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Water table decline alters growth and survival of *Salix gooddingii* and *Tamarix chinensis* seedlings

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Abstract

In the western United States, many native riparian forests are declining downstream from dams and diversions, primarily due to a lack of successful regeneration of native species. Conceptual models have been described that incorporate stream flow characteristics that promote successful regeneration of western riparian *Populus* seedlings. However, these models need to be calibrated for additional species and specific stream characteristics. In this study, we examined the growth and survival of two dominant Sonoran desert riparian tree species, a native *Salix gooddingii*, and an exotic, *Tamarix chinensis*, to simulated water table declines at rates of 0, 1, 2, and 4 cm/day. *Salix* seedlings performed best in the 0 cm/day treatment in which the soil was saturated and showed decreasing survival and growth with increasing rates of water table decline. Root-to-shoot ratios were high for *Salix*, but root elongation rates were low with an emphasis on lateral root development. This root growth pattern may be an adaptation to habitat where *Salix* typically grows, near the stream channel where the water table is shallow but the likelihood of flood scour is high. Lateral root development may help to protect *Salix* seedlings from late season flood scour. *Tamarix* seedlings showed consistently high survival across all treatments and had the greatest growth in the 0 and 1 cm/day treatments. *Tamarix* seedlings had greater root elongation rates in response to water table decline relative to the control, with the greatest elongation in the 1 cm/day treatment. Greater root elongation rates and higher drought tolerance allowed *Tamarix* seedlings to persist in dry soils where *Salix* seedlings died. Differences in growth and survival of these two species in response to water table decline will need to be incorporated into management practices to promote successful native riparian tree regeneration. © 2001 Elsevier Science B.V. All rights reserved.

Keywords: *Salix gooddingii*; *Tamarix chinensis*; Seedling establishment; Water table decline; Riparian ecology

1. Introduction

Riparian ecosystems in the American Southwest compose less than 3% of the landscape area (Naiman and Decamps, 1997), however, they are highly valued for wildlife habitat, biodiversity, recreation, flood

attenuation, and water quality (Carothers, 1977; Patten, 1998). Despite their importance, demands for water and subsequent development projects, including dams and diversions, have contributed to a decline of southwestern riparian forests (Stromberg, 1993; Busch and Smith, 1995; Stromberg et al., 1996; Patten, 1998). Dam operations alter the hydrology of rivers, often reducing sediment loads and increasing erosive power causing greater channel incision and water table decline (Reily and Johnson, 1982). The abrupt

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downstream decline of alluvial water tables caused by dams and diversions has been proposed as a mechanism of riparian forest decline (Rood and Heinze-Milne, 1989; Rood and Mahoney, 1990; Mahoney and Rood, 1991, 1992). Also, flood attenuation and altered timing of peak flows by dams and diversions can limit regeneration by downstream native trees (Fenner et al., 1985; Bradley and Smith, 1986; Rood and Heinze-Milne, 1989; Rood and Mahoney, 1990; Mahoney and Rood, 1998) and promote the establishment of exotics that are more competitive than natives under drier conditions (Smith et al., 1991; Busch and Smith, 1995; Cleverly et al., 1997; Smith et al., 1998). Chronic regeneration failures by native riparian trees can shift community composition towards dominance by exotic and more xeric species (Friedman et al., 1995).

The germination requirements of many western riparian trees are well known (Stromberg, 1993; Braatne et al., 1996; Mahoney and Rood, 1998). High spring flows typically scour competing vegetation and deposit sediment, creating safe sites for germination. Most native riparian trees are adapted to this disturbance regime and produce seeds prolifically in synchrony with flood water recession in early spring (Stromberg, 1993). The presence of significant numbers of seedlings every year suggest that seed availability is not limiting to establishment, although many of these seedlings do not survive the first year (Stromberg, 1993; Scott et al., 1997; Mahoney and Rood, 1998). The primary causes of mortality are typically water stress caused by rapid water table declines (Mahoney and Rood, 1991; Stromberg, 1993; Mahoney and Rood, 1998) and scouring by late summer and fall floods (Stromberg, 1993). A key to seedling establishment is rapid root growth as the water table declines (Mahoney and Rood, 1991, 1992). Often the rate of water table decline on dam-regulated rivers is very rapid, which can cause extensive water stress and mortality in new seedling populations (Mahoney and Rood, 1998). *Populus* seedlings are known to have root growth rates of 0.6–1.3 cm/day, resulting in 72–162 cm of root growth by the end of their first season (Fenner et al., 1984; Mahoney and Rood, 1998), however, it has been reported that *Populus* seedlings can survive ground water decline rates of 2–4 cm/day (Mahoney and Rood, 1991, 1992; Segelquist et al., 1993). These findings suggest that some riparian tree

seedlings can use water from the capillary fringe above the alluvial water table (Mahoney and Rood, 1998). The thickness of the capillary fringe can range from less than 10 cm in coarse cobbles to greater than 100 cm in fine silts (Mahoney and Rood, 1998).

The 'recruitment box' conceptual model of *Populus* seedlings based on these ideas combines root growth rates with rates of water table and capillary fringe declines to estimate successful establishment sites (Mahoney and Rood, 1998). Utilizing a 2.5 cm/day rate of water table decline combined with *Populus* root growth rates and the thickness of the capillary fringe, Mahoney and Rood (1998) determined that for many *Populus* species, successful establishment would occur at elevations 0.6–2 m above the late summer low flow stream stage. The model was used successfully on the Truckee River in Nevada to promote *Populus* regeneration by regulating rates of water table decline in a controlled flood. This model should have applications in other semi-arid riparian areas around the world, and may be an important tool in conservation and restoration of riparian habitats. However, the model will need calibration for different species and specific stream conditions (Mahoney and Rood, 1998; Shafroth et al., 1998). The estimated survivable rate of ground water decline of 2.5 cm/day used by Mahoney and Rood (1998) may not be applicable in southwestern riparian ecosystems, which are typically much hotter and drier than the systems reviewed in their study. In addition, *Salix gooddingii* Ball has been shown to be more sensitive to changes in ground water availability than the co-occurring *Populus fremontii* S. Wats. (Stromberg, 1993) and grows well in saturated soils (Stromberg, 1997). In contrast, *Tamarix chinensis* Lour. has been reported to be more drought tolerant than native species (Cleverly et al., 1997; Smith et al., 1998) and is able to persist indefinitely in drier soils (Everitt, 1980).

In the Sonoran desert, low elevation (<1250 m) riparian forests were traditionally dominated by *P. fremontii* and *S. gooddingii* (Stromberg, 1993). However, in response to water development, many of these native populations have been invaded and often replaced by the exotic, *T. chinensis*, (Christensen, 1962; Stromberg, 1993; Brock, 1994; Busch and Smith, 1995). Whereas field observational studies have provided insight into the factors that regulate establishment of these southwestern riparian species

(Stromberg, 1993, 1997), more information is needed on the effects of different rates of water table decline on seedling establishment and growth. In this study, we utilized rhizopods (Mahoney and Rood, 1991, 1992) to investigate the effects of differing rates of ground water decline on growth and survival of one important, native riparian tree species, *S. gooddingii*, and one invasive exotic, *T. chinensis*.

2. Materials and methods

Seeds were collected on 16 May 1998 from natural populations of both *S. gooddingii* and *T. chinensis* along the Hassayampa and Bill Williams Rivers in Arizona. Seeds were frozen and stored in the dark in sealed jars containing silica gel desiccant for 7 months until they were germinated.

Rhizopods (see Mahoney and Rood, 1991, 1992 for construction details) were constructed in a greenhouse to simulate alluvial water table decline. Each rhizopod consisted of 15 growth tubes (pods) connected to a central reservoir. Water levels in the pods were controlled by changing the water level in the central reservoir. Rates of ground water decline of 0, 1, 2, and 4 cm/day were used in this experiment. The rates used in this study were based on field observations of alluvial water table dynamics at each river where seeds were collected (J. Horton, unpublished data).

Each growth pod was filled with a 3:1 by volume sand to river gravel mixture to simulate a natural river substrate. Each treatment was applied to one rhizopod; the four rhizopods were identical in design and were all located within a 25 m² area with consistent environmental conditions (irradiance, humidity, and temperature). In each rhizopod, each species (*S. gooddingii* and *T. chinensis*) was grown singularly in seven tubes. The 15th tube was used to measure volumetric water content of the substrate (0–30 cm depth) using time domain reflectometry (Trase System 1, Soil Moisture Corp., Santa Barbara, CA).

Seeds were germinated in a greenhouse on 29 January 1999 (Day 0) in trays of moist sand, transplanted to growth tubes on Day 14, and then thinned to seven seedlings per tube on Day 21. The water table was kept constant during this initial growth period and the treatments were started on Day 25. A 12 h light/dark cycle was maintained with 500 W metal halide

growth lamps. Climate conditions ranged from 17°C/30% relative humidity (RH) at night to 24°C/20% RH in the daytime, which are similar to the range in temperature observed in April at the Bill Williams and Hassayampa Rivers (J. Horton, unpublished data).

Seedling mortality and the plant height of the surviving plants in each pod were typically measured twice weekly. Plants were harvested on Day 67 after water levels in both the 2 and 4 cm/day treatments reached the bottom of the central reservoir. At harvest, seedlings were gently shaken out of each pod and the length of the longest recovered root was measured. Leaf area was measured with an image analysis system (Decagon Devices, Inc, Pullman WA) at harvest. Roots and shoots were oven dried at 70°C for 48 h and then weighed.

Seedling survival and growth characteristics were averaged for each pod and each pod was used as a replicate ($n=7$ for each species \times treatment combination). Data on seedling height and survivorship were analyzed at both the mid-point (Day 46) and the end (Day 67) of the water table manipulations. Total biomass, root length, leaf area, and root-to-shoot ratios were compared after harvest. All comparisons were made with a two-factor analyses of variance with rate of water table decline and species being the two factors. Multiple paired comparisons were performed by Fisher's PLSD tests with a significance level of $p=0.05$ (Statview v 4.5, Abacus Software Inc., Berkeley, CA).

3. Results

There were distinct differences in volumetric soil moisture content (θ_v) at depths of 0–30 cm in the four treatments throughout the course of the water manipulations (Fig. 1). In the 1 cm/day treatment the capillary fringe persisted in the surface soil for 22 days (Day 47) after the water table started declining, after which the surface soil dried more rapidly. In the 2 cm/day treatment this rapid drying phase began after 8 days (Day 33), and had begun by the first measurement (Day 28) in the 4 cm/day treatment.

Halfway through the water manipulations (Day 46), there were significant treatment and species effects on seedling survival (Table 1). The 0 and 1 cm/day treatments had greater survival than the 2 and 4 cm/

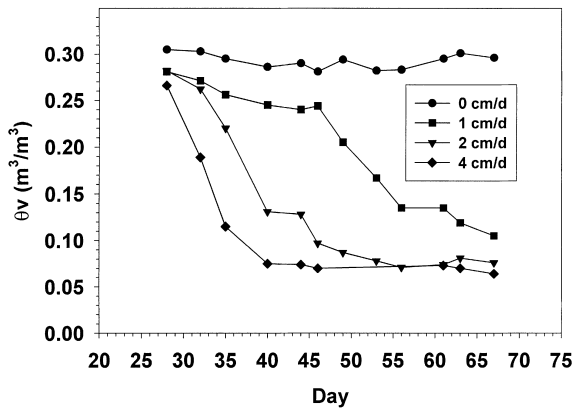


Fig. 1. Soil volumetric water content (θ_v) in the first 30 cm of soil for 42 days of ground water decline at rates of 0, 1, 2, and 4 cm/day.

day treatments for both species (Fig. 2). *Tamarix* had fairly consistent survival across all treatments (86–92%), while *Salix* showed decreasing survival with increasing rate of water table decline; however, the species \times treatment interaction was not significant.

At this time the surviving *Tamarix* seedlings were significantly taller than the surviving *Salix* seedlings in all treatments (Table 1, Fig. 3).

At the time of harvest (Day 67), the trends observed at Day 46 were even more pronounced and there was greater differentiation between the species. In particular, the species \times treatment interaction was significant for both survival and height (Table 1). *Tamarix* survival was fairly consistent across all treatments (80–88%), while *Salix* decreased with increasing rate of ground water decline (Fig. 2). Surviving *Tamarix* seedlings were taller than *Salix* in all treatments (Fig. 3). *Salix* height growth was reduced significantly by all decline treatments, with a greater reduction in the 4 cm/day treatment (64% growth reduction relative to the control) than in the 1 and 2 cm/day treatments (46 and 52%, respectively). In contrast, *Tamarix* height was similar in the 0 and 1 cm/day, while the 2 and 4 cm/day treatments decreased similarly (36 and 40% reductions relative to the control, respectively).

There was a decrease in total plant biomass with increasing rate of water table decline for both species. However, there was a significant species \times treatment

Table 1

Results of a two factor analysis of variance on seedling height and survival at the mid-point of water manipulations (Day 46) and at harvest (Day 67)

Parameter source of variation	d.f	F- value	P- value
Mid-point survival			
Species (S)	1	5.287	0.0259
Treatment (T)	3	3.725	0.0173
S \times T interaction	3	1.984	0.1289
Error	48	MS=598.7 ^a	
Mid-point height			
Species (S)	1	6.756	0.0125
Treatment (T)	3	1.200	0.3202
S \times T interaction	3	1.924	0.1389
Error	48	MS=95.1 ^a	
Harvest survival			
Species (S)	1	7.691	0.0003
Treatment (T)	3	12.890	0.0008
S \times T interaction	3	5.689	0.0020
Error	48	MS=525.7 ^a	
Harvest height			
Species (S)	1	86.076	<0.0001
Treatment (T)	3	15.292	<0.0001
S \times T interaction	3	3.953	0.0136
Error	48	MS=31.3 ^a	

^a Mean squares value.

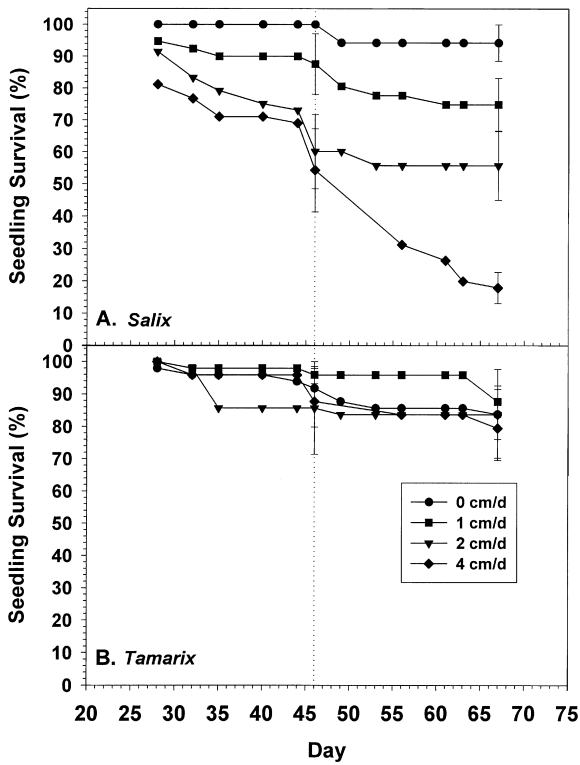


Fig. 2. Seedling survival for *Salix* (A) and *Tamarix* (B) for 42 days of water table decline at rates of 0, 1, 2, or 4 cm/day. Each point represents the mean of seven measurements. The dotted line represents the midpoint of water manipulations (Day 46). Error bars (± 1 standard error of the mean) are included for the mid-point and harvest date measurements.

interaction, suggesting different responses for each species. For *Salix* total biomass had greater reduction in the 4 cm/day treatment (84% reduction relative to the control) than in the 1 and 2 cm/day treatments (42 and 50% reductions, respectively). In contrast, *Tamarix* total biomass was similar in the 0 and 1 cm/day treatments, with significant reductions occurring in the 2 and 4 cm/day treatments (56 and 71%, respectively). Surprisingly, total biomass at harvest was greater for *Salix* than *Tamarix* in all treatments, with greatest biomass in the 0 cm/day treatment (Fig. 4).

Salix also had much greater biomass allocation to roots than *Tamarix* as evidenced by greater root-to-shoot ratios (Fig. 5) and greater root biomass (data not shown) across all treatments. There were no significant treatment or species \times treatment interaction effects on root-to-shoot ratios, suggesting that the

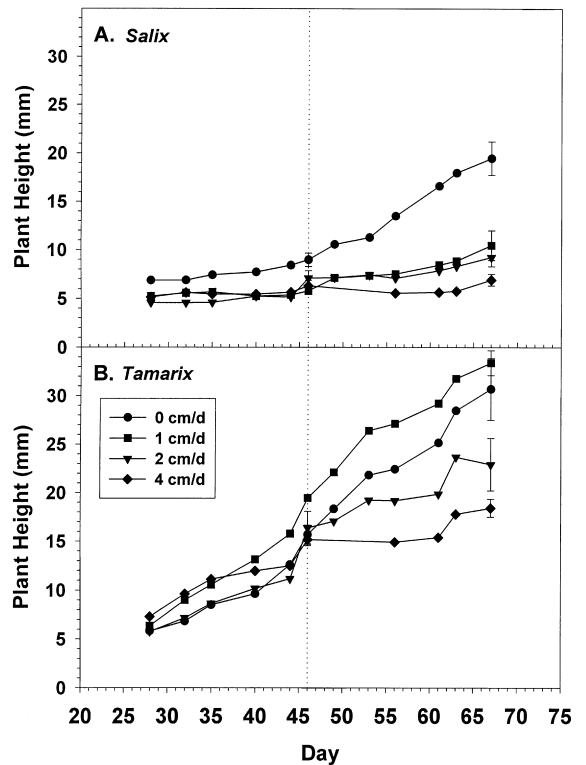


Fig. 3. Seedling height for *Salix* (A) and *Tamarix* (B) for 42 days of water table decline at rates of 0, 1, 2, or 4 cm/day. Each point represents the mean of seven measurements. The dotted line represents the midpoint of water manipulations (Day 46). Error bars (± 1 standard error of the mean) are included for the mid-point and harvest date measurements.

relative allocation to roots was similar in all treatments and was consistently greater for *Salix*. However, root length was greater in *Tamarix* than in *Salix* (Fig. 6). There was a significant species \times treatment interaction, suggesting different responses by each species. *Salix* root length increased in the 1 and 2 cm/day treatments (38 and 32% increases relative to the control, respectively), but decreased in the 4 cm/day treatment (32% reduction relative to the control). *Tamarix* root length increased in all treatments relative to the control with the greatest increase occurring in the 1 cm/day treatment (190%) and lesser increases occurring in the 2 and 4 cm/day treatments (71 and 45%, respectively). Upon harvest, we noticed that *Salix* seedlings in all treatments had much greater lateral root development than *Tamarix*, although lateral root length was not measured.

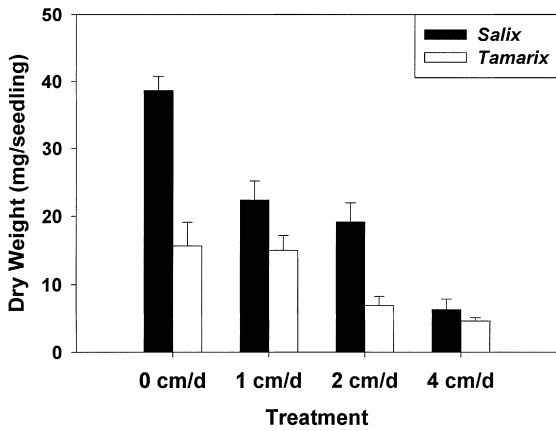


Fig. 4. Total plant biomass at harvest for *Salix* and *Tamarix* seedlings after 42 days of water table decline at rates of 0, 1, 2, or 4 cm/day. Vertical bars represent 1 standard error of the mean. (ANOVA: Species $F=29.0$, $p<0.0001$; Treatment $F=43.1$, $p<0.0001$, $S \times T$ interaction, $F=7.2$, $p=0.0005$).

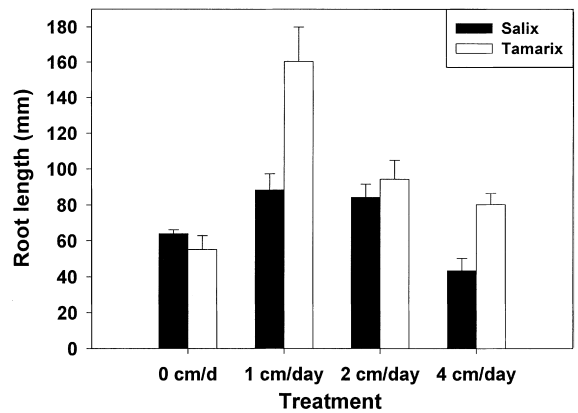


Fig. 6. Root length at harvest for *Salix* and *Tamarix* seedlings after 42 days of water table decline at rates of 0, 1, 2, or 4 cm/day. Vertical bars represent 1 standard error of the mean. (ANOVA: Species $F=18.4$, $p<0.0001$; Treatment $F=15.1$, $p=0.0003$, $S \times T$ interaction, $F=6.2$, $p=0.0012$).

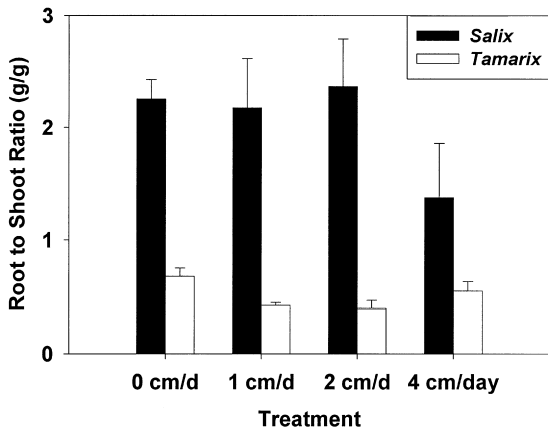


Fig. 5. Root-to-shoot ratios at harvest for *Salix* and *Tamarix* seedlings after 42 days of water table decline at rates of 0, 1, 2, or 4 cm/day. Vertical bars represent 1 standard error of the mean. (ANOVA: Species $F=1.2$, $p=0.31$; Treatment $F=60.3$, $p<0.0001$, $S \times T$ interaction, $F=1.6$, $p=0.21$).

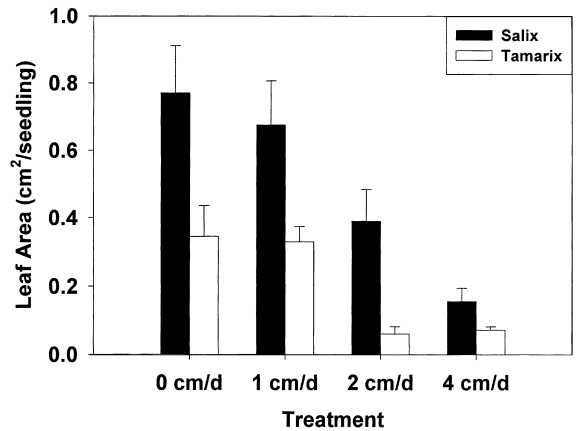


Fig. 7. Projected leaf area at harvest for *Salix* and *Tamarix* seedlings after 42 days of water table decline at rates of 0, 1, 2, or 4 cm/day. Vertical bars represent 1 standard error of the mean. (ANOVA: Species $F=22.3$, $p<0.0001$; Treatment $F=11.5$, $p<0.0001$, $S \times T$ interaction, $F=1.13$, $p=0.29$).

There was no significant species \times treatment effect on projected leaf area and both species showed reduced leaf area with increasing rate of water table decline (Fig. 7). Projected leaf area was greater in *Salix* than in *Tamarix* across all treatments, however, when comparing leaf production on a mass basis, there was no difference between species in any treatment ($p=0.37$).

4. Discussion

It is evident from the results of our experiment that the exotic, *T. chinensis*, is more tolerant of ground water declines than the native, *S. gooddingii*. *Tamarix* is known to be a facultative phreatophyte (Turner, 1974), that is able to use water from the alluvial water table and associated capillary fringe, but that is also

able to extract water and survive indefinitely in unsaturated soils (Everitt, 1980; Busch and Smith, 1995). This attribute was demonstrated by the high survival of *Tamarix* seedlings in all treatments. On the other hand, *Salix* is considered to be an obligate phreatophyte (Turner, 1974) that relies solely on ground water and the associated capillary fringe. As such, *Salix* may require saturated soils but is less tolerant of dry soils (Stromberg, 1993). Stromberg (1997) reported that *Salix* seedlings occurred more frequently in and had highest stem growth in saturated soils compared to drier soils. In drier soils, *Salix* may experience significant water stress which reduces productivity and causes mortality. This pattern was observed in this study for *Salix* with less biomass and greater mortality in the water table decline treatments compared to the 0 cm/day treatment in which the soil was saturated.

It has been reported that *Tamarix* seedlings have slower growth than many native riparian species (Everitt, 1980). Stromberg (1997) reported that, in moist soils, native *Populus* and *Salix* seedlings were taller than *Tamarix* seedlings, although all species were equally short on drier soils, however, in this study, stem elongation was greater in *Tamarix* across all treatments and root elongation was greater (1.3–3.8 mm/day) in the treatments in which the water table decreased. The optimal rate of ground water decline for *Tamarix* growth in this study was 1 cm/day. This optimal rate of ground water decline was also observed in a field study at the Bill Williams River in Arizona, in which *Tamarix* seedling establishment occurred most in areas with a maximum water table decline of 1.2 cm/day (Shafroth et al., 1998).

Even though stem and root elongation were greater in *Tamarix* than in *Salix*, total plant biomass was greater for *Salix* in all treatments. In addition, allocation to roots was greater in *Salix* across all treatments as evidenced by a higher root-to-shoot ratio and total root biomass. This growth pattern may be an adaptation to the areas that *Salix* typically inhabits. Mature *Salix* trees produce seed from late March to mid-June (Stromberg, 1993; Shafroth et al., 1998) after flood waters have receded, and *Salix* seedlings become established near the stream channel (Stromberg, 1993). In one field study, the highest elevation of *Salix* seedling establishment was 78 cm above the mean low water line (Shafroth et al., 1998). At these low positions, the seedlings are closer to the alluvial

water table, but are more likely to experience late season flood scour. Stromberg (1997) reported that *Salix* seedlings are more tolerant of scour than *Tamarix* seedlings. In our study, root growth rates of *Salix* were slow (1.0–2.1 mm/day), even when rates of ground water decline were relatively rapid. Perhaps vertical root growth is slow for *Salix* seedlings because ground water is relatively shallow in its typical habitat. Instead, early development in *Salix* seedlings may emphasize lateral root development in order to anchor the seedlings to protect them from late season scour. This may explain the patterns of root allocation and lateral root development observed in this study, although a more rigorous assessment of lateral root growth is needed. The higher rates of stem growth that have been reported for *Salix*, relative to *Tamarix*, may occur later in the growing season once they are established with ample lateral roots. In field observations from the Hassayampa River, *Salix* seedlings that germinated in mid-April 1998 initially grew slowly reaching heights of 12–47 mm by mid-June, with more rapid stem growth occurring later, with seedlings reaching heights of 50–125 mm by mid-July. In the short duration of this study (67 days), the seedlings may not have entered the stage of rapid stem elongation that has been reported by others for *Salix*. Likewise, leaf area measurements of *Salix* in our study are smaller than those reported for a *Populus* hybrid after 46 days of growth (Mahoney and Rood, 1991). However, *Salix* leaves are more narrow than *Populus* and seedlings would likely have lower leaf area with the same number of leaves. In our study, *Salix* seedlings had between 4 and 6 fully expanded leaves per seedling, similar to the number reported for 46-day old hybrid *Populus* seedlings (Mahoney and Rood, 1991).

In order to manage stream flow to promote the establishment of native riparian trees, appropriate timing between seed dispersal and the generation of safe germination sites with adequate soil moisture is needed (Everitt, 1980). Flows should peak before the onset of seed production of native species (late March for *Salix*) and then subside creating germination sites as the seeds are dispersed (Stromberg, 1997). *Tamarix* produces seeds later than native *Populus* and *Salix*, but produces them for a longer period of time with a bimodal distribution pattern (Warren and Turner, 1975). Seed production for *Tamarix* begins in April or May with a peak in mid-June and a smaller peak in

August and continues until September or October (Everitt, 1980; Shafroth et al., 1998). For successful establishment, *Tamarix* needs moist, open sites (Everitt, 1980) as it does not establish well in areas with high vegetative cover (Everitt, 1980; Stromberg, 1997; Shafroth et al., 1998). However once established, *Tamarix* seedlings are better able to survive water stress induced by low flows, and would be more likely to persist until water is more available than *Salix* seedlings. This may be one mechanism, by which *Tamarix* successfully invades disturbed riparian ecosystems.

4.1. Implications for managed flow regimes

There is interest in ‘naturalizing’ flow regimes in managed river systems to promote the establishment of native riparian vegetation for conservation and restoration of these important habitats (Stromberg, 1997; Poff et al., 1997; Mahoney and Rood, 1998; Shafroth et al., 1998). Conceptual models, like the ‘recruitment box’ model of Mahoney and Rood (1998), may be utilized to determine the flows necessary to encourage native and discourage exotic regeneration. However, to effectively export this model to different systems and different species, it is first necessary to determine the establishment requirements of those species in the context of the stage discharge characteristics of the system (Mahoney and Rood, 1998; Shafroth et al., 1998). Seed production phenology, root growth rates, tolerance of drought, inundation, and scour are all characteristics that need to be understood for each species in order for managed flow regimes to be successful. In our study, both species had much slower root growth rates (1.0–2.1 mm/day for *Salix* and 1.3–3.8 mm/day for *Tamarix*) than the *Populus* species reviewed by Mahoney and Rood (1998). *Salix* had greater lateral root development than the exotic, *Tamarix*, which may make it more resistant to flood scour, but its slower root growth make it more susceptible to water stress induced by rapid water table decline. *Tamarix*, had lower biomass productivity, but had a higher rate of root elongation than *Salix*, allowing it to persist in dry soils under rapid rates of water table decline where most of the native *Salix* seedlings died. Regeneration of *S. gooddingii* may benefit by considering the pronounced difference in survival and growth response

to water table decline between this species and the invasive exotic, *T. chinensis*.

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