MECHANISMS ASSOCIATED WITH DECLINE OF WOODY SPECIES IN RIPARIAN ECOSYSTEMS OF THE SOUTHWESTERN U.S.¹

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Abstract. Throughout western North America, riparian ecosystem function has been transformed by anthropogenic influences on riverine environments. Modified flood frequency, duration, or intensity; depressed floodplain water tables; and increased alluvium salinity have contributed to change in riparian forest communities formerly dominated by Populus fremontii and Salix gooddingii. The invasion of the naturalized arborescent shrub, Tamarix ramosissima, potentially alters competitive hierarchies and disturbance regimes in these riparian ecosystems. We evaluated the structure and function of two southwestern riparian communities that differed in the degree of streamflow perturbation to which they had been subjected: the highly regulated lower Colorado River and the less tightly regulated Bill Williams River. Ordination analyses provided evidence that these riparian communities are structured along gradients relating to moisture, salinity, disturbance from fire, and community maturity, with Colorado River sites being more xeric and saline than those on the Bill Williams River.

Foliar elemental analyses revealed high sodium concentrations in Tamarix (Na:K ratio = 1.87) and in the native shrub Tessaria sericea (Na:K = 1.56). Evaluation of tissue water relations parameters showed that Tamarix had lower osmotic potentials than sympatric woody taxa, helping to confirm that Tamarix is halophytic and probably capable of greater osmotic adjustment than native species. Carbon isotopic discrimination (Δ) provided evidence for higher water use efficiency in Tamarix than in Populus, Salix, and Tessaria. Tamarix Δ averaged over 1% less than that of the other riparian taxa. Experimental removal of Tamarix from stands where Salix was codominant resulted in growth augmentation, less negative water potentials, and higher leaf conductance in Salix, all providing evidence of interspecific competition. The persistence of Salix, but not Populus, on the Colorado River appears to be due to greater water- and salinity stress tolerance in Salix than in Populus. A preponderance of senescent Populus along the Colorado River is an indication that this formerly dominant species is effectively approaching local extinction in parts of this ecosystem.

Key words: Bill Williams River; carbon isotope ratios; Colorado River; experimental vegetation removal; morphology; ordination; plant water relations; Populus fremontii; Salix gooddingii; Tamarix ramosissima; Tessaria sericea; water use efficiency.

INTRODUCTION

In spite of their arid surroundings, the native trees dominating low elevation alluvial plant associations of the southwestern United States have their closest phylogenetic relationships with taxa from montane and mesic forest communities in North America. However, this is not an indication that the biotic and abiotic processes acting to structure forest communities in these disparate regions are uniform. Southwestern riparian communities owe their existence to mesic microenvironments along the floodplains of perennial watercourses. Functional attributes such as disturbance, regeneration, and competition operate differently in southwestern riparian ecosystems than in other North American temperate deciduous forest systems. The influences of xerophytic or halophytic taxa are also important in setting southwestern riparian forest and scrub communities apart.

Flooding is a form of disturbance to which many of the taxa occurring in riparian communities appear well adapted. Decreased frequency or intensity of flooding as a result of damming, water diversion, and flow regulation has major effects on riparian ecosystems.

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Downstream effects of impoundment include altered river discharge, decreased suspended sediment, channel incision, and floodplain narrowing (Williams and Wolman 1984). Accompanying such changes in the alluvial environment are shifts in riparian plant community composition. Water management practices have been implicated in reducing Populus recruitment in riparian forests and the over-representation of senescent individuals in these populations (Rood and Heinz-Milne 1989, Howe and Knopf 1991). Perturbation of floodplain hydrology resulting in the depression of floodplain water tables may also result in water stress in riparian trees and shrubs, given the phreatophytic habit of the taxa dominating floodplain communities (Busch et al. 1992). Such stress may accelerate plant senescence or reduce the ability of woody species to resist a variety of damaging agents (Runeckles 1982, Franklin et al. 1987).

The invasion of exotic vegetation in riverine ecosystems is a cosmopolitan phenomenon (Loope et al. 1988, McIntyre et al. 1988, Griffin et al. 1989, Thebaud and DeBussche 1991). Rapid invasion by naturalized Tamarix ramosissima in floodplain ecosystems of the southwestern United States has profoundly altered riparian community composition (Crins 1989). The invasion of Tamarix has also fundamentally altered riparian ecosystem properties. Tamarix is capable of desiccating watercourses (Vitousek 1990) and appears to induce novel riparian ecosystem disturbance regimes, including those associated with fire (Busch and Smith 1993). Given that the invasion of Tamarix often involves the displacement of native Salix gooddingii and Populus fremontii (Ohmart and Anderson 1982, Vitousek 1990, Stromberg et al. 1991), it appears that anthropogenic hydrological perturbation may also affect competitive interrelationships among woody riparian taxa.

While research on riparian communities has clarified germination and establishment with respect to abiotic factors for a variety of riparian species, those factors contributing to long-term survival or community change remain largely unidentified. An understanding of riparian community dynamics based only upon information collected during germination and initial establishment is insufficient because survival through these early stages is infrequent in natural forest populations (Peet and Christensen 1987). In addition, ecophysiological differences in juvenile and adult woody plants may lead to differential mortality between age classes (Donovan and Ehleringer 1991). Consequently, geomorphic and hydrologic instability in riparian ecosystems often makes the sites that are most favorable for germination among the most unlikely for survivorship through subsequent age classes (Asplund and Gooch 1988, Stromberg et al. 1991). Although the physicochemical and biotic interactions occurring after establishment are of considerable importance to riparian community structure, such interactions have not been addressed in past studies of riparian community ecology or controlled experimentation with seeds or seedlings.

Perspectives based on isolated components of the terrestrial–aquatic interface have only limited value to the understanding of riparian ecosystems (Gregory et al. 1991). Thus, hydrologic, geomorphic, and edaphic gradients are of key importance in riparian community organization. Because of the increasing rarity of pristine riparian ecosystems in the southwestern United States, it is vital that experimental approaches contrast unperturbed riparian sites showing evidence of community vigor with those showing indications of incipient or chronic environmental stress. Interactions of dominant woody riparian taxa of the lower Colorado River system were evaluated under two primary hypotheses: (1) that hydrologic variation has significant effects on riparian plant community structure and function; and (2) that varying salinity in floodplain environments also affects these attributes. We used data on site physical characteristics and plant moisture and salinity relations, together with multivariate community analyses, to evaluate how environmental influences and ecophysiological responses of the dominant woody taxa govern riparian community structure. We also hypothesized that the invasion of Tamarix has led to the alteration of competitive hierarchies in riparian communities of the southwestern United States. Experimental manipulation of plant populations was used to examine this phenomenon at sites subject to chronic hydrological perturbation, where plant interactions were likely to be intense due to potential limitation in the groundwater moisture source.

**STUDY AREA**

Research was conducted in two areas of west-central Arizona near the lower Colorado River (Fig. 1, Plate 1). The first of these was in the Colorado River flood-
PLATE 1. Study areas. Top: riparian gallery forest of *Salix gooddingii* and *Populus fremontii* lining the active Bill Williams River channel. Bottom: riparian scrub habitat dominated by *Tamarix ramosissima* and *Tessaria sericea* covering the lower Colorado River floodplain.

plain (34°50’ N, 114°35’ W, elevation 150 m). The second was in the Bill Williams River floodplain east of Lake Havasu (34°15’ N, 114°0’ W, elevation 150 m). Throughout the general study area, January temperatures average 10°–13°C, while average July temperatures are >32° (Hecht and Reeves 1981). Precipitation averages 13 cm annually (Sellers and Hill 1974). Hyperthermic Aridosols are the characteristic soils of the lower elevations of western Arizona; study site soils are from the Torrifluvents Association, the well-drained, sandy, recently mixed alluvium of floodplains in southwestern Arizona (Hendricks 1985). The surrounding upland vegetation was representative of the Lower Colorado subdivision of the Sonoran Desert-scrub formation (Turner and Brown 1982).

The Colorado and Bill Williams Rivers possess fundamental differences relating principally to their physiographic characteristics. With its headwaters in the Rocky Mountains ≈2700 km to the northeast and 4000 m higher than its lower reach, the Colorado River is one of the major rivers of the southwestern United States, draining a 630,000 km² basin. Historically, this lower perennial river transported large quantities of sediment which were deposited laterally in episodic
floods, creating a broad, deep floodplain alluvium where the river was not constrained in canyons. At such sites, deciduous woody taxa formed closed canopy riparian gallery forests. The construction of several large dams on the river during the middle of the twentieth century allowed regulation of river discharge to meet flood control, agricultural, and electrical power generation requirements. Channel aggradation and degradation have been altered by the presence of impoundments and by dredging and bank stabilization programs. Sites in the Colorado River floodplain that were selected for this research were 54 km downstream from Davis Dam, one of the major impoundment points. Amplitude and frequency of river discharge in this reach were profoundly affected by dam operation.

The Bill Williams River is a tributary to the Colorado River and drains a more localized (12,300 km²) basin. There is nearly continuous riparian forest and scrub vegetation along the lower 23 km of the Bill Williams River floodplain. Above this reach, the river is restricted to a narrow canyon extending another 30 km upstream to where it is impounded at Alamo Dam. Although subjected to some of the same sorts of hydrologic perturbation that affect the Colorado, flows in the Bill Williams River are more variable and less predictable, based on long-term averages. Unlike the Colorado River, the Bill Williams River channel is not confined by anthropogenic channelization or natural channel incision, so its floodplain is subject to periodic flooding.

Szaro (1989) characterized the forest vegetation native to the Colorado River riparian zone as the Populus fremontii–Salix gooddingii association. The Tamarix pentandra (nom. illeg.) community type (Szaro 1989) is abundantly distributed along the Colorado River and its tributaries, and is a riparian scrub formation dominated by the woody taxa Tamarix ramosissima, Tessaria sericea, Prosopis glandulosa, Prosopis pubescens, and Atriplex lentiformis. Central to the goals of this study was an examination of the interrelationships of Tamarix, Tessaria, Populus, and Salix. Because much of the Colorado River floodplain is now dominated by monotypic Tamarix, study site selection on the two rivers was limited to stands with remnant Populus or Salix. Areas delineated as Populus–Salix habitats (Younker and Anderson 1986, Ohmart et al. 1988) generally have Populus or Salix present, although often at low densities relative to Tamarix or Tessaria.

Two types of sites on the Bill Williams River were selected for ecophysiological data collection, both types having Tamarix, Salix, and Populus in a riparian forest assemblage. Hydrogeologic characteristics were the basis for the distinction between Bill Williams River areas. In upstream portions of the study reach, the stream and alluvial aquifer maintain a hydraulic connection, but downstream the lack of such a connection leads to much more extensive seepage into the alluvium (Rivers West 1990). Thus, our “upstream” sites (n = 3) were in an effluent stream reach where stand evapotranspiration and water table declines did not substantially deplete stream discharge. An initial demographic assessment of these sites depicted apparent vigor among the native taxa due to the presence of seedlings (evidence of recent germination) and a low proportion of mature tree senescence or mortality. Although floristically similar to upstream sites, “downstream” sites on the Bill Williams River (n = 3) were located where streamflow was intermittent. Trees on these sites had experienced crown dieback and mortality. All study sites were within 300 m of the active Bill Williams River channel.

Populus has become localized and rare in the lower Colorado River floodplain. Although the sites chosen to represent this area in comparisons with Bill Williams River sites were classified within the Populus–Salix association (Younker and Anderson 1986), Salix and Tamarix dominated these sites. Tessaria was locally abundant as an understory shrub. Disturbance-associated increases in Tessaria riparian coverage (Busch 1995) led to its inclusion in the study design for the Colorado River in the place of Populus. Colorado River “control” sites (n = 4) had nearly complete canopy cover by tall Tamarix–Salix thicket vegetation. Based on their shoot architecture, the spread of Salix and Tamarix in these areas appeared to be largely clonal. Crown dieback was evident in most of the Salix thickets. Colorado River sites were <400 m from the river’s channel. “Experimental” sites (n = 4) on the Colorado River were plots where vegetation removal was conducted.

**Methods**

**Hydrology and soil moisture**

All sites were within 7 km of U.S. Geological Survey (USGS) river gauges. Hydrographic data were obtained electronically from the USGS Arizona data base for the years 1949–1990 on the Colorado River, and 1940–1990 on the Bill Williams River. Median flows and ranges in flow were determined on a monthly basis using daily discharge data for the years of field study (1989–1990). Comparisons of study period discharge with historical hydrographs were made using monthly flow averages over the periods for which data were available from this data base.

Observation wells were installed to measure groundwater depth in the unconfined alluvial aquifers at all study sites. Depths from the soil surface to the water table were measured to characterize this potential moisture source. Four groundwater observation wells were placed on the upstream and downstream sites adjacent to the Bill Williams River. Three wells were located near the complex of control and experimental sites in the Colorado River floodplain.

Time-domain reflectometry (TDR) has been used to measure dielectric properties of many materials, and
can be used to accurately measure volumetric moisture percentage (θ) in surface soils (Topp and Davis 1985). At each study site, arrays (n = 3 or 4) of four stainless steel TDR probes were implanted vertically in the alluvium. Two 90-cm probes served as electromagnetic wave guides, with single 60- and 30-cm probes paired with a 90-cm probe to estimate θ over each 30 cm depth interval. Vertical probe orientation resulted in an integrated θ measurement over the upper 90 cm of the soil profile (θs), and measurements for the 0–30, 30–60, and 60–90 cm depth intervals (θd).

**Soil and water analyses**

Soil samples were collected by soil auger at randomly selected points at each of the study sites for nutrient and salinity analyses. Sampling depth intervals corresponded to those used in TDR soil moisture measurements (i.e., 0–30, 30–60, and 60–90 cm; n ≥ 8 for each depth on each site). Groundwater samples were obtained by hand pumping water from study site wells once every two months. To avoid taking water standing in wells, three well volumes were withdrawn prior to taking a 500 ml aliquot for analysis. Water samples were grouped by river system for comparisons of aquifer water characteristics.

With only minor modifications, soil extract and water analyses followed identical protocols. Sample electrical conductivity (EC) and pH were determined using an electrical conductivity probe and pH meter, respectively. Total dissolved solids (TDS) determinations were made on water samples by evaporating the water and then weighing the residual evaporate. Water and soil extract sample carbonate (CO3) and bicarbonate (HCO3) concentrations were determined by colorimetric titration with a 0.1 or 0.04 mol/L sulfuric acid solution. Chloride (Cl) concentrations were ascertained by titration with 0.1 mol/L silver nitrate. Sample sulfate (SO4) concentrations were determined by titration with 0.00521 mol/L barium perchlorate. An atomic absorption spectrophotometer (Perkin–Elmer 2380, Norwalk, Connecticut) was utilized in assays of sample extract potassium (K), calcium (Ca), magnesium (Mg), and sodium (Na) concentrations. Nitrate (NO3) concentrations were determined using ultraviolet spectrophotometry on soil extracts. Extract fluoride (F) concentrations were ascertained using a fluoride electrode in combination with a pH meter. A spectrophotometer was used to evaluate boron (B), phosphate (PO4), and ammonium (NH4) concentrations of sample extracts (Wolf 1971, Greenberg et al. 1981). Saturation percentages (Sat, %) for the soil sample extracts were determined by over-night drying of the soil paste. Sodium absorption ratios (SAR), an expression of the activity of Na ions in exchange reactions with soils (Hillel 1980), were calculated for water samples.

**Plant measurements**

On a seasonal basis, terminal segments of *Populus* and *Salix* branches were removed for morphological analysis. This analysis was limited to these taxa, where proleptic growth produced bud scale scars making annual growth increments identifiable. Stem segments were randomly taken from sunlit branches at the mid-canopy level from each of the study sites. On each branch sample, stem elongation was measured as the distance from the most terminal bud scale scar to the branch apex. Annual leaf production was quantified by counting the leaves with petiole insertions on these terminal segments, and by measuring the leaf area of individual leaves from annual growth increments with a leaf area meter (Decagon Delta-T, Pullman, Washington). Leaves were then rinsed, oven-dried at 65°C for 72 h, and weighed. Specific leaf area (SLA) was calculated as leaf area per unit dry leaf tissue mass.

Oven-dried leaf tissue was used in interspecific foliar element comparisons. These analyses were extended to *Tamarix* and *Tessaria* leaf tissue which were sampled and prepared in a similar manner. Dried leaf tissues were ground using a Wiley mill to produce homogenous samples. Leaf tissue samples taken from 5–10 individuals were bulked so that each species–study site combination was represented in the foliar analyses (n = 18) for each of the taxa investigated. Tissue samples were subjected to a nitrate digest and analyzed for dry weight concentrations of P, K, Ca, Mg, Na, Zn, Fe, Mn, Cu, and B using a Jarrell–Ash Atomcomp 975 inductively-coupled plasma atomic emission spectrometer (Franklin, Massachusetts). Total N was determined using a micro-Kjeldahl procedure.

**Plant water relations**

At each study site, three individuals of each species were selected for intensive monitoring. At Bill Williams River sites, *Tamarix, Salix,* and *Populus* were sampled. For the Colorado River, *Tessaria* replaced *Populus* in the study design. Water relations data were collected on a monthly basis, from April through October (full leaf expansion to senescence), over a 2-yr period. Data on leaf stomatal conductance (g), transpiration (E), leaf temperature (Tl), and photosynthetic photon flux (PPF) were collected by making repeated measurements at two-hour intervals on fully-expanded, mid-canopy leaves of each individual using a steady-state porometer (Licor LI-1600 with a LI-190S-1 quantum sensor, Lincoln, Nebraska). Data collection was confined to clear days, but leaves were not always sunlit due to mutual shading. A cylindrical chamber (Licor LI-1600–07) was used to measure g and E from both leaf surfaces of these amphistomatous species. Area-specific porometry results for all species were calculated using a single leaf surface derived from leaf area meter measurements.

Plant water potential (ψ) determinations were made twice daily with a pressure chamber (PMS Model 1000, Corvallis, Oregon) on two to four 5–10 cm terminal branch segments that were clipped from the mid-canopy level of study site individuals. Water potentials
were determined before dawn and near midday (1100–1300) at times corresponding to maximum and minimum daily \( \psi \), respectively, as determined by diurnal \( \psi \) trials.

Water potential components were estimated for *Populus, Salix, Tессария*, and *Tamarix* using pressure–volume analyses (Turner 1988). Analyses were performed seasonally (April, July, and October) on rehydrated cuttings from riparian stands near Las Vegas Wash, Nevada (36°5’ N, 114°50’ W, elevation 600 m; Fig. 1), a tributary of the Colorado River. This site was chosen because of its ecological similarity to our field sites and its proximity to a laboratory with facilities for tissue water relations quantification. Evidence of rehydration-induced shifts in pressure–volume parameters in trees from xeric sites has led to the recommendation of short (i.e., 1–3 h) rehydration periods for mesophytic trees (Dreyer et al. 1990, Kubiske and Abrams 1991). After rehydration for 1.5–2.5 h, terminal branch segments \( \approx 10 \) cm in length were detached and rapidly weighed, followed by pressurization in the pressure chamber. For each branch segment \( n = 10 \) for each species in each season), this process was repeated 7–11 times, or until xylem sap no longer exuded from the cut surface under pressure. Following this procedure, segments were dried at 65° for 72 h prior to dry mass determination. Sample water volumes were then calculated as the segment tissue mass less the oven-dry mass. Tissue water relations parameters were developed from pressure–volume plots of the reciprocals of chamber balancing pressure (1/\( P \)) versus relative water content (\( R \)) for each sample. A computer-assisted analytical technique (Schulte and Hinckley 1985) was employed to estimate relative water content at zero turgor (\( R_0 \)), osmotic potential at full turgor (\( \psi_{10^9} \)), osmotic potential at the turgor loss point (\( \psi_\text{t} \)), and bulk modulus of elasticity (\( \psi_e \)).

Carbon isotope fractionation occurring via CO\(_2\) assimilation was used to evaluate potential differences in water use efficiency (WUE) among the four taxa investigated. The ratio of carbon isotopes in leaf tissue samples (\( R_{\text{leaf}} \)) relative to that of the Pee Dee Belemnite standard (\( R_{\text{std}} \)) was used to express carbon isotope compositions on a parts per thousand (‰) basis:

\[
\delta^{13}C = \frac{[R_{\text{leaf}} - R_{\text{std}}]}{R_{\text{std}}} \times 10^3
\]

Carbon isotopic ratios were determined on oven-dried leaf tissues that were prepared as for the leaf elemental analyses. Samples \( (n = 20 \) for *Salix* and *Tamarix*, \( n = 12 \) for *Populus*, and \( n = 4 \) for *Tessarия*) were taken across all study sites where these taxa occurred. Isotopic analyses involved combustion of a 2–3 mg subsample of the dried leaf tissue for 6 h at 850° to produce CO\(_2\) in sealed evacuated Victor tubes containing cupric oxide and silver foil. Following cryogenic purification of the CO\(_2\) produced, sample \( \delta^{13}C \) values were determined on a Finnigan MAT delta E isotope ratioing mass spectrometer (San Jose, California). Carbon isotopic analyses were conducted at the University of Utah Stable Isotope Ratio Facility for Environmental Research, where instrument error associated with each observation has been estimated at 0.01‰, and error between repeated analyses at \( \pm 0.14‰ \) (Ehleringer 1990). Assuming a \( \delta^{13}C \) for atmospheric CO\(_2\) of \( -8.0\% \), carbon isotopic discrimination values (\( \Delta \)) for leaf tissues with \( \delta^{13}C \) measured as \( \delta_e \) were calculated using:

\[
\Delta = (-8.0 - \delta_e)/(10^3 + \delta_e)
\]

Farquhar et al. (1989a, b) have shown that \( \Delta \) is related to the ambient and intercellular partial pressures of CO\(_2\); ratios of these partial pressures are related to WUE and thereby also to \( \Delta \).

**Tamarix removal experiment**

To evaluate possible competitive interactions between a native riparian dominant and exotic *Tamarix*, plant community manipulations were conducted in the vicinity of the Colorado River control site. During the period of winter dormancy, *Salix* was left standing while surrounding vegetation was mechanically removed at four sites interspersed among the control sites. Clearing was accomplished by bulldozer, and involved complete aboveground removal of *Tamarix* from around the base of *Salix* clones. Given the low precipitation of the study area, it is unlikely that the cleared areas benefitted from additional surface soil moisture as the result of *Tamarix* removal. Surface disruption or incomplete removal of downed vegetation may have added nutrients or elevated salinities in the cleared areas, although attempts were made to minimize and document such effects.

Experimental and control *Salix* were irregularly distributed and \( >50 \) m apart. The plant removal areas were roughly circular, extending \( \approx 20 \) m from the base of the remaining *Salix* individuals. This radial distance was approximately three times the height and seven times the crown diameter of the remaining *Salix*. The lack of resprouting *Tamarix* during the data collection period obviated the need for reclearing efforts and provided an indication that experimental *Salix* were freed from both belowground and aboveground interspecific influences. Data on soil moisture, soil chemistry, plant morphology, and plant water relations were collected. In this manner, data from *Salix* on these experimental sites were available for comparison to *Salix* data from the interspersed Colorado River control sites, as well as to data from Bill Williams River study areas.

**Community structure**

Data for an analysis of plant community structure were collected from 97 circular plots (of area \( 200 \) m\(^2\)) selected from a wide range of microhabitats throughout the Colorado River \( (n = 63) \) and Bill Williams River \( (n = 34) \) floodplains. Studies of the variability in species richness relative to the number of plots sampled in southwestern riparian vegetation (Szaro and King
1990) indicate that these sample sizes were statistically adequate. Plots were restricted to vegetation stands classified within the *Populus–Salix* association (Younger and Anderson 1986); thus vegetation quantification was restricted to floodplain sites with evidence of recent dominance by one or both of these taxa. Estimation of perennial plant cover followed the Daubenmire (1959) method for classifying vegetation canopy coverage in six classes. A demographic aspect was introduced into this classification by subcategorizing *Populus* and *Salix* by size. Preliminary analyses of *Salix* at our study areas indicated that the frequency distribution of diameter at breast height (DBH) for reproducing individuals did not differ significantly from normal (Kolmogorov–Smirnov test, *P* > 0.99, *n* = 39), and that the lower quartile of this distribution fell at 10 cm DBH. Comparable results for reproductive *Populus* led to the adoption of a DBH criterion of ≤10 cm for defining a “juvenile” size class in these taxa. Trees of greater DBH were assigned to an “adult” class, unless standing dead branches contributed >20% of the canopy volume, in which case trees were classified in a “senescent” age class (Gatsuk et al. 1980). Demographic classification was based on primary stems, without accounting for the clonal nature of various riparian species.

Relative cover and relative frequency percentages were calculated for those taxa demonstrating ≥5% relative cover over the general study area. Detrended correspondence analysis (DCA; Hill 1979) was employed to produce ordinations of all stands and perennial species. Study areas were highlighted in stand ordinations to assess the assumption that these sites adequately depicted microsite structural variation within their respective ecosystems. Axes of variation in ordination studies frequently reflect regeneration characteristics of plant communities (Grubb 1977). Thus, in addition to correlation with physical or physiological parameters, association with disturbance or re-establishment features was also investigated.

Data analysis

Statistical significance was assumed at the five percent level of probability (*P* ≤ 0.05). Because the various soil elemental concentrations deviated highly and were expressed using different units, standard scores for these variables were calculated to aid in study site and subsurface depth comparisons. Standard scores (*C*) for a given soil constituent were calculated as the average deviation of each site–depth combination from the overall mean:

\[ C = (\bar{X}_i - \bar{X}_e)/s_e \]

where \( \bar{X}_i \) represents the mean from each unique site–depth combination, \( \bar{X}_e \) is the mean for each constituent from all sites and depths, and \( s_e \) is the standard deviation associated with \( \bar{X}_e \).

Where normality, independence, and randomness were reasonable assumptions for sample data and sampling regimes, procedures to test the equality of treatment means were carried out using parametric statistical techniques. Generally, this involved analysis of variance (ANOVA) followed by multiple range analysis using the Student Newman–Keuls (SNK) test in cases where ANOVA results indicated significant differences of ≥ 2 means. A posteriori residual and normal probability plots were used to assess the adequacy of ANOVA model assumptions and, where used, departures from these assumptions were minor.

Where the above assumptions were not valid, non-parametric statistics (Conover 1980) were employed in hypothesis testing. For groundwater constituents, the Mann–Whitney test was used to compare distribution functions for the two river systems. The Kruskal–Wallis test was employed to examine the null hypothesis that study area soil parameters were identical. Stand positions relative to DCA axes were treated as ordinal data. Spearman rank correlation coefficients (ρ) were used to clarify possible associations between study site positions along ordination axes and gradients of physical or physiological factors at these sites.

Sequential sampling of the same experimental material violates the independence assumption associated with the univariate ANOVA test. This was unavoidable for analyses of soil moisture and plant water relations where a considerable investment of effort was required to establish study sites, install soil probes, etc. For comparisons of ecophysiological responses collected on a sequential basis, repeated measures analysis of variance (ANOVAR) or “profile analysis,” has been advocated (Moser et al. 1990, Potvin et al. 1990). Using the SPSS-X profile analysis procedure (SPSS 1988), ANOVAR was employed in site comparisons of \( O_n \), g, E, and predawn and midday \( \psi \). Monthly and hourly data collections were treated as the repeated factors. Mauchly’s criterion was used to evaluate the assumption of compound symmetry of the variance–covariance matrix of these data sets.

Results

Hydrogeology

Colorado River discharge was approximately three orders of magnitude greater than that of the Bill Williams River (Fig. 2). Over the course of the study, highly regulated Colorado River flows were nearly identical to the long-term average (1949–1988) in terms of monthly discharge and its fluctuations. Daily and annual variation in discharge was high in the Colorado River. As a result of upstream dam releases, the range in daily flows was as much as 63% of the monthly median. The range in monthly discharge was 144% of the annual average flow for 1989. Throughout the study, Bill Williams River discharge was much more stable on an absolute basis than that of the Colorado River. The range of daily variability was <32% of the
monthly median, with monthly variation for 1989 only 19% of the annual average discharge. Monthly flow variation appeared to be attributable to localized precipitation and runoff events on the Bill Williams River.

Declining water tables during the 1990 growing season (Fig. 3) coincided with surface flow attenuation in the Bill Williams River (Fig. 2), but were also coincident with the midsummer peak in potential evapotranspiration. Variation among groundwater observation points was less for Bill Williams River floodplain sites than it was for the Colorado River study areas. Mean monthly water table depth ranged from 3 to 4.5 m for the Colorado River study sites and from 1.5 to 3 m for Bill Williams River sites. The annual progression in water table depth for the Colorado River floodplain appeared to follow the Colorado River hydrograph closely. Volumetric soil moisture ($\Theta_s$) varied significantly ($F = 7.98; P < 0.02; 2.7 \text{ df}$) among the four study areas (Fig. 4). Bill Williams River upstream sites had the greatest ($\bar{X} \pm \text{ se} = 12.2 \pm 2.2\%$) annual mean soil moisture integrated over the upper 90 cm of the floodplain alluvium ($\Theta_i$). As expected for locations where the principal source of soil moisture replenishment is the alluvial aquifer, $\Theta_s$ increased with subsurface depth at Bill Williams River upstream sites. The lack of change in $\Theta_s$ with depth at Bill Williams River downstream sites suggests that groundwater and moisture in surface soils were not closely connected. Soil moisture in the upper 90 cm ($\Theta_i$) averaged 7.4 ± 1.6% for these sites. Likewise, the Colorado River areas exhibited no clear trend in $\Theta_s$ with subsurface depth. Both areas were characterized by substantially lower mean $\Theta_i$ (5.0 ± 0.5% and 4.6 ± 0.4% for control and experimental areas, respectively) relative to Bill Williams River floodplain areas.

**Alluvium, water, and tissue analyses**

There were few differences among study areas with regard to the texture of floodplain soils (D. E. Busch, *unpublished hydrometer data*). Results of soil elemental analyses indicate a tendency for cation and anion concentrations to be statistically indistinguishable be-

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**Fig. 2.** Hydrographs for the Colorado and Bill Williams Rivers in 1989 and 1990, derived from the U.S. Geological Survey Arizona stream gauge database. Boxes depict second and third quartiles (i.e., the bounds of the middle 50%) of daily discharge for each month, with medians indicated by the lines inside each box. Line extensions indicate range of daily discharges for each month that are ±1.5 interquartile ranges from the second and third quartiles. Outlying points are plotted individually with flows >3 interquartile ranges below the second, or above the third, quartiles indicated with a “+” mark. Note contrasting ordinate scales for the two rivers.

**Fig. 3.** Alluvial water table depth in study region floodplains during 1990. Means are presented for the Colorado (filled squares; $n = 3$ wells) and Bill Williams (open circles; $n = 4$ wells) Rivers. Spatial variability among groundwater wells is represented by vertical bars extending ± 1 sd from the means.
TABLE 1. Analysis of soil extracts for Colorado River and Bill Williams River study sites. Data represent means ± 1 SE, n = 24. Entries not sharing common letter superscripts denote between-site statistical difference at P ≤ 0.05 in Kruskal-Wallis and multiple range tests.

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<th>Factor</th>
<th>Bill Williams River</th>
<th>Colorado River</th>
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<td></td>
<td>Upstream</td>
<td>Downstream</td>
</tr>
<tr>
<td>pH</td>
<td>7.4 ± 0.7a</td>
<td>8.0 ± 0.1b</td>
</tr>
<tr>
<td>Sat.%* (%)</td>
<td>30.5 ± 0.1a</td>
<td>34.3 ± 0.9b</td>
</tr>
<tr>
<td>EC+ (dS/m)</td>
<td>1.6 ± 1.6a</td>
<td>5.1 ± 1.7b</td>
</tr>
<tr>
<td>B (mg/L)</td>
<td>0.3 ± 0.2a</td>
<td>1.2 ± 0.2b</td>
</tr>
<tr>
<td>Na (mg/L)</td>
<td>131.1 ± 388.7a</td>
<td>825.7 ± 420.9a</td>
</tr>
<tr>
<td>K (mg/L)</td>
<td>11.7 ± 17.9a</td>
<td>42.9 ± 19.1a</td>
</tr>
<tr>
<td>Ca (mg/L)</td>
<td>175.2 ± 45.8a</td>
<td>252.0 ± 49.4a</td>
</tr>
<tr>
<td>Mg (mg/L)</td>
<td>36.4 ± 37.9a</td>
<td>85.2 ± 40.9a</td>
</tr>
<tr>
<td>F (mg/L)</td>
<td>1.8 ± 0.2a</td>
<td>3.5 ± 0.2b</td>
</tr>
<tr>
<td>CO₂ (mg/L)</td>
<td>0.0 ± 0.0a</td>
<td>5.7 ± 0.7b</td>
</tr>
<tr>
<td>HCO₃⁻ (mg/L)</td>
<td>152.5 ± 19.9a</td>
<td>201.3 ± 21.5a</td>
</tr>
<tr>
<td>Cl (mg/L)</td>
<td>156.2 ± 394.1a</td>
<td>990.5 ± 422.5a</td>
</tr>
<tr>
<td>SO₄²⁻ (mg/L)</td>
<td>518.4 ± 537.6a</td>
<td>1200.0 ± 580.8a</td>
</tr>
<tr>
<td>NO₃⁻ (mg/L)</td>
<td>6.8 ± 5.2a</td>
<td>16.8 ± 5.6a</td>
</tr>
<tr>
<td>NH₄⁺ (mg/L)</td>
<td>0.6 ± 0.6a</td>
<td>4.0 ± 0.7b</td>
</tr>
<tr>
<td>PO₄³⁻ (mg/L)</td>
<td>0.0 ± 0.1a</td>
<td>0.6 ± 0.1b</td>
</tr>
<tr>
<td></td>
<td>Control</td>
<td>Experimental</td>
</tr>
<tr>
<td>pH</td>
<td>7.8 ± 0.1c</td>
<td>7.8 ± 0.1c</td>
</tr>
<tr>
<td>Sat.% (%)</td>
<td>34.2 ± 0.7b</td>
<td>33.7 ± 0.9b</td>
</tr>
<tr>
<td>EC+ (dS/m)</td>
<td>11.7 ± 1.2b</td>
<td>12.8 ± 1.6b</td>
</tr>
<tr>
<td>Na (mg/L)</td>
<td>2440.3 ± 308.2b</td>
<td>2601.3 ± 411.7b</td>
</tr>
<tr>
<td>Cl (mg/L)</td>
<td>105.3 ± 14.0b</td>
<td>92.0 ± 19.0c</td>
</tr>
<tr>
<td>SO₄²⁻ (mg/L)</td>
<td>278.8 ± 36.2a</td>
<td>398.0 ± 48.6c</td>
</tr>
<tr>
<td>NO₃⁻ (mg/L)</td>
<td>217.2 ± 30.0a</td>
<td>310.8 ± 40.1b</td>
</tr>
<tr>
<td>NH₄⁺ (mg/L)</td>
<td>2.4 ± 0.2a</td>
<td>2.4 ± 0.2a</td>
</tr>
<tr>
<td>PO₄³⁻ (mg/L)</td>
<td>0.1 ± 0.1a</td>
<td>0.1 ± 0.1a</td>
</tr>
<tr>
<td></td>
<td>207.4 ± 15.8a</td>
<td>225.7 ± 21.1a</td>
</tr>
<tr>
<td>pH</td>
<td>2154.9 ± 312.4b</td>
<td>2548.9 ± 418.9b</td>
</tr>
<tr>
<td>Sat.% (%)</td>
<td>3595.2 ± 422.4b</td>
<td>4022.4 ± 566.4b</td>
</tr>
<tr>
<td>EC+ (dS/m)</td>
<td>4.5 ± 4.1a</td>
<td>6.8 ± 5.5a</td>
</tr>
<tr>
<td>Na (mg/L)</td>
<td>5.2 ± 0.5a</td>
<td>3.7 ± 0.7a</td>
</tr>
<tr>
<td>Cl (mg/L)</td>
<td>0.2 ± 0.1a</td>
<td>0.1 ± 0.1a</td>
</tr>
</tbody>
</table>

* Saturation percentage.
† Electrical conductivity.
Fig. 5. Standard scores for soil extract analysis variables. Each parameter value was subtracted from the grand mean for that parameter, at all sites and depths. The resultant difference was divided by the standard deviation associated with the grand mean to calculate a standard score in standard deviation units.

Variations, resulted in higher mean SAR values in Bill Williams groundwater relative to that of the Colorado River. There were higher mean HCO₃ levels in Bill Williams River study area samples than in Colorado River groundwater, but no significant difference in groundwater pH between the two river systems.

Table 2. Groundwater analysis results for samples from wells near the Bill Williams (n = 16) and Colorado (n = 11) Rivers. Data represent mean ± 1 se for each factor.

<table>
<thead>
<tr>
<th>Factor</th>
<th>Bill Williams River</th>
<th>Colorado River</th>
</tr>
</thead>
<tbody>
<tr>
<td>pH</td>
<td>7.70 ± 0.02</td>
<td>7.73 ± 0.02</td>
</tr>
<tr>
<td>Na (mg/L)*</td>
<td>113.39 ± 0.46</td>
<td>98.90 ± 1.61</td>
</tr>
<tr>
<td>K (mg/L)^*</td>
<td>7.80 ± 0.13</td>
<td>5.07 ± 0.20</td>
</tr>
<tr>
<td>Ca (mg/L)**</td>
<td>66.56 ± 3.01</td>
<td>91.40 ± 2.68</td>
</tr>
<tr>
<td>Mg (mg/L)**</td>
<td>20.40 ± 0.64</td>
<td>27.24 ± 0.72</td>
</tr>
<tr>
<td>SO₄ (mg/L)**</td>
<td>252.00 ± 2.40</td>
<td>252.00 ± 2.40</td>
</tr>
<tr>
<td>HCO₃ (mg/L)**</td>
<td>310.49 ± 12.71</td>
<td>218.99 ± 9.29</td>
</tr>
<tr>
<td>Cl (mg/L)**</td>
<td>106.20 ± 1.07</td>
<td>81.07 ± 1.42</td>
</tr>
<tr>
<td>SAR***</td>
<td>3.15 ± 0.03</td>
<td>2.32 ± 0.03</td>
</tr>
<tr>
<td>EC (dS/m)*</td>
<td>1.00 ± 0.01</td>
<td>1.08 ± 0.01</td>
</tr>
<tr>
<td>TDS (mg/L)**</td>
<td>606.6 ± 2.4</td>
<td>731.6 ± 6.6</td>
</tr>
</tbody>
</table>

Asterisks indicate significant differences between means using the Mann–Whitney test at P ≤ 0.05 (*) or P ≤ 0.001 (**).

Foliar analyses revealed that Tamarix tended to concentrate cations in leaf tissue (Table 3). Calcium, Mg, Na, and Fe were all found at significantly higher levels in Tamarix than in leaf samples from the other three taxa. Salix and Populus had higher mean leaf tissue concentrations of P, K, and Zn relative to Tamarix and Tessaria. Strikingly high Mn concentrations in Salix and the relatively high leaf tissue Ca in Populus were exceptions to the tendency of Salix and Populus to have similar concentrations of the same elements. Like Tamarix, Tessaria had high levels of Na and Fe. There were also elevated levels of Cu and B in Tessaria leaf tissue. Concentrations of B were greater in Salix and Populus than in Tamarix. There were no significant interspecific differences in leaf N.

Growth and morphology

Annual stem elongation, leaf area, and specific leaf area (SLA) were all significantly greater for Salix from Bill Williams River upstream sites than they were at control sites on the Colorado River (Table 4). The number of leaves produced annually showed little variation among any of the study sites in Salix. Morphological measurements indicated distinct differences between
upstream and downstream site *Populus*, but not *Salix*, along the Bill Williams River. *Salix* SLA was greater at the downstream Bill Williams River sites compared to the upstream sites. Stem elongation was 62% greater and leaf area was 88% greater in Colorado River experimental *Salix* than at control sites. Although there was no significant difference in *Salix* SLA between experimental and control sites on the Colorado River, annual growth increments had 60% greater leaf area on the experimental plots.

### Plant water relations

*Salix* stomatal conductance (g) was similar among areas, although Bill Williams River downstream sites tended to have slightly lower midday $g$ than at Bill Williams River upstream or Colorado River control sites (Fig. 6). *Tamarix* from Colorado River control sites exhibited markedly higher transpiration ($E$) than on either of the sites on the Bill Williams River. Overall, *Salix* showed a graded response ($F = 4.70; P < 0.05; df = 2.7$) with $g$ lowest at Bill Williams River downstream sites, and the Bill Williams River upstream, Colorado River control, and Colorado River experimental sites successively higher. *Salix* $E$ at the Colorado River study areas was greater than at Bill Williams River areas. Differences in $E$ were less distinct between sites within the river systems. *Populus* from the Bill Williams River exhibited $g$ and $E$ responses similar to those for *Salix* from the Bill Williams River.

Predawn and midday water potential ($\psi$) in *Tamarix* (Fig. 7) differed significantly between areas ($F = 36.9; P < 0.001; df = 2.7$). Both predawn and midday $\psi$ were higher for *Tamarix* at the Bill Williams River upstream sites than for either the Bill Williams River downstream or the Colorado River control sites. Midsummer declines in $\psi$ were greatest for the Bill Williams River downstream areas. Significant ($F = 20.0; P < 0.01; df = 2.7$) differences were exhibited in midday $\psi$ for *Salix*, where late growing season differences

### Table 3. Leaf element concentrations (mean ± 1 se, $n = 18$) for woody taxa sampled at Bill Williams River and Colorado River study areas. Concentrations are presented on a leaf tissue dry weight basis. Entries not sharing letter superscripts along rows indicate significant interspecific differences indicated by ANOVA and Student Newman–Keuls multiple range analysis ($P \leq 0.05$).

<table>
<thead>
<tr>
<th>Element</th>
<th>Tamarix</th>
<th>Salix</th>
<th>Populus</th>
<th>Tessaria</th>
</tr>
</thead>
<tbody>
<tr>
<td>N (mg/g)</td>
<td>20.4 ± 1.0$^a$</td>
<td>21.3 ± 1.0$^a$</td>
<td>20.3 ± 1.2$^c$</td>
<td>16.6 ± 2.2$^c$</td>
</tr>
<tr>
<td>P (mg/g)</td>
<td>1.2 ± 0.1$^a$</td>
<td>1.7 ± 0.1$^a$</td>
<td>1.9 ± 0.1$^d$</td>
<td>1.6 ± 0.2$^b$</td>
</tr>
<tr>
<td>K (mg/g)</td>
<td>9.7 ± 0.6$^a$</td>
<td>15.0 ± 0.6$^b$</td>
<td>18.5 ± 0.8$^c$</td>
<td>7.2 ± 1.4$^d$</td>
</tr>
<tr>
<td>Ca (mg/g)</td>
<td>25.9 ± 1.1$^a$</td>
<td>9.9 ± 1.0$^d$</td>
<td>23.0 ± 1.2$^c$</td>
<td>10.9 ± 2.4$^c$</td>
</tr>
<tr>
<td>Mg (mg/g)</td>
<td>11.2 ± 0.3$^a$</td>
<td>3.7 ± 0.3$^b$</td>
<td>5.6 ± 0.3$^e$</td>
<td>6.1 ± 0.6$^d$</td>
</tr>
<tr>
<td>Na (mg/g)</td>
<td>18.1 ± 0.7$^a$</td>
<td>0.7 ± 0.7$^b$</td>
<td>1.1 ± 0.8$^c$</td>
<td>11.2 ± 1.5$^e$</td>
</tr>
<tr>
<td>Zn (mg/g)</td>
<td>40.0 ± 13.5$^c$</td>
<td>160.5 ± 13.1$^d$</td>
<td>248.8 ± 15.8$^c$</td>
<td>70.1 ± 30.6$^d$</td>
</tr>
<tr>
<td>Fe (mg/g)</td>
<td>183.5 ± 11.5$^d$</td>
<td>117.7 ± 11.3$^c$</td>
<td>63.4 ± 13.5$^c$</td>
<td>280.4 ± 26.3$^e$</td>
</tr>
<tr>
<td>Mn (mg/g)</td>
<td>55.5 ± 58.8$^b$</td>
<td>1059.0 ± 57.4$^a$</td>
<td>8.2 ± 68.8$^c$</td>
<td>153.7 ± 133.8$^b$</td>
</tr>
<tr>
<td>Cu (mg/g)</td>
<td>4.7 ± 0.6$^a$</td>
<td>6.2 ± 0.6$^c$</td>
<td>6.8 ± 0.7$^e$</td>
<td>19.5 ± 1.4$^d$</td>
</tr>
<tr>
<td>B (mg/g)</td>
<td>45.7 ± 8.5$^a$</td>
<td>75.6 ± 8.3$^a$</td>
<td>93.4 ± 9.9$^b$</td>
<td>114.7 ± 19.3$^a$</td>
</tr>
</tbody>
</table>

### Table 4. Morphological measurements for *Populus fremontii* and *Salix gooddingii* from study sites on the Colorado and Bill Williams Rivers. Data are the stem elongation of the 1990 growth increment and the leaf number, leaf area, and specific leaf area of the branch segment making up this increment. Values presented are means ± 1 se ($n = 30$) for each measurement factor, with unshared letter superscripts indicating significant ($P \leq 0.05$) between-site differences within rows using ANOVA and Student Newman–Keuls tests.

<table>
<thead>
<tr>
<th>Study site</th>
<th>Bill Williams River</th>
<th>Colorado River</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Stem elongation (cm)</td>
<td>Control</td>
</tr>
<tr>
<td><em>Salix</em></td>
<td>24.4 ± 1.9$^a$</td>
<td>12.4 ± 1.5$^b$</td>
</tr>
<tr>
<td><em>Populus</em></td>
<td>173.0 ± 15.6$^a$</td>
<td>70.1 ± 15.3$^b$</td>
</tr>
<tr>
<td><em>Salix</em></td>
<td>19.0 ± 1.1$^a$</td>
<td>17.3 ± 1.1$^a$</td>
</tr>
<tr>
<td><em>Populus</em></td>
<td>12.8 ± 0.7$^a$</td>
<td>8.0 ± 0.7$^b$</td>
</tr>
<tr>
<td><em>Salix</em></td>
<td>122.3 ± 12.3$^c$</td>
<td>101.5 ± 12.4$^a$</td>
</tr>
<tr>
<td><em>Populus</em></td>
<td>189.8 ± 11.9$^a$</td>
<td>57.0 ± 11.9$^c$</td>
</tr>
<tr>
<td><em>Salix</em></td>
<td>126.6 ± 3.6$^a$</td>
<td>136.8 ± 3.7$^b$</td>
</tr>
<tr>
<td><em>Populus</em></td>
<td>137.5 ± 5.4$^a$</td>
<td>118.6 ± 5.4$^b$</td>
</tr>
</tbody>
</table>
as great as 0.5 MPa were observed between the Colorado River control sites and the upstream sites on the Bill Williams River. Water potentials in Bill Williams River *Populus* were greater for upstream sites relative to downstream sites \( (F = 18.63; P < 0.05; \text{df} = 1.4) \). This difference became more pronounced as the growing season progressed.

Despite the close taxonomic relationship of *Populus* and *Salix*, estimates of *Salix* tissue water relations parameters were often closer to those of *Tessaria* or *Tamarix* than to *Populus* (Table 5). Relative water content at zero turgor \((R^0)\) was similar in *Tamarix* and *Salix* and was significantly lower than that for *Populus*. *Tessaria* had the lowest \(R^0\) of any species. Osmotic potential at the turgor loss point \((\psi_l^0)\) was most negative in *Tamarix*, intermediate in *Tessaria* and *Salix*, and highest in *Populus*. Although there was a similar relationship for osmotic potential at full turgor \((\psi_F^0)\), *Salix* and *Populus* \(\psi_F^0\) values were significantly higher than those of *Tamarix* and *Tessaria*. There were no significant differences among *Tamarix*, *Salix*, and *Populus* in bulk modulus \((e^{100})\), but lower \(e^{100}\) in *Tessaria* relative to the other taxa provided an indication of greater tissue elasticity in this species.

*Tamarix* leaf tissue carbon isotope discrimination \((\Delta)\) was significantly \( (F = 6.98; P < 0.005; 3.47 \text{df}) \) lower than that of the other taxa examined (Fig. 8), providing an indication of higher water use efficiency (WUE) in this species. Two-way ANOVA indicated that photosynthetic photon flux (PPF) at the mid-canopy level did not differ significantly between Colorado and Bill Williams River sites. Interspecific differences in PPF between *Salix* and *Tamarix* were also insignificant. *Salix* PPF was significantly \( (t = 4.61; P < 0.01; n = 660) \) greater on experimentally cleared sites \((\bar{X} \pm 1 \text{SE} = 491.2 \pm 27.8 \mu\text{mol m}^{-2} \text{s}^{-1})\) than at control sites on the Colorado River \((306.8 \pm 25.8 \mu\text{mol m}^{-2} \text{s}^{-1})\). Leaf temperatures \((T_l)\) did not differ significantly between the two ecosystems, but there were significant \( (F = 4.85; P < 0.05; 1, 938 \text{df}) \) differences in \(T_l\) between *Salix* \((27.80 \pm 0.4 \degree\text{C})\) and *Tamarix* \((29.00 \pm 0.4 \degree\text{C})\). *Salix* \(T_l\) did not vary significantly between experimental and control sites on the Colorado River.
Vegetation community structure

Colorado River riparian vegetation structure was characterized by high relative cover and relative frequency of *Tessaria*, *Tamarix* and *Salix* (Fig. 9). *Prosopis pubescens*, *Baccharis glutinosa*, and *Populus* were represented in the riparian community, but at lower abundance values. *Populus* was represented largely by senescent individuals in the Colorado River ecosystem. The largest proportion of *Salix* was also senescent, but adult and juvenile segments were clearly identifiable for the Colorado River. Based on relative cover, *Tamarix* and *Salix* dominated the Bill Williams River riparian community. *Populus* and *Salix* both had greater importance in the Bill Williams River floodplain than that of the Colorado River. Juvenile and adult population segments were also much better represented for *Populus* on the Bill Williams River than on the Colorado River. While juvenile and adult population segments were also identified in the *Salix* age structure for the Bill Williams River, the proportion of senescent individuals in this population was greater than that of the Colorado River.

Detrended correspondence analysis (DCA) results for riparian vegetation from throughout the Bill Williams and Colorado River floodplains are presented in Figs. 10–12. The three axes derived from this ordination had eigenvalues of 0.41, 0.23, and 0.17, and accounted for ≈81% of the variation in the community.

**Table 5.** Results of pressure–volume analyses for riparian woody taxa. Data represent means ± 1 SE. Entries are followed by an indication of significant ($P \leq 0.05$) difference in average values (entries not sharing letter superscripts) as shown by ANOVA and Student Newman–Keuls multiple comparison tests.

<table>
<thead>
<tr>
<th>Species</th>
<th>Tamarix (n = 23)</th>
<th>Salix (n = 26)</th>
<th>Populus (n = 31)</th>
<th>Tessaria (n = 29)</th>
</tr>
</thead>
<tbody>
<tr>
<td>$R^0$</td>
<td>0.79 ± 0.01</td>
<td>0.78 ± 0.01</td>
<td>0.83 ± 0.01</td>
<td>0.87 ± 0.01</td>
</tr>
<tr>
<td>$\phi_0$ (MPa)</td>
<td>-2.93 ± 0.09</td>
<td>-2.54 ± 0.09</td>
<td>-2.29 ± 0.08</td>
<td>-2.59 ± 0.08</td>
</tr>
<tr>
<td>$\phi^{100}$ (MPa)</td>
<td>-2.40 ± 0.08</td>
<td>-1.94 ± 0.08</td>
<td>-1.77 ± 0.07</td>
<td>2.26 ± 0.07</td>
</tr>
<tr>
<td>$\epsilon^{100}$ (MPa)</td>
<td>15.80 ± 1.47</td>
<td>17.38 ± 1.38</td>
<td>17.31 ± 1.26</td>
<td>11.48 ± 1.30</td>
</tr>
</tbody>
</table>

* $R^0$ = relative water content at the turgor loss point; $\phi_0$ = osmotic potential at zero turgor; $\phi^{100}$ = osmotic potential at full turgor; and $\epsilon^{100}$ = bulk modulus of elasticity at full turgor.
analysis data set. There was a tendency for salt- or water stress-tolerant taxa to have lower values, and for hydrophytes and mesophytes to have higher values along DCA axis 1 (Fig. 10). Examples of taxa that fit this pattern include *Prosopis pubescens* and *Tessaria* (values <100), and *Typha latifolia*, and juvenile *Salix* and *Populus* (values >200). Evidence for a community maturity gradient was indicated along DCA axis 1 where senescent *Salix* and *Populus* tended to have lower weights than juvenile classes for these taxa. However, this trend is more clearly indicated by DCA axis 2 where higher loadings were characteristic of senescent *Populus* and *Salix* relative to juvenile age classes. Ruderal (*Suaeda torreyana* and *Tessaria*) and late successional (*Prosopis* spp.) taxa also occurred near opposite extremes of DCA axis 2.

Stands from the Bill Williams River were segregated from Colorado River vegetation plots relative to DCA axis 1 (Fig. 11). Exceptions to this included stands from areas of the Colorado River floodplain that have shallow water tables and clustered on the ordination with Bill Williams River stands. Evidence for community organization along moisture gradients is reinforced by the significant correlation of DCA axis 1 with depth to the water table, $\Theta$, and $\psi$ (Table 6). This axis may depict community organization along salinity and nu-
Fig. 10. Ordination of perennial plant taxa on Colorado River and Bill Williams River vegetation plots against the first two detrended correspondence analysis (DCA) axes. Demographic classes for Salix gooddingii and Populus fremontii are coded J for juvenile, A for adult, and S for senescent.

Fig. 11. Ordination of 97 Bill Williams River and Colorado River riparian stands against the first two DCA axes. Stands denoted as B were from the Bill Williams River and those with a C are from the Colorado River. Asterisks (*) indicate the Colorado River control and Bill Williams River upstream sites, while pluses (+) represent the Bill Williams River downstream sites.
trient gradients as well, based on correlations with electrical conductivity (EC), total dissolved solids (TDS), and NO₃. DCA axis 2 was correlated with soil NO₃, a finding consistent with our species ordination, indicating that this axis depicts community maturity. The addition of DCA axis 3 (Fig. 12) shows how disturbance is also important in riparian community organization. Stands that showed evidence of recent burning tended to have lower values along DCA axis 3 than stands not exhibiting signs of such disturbance. The negative correlations of soil PO₄ and PPF with this axis provide additional evidence that fire is an important form of disturbance in this ecosystem (Table 6).

**DISCUSSION**

**Hydrogeology**

There were clear hydrological differences between the two river systems, but within each system site differences were less well defined. The Colorado River possesses nearly all of the physical effects characteristic of impounded riparian ecosystems, including increased channel incision and confinement, and augmented daily flow variation (Williams and Wolman 1984). The Colorado River differs from the unregulated discharge pattern prior to river impoundment in that peak flows occur in midsummer rather than the spring, and because flows rarely overtop the riverbanks, thus eliminating flooding in this ecosystem. In contrast, the Bill Williams River exhibits a more natural flow pattern for the region (Stromberg et al. 1991) with peak runoff in the spring and flooding occurring over much of the floodplain in wet years.

The midsummer peak in groundwater elevation at Colorado River floodplain sites resembles the pattern for surface flows and demonstrates the linkage of the river and the alluvial aquifer. Diel variation in groundwater depth tracked diel discharge fluctuations, indicating that surface flows and water table depth were closely coupled. High groundwater levels during the summer months also are contrary to the pre-development pattern, in which increased evapotranspiration and reduced runoff would have tended to depress water tables at this time. Although Bill Williams River surface flow curtailment was reported in both study years,
it was more likely to affect downstream sites than upstream sites where flows diminished but were detectable throughout the study period. Mean water table depths at Bill Williams River study sites were always shallower (\(\leq 2.8\) m) than those for the Colorado River.

Low values for moisture content in the surface soils of Colorado River study sites were the result of depressed floodplain water tables, lack of moisture replenishment by flooding, low precipitation, and high potential evapotranspiration. Although the latter two factors also typify the Bill Williams River ecosystem, floodplain soils had higher moisture content than those of the Colorado River due to shallower water tables and periodic flooding. Lower soil moisture and deeper water tables at the downstream sites were similar to the Colorado River sites, in that surface soils were severed from groundwater moisture sources.

**Nutrients and salinity**

Where water table incursion into the unsaturated zone was infrequent, leaching of soil nutrients was also reduced. This contributed to elevated values for Na, K, Mg, Cl, SO\(_4\), and NH\(_4\) ions in the alluvium of Colorado River study sites, and also contributed to high electrical conductivities (EC) and saturation percentages (Sat.\%) in Colorado River soil extracts. Colorado River floodplain study areas can be characterized as high in salinity and marginally low in nutrient status relative to those on the Bill Williams River. Soil element concentrations in the upper 30 cm contributed most strongly to this pattern. This demonstrates that elements are not dispersed uniformly through the soil profile by aqueous transport due to the infrequency of precipitation and the rarity of flooding or groundwater incursion into the unsaturated zone in the Colorado River ecosystem. In contrast, periodic flooding and groundwater incursion into surface soils tend to decrease salinity in the Bill Williams River floodplain soils.

Total dissolved solids (TDS) and EC values in Colorado River groundwater were high and were positively correlated with soil concentrations, indicating that this is the more saline ecosystem. Soil EC at Colorado River sites exceeded salinities equivalent to those shown to reduce growth in *Populus* and *Salix* seedlings (Jackson et al. 1990), while *Tamarix* and *Tessaria* appear to be within their salinity tolerance limits at all sites. Soil EC also approached stressful levels for *Populus* and *Salix* at downstream Bill Williams River sites, while salinities at upstream sites were relatively low. Based on EC and TDS measurements, groundwater salinities were beneath salinity stress thresholds (Jackson et al. 1990) for all four taxa in both river systems.

Variation in leaf nutrient levels in natural vegetation is often less than in soil samples because rapid growth on fertile sites tends to dilute the tissue nutrient pool, whereas nutrient concentration in plant tissues may occur on infertile sites (Chapin 1980). In this study, differences in leaf element concentrations followed a halophyte–glycophyte dichotomy. Specifically, *Tamarix* and *Tessaria* leaf tissue Na:K ratios (1.87 and 1.56, respectively) deviated strongly from those of glycophytic *Populus* and *Salix* (Na:K < 0.1 in both). While glycophytes generally rely on ion exclusion at the root endodermis, *Tamarix* is thought to survive in saline soils by maintaining high uptake of ions in conjunction with salt extrusion, cellular compartmentation, and utilization for osmoregulation (Greenway and Munns 1980). *Tamarix* possesses glands that produce a salty exudate, but this plant also may use inorganic ions for turgor maintenance at low water potentials (Berry 1970). The ions detected in high concentrations in *Tamarix* leaf tissue were also found at high concentrations in both the soil and groundwater. There is thus evidence for a lack of selectivity in *Tamarix* ion uptake, concentration, and excretion, as has been shown in *Tamarix* solution culture experiments (Berry 1970, Kleinkopf and Wallace 1974). Furthermore, the observation that high root zone concentrations of Na lead to decreased K uptake in *Tamarix* (Kleinkopf and Wallace 1974) appears to be substantiated here for *Tamarix* as well as *Tessaria*. An alternate strategy is suggested for *Populus* and *Salix*. These glycophytes showed evidence of Na exclusion combined with concentration of K in leaf tissues.

**Tissue level water relations**

Water relations characteristics estimated in pressure-volume analyses provide evidence for adaptations favoring the competitive status of *Tamarix* and *Tessaria*, and for the persistence of *Salix* in perturbed ecosystems. Studies of temperate deciduous hardwoods indicate that acclimation to water deficits are made through adjustments in osmotic potential (\(\psi_h\)) rather than changes in cell wall elasticity (Tyree et al. 1978, Dawson 1990, Dreyer et al. 1990, Ranney et al. 1990). However, osmotic adjustment may result in potentially maladaptive solute concentrations through water loss or membrane damage (Morgan 1984). Trees capable of accumulating solutes have been shown to maintain turgor and high leaf conductance (\(g_l\)) as tissue water potential (\(\psi_h\)) declines, while others maintain turgor only through stomatal closure (Osonubi and Davies 1978).

Interspecific differences in bulk modulus (\(\epsilon\)) may be important in riparian plant responses to water or osmotic stress. Low \(\epsilon\) values (high elasticity) allow the maintenance of turgor as tissue water content varies and may be of physiological or ecological advantage where there are short-term fluctuations in soil moisture; high \(\epsilon\) ensures that changes in water content and cell solute concentration are relatively small as \(\psi_h\) changes (Zimmermann 1978). High \(\epsilon\) is thought to offer advantages in maintaining water uptake in xeric environments or microsites, but the utility of low \(\epsilon\) in maintaining turgor is more apparent than are claims that increases in \(\epsilon\) enhance water uptake (Monson and Smith 1982, Abrams 1988, Abrams et al. 1990, Schulte 1992).
Low bulk modulus at saturation ($e^{100}$), taken in conjunction with high relative water content at the turgor loss point ($R^0$), reflect leaf succulence in *Tessaria*. Tissue elasticity could thus contribute to turgor maintenance under desiccating conditions in this species.

The variability in *Tamarix* water potential ($\psi$) among field sites indicates that the choice of a representative location for tissue water relations determinations was difficult. This potential problem was minimized by collecting *Tamarix* at a variety of locations. Also, field $\psi$ was consistently lower in *Tamarix* than in the other taxa, indicating that the differences observed in pressure–volume analyses were valid. *Tamarix* osmotic potentials at saturation ($\psi_{w}^{\infty}$) were lower than those in *Populus* and *Salix* and at the point of turgor loss, osmotic potentials ($\psi_{t}$) in *Tamarix* were lower than all three other species. This would prove advantageous to *Tamarix* where water uptake and transport depend on low plant $\psi$ due to elevated soil salinity or water table depression. High tissue tolute levels in this species are presumably involved with the adaptations of this species to generate low $\psi_c$.

Measurements of $\psi_{w}^{\infty}$ and $\psi_{t}$ in *Populus* and *Salix* were within ranges of values reported from *Populus* and *Salix* species growing in mesic climates (Tyree et al. 1978, Tschaplinski and Blake 1989, Dawson 1990, Gebre and Kuhns 1991). However, interspecific differences in tissue water relations between *Salix* and *Populus* demonstrate the potential for ecological heterogeneity between these taxonomically related, sympatric taxa. Lower osmotic potentials ($\psi_{t}$) in *Salix* may favor its persistence over *Populus* under conditions of high salinity or moisture stress in southwestern riparian ecosystems. As in *Tamarix* and *Tessaria*, the ability of *Salix* to maintain turgor at lower values of $\psi$ would allow it to operate under conditions of reduced moisture availability.

**Whole plant water relations**

Predawn and midday $\psi$ levels were significantly lower in *Tamarix* from the Colorado River than in plants at Bill Williams River upstream sites. Comparably low $\psi$ was previously reported for Colorado River *Tamarix* (Gay and Sammis 1977), but $\psi$ appears to be maintained at a higher level in *Tamarix* from more mesic environments (Wilkinson 1972, Anderson 1982). Bill Williams River downstream *Tamarix* showed a seasonal decline in $\psi$ from levels approximately equivalent to those of the upstream sites to levels approximating those at the Colorado River control sites. However, low $\psi$ levels in *Tamarix* were not accompanied by pronounced reductions in stomatal conductance or transpiration, indicating that they were not stressful for this species. *Tamarix* thus shows similarities to plants that maintain turgor and stomatal function through osmotic adjustment or tissue elasticity under conditions of reduced moisture availability (Osonubi and Davies 1978, Abrams 1988).

*Tamarix, Populus,* and *Salix* all demonstrated midmorning peaks in stomatal conductance ($g$), with afternoon declines varying among species. Transpiration ($E$) increased throughout the day in these taxa, tending to reach maximal values in the early afternoon in conjunction with maximum leaf-to-air vapor pressure deficit (VPD). Gay and Sammis (1977) and Anderson (1982) demonstrated similar diurnal responses in *Tamarix* $g$, but these responses were associated with more immediate declines in $E$. Transpiration in *Tamarix* is thought to follow the evaporative demand of the ambient air (Hagemeyer and Waisel 1989). Higher VPDs are likely for the Colorado River floodplain due to reduced soil moisture and tree canopy cover. Such differences would explain higher *Tamarix* $E$ on the Colorado despite the similarity in $g$ between river systems. Neither radiation flux (PPF) nor leaf temperature ($T_l$) varied significantly between ecosystems so that higher VPD along the Colorado River is likely to cause these differences.

*Tamarix* has been described as possessing inherently low water use efficiency (Anderson 1982), a characterization that has also been applied to aridland phreatophytes in general (Smith and Nobel 1986). It is thus of note that water use efficiency (WUE) in *Tamarix* is the highest of the woody riparian taxa investigated, based on our interspecific comparison of carbon isotope discrimination ($\Delta$). Carbon isotopic ratios can vary temporally and spatially as a function of topography or position within the tree canopy (Garten and Taylor 1992). By obtaining leaf samples from trees and shrubs that were sympatric and often possessed overlapping canopies, and by consistently sampling at approximately the same time and canopy height, microenvironmental contributions to $\Delta$ were minimized. Unambiguous ranking of species WUE using foliar $\Delta$-value differences of <1.0%o requires that $T_l$ not differ by >2.5 °C between species (Ehleringer et al. 1992). Although there was little overall $T_l$ difference between ecosystems, *Tamarix* $T_l$ was ≈1.2 ° greater than that in *Salix*. The 1.0–1.6% differences in $\Delta$ between *Tamarix* and the other taxa evaluated thus provide a measure of reliability to indications that WUE is significantly greater in *Tamarix*.

Fractionation of carbon isotopes in halophytes under elevated salinities may occur through diffusional processes or carboxylation in the leaf (Farquhar et al. 1982). Concurrent measurements of photosynthesis and $E$ have shown that increasing environmental salinity causes higher WUE due to reduced $E$ (McCree and Richardson 1987, Plaut et al. 1990). Halophytes that are well supplied with moisture may salinize soils, thereby reducing water uptake and transpiration (Passioura et al. 1992). In addition to their role in osmotic regulation, *Tamarix* salt glands may also provide a mechanism for carbon concentration via a process of carbonate secretion and CO$_2$ release (Waisel 1991a).

High WUE in *Tamarix* thus appears to have a functional
basis that is related to its halophytic life history. An hypothesized dichotomy between halophytes without solute-excreting mechanisms that could reduce salt uptake by decreasing \( E \) and increasing WUE and those with salt glands, which would tend to have lower WUE (Guy et al. 1989), does not appear to be supported. This is because *Tamarix* WUE was greater (based on significantly lower \( \Delta \)) than that in *Tessaria*, which is not known to excrete salts.

Senescing leaves from hardwood trees have been shown to maintain turgor by decreasing stomatal conductance (Gee and Federer 1972). A similar mechanism could occur in riparian plants that are senescent due to moisture or salinity stress. Regulation of leaf conductance has been documented in *Populus* clones as a moisture stress avoidance mechanism (Pallardy and Kozlowski 1981, Tschapinski and Blake 1989) and in *Salix* species adapted to xeric extremes of soil moisture gradients (Dawson 1990). Diurnal patterns of \( g \) in *Salix* from both ecosystems, and in *Populus* from Bill Williams River sites, support the concept of stomatal regulation as a mechanism for maintaining \( \psi \) in riparian trees. In both taxa, lower \( g \) was characteristic of drier downstream sites relative to upstream sites on the Bill Williams River.

*Populus* and *Salix* exhibited \( \Delta \) values that suggest that WUE is low in these riparian taxa relative to the desert perennials found in surrounding upland habitats (Ehleringer 1989). Carbon isotope discrimination in *Salix gooddingii* in this study approximated that reported for *S. exigua* from a semi-arid habitat (Donovan and Ehleringer 1991). Individuals that conserve water may be at a competitive disadvantage to those that do not possess high WUE (Davies and Zhang 1991). This may apply well in pristine riparian forest ecosystems where taxa with low WUE but high growth rates may be superior competitors for limiting space or light. Where water has become less available due to hydrologic perturbations, elevated plant WUE may become important. Consequently, species with higher WUE (*Tamarix*) are likely to have advantages when moisture supply is less abundant or varies substantially.

**Morphological responses**

Variation in shoot morphology is closely related to successional status or growth conditions in deciduous trees (Marks 1975). Such variation is likely to be integrated with other moisture and salinity responses to determine plant productivity, competitive status, and riparian community structure. There were distinct differences in morphology between *Populus* individuals growing on upstream and downstream sites in the Bill Williams River floodplain. This was not the case in *Salix*, although *Salix* morphology did differ significantly between the two river systems. For the 1990 growth increment, leaf number per shoot was consistent among sites in *Salix*, as is typical for plants exhibiting determinate extension growth (Marks 1975). For this species, adjustments to water deficits appeared to occur through reductions in the area of new leaves produced or via reduced stem elongation.

Stem elongation, leaf number, and leaf area were all greater at upstream relative to downstream sites in *Populus* on the Bill Williams River. *Populus* spp. have been described as indeterminate in their extension growth, with early senescence contributing to decreased leaf production (Marks 1975, Waisel 1991). The reduction in leaf number at downstream Bill Williams River sites is considered a typical desiccation response. Premature leaf abscission may also have contributed to reduced leaf number at these sites. Thus, adjustments in leaf area appear to be among the mechanisms mediating responses to water or salinity stress in *Populus*.

Trends in specific leaf area (SLA) can be viewed in terms of the adaptive value that xeromorphy brings to trees exposed to water or salinity stress. Leaves with lower SLA tend to be smaller in surface area, thicker in cross section, have lower maximum leaf conductances, and fewer but larger stomata; they are, thus, better suited for xeric habitats (Hinckley et al. 1989, Abrams et al. 1990). Lower SLA in *Populus* from the Bill Williams River downstream site indicates a trend toward xeromorphy due to drying soils or increased salinity. Stomatal conductance was also lower during peak diurnal time periods for downstream site *Populus*. A similar morphological relationship exists in comparisons of *Salix* between the Colorado and Bill Williams Rivers, but \( g \) was higher in Colorado River trees with reduced SLA. The tendency of *Salix* at the Bill Williams River downstream site to have greater SLA but lower \( g \) in comparison to upstream site individuals indicates that this species may rely more on stomatal regulation than morphological adaptations in short-term stress responses. Tissue level adaptations in *Salix* allowing osmotic adjustment during periods of desiccation could also delay the onset of morphological responses as witnessed in Bill Williams River *Populus*. Such adaptations may also allow *Salix* persistence with reduced leaf area and annual growth on the Colorado River, where such stress is chronic. An absence of osmotic regulatory capabilities may contribute to morphological declines that would lead to reduced productivity in *Populus* at the Bill Williams River downstream area, and to its near-extirpation from the Colorado River.

**Competitive relationships**

There was little evidence for altered soil moisture availability following *Tamarix* removal on the Colorado River. Experimental and control sites were interspersed too closely to permit measurement of change in water table depth or river discharge, and no differences in moisture content of surface soils were observed. Clearing of woody vegetation over spatial scales that were both more intensive locally, and more extensive regionally, indicate that aquifer and stream
baseflow responses are difficult to detect and may develop at nearly imperceptible rates (Weeks et al. 1987, Allison et al. 1990). Thus, measurable aquifer or stream recharge was not expected from the relatively small-scale clearing described here. The lack of a soil moisture response indicates either that increased water uptake in the remaining Salix prevented groundwater enhancement of surface soil moisture, or that bare surface evaporation rates depleted soil moisture at a rate comparable to evapotranspiration occurring prior to vegetation removal. Because desiccated surface soils, depressed water tables, and phreatophytic water uptake made substantial increases in surface evaporation unlikely, augmentation of Salix moisture supply is suggested.

Plant competitive abilities have been linked to rates of water extraction (Caldwell 1988, Eissenstat and Caldwell 1988). Based on values of $\Delta$, Tamarix WUE surpasses that of Salix, indicating that Salix may possess an advantage in water acquisition where free water is readily available. Removal of neighboring vegetation increased $\psi$ in desert shrubs (Fonteyn and Mahall 1978), but where water availability and leaf areas are high, $\psi$ may decline due to higher transpiration rates (Pothier and Margolis 1990). There is also evidence that $\psi$ may remain stable in plants with access to groundwater sources following the removal of neighbors (Manning and Barbour 1988). Because uptake is largely phreatophytic in Salix and Tamarix (Busch et al. 1992), we hypothesized that water status changes would not occur in Salix following the removal of neighboring Tamarix. However, the results showed distinguishable increases in midday $\psi$ (up to 0.5 MPa) in Salix on cleared sites. Increased $\psi$ coincided with higher leaf conductance, indicating that reduced water stress was associated with enhanced gas exchange in experimental Salix.

The removal of the shading effects of neighboring Tamarix led to the exposure of experimental site Salix to ~60% greater PPF at the mid-canopy level. Stomatal responses to increased radiation flux may thus be implicated in the higher $g$ characteristic of Salix following the removal of Tamarix. This suggests that competition for light may also be a factor acting to structure southwestern riparian communities, particularly where Salix and Tamarix thicketts overlap. Experimental clearing of Tamarix from around established Salix thicketts on the Colorado River resulted in a positive growth response in Salix shoots. Although tree architecture appears to have evolved in response to competition for light, water may act as a “cost” limiting tree height (King 1990). The shorter, thicket morphology typical of Colorado River Salix differs from the taller, arborescent form on the Bill Williams River. Such morphological variation is a probable result of decreased water availability, and may intensify competition with Tamarix for light in dense riparian stands.

Community structure

Low community abundance of Populus shows that this formerly dominant tree is in danger of local extirpation in the Colorado River floodplain. Canonical discriminant analysis of southwestern riparian community types indicated a trend toward Salix dominance on low-elevation sites, and codominance of this species with Populus at middle elevations (Szaro 1989). However, we have shown that hydrologic and salinity factors also contribute to Populus and Salix growth. The tendency for hydrological perturbations to become more prevalent in riparian ecosystems at the lower end of southwestern elevational gradients makes it probable that elevation is confounded with other physical or physiological factors driving such patterns.

Analysis of the age structures of Salix and Populus populations revealed large senescent segments on both the Colorado and Bill Williams Rivers. Despite this, an abundance of juvenile and adult Salix along both rivers demonstrates that ramet sprouting and establishment occur frequently. The same holds true for Populus on the Bill Williams River. The presence of juvenile cohorts in these populations cannot be taken as evidence for establishment of new individuals, because genets were not differentiated in our community analyses. As proposed by Neilson (1986), clonal growth appears to uncouple riparian plants from environmental stress that affects sensitive stages of their life cycles and presents limitations to dispersal and colonization.

Novel, monospecific community types may be formed as a consequence of human perturbation reflecting natural processes in environmental mosaics (Whittaker and Levin 1977). Our results indicate that Tessaria and Tamarix are functionally suited to exploit the environmental conditions present in riparian areas subject to perturbation. The community importance of these shrub species appears to have increased as native trees (Populus and Salix) have declined. Tamarix and Tessaria now dominate the Colorado River floodplain, with Tamarix extending its importance to the Bill Williams River riparian community. Because the Bill Williams River and Colorado River riparian zones were contiguous, it is doubtful that the recent (~40-yr) isolation imposed by river impoundment explains the differences in community structure between the two river systems. Thus, the environments available for colonization by shrubby taxa are presumably less extensive on the Bill Williams River than on the Colorado River.

Ordination analyses often reveal combinations of attributes which suggest causes for vegetation patterns not initially obvious from the geographic distribution of stands (James and McCulloch 1990). While our analysis revealed distinct patterns of salinity response in riparian species, it was more difficult to differentiate the Bill Williams River from the Colorado River floodplains in terms of salinity. Rank correlation analysis revealed that the first DCA axis was negatively asso-
citary with gradients in plant moisture stress and salinity, and positively associated with moisture availability and soil NO₃. This makes it evident that riparian species in the vicinity of the lower Colorado River do aggregate into communities along lines of moisture availability and salinity.

In addition to measurable features of the physical environment, ordination axes can also clarify population regeneration characteristics (Grubb 1977). The second DCA axis was significantly correlated with soil NO₃ levels. This is consistent with reported accumulation of organic matter as riparian stands age (Johnson et al. 1976). It also supports our interpretation of riparian community organization along the lines of maturity, as suggested by species (and Salix and Populus age class) loadings on DCA axis 2. The third DCA axis, which was negatively correlated with PPF and PO₄, also appeared to be associated with the occurrence of fire. Ecophysiological studies with mesophytic and riparian forest communities have demonstrated that increased PPF and increased soil nutrient concentrations are characteristic of post-fire environments (Reich et al. 1990, Busch and Smith 1993). Given evidence for increased abundance of halophytic shrubs following riparian zone fires (Busch 1995), episodic burning appears to be an important factor influencing community structure in the riparian ecosystems evaluated.

Successful invaders are often characterized by broad niches with respect to resource use (Bazzaz 1986). Similarly, a “general-purpose genotype” has been proposed for Tamarix (Brotherson and Von Winkel 1986). The osmotic and dehydration tolerances demonstrated here provide evidence for adaptations supporting Tamarix survival in desiccated or salinized riparian environments. Such tolerance does not preclude its survival or vigor in more mesic or less saline habitats, however. Accordingly, Tamarix was located near the center of the perennial species ordination, suggesting that this species may combine stress tolerance with adaptations promoting rapid growth in less stressful environments. Halophytic adaptations and apparent low WUE were characteristic of Tessaria and may help to explain its extreme position relative to the first ordination axis. Such adaptations are likely to facilitate the apparent expansion of these species in Colorado River riparian habitats where hydrological perturbation has been intense. Juvenile and adult Populus occupied positions in species ordination space indicative of a mesophytic niche. Relative to Populus, juvenile and adult Salix were displaced slightly toward the halophytic/xerophytic pole of DCA axis 1. Osmotic adjustment, which appears to allow more vigorous water- or salinity stress responses in this species relative to Populus, may thus be an important adaptation permitting the persistence of Salix in perturbed riparian environments.

Conclusions

The objective of this study was to provide a functional interpretation of the transition from Populus – Salix forest to domination by Tamarix or Tessaria scrub in southwestern riparian ecosystems. A comparison of adjacent alluvial ecosystems that were relatively pristine (Bill Williams River) and highly perturbed (lower Colorado River) was fundamental to this approach. Contrasts between Colorado River control sites and interspersed experimental sites, at which surrounding Tamarix was cleared from the bases of Salix thickets, helped elucidate potential competitive mechanisms acting to structure these communities. Comparisons were also made within the Bill Williams River ecosystem between upstream sites, which supported healthy age structures and vigorous growth of the dominant native riparian taxa, and downstream sites, which exhibited morphological and demographic indications of decline. The physical differences between these sites were subtle, thus challenging us to discriminate more finely among potential causes for incipient physiological stress.

Tissue water relations characteristics and leaf elemental analyses confirmed that Tamarix is likely to be tolerant of a relatively high degree of salinity or water stress. Based on carbon isotopic ratios, Tamarix also has significantly greater water use efficiency than the other riparian taxa examined. These adaptations are likely to be beneficial where salinities are elevated or water tables depressed, conditions characteristic of perturbed riparian environments. On the Colorado River, halophytic adaptations allowed Tamarix to operate at lower water potentials with higher leaf conductances relative to the other species and ecosystems examined. While high water use efficiency is not universally regarded as providing a competitive advantage, it may be beneficial in desiccated riparian habitats. Such characteristics are thought to confer advantages to Tamarix in its role as an invader in riparian ecosystems. It appears that Tessaria combines halophytic adaptations with leaf succulence and low water use efficiency, traits that appear to contribute to increases in the abundance of this shrub following disturbance in riparian ecosystems.

Growth and water relations responses to experimental clearing suggested a close interaction between neighboring Salix and Tamarix on the Colorado River. Higher stomatal conductance in experimental Salix relative to controls may have been attributable to enhanced radiation flux following Tamarix removal. However, increased water potentials and consideration of the water cost of height maintenance in trees indicates that competition for moisture is probable as well. Ecophysiological variation thus helps explain community dynamics along competitive hierarchies that may have intensified due to hydrological perturbation in riparian ecosystems.
The ecological roles for *Populus* and *Salix* in riparian ecosystems were previously assumed to be relatively uniform. However, it appears that there is a physiological basis for individualistic responses to riparian ecosystem perturbation between these taxa. *Salix* tended to exhibit tissue water relations values that were intermediate between those of *Tamarix*, a salt-tolerant facultative phreatophyte, and *Populus*, a mesophytic obligate phreatophyte. Because these taxa may operate near the limits of their water and salinity stress response capabilities in low elevation southwestern riparian habitats, this distinction helps explain the persistence of *Salix*, and not *Populus*, in hydrologically perturbed environments such as the Colorado River floodplain. Such adaptations may also have been responsible for the lack of obvious morphological adjustments in *Salix* to short-term desiccation stress on the Bill Williams River, while morphological and water relations responses of *Populus* were indicative of a low tolerance to moisture or salinity stress.

Moisture was clearly a variable to which riparian plant populations responded. Distinct differences were evident in surface- and groundwater hydrology in the two ecosystems, and species water-relations characteristics tended to vary according to such differences. The Colorado River ecosystem offered the more saline and moisture-deficient environment, but downstream attenuation of Bill Williams River flow induced stress related to soil moisture declines and elevated salinity. Ordination analyses revealed that the riparian communities of the Colorado and Bill Williams Rivers are structured along moisture and salinity gradients. With the prevalence of desiccated floodplain environments, *Tamarix* and *Tessaria* have increased in importance in riparian plant communities while *Salix* and *Populus* have declined, the latter more precipitously than the former. Distinct adaptations for dealing with salinity and water stress among these taxa are apparently responsible for the shifts in riparian community structure which accompany ecosystem change. These shifts include fundamental transformations in vegetation physiognomy, from gallery forest to riparian scrub or thicket habitats, that have accompanied hydrological perturbation in southwestern river systems.

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