ESTABLISHMENT PATTERNS OF NATIVE POPULUS AND SALIX IN THE PRESENCE OF INVASIVE NONNATIVE TAMARIX

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Abstract. Despite growing concern and research interest in plant invasions, we know very little about ecological processes involved during invasion episodes. Understanding these dynamics is especially important for habitats subject to reestablishment of historical disturbance regimes; because many invasive species respond positively to disturbance, interactions between colonizing natives and nonnatives at the seedling stage may determine success of invasions. In the American Southwest, reduced flood disturbance in this century has been associated with the invasion of nonnative Tamarix ramosissima, with Tamarix appearing to displace native flood-dependent species of Populus and Salix. We studied two riparian communities of these woody species that had established after over-bank flooding was allowed to occur in two protected areas in New Mexico. Growth and mortality were monitored for each individual within 1-m² plots of seedling communities within these sites for 2–4 yr. Abiotic conditions measured for each plot included soil salinity, texture, and nitrogen and phosphorus concentration. Although Tamarix seedling densities were an order of magnitude greater than those of the native species at initial establishment, mortality of Tamarix was also much greater than for Populus or Salix and occurred primarily in plots where native species were the most dense. Both natives were taller and grew faster above ground than Tamarix in the first 4 yr, and growth of Tamarix was negatively correlated with neighbor densities. In contrast, Populus and Salix growth and survival were never correlated with Tamarix densities. For all species, none of the abiotic variables measured was as important as neighbor density for explaining growth and survival patterns. These results have positive implications for managers who wish to reestablish the native dominants of riparian forests through reinstatement of flooding. Although Tamarix can respond positively to flooding, a range of conditions clearly exists in which Populus and Salix establishment can be stimulated by flooding, even when Tamarix seedlings are present. Furthermore, the presence of such natives even at the seedling stage may help to reduce densities of invasive Tamarix seedlings.

Key words: competition; disturbance; invasion; Populus deltoides; riparian communities; Salix exigua; Tamarix.

INTRODUCTION

Plant community structure and composition are often considered in terms of how plants with similar niches coexist in a habitat, and under what conditions one species will exclude another (Bengtsson et al. 1994). The issue of species distributions is especially significant within the context of detrimental plant invasions, due to their potentially severe economic, ecological, and aesthetic impacts. It is critical that we understand the mechanisms of invasives for retaining dominance, that is, how persistence is maintained through multiple generations and how new areas are colonized. By understanding the relative roles of abiotic vs. biotic factors affecting establishment of invasive species, we also inform efforts to control and predict invasions. Here we investigate seedling recruitment, growth, and mortality patterns of an invasive species that has established among native species in two field sites.

There is considerable debate within the literature regarding which species traits or ecosystem processes are most important for allowing invasions to occur (for reviews see Mooney and Drake 1987, Cronk and Fuller 1995). In particular, increases and decreases in disturbance frequency or magnitude are often associated with plant invasions (Forcella and Harvey 1983, Crawley 1987, Hobbs 1989, Hobbs and Huenneke 1992, Burke and Grime 1996, Sher and Hyatt 1999). Increasing disturbance often promotes invasion by reducing competition from established vegetation. However, increasing disturbance is sometimes necessary in ecosystems that are historically prone to disturbance; in many cases, native species will even require disturbance for reproduction or establishment. Management of these systems by increasing disturbance will risk making habitat available for unwanted invasive colonization as well. Thus, it is especially important to understand which environmental factors affect the relative success of dis-
turbance-stimulated native vs. invasive species at the establishment stage.

River ecosystems are an important example of such a management paradox. Riparian corridors will often support disturbance-adapted species assemblages, and they may be especially prone to invasion. It has been suggested that the apparent high invasibility of riparian ecosystems is because of their high degree of hydrological disturbance (Tabacchi 1995), because they are often nutrient rich and therefore generally species rich (Planty-Tabacchi et al. 1996), and because rivers are vectors of dispersal (Pysek and Prach 1994). Invasion of riparian zones seems especially likely when historical flooding patterns are changed in intensity or frequency. The association between flow regulation and invasion of riparian communities has been documented in North America, Australia, Europe, and Africa (Baker 1986, Lonsdale 1993, Busch and Smith 1995, Décamps et al. 1995, Springuel et al. 1997, Shafrroth et al. 1998). Management of native riparian habitats may therefore include restoring or recreating historical hydrological regimes, including increasing flooding intensity or frequency. However, research is needed to determine the effectiveness of such a strategy for controlling invasions, especially in cases where flooding disturbance is as likely to stimulate invasive species as native species.

Tamarix invasions of riparian communities offer an opportunity to study invasion episodes as they occur in an ecosystem where disturbance is likely to be important. Tamarix sp. is a significant invasive species along many rivers in the American Southwest, including extensive distributions in Mexico (Glenn et al. 1998), New Mexico (Hink and Ohmart 1984), Arizona (Stromberg 1998), and Utah (Irvine and West 1979, Busch and Smith 1995). Tamarix is also invasive in Egypt (Springuel et al. 1997) and is beginning to show signs of invasiveness in new regions such as Israel (L. Whittaker, personal communication). Tamarix is capable of forming dense monocultures and dramatically changing vegetation structure (Busch and Smith 1995), animal species diversity (Ellis 1995), soil salinity (Taylor et al. 1999), and hydrology (Graf 1978) of sites where it has become dominant.

In the American Southwest, floodplains have been historically dominated by native cottonwood (*Populus* sp.) and willow (*Salix* sp.), but since introduction a century ago, *Tamarix ramosissima* and *T. chinensis* have replaced these natives as the dominant genus, particularly along dammed rivers (Campbell and Dick-Peddie 1964, Howe and Knopf 1991, Busch and Smith 1995). Seeds of these three genera are wind and water dispersed in the early summer, and seedlings become established in high densities on riverbanks when overbank flooding has created an open wet environment (Horton et al. 1960, Fenner et al. 1984). While there is evidence that mature *Tamarix* trees have a competitive effect on neighboring species (Busch and Smith 1995), competition experiments on seedlings suggest that *Tamarix* may not be a good competitor at the seedling stage (Sher et al. 2000). If *Tamarix* is competitive as a seedling, reestablishment of the disappearing *Populus* will be unlikely through any process that simply promotes seedling establishment. Management plans to restore historical disturbance regimes to stimulate natives will only be successful if these native trees can reestablish in the presence of the invasive species.

Using this community, we asked the following questions:

1) Do the native and nonnative species establish in the same microsites after flooding disturbance?

2) Are there density-dependent patterns of survival or growth? Do they differ between the native and non-native species?

3) Do abiotic variables explain distributions and growth?

4) Can flooding disturbance promote successful establishment of native *Populus* and *Salix* even if there is concurrent *Tamarix* establishment?

**Study Species**

We studied the species assemblage found along the Middle Rio Grande, in New Mexico, USA, comprising plains cottonwood, *Populus deltoides* subsp. *wislizenii* (Eckenwalder 1977; these populations have been previously identified as *P. fremontii*), coyote willow (*Salix exigua*), and *Tamarix ramosissima* (identified previously as *T. chinensis*). Typically, *Populus* establishes gallery forests while *Salix* occupies the wetter, more open regions along the riverbanks of the Rio Grande (Hink and Ohmart 1984). *Salix exigua* is a prolific vegetative reproducer, and can spread very quickly within wet environments (Irvine and West 1979). This species has a high transpiration rate compared to other riparian woody species and is very vulnerable to water stress (Cleverly et al. 1997). *Populus* appears to depend more on sexual reproduction than on vegetative spread (Howe and Knopf 1991), and seedlings are very vulnerable to desiccation during establishment (Mahoney and Rood 1998). This may account for the decline of *Populus–Salix* assemblage forests in New Mexico, since “safe-sites” (i.e., places where conditions are favorable for seedling germination and establishment) are less available than they were before damming of the rivers (Howe and Knopf 1991, Busch and Smith 1995, Stromberg 1998). Successful seedling establishment requires the moist open substrate created by scouring floods (Horton et al. 1960, Fenner et al. 1984, Bradley and Smith 1986, Rood et al. 1998), which no longer occur due to damming and channelization of rivers (Williams and Wolman 1984, Crawford et al. 1993).

*Tamarix* is similar to *Populus* and *Salix* in several respects. All three taxa use groundwater; however, *Tamarix* is only facultatively phreatophytic and therefore may be better able to take advantage of surface water
Like both natives, *Tamarix* produces seed in the spring and it also readily exploits the same habitats for germination (Horton et al. 1960, Taylor et al. 1999). However, *Tamarix* produces seeds for many more months of the year, extending well past the historical spring flooding season, and seedlings may not be as flood dependent as *Populus* (Horton et al. 1960). Therefore, seeds produced late in the season may be able to exploit substrate that becomes available due to disturbance after *Populus* and *Salix* have finished producing seeds, such as late floods, fire, or human-created clearings. In addition, *Tamarix* seeds and seedlings have adaptations to the salinity, drought, and fire associated with decreased over-bank flooding (Horton et al. 1960, Busch and Smith 1993, 1995, Shafroth et al. 1995, 1998, Cleverly et al. 1997, Smith et al. 1998). All of these differences may contribute to *Tamarix's* establishment success over much of the Rio Grande floodplain since the cessation of over-bank flooding.

**Study Sites and Methods**

**Bosque del Apache**

The first field site was located at the Bosque del Apache Wildlife Refuge, 20 km south of the city of Soccorro, New Mexico, USA, 33°48' N, 106°53' W. Eight 50 x 50 m quadrats adjacent to the Rio Grande were cleared of dense *Tamarix* in 1993, and within each quadrat, nine 1-m² plots were created along crossing diagonal transects (Fig. 1; Taylor et al. 1999). Over-bank floods were released after clearing in the spring of 1993, resulting in natural seedling establishment. Although the Rio Grande is a dammed river, the timing and character of this flood was controlled to simulate historical spring flows (Taylor et al. 1999). Abundant seed for both species was provided from uncleared *Tamarix* trees surrounding the cleared quadrats and from *Populus* populations north and south of the study site via both wind and water dispersal of seed.

The following abiotic variables were measured in each of the 72 plots (Taylor et al. 1999): elevation (feet above sea level), soil texture, salinity, and soil nutrients. Soil samples were collected in July 1993 using a 2 cm diameter soil bucket auger for particle size determination using the hydrometer method (Gee and Bauder 1986). Clay, silt, and sand proportions from each sample were assigned soil texture classifications using a soil triangle (Brady 1974); each soil class was given a numeric value as follows: 0 = sandy, 1 = loamy sand and sandy loam, 2 = loam and silt loam, 3 = silt and clay loam, 4 = sandy clay loam and silty clay loam, 5 = sandy clay and silty clay, 6 = clay (from Taylor et al. 1999). In October 1993, soil salinity was determined across the 0.75-m soil profile (upper salinity; EM38H, “HEC” in tables) and across the 1.5-m soil profile (lower salinity; EM38V, “VEC” in tables) using the electromagnetic induction method (Sheets et al. 1994). In August 1994, four 10-cm soil cores were collected per 1-m² plot, and we digested them using the Kjeldahl extraction method (Schuman et al. 1973). These samples were then analyzed for NH₄ and PO₄ content (milligrams per gram of soil) using an autoanalyzer.

Seedling counts were made by species within each plot from establishment in June of 1993 through September of 1996; three times in the first growing season (June 1993, July 1993, September 1993), three times in the second season both before (April 1994) and after flooding (June 1994, September 1994), and then once yearly in the third and fourth seasons after flooding (August 1995, September 1996). In 1994, all woody seedlings in the plots were tagged, such that individuals could be tracked. *Populus* and *Tamarix* were tagged in July, while *Salix* was not included in individual data collection until the next census in September, when increasing numbers of *Salix* indicated that it could potentially impact the competitive environment. At the time of tagging, individuals were classified into one of
three distinct size classes: new 1994 seedlings (<5 cm), vegetative sprouts from roots in 1993 (>100 cm and/or >5 shoots), or intermediate size (1994 vegetative sprouts or 1993 seedlings). The distinction between the last two categories within the intermediate size class could not be determined nondestructively. Additional data collected on each individual included mortality, basal diameter, height, and number of shoots. These data were taken twice, in summer and fall of the second growing season (July 1994, September 1994), and then once yearly for the third and fourth years (fall of 1995, 1996). At each census, new individuals were tagged and origin identified (as either a seedling or a root sprout). New seedlings were identifiable by their small size and the presence of cotyledons. Previously untagged larger individuals were considered new root sprouts (rather than a shoot of a neighboring sapling) if we could find no point of attachment to another individual to a depth of 5 cm, and it had formed its own roots. In 1997, a subsample of plots was harvested. At least one plot was harvested from each quadrant, and plots were chosen to represent a range of densities and species ratios, as both density and ratio have been shown to affect aboveground growth of *Populus–Tamarix* mixtures (Sher et al. 2000). Aboveground biomass of all individuals in harvested plots was dried at 45°C for one week and weighed.

**Escondida**

A second field site was found in the spring of 1996 at Escondida, 32 km north of Bosque del Apache, in an area managed by the U.S. Bureau of Land management (39°54' N, 106°54' W). Unlike Bosque del Apache where mechanical clearing of established vegetation created substrate, at Escondida the natural meandering of the river had created an open area for seedling establishment. This used to be a common occurrence for *Populus* seedling establishment (Howe and Knopf 1991). High flows that facilitated germination at Bosque del Apache in 1993 had also resulted in natural seedling establishment at Escondida, filling a 400 × 40 m area on the sandbar with *Salix, Populus*, and *Tamarix*. The soil at Escondida was generally more sandy than Bosque del Apache, and appeared to be more xeric.

At 10-m intervals, 1-m² plots were established at random distances from the edge of the seedling population for a total of 40 plots. As in the Bosque del Apache plots, all individuals within a 1-m² plot were tagged and measured for height, basal diameter, and number of shoots. This site was censused again in spring of 1997. We collected soil samples from each plot in 1996 by taking four 10 cm deep cores, which were analyzed in the laboratory for electroconductivity (i.e., salinity), soil texture, and concentrations of NH₄ and PO₄. Mineral nutrient availability was determined by the same methods as used for Bosque del Apache samples (see Study sites and methods: Bosque del Apache).

**Statistical Analysis**

For both sites, analyses used mean measurements of height per 1-m² plot per quadrant. At Bosque del Apache, the first 50-m² quadrant was bulldozed the summer of 1996 to create a firebreak. Therefore the sample size for the final sampling period is smaller, and individuals growing in the first quadrant are excluded from analyses that use environmental variables to predict mortality. Also, for analyses of height and species distributions, only those plots that contained saplings were included; thus, the final sample sizes of the Bosque del Apache and Escondida sites were comparable (i.e., 40 1-m² plots).

Due to the nested nature of the plot design at Bosque del Apache, it was necessary to determine the degree to which variation between 1-m² plots could be attributed to their location within a 50-m² quadrant. The variation of species densities due to plot assignment was first tested using an intraclass correlation. This analysis was performed using densities at establishment (t < 1 mo) and after one year (t = 14 mo) to account for potential changes in plot similarity after high mortality during the first year.

We examined the abiotic (i.e., soil characters) and biotic (densities of species, growth measurements) environment of the plots in the following ways. We first investigated the relationship between densities of each species for each sampling period with linear regressions, and then we measured the relationships among abiotic variables with Pearson correlations. Due to the large number of abiotic variables and high level of correlations among them at Bosque del Apache, we used principal component analysis (PCA) to create uncorrelated variables for abiotic plot descriptors (PROC PRINCOMP; SAS 1990). At Escondida, PCA was used to create a single soil texture variable based on percent sand, silt, and clay. No principal component could be developed for a combination of all of the abiotic variables at Escondida that explained a high percentage of the variation; therefore these variables were retained as individual variables in the analyses. We then used these principal component values of the biotic and abiotic plot descriptors as independent variables in other analyses.

We then investigated change in density over time with the following analyses. Differences between species were tested with repeated-measures ANOVA. This was done both including and excluding the first growing season for Bosque del Apache, when the greatest amount of mortality occurred. Different analyses were then used to investigate how environmental variables influenced density pattern change in the first year vs. mortality patterns in subsequent years.

To examine the abilities of different variables to predict which species gained dominance in individual
plots by the end of the second growing season \((t = 14 \text{ mo})\) at Bosque del Apache, we used a multivariate discriminant analysis. Because seedling densities of \textit{Populus} and \textit{Tamarix} were positively correlated at establishment and there was very little new recruitment the second year, dominance of one or the other species after two growing seasons reflected differential mortality during early establishment. This analysis addressed whether the pattern of mortality (as reflected by dominance of only one species) was related to initial density and/or soil characters. Plots \((1 \text{ m}^2 \text{ in size})\) were classified as either \textit{Populus} dominated \((>75\% \text{ by density})\), \textit{Tamarix} dominated \((>75\% \text{ by density})\), or mixed. \textit{Salix} densities were not high enough or concentrated enough to be given their own category. Those plots with no seedlings were excluded from the analysis. We then used canonical discriminant analysis (PROC CAN- DISC; SAS 1990) to determine whether abiotic and biotic environmental variables could be used to discriminate between plots with different species dominance. Initial densities of each species, elevation, soil texture, salinity, and nutrient content \((\text{NH}_4, \text{PO}_4)\) were the independent variables included to differentiate between plot types. This analysis produces linear combinations of the independent variables (abiotic and biotic environmental factors) that most separate categories (species dominance groups). This classification rule can then be tested for degree of accuracy by comparing the predicted against actual classifications.

To investigate the effect of environmental factors on survival after the first year when we have data on specific individuals, we analyzed mortality patterns of those individuals using an accelerated failure time analysis \((\text{AFTA, PROC LIFEREG; SAS 1990})\). This analysis describes the effect of independent variables (species densities initially and after one year and abiotic plot descriptors) on how quickly an event occurs—in this case, the event of death. Independent variables for the AFTA were initial and \(t = 14 \text{ mo}\) densities of \textit{Populus} and \textit{Tamarix}, the PCA of abiotic variables, and plot location.

We investigated growth (i.e., change in height over time) differences between species across habitat types using repeated measures ANOVA \((\text{PROC GLM; SAS 1990})\). Multiple regression models were tested for each species separately with independent variables of abiotic plot descriptors, initial density (for Bosque del Apache only), and density at the beginning of the sampling period for height (for both Bosque del Apache and Escondida).

\section*{Results}
\subsection*{Bosque del Apache, the cleared site}
A plot of mean densities over time reveals that while \textit{Tamarix} was more abundant by an order of magnitude than either \textit{Populus} or \textit{Salix} in the first season, \textit{Tamarix} mortality was much greater than in either native species, resulting in much more similar densities at \(t = 36 \text{ mo}\) (Fig. 2). Change in densities over time was significantly different between species, even when the high mortality of the first year was excluded (repeated-measures ANOVA, \(n = 61, F_{1.56} = 11.7, P < 0.001\)).

Variability in density among plots was not explained well by quadrant for either \textit{Tamarix} \((R^2 = 0.20 \text{ for } t = 1 \text{ mo} \text{ and } 0.23 \text{ at } t = 36 \text{ mo})\) or \textit{Populus} \((R^2 = 0.02 \text{ and } 0.11)\). With this caveat, the sample sizes for all analyses were based on plot \((\text{maximum } n = 72 = 8 \text{ quadrats } \times 9 \text{ plots/quadrat})\) rather than a mean value across plots for each 50-m\(^2\) quadrat. Although quadrant did not significantly explain variation in density among plots, plot location (i.e., quadrant) was included as a variable in the analyses of mortality after 14 mo and growth. We used an index variable for plot location to account for possible spatial variation in environmental characteristics, with lower numbers indicating more northerly quadrats.

Initial densities of \textit{Populus}, \textit{Tamarix}, and \textit{Salix} were highly positively correlated with each other (Fig. 3A), with most plots dominated by \textit{Tamarix}. However, spatially nonrandom mortality resulted in a change in this relationship over time. For each successive time period, the positive relationship of \textit{Salix} and \textit{Populus} with \textit{Tamarix} became weaker, and by \(t = 38 \text{ mo}\) had become negative (Fig. 3B). Densities of \textit{Populus} and \textit{Salix} remained positively, but weakly, correlated \((R^2 = 0.15, P < 0.01)\). The negative relationship between \textit{Populus} and \textit{Tamarix} was such that 89\% of occupied plots were dominated (in number and biomass) by one or the other species at the end of the second growing season in 1994.

A single canonical vector could discriminate between \textit{Populus}, \textit{Tamarix}, and mixed-dominance plots using the site characters measured, most particularly initial \textit{Populus} density (Table 1). Soil texture, salinity, soil N and P contributed approximately equally to the

\begin{figure}
\centering
\includegraphics[width=\textwidth]{fig2}
\caption{Changes in densities over time for \textit{Tamarix}, \textit{Populus}, and \textit{Salix}. Note log scale of the y-axis. Growing seasons begin in April (i.e., after last frost).}
\end{figure}
model, while initial Tamarix density was very weakly weighted. Mean values of each site character by plot type revealed that Tamarix-dominated plots had lower initial densities of both Populus and Tamarix, and a higher mean NH₄ concentration and soil texture index (heavier, less sandy soils) than Populus plots (Table 1). A comparison of predicted vs. actual classifications showed that the model accurately classified 42 out of 47 plots. No pattern or clear explanation could be made for the misclassified plots. The only gross misclassifications were a mixed plot that had a CAN1 value that should have placed it in the Populus-dominated group, and a Populus plot with a CAN1 value more similar to Tamarix plots (Fig. 4).

Accelerated failure time analysis on individual sapling mortality patterns showed that even after the high mortality of seedlings the first year (i.e., starting in autumn 1994 when tracking of individuals began), Tamarix mortality was more rapid than for either native species (Fig. 5) and was more highly correlated with neighbor densities (Table 2). Both Tamarix and Populus densities significantly explained time to death of Tamarix, whereas Populus mortality rate was negatively correlated with initial Populus density. Salix mortality was not explained by densities of any species. Second through fourth year mortality patterns were also significantly associated with plot location for all three species, with shorter life-spans of Tamarix farther upstream, whereas Populus and Salix died more quickly downstream. Plot location was significantly correlated (Pearson correlation (C), P < 0.01) with some but not all of the abiotic variables; plots became lower in elevation (C = −0.34), higher in N (C = 0.58), and heavier in texture (C = 0.52) as sampling location moved downstream. A PCA vector of these abiotic variables did not explain a significant portion of mortality patterns of the second through fourth years for any of the species.

**Table 1.** Discriminant analysis results to distinguish between 1-m² subplots dominated by *Populus, Tamarix,* or both at time (t) = 14 mo.

<table>
<thead>
<tr>
<th>Independent variable</th>
<th>CAN1</th>
<th>Mean values in subplots</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>P</td>
<td>Populus</td>
</tr>
<tr>
<td>Tamarix density (t = 0)</td>
<td>−0.033</td>
<td>557.8</td>
</tr>
<tr>
<td>Populus density (t = 0)</td>
<td>1.25</td>
<td>21.7</td>
</tr>
<tr>
<td>Soil texture</td>
<td>−0.209</td>
<td>2.0</td>
</tr>
<tr>
<td>Elevation (relative measure)</td>
<td>−0.017</td>
<td>−0.04</td>
</tr>
<tr>
<td>VEC/salinity</td>
<td>0.310</td>
<td>39.89</td>
</tr>
<tr>
<td>NH₄</td>
<td>−0.146</td>
<td>0.477</td>
</tr>
<tr>
<td>PO₄</td>
<td>0.254</td>
<td>0.224</td>
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</tbody>
</table>

**Notes:** Values in first column are coefficients for each independent variable in the first canonical vector (CAN1) and reflect weighting of each variable in the model. Mean values are reported for each independent variable used in the analysis.
Despite mortality in all species throughout the survey period, the number of individuals was fairly constant after the first year due to the appearance of new individuals. The relative abundance resulting from each reproductive strategy differed between species and between years (Fig. 6). *Populus* and *Tamarix* had pulses of sexual reproduction after flooding in the first years, but depended on vegetative reproduction in later years when the canopy had been established. *Salix* produced very few seedlings at any sampling period, but new vegetative sprouts appeared each year after 1993.

Growth of each species was measured in several ways; however, height proved the most useful indicator. Basal diameter was highly correlated ($P < 0.001$) with height at the first census for both *Populus* ($n = 171$, $F_{1,169} = 1000.16$, $R^2 = 0.94$) and *Tamarix* ($n = 544$, $F_{1,542} = 287.13$, $R^2 = 0.81$). A PCA was conducted to determine if a composite variable of the three size descriptors (height, basal diameter, number of shoots) would provide an improved dependent variable for growth; however, 99% of the variation in these variables was explained by a PCA vector that was 99% based on height. Linear regressions on biomass from subsamples of harvested individuals in 1997 revealed that biomass was also very highly correlated with height ($P < 0.0001$) for *Salix* ($n = 77$, $F_{1,75} = 350.4$, $R^2 = 0.82$), *Populus* ($n = 34$, $F_{1,32} = 273.7$, $R^2 = 0.92$), and *Tamarix* ($n = 27$, $F_{1,25} = 127.0$, $R^2 = 0.83$). Therefore, height was used for all growth analyses.

*Populus* had the greatest height and grew the most rapidly of the three species (repeated-measures ANOVA: $df = 2, 422, \text{Wilks Lambda } F = 102.73, P < 0.0001$; Fig. 7). Total initial density was negatively correlated with *Tamarix* growth but positively correlated with *Populus* growth (Table 3). Plot location was also significant, with increasing total growth as plots were farther upstream for both *Tamarix* and *Populus*.

The model using plot location, abiotic PCA, and plot densities was not able to significantly explain variation in *Salix* growth.

**Escondida, the sandbar site**

As at Bosque del Apache, *Tamarix* mortality was greatest in plots with dense *Tamarix* and *Populus* neighbors (Table 4). *Salix* mortality was correlated only with density of conspecifics, and *Populus* mortality was not explained by neighbor density of any species. Abiotic variables measured did not explain mortality of any species. Unlike at Bosque del Apache, *Tamarix* densities were much less than those of either *Populus* or *Salix* at Escondida, even after severe mortality of *Populus* in 1996 (Table 5). All species suffered mortality at this site, and there was no recruitment over the two years surveyed.

Pairwise regressions of densities of each species at each sampling period revealed a significant relationship only between *Salix* and *Tamarix* densities (positive) in 1996, but this explained <10% of the variation (Fig. 8; $n = 89$, $F = 1$, $P < 0.02, R^2 = 0.06$). There were proportionally fewer *Tamarix* at this site, making relationships between species densities more difficult to measure. All other species comparisons in all other years were not significant; however, 88% of *Tamarix* seedlings were concentrated in only seven out of 40 total plots. Chi-square analysis on presence vs. absence of species in plots was significantly nonrandom ($df = 2, \chi^2 = 38.06, P < 0.001$).

Growth patterns also differed significantly between species at Escondida, with *Populus* and *Salix* being significantly taller and growing more quickly than *Tamarix* (Table 5), as seen at Bosque del Apache. Growth rate was not negatively correlated with increasing neighbor density for any species; in fact, both *Salix* and *Populus* grew best in plots where *Salix* was most dense (Table 6). Abiotic plot characteristics were generally not good predictors of growth rate, with the exception of a positive correlation between P concentration and *Salix* growth.

**Discussion**

This field survey documents successful seedling establishment of native *Populus* and *Salix* in the presence of invasive nonnative *Tamarix* at both a mechanically cleared and a naturally cleared site along the Middle Rio Grande. At both sites, survival and/or growth of *Tamarix* was negatively correlated with densities of native species, and in no case was there evidence of *Tamarix* having an effect on native species survivorship or growth.
Tamarix and Populus t may compete for light. There is also evidence of competition for mineral nutrients. The plots where Tamarix seedlings were most dense had lowered soil N in the cleared site, and research has shown that increasing Populus density reduces concentrations of nitrogen in leaf tissues of both Populus and Tamarix at initial \( t = 0 \) mo and second year \( t = 14 \) mo densities. Significant variables for the model are in bold type.

### Establishment and density dependence

Flooding can stimulate natural establishment of Tamarix, Populus, and Salix in high densities without manual planting, both where existing vegetation is removed mechanically and where it is cleared naturally. However, it appears that mortality and growth of only Tamarix is highly density dependent. Even with the much higher densities of Tamarix, the native Populus and Salix appeared impervious to its presence. Pairwise pot experiments have shown Populus to be a superior competitor against Tamarix (Sher et al. 2000), and these field observations support the hypothesis that natural conditions exist in which interspecific competition will favor Populus.

The mechanism of superior seedling competition in Populus and Salix may be both above- and belowground. These native trees were initially taller and grew faster aboveground than Tamarix in both locations. It has been observed that neither species will establish in the shade of the other (Campbell and Dick-Peddie 1964), and there was very low seedling recruitment at our sites after the canopy closed, suggesting that these species may compete for light. There is also evidence of competition for mineral nutrients. The plots where Populus seedlings were most dense had lowered soil N in the cleared site, and research has shown that increasing Populus density reduces concentrations of nitrogen in leaf tissues of both Populus and Tamarix (Sher et al. 2000). Additional research on belowground interactions and physiological response is necessary to determine the most important mechanisms for this competitive interaction.

### The role of abiotic factors

We found that abiotic variables, including salinity, were not good predictors of growth or survival after establishment, in contrast to expected results. It has often been argued that because Tamarix has adaptations to saline soils, salt tolerance should be an important mechanism of Tamarix invasion (Busch and Smith 1995, Smith et al. 1998). In greenhouse experiments, high-salinity solutions (1.5–2 g/L NaCl) have been shown to have a greater negative effect on Salix sp. and Populus fremontii cuttings (Glenn et al. 1998) and seedlings (Jackson et al. 1990) than on Tamarix. However, comparisons in seeds and seedlings of Tamarix and Populus across ranges of river water salinity have shown less difference in salt tolerance than expected.
with Populus equally tolerating even five times the salinity of the Rio Grande (2.5 g/L; Shafroth et al. 1995). That salinity was usually unimportant in our models to explain survival and growth may be because our soils were not highly saline, possibly due to the overbank flooding our sites received. These results suggest that soil salinity levels must be at high levels (as would be likely in less flooded areas) before salinity becomes an important differentiating mechanism for establishment.

Although the abiotic characters we measured were generally insignificant for explaining growth or sapling survival, stream-bank location was. Generally, Populus dominated more northern sites, while Tamarix persisted in the more southern sites. The northern end of the site had the most active river flows. Although the upstream sites had higher elevation, water access to the downstream sites required crossing an elevationally high area, and therefore downstream plots were less likely than upstream plots to be under water or to have silt deposited. Populus may have done better than Tamarix in upstream plots because of greater flood tolerance, since research has shown that, due to their slower aboveground growth, Tamarix seedlings are more likely than Populus to be covered by silt or water and

### Table 3. Multiple regressions for Tamarix and Populus to explain mean change in height at Bosque del Apache from September 1994 to November 1995 (1996 data were not used due to destruction of quadrat 1 in 1996).

<table>
<thead>
<tr>
<th>Independent variable</th>
<th>Tamarix $^\dagger$</th>
<th>Coefficient $P$</th>
<th>Coefficient $P$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Plot location</td>
<td>-2.61</td>
<td>0.05</td>
<td>-1.55</td>
</tr>
<tr>
<td>Abiotic PCA§</td>
<td>0.41</td>
<td>NS</td>
<td>0.09</td>
</tr>
<tr>
<td>$t = 0$ total density</td>
<td>-13.41</td>
<td>0.001</td>
<td>21.34</td>
</tr>
<tr>
<td>$t = 1$ yr total density</td>
<td>-6.50</td>
<td>0.00</td>
<td>-20.03</td>
</tr>
</tbody>
</table>

$^\dagger$ Model $R^2 = 0.60, P < 0.001$, intercept = 127.17.

$^\ddagger$ Model $R^2 = 0.040, P < 0.015$, intercept = 73.19.

§ APRIN1 = (0.035ST + 0.74HEC + 0.005M) − (0.0060E + 0.0027P). This PCA vector explains 95.1% of the variation in soil texture (ST), vertical and horizontal electrical conductivity (VEC/HEC), elevation ($E$; a standardized relative measure based on elevation above sea level), NH$_4$ ($N$), and PO$_4$ ($P$).
had the greatest growth in the most flooded plots, Populus, Tamarix, and Salix in 1996 plot descriptors at Escondida, the sandbar site.

<table>
<thead>
<tr>
<th>Independent variable</th>
<th>Populus(\dagger)</th>
<th>Tamarix(\ddagger)</th>
<th>Salix$\S$</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Coefficient</td>
<td>(P)</td>
<td>Coefficient</td>
</tr>
<tr>
<td>Populus density</td>
<td>0.26</td>
<td>NS</td>
<td>3.07</td>
</tr>
<tr>
<td>Tamarix density</td>
<td>0.042</td>
<td>NS</td>
<td>0.19</td>
</tr>
<tr>
<td>Salix density</td>
<td>1.48</td>
<td>NS</td>
<td>6.73</td>
</tr>
<tr>
<td>Salinity</td>
<td>-0.018</td>
<td>NS</td>
<td>0.055</td>
</tr>
<tr>
<td>Soil texture</td>
<td>0.20</td>
<td>NS</td>
<td>-1.54</td>
</tr>
<tr>
<td>(N)</td>
<td>-0.11</td>
<td>NS</td>
<td>0.0004</td>
</tr>
<tr>
<td>(P)</td>
<td>-0.025</td>
<td>NS</td>
<td>8.80</td>
</tr>
</tbody>
</table>

Notes: Difference in species density patterns between the two years were attributable solely to mortality (i.e., there were no new individuals in 1996).

\(\dagger\) Intercept = 88.56, model \(R^2 = 0.01\), NS, model df = 7, error df = 30.  
\(\ddagger\) Intercept = -227.52, model \(R^2 = 0.56\), \(P = 0.08\), model df = 7, error df = 6.  
§ Intercept = 40.84, model \(R^2 = 0.21\), \(P = 0.07\), model df = 7, error df = 25.  
\| Soil texture is represented by PCA vector PRIN1 = 0.60(%silt) + 0.17(%clay) - 0.78 X (%sand); this vector can be understood as a weighted average of silt and clay against sand, such that lower values represent greater percentages of larger particles. It should be noted that this is the same trend as for the index of soil texture used for Bosque del Apache.

Although intrasite variation in the abiotic variables was not important for describing growth, differences between study sites did indicate abiotic effects on growth. The soils of the sandbar site were coarser and had less organic material than the cleared site soils, which possibly explains the reduced growth at the sandbar site and also the weaker density dependence there. The response to the abiotic environment may have been so strong as to preempt most competitive effects (Grime 1979). That there are differences between the sites makes all the more striking the similarities in the way the trees behaved: most particularly, that Tamarix seedlings were shorter and demonstrated much greater density dependence than native species.

Implications for management of Tamarix invasion

Previous research has suggested that decline in Populus and/or Salix along southwestern rivers may be due in part to competitive exclusion by the nonnative Tamarix (Howe and Knopf 1991, Busch and Smith 1995), from which one might conclude that flooding would not be a good management strategy because it is known to stimulate Tamarix establishment. However, our results suggest that under conditions favorable for native species establishment, i.e., if there is open substrate with spring flooding, native species will not be competitively excluded at the seedling stage by colonizing Tamarix seedlings or vegetative sprouts. These observations support recent documentation of co-occurrence of Populus, Salix, and Tamarix in areas with restored or natural flood disturbance (Stromberg 1998), and a characterization of Tamarix invasion as passive (Evett 1998). Tamarix distributions in our sites were rel-

Table 4. Summary of multiple-regression analyses of probability of mortality ([density 1996 - density 1997]/density 1996) × 100) per plot for each of the three species vs. abiotic (salinity, soil texture, N, and P) and biotic (density of Populus, Tamarix, and Salix) parameters.

Table 5. Mean heights and densities (±1 se) for each species in 1996 and 1997 with summary statistics for repeated-measures ANOVA on differences between species over time at Escondida.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Populus</th>
<th>Tamarix</th>
<th>Salix</th>
</tr>
</thead>
<tbody>
<tr>
<td>Density (no./m²)(\ddagger)</td>
<td>29.48 (± 2.43)</td>
<td>9.28 (± 1.07)</td>
<td>8.92 (± 3.51)</td>
</tr>
<tr>
<td>Height (cm)(\ddagger)</td>
<td>70.07 (± 1.81)</td>
<td>74.33 (± 2.25)</td>
<td>27.50 (± 5.56)</td>
</tr>
</tbody>
</table>

Note: \(N = 40\).

\(\ddagger\) Repeated-measures ANOVA for effect of time × species: \(F_{1,90} = 3.18, P < 0.05\).  
\(\ddagger\) Repeated-measures ANOVA for effect of time × species: \(F_{1,97} = 13.96, P < 0.01\).
between native species establishment will give rise to competitive and environmental constraints across a heterogeneous substrate.

Mechanical clearing and floodwater management that simulate the critical effects of historical scouring to allow native species establishment will give *Tamarix* fewer colonization opportunities. That *Tamarix* does less well in the presence of native species suggests that, for new colonization events, competitive release from native trees may be an important factor for the promotion of *Tamarix* invasion. Even though flooding disturbance positively stimulates *Tamarix* initial establishment and growth, the presence of flood-adapted species does not. This is significant because, although disturbance is often cited as facilitating plant invasions by removing native competitors (Crawley 1986, Mooney and Drake 1987, Hobbs 1989, Cronk and Fuller 1995, Burke and Grime 1996), our results support the hypothesis that disturbance can favor natives over nonnatives in an ecosystem adapted to disturbance (Hilleryard 1985). Any alteration to the disturbance regime, including decreases in disturbance, can therefore promote species invasions (Hobbs and Huenneke 1992, Sher and Hyatt 1999).

Decrease in flooding disturbance due to damming is widely recognized as the most powerful mechanism of change in floodplain ecosystems throughout the world, affecting hydraulics, geomorphology, chemistry, and biological communities (Williams and Wolman 1984, Auble et al. 1994, Bayley 1995, Jansson et al. 2000). During the last 250 yr, most major temperate-zone rivers have been transformed by human engineering (Gore and Shields 1995), and the resulting loss of floodplains poses a significant threat to global biodiversity (Sparks 1995). It is clear that management of *Populus–Salix* forests in the American Southwest requires some reinstatement of historical hydrographs (Fenner et al. 1984, Bradley and Smith 1986, Molles et al. 1998), and flooding is more important for *Populus* establishment than other factors such as an absence of grazing (Asplund and Gooch 1988).

As management strategies are beginning to incorporate restoration of disturbance regimes, it is crucial to understand how reestablishing natives will be able to respond in the presence of potentially invasive species. *Tamarix* invasion has been a significant problem in riparian ecosystems across the globe, and flooding can stimulate seedling establishment. However, this research suggests that promoting native *Populus* and *Salix* establishment with flooding disturbance along the middle Rio Grande is not only possible in the presence

![Figure 8](image-url)  
**FIG. 8.** Linear regression of pairwise comparison of densities between *Salix* and *Tamarix* at the first sampling period (1996) at the Escondida site. Density is number of individuals per 1-m² plot.

<table>
<thead>
<tr>
<th>Independent variable</th>
<th><em>Populus</em> Coefficient</th>
<th><em>Tamarix</em> Coefficient</th>
<th><em>Salix</em> Coefficient</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td><em>P</em></td>
<td><em>P</em></td>
<td><em>P</em></td>
</tr>
<tr>
<td><em>Populus</em> density</td>
<td>0.007</td>
<td>0.566</td>
<td>-0.182</td>
</tr>
<tr>
<td><em>Salix</em> density</td>
<td>-0.034</td>
<td>-0.022</td>
<td>-0.102</td>
</tr>
<tr>
<td>Salinity</td>
<td>0.657</td>
<td>1.123</td>
<td>0.442</td>
</tr>
<tr>
<td><em>NH₄</em></td>
<td>-0.001</td>
<td>0.005</td>
<td>-0.008</td>
</tr>
<tr>
<td><em>PO₄</em></td>
<td>0.102</td>
<td>-0.661</td>
<td>0.654</td>
</tr>
<tr>
<td>Soil texture</td>
<td></td>
<td>0.049</td>
<td>-0.253</td>
</tr>
</tbody>
</table>

† Intercept = 18.951, $R^2 = 0.44$, $P = 0.02$.
‡ Intercept = -14.868, $R^2 = 0.75$, NS.
§ Intercept = 31.793, $R^2 = 0.42$, $P = 0.04$.
∥ Soil texture is represented by PCA vector PRIN1 = 0.60(−%silt) + 0.17(%clay) - 0.78 × (%sand); this vector can be understood as a weighted average of silt and clay against sand, such that lower values represent greater percentages of larger particles. It should be noted that this is the same trend as for the index of soil texture used for Bosque del Apache.
of Tamarix, but that the presence of natives may even be detrimental for Tamarix establishment. Additional research is clearly needed to determine if other invaded riparian areas may similarly benefit from reinstating historical disturbance patterns.

Acknowledgments

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