998). In the delta of the Colorado River, *Tamarix* penetrates into the intertidal zone, growing in salinities up to approximately  $34 \text{ dS m}^{-1}$ , but gives way to extensive *Distichlis palmeri* and *Allenrolfia occidentalis* stands as seawater salinity is approached (Glenn et al. 1998). Glenn et al. (1998) noted a 70 % survival rate of *Tamarix* at salinities exceeding three times this level ( $102 \text{ dS m}^{-1}$ ). Regardless of the source of salinity, be it concentration from evaporation, loss of flushing flood flows, or concentration from exudation and litterfall, *Tamarix* appears to be favored over glycophytic native species in saline soils.

Our results suggest that salt concentrations on the lower Colorado River were sufficiently high (average and maximum EC of 99 and  $162 \text{ dS m}^{-1}$ ; and salinity of  $1,459$  and  $2,920 \text{ mg l}^{-1}$ ) to limit vegetation to only halophytes across the *Tamarix* chronosequence at most sites (Beauchamp et al. 2009; Shafroth et al. 2008). Soil salinity levels were sufficient to limit salt-intolerant trees such as *S. gooddingii* and *P. fremontii* in most (all but 5) plots along the lower Colorado River (Table 1). In contrast, only four plots along the upper Colorado exceeded this concentration; each in *Tamarix* stands greater than 30 years old. Despite the fact that EC commonly exceeded threshold salinity levels on the lower Colorado, *Populus* dominated plots with surface soil EC as high as  $56.8 \text{ dS m}^{-1}$ . This is likely due to concentrations of salt in the upper soil horizons, which may not correspond to the portion of the soil column where roots are concentrated. In northeastern Montana, salt concentrations recorded in *Tamarix*-dominate stands were found to be within the tolerance range of native vegetation ( $<4 \text{ dS m}^{-1}$ ) (Lesica and DeLuca 2004).

Specific ions or particular combinations in soil and groundwater can also affect growth, germination, and mortality; thus, salinity and EC are only coarse indicators of a species' ability to grow on a site (Ungar 1978). At low levels, certain ions exuded or otherwise delivered to soils following translocation through plants may have positive interspecific effects on plant growth. Lesica and DeLuca (2004) found that *Agropyron smithii*, a native grass, grown in soils collected beneath *Tamarix* was 73 % larger than when grown in soils collected from adjacent areas outside of the *Tamarix* canopy. In addition, shoot:root ratio was 29 % greater for plants grown in *Tamarix* affected soil. Inorganic N and P were higher in *Tamarix* stands,

compared to other vegetation types, suggesting a fertilizing effect of *Tamarix* leaf fall or leaf secretions (Lesica and DeLuca 2004).

In the current study,  $\text{NH}_4$  was greater, and  $\text{NO}_3$  and total inorganic N were much lower, in mature *Tamarix* stands than in mature *Populus*-dominated stands along the upper Colorado River. The lower total inorganic N in *Tamarix* stands is surprising, because *Tamarix* tends to have greater leaf N concentrations (nearly double) and contribute greater N inputs to soil than *Populus* (Moline and Poff 2008; Tibbets and Molles 2005). N mineralization rates may be suppressed in *Tamarix*-influenced soils despite greater organic N, perhaps because of inhibitory effects of slightly elevated soil salinity on N-mineralizing soil microbiota. The greater  $\text{NH}_4$  concentrations in *Tamarix* stands may also have been due to elevated salinity, which can inhibit both nitrifying soil microbiota (Laura 1977) and root  $\text{NH}_4$  absorption (Fageria et al. 2011). Other studies, however, have documented decreases in  $\text{NH}_4:\text{NO}_3$  ratios under *Tamarix* canopies (Lesica and DeLuca 2004). Our results contrast with studies of other non-native, invasive species, which often report greater N litter decomposition and N mineralization rates (particularly nitrification) in sites occupied by invasive species (Ehrenfeld 2003).

The abundance of certain ions (including those that are beneficial or necessary at trace levels) can overwhelm other indicators of habitat suitability for certain species (e.g., ranges of tolerable EC levels or other salinity indicators). For example, B is known to have negative effects on domestic crops and crop yield decrease is exacerbated (additive effect) where salinity occurs simultaneously with toxic ions such as B (Shani and Hanks 1993). *Populus* and *Salix* exhibit a low tolerance to B (Di Tomaso 1998). B concentrations were particularly high in soils in older *Tamarix*-dominated stands in the current study, suggesting that *Tamarix* may preferentially exude B. The detrimental effects of B on *Populus*, and the relative tolerance of *Tamarix* to this element, has led some researchers to recommend *Tamarix* planting for stabilization and remediation of soils with high B levels (Pavlovic et al. 2004).

## Conclusions

By contrasting chronosequences of non-native *Tamarix*-dominated riparian forest with native *Populus*

and *Salix*-dominated forest along moderately- and heavily-regulated reaches of the Colorado River, our results demonstrate that *Tamarix* can affect soil salinity to the possible detriment of native riparian plants. However, alteration of natural fluvial processes by flow regulation and channelization may contribute to severe soil salinization in areas where *Tamarix* is present and cause soil salinization even in the absence of *Tamarix*. The contention that *Tamarix* has directly contributed to the decline of western riparian areas has resulted in expenditures of tens of millions of dollars by agencies attempting in many cases to “restore” riparian habitats through large-scale removal of *Tamarix* from river margins (Shafroth and Briggs 2008). A recurring objective of resource managers along western USA rivers is to replace stands of *Tamarix* with native vegetation such as *Populus* and *Salix* (Shafroth et al. 2008; Taylor et al. 2006). Without the restoration of natural processes, including those that flush salts from floodplain soils, control efforts are unlikely to result in restoration of floodplain functions or native riparian vegetation (Merritt and Poff 2010; Stromberg 2001; Stromberg et al. 2007). Through restoring these processes, the effects of *Tamarix* on soil properties can be mitigated while at the same time providing a range of other important functions of riverine ecosystems. In cases where some degree of restoration of fluvial and hydrologic processes is not possible, soil remediation and tailoring plant species lists to existing (or forecasted) soil salinities is advisable (Beauchamp et al. 2009; Shafroth et al. 2008). Understanding salinity tolerance of replacement taxa is important in evaluating the potential effects of elevated soil salinity on rates of colonization, success of establishment, and compositional potential of replacement communities.

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