

WOODY RIPARIAN VEGETATION RESPONSE TO DIFFERENT ALLUVIAL WATER TABLE REGIMES

Patrick B. Shafroth^{1,2}, Juliet C. Stromberg¹, and Duncan T. Patten¹

ABSTRACT.—Woody riparian vegetation in western North American riparian ecosystems is commonly dependent on alluvial groundwater. Various natural and anthropogenic mechanisms can cause groundwater declines that stress riparian vegetation, but little quantitative information exists on the nature of plant response to different magnitudes, rates, and durations of groundwater decline. We observed groundwater dynamics and the response of *Populus fremontii*, *Salix gooddingii*, and *Tamarix ramosissima* saplings at 3 sites between 1995 and 1997 along the Bill Williams River, Arizona. At a site where the lowest observed groundwater level in 1996 (–1.97 m) was 1.11 m lower than that in 1995 (–0.86 m), 92–100% of *Populus* and *Salix* saplings died, whereas 0–13% of *Tamarix* stems died. A site with greater absolute water table depths in 1996 (–2.55 m), but less change from the 1995 condition (0.55 m), showed less *Populus* and *Salix* mortality and increased basal area. Excavations of sapling roots suggest that root distribution is related to groundwater history. Therefore, a decline in water table relative to the condition under which roots developed may strand plant roots where they cannot obtain sufficient moisture. Plant response is likely mediated by other factors such as soil texture and stratigraphy, availability of precipitation-derived soil moisture, physiological and morphological adaptations to water stress, and tree age. An understanding of the relationships between water table declines and plant response may enable land and water managers to avoid activities that are likely to stress desirable riparian vegetation.

Key words: groundwater, riparian habitat, *Populus*, *Salix*, *Tamarix*, Arizona, root distribution.

Although surface water flows and associated fluvial processes exert strong influences on woody riparian establishment in arid and semi-arid regions (Stromberg et al. 1993, Scott et al. 1996), the alluvial groundwater and associated capillary fringe and unsaturated zone are water sources upon which many riparian plants rely for most of the year (Busch et al. 1992, Kolb et al. 1997, Snyder et al. 1998). The importance of alluvial groundwater is pronounced in intermittent or ephemeral streams and in regions with little precipitation, such as the southwestern United States (Robinson 1958, Snyder et al. 1998). The need for high water tables (often <1.5 m from the ground surface) for successful seedling establishment of woody riparian plants has been observed at numerous sites (Mahoney and Rood 1998) and experimentally demonstrated for *Populus* (Mahoney and Rood 1991, 1992, Segelquist et al. 1993). In addition, mature riparian trees and shrubs are often associated with water tables <3 m deep (Stromberg et al. 1996).

Floodplain water tables can fluctuate considerably over time, resulting from a variety of natural and anthropogenic phenomena. Natural

variability in stream flow and evapotranspiration can result in intra- and interannual changes in alluvial water tables. Fluvial processes such as channel incision or bed aggradation may also cause groundwater regimes to change. Human activities such as groundwater pumping, surface flow diversion, or in-stream sand and gravel mining may lead to declines in riparian water tables (Groeneveld and Griepentrog 1985, Stromberg et al. 1992, Stromberg and Patten 1996, Kondolf 1997).

Water table declines can reduce riparian plant growth and potentially lead to mortality (Scott et al. 1999). Declines in alluvial water tables also may change the distribution and abundance of different riparian plant associations, which tend to thrive under different groundwater conditions (Bryan 1928, Stromberg et al. 1996). Of particular research and management interest are conditions influencing the relative abundance of dominant woody floodplain species, including native *Populus* and *Salix* spp. and exotic *Tamarix* spp. *Populus* and *Salix* require relatively shallow groundwater and are sensitive to drought associated with groundwater declines (Busch et al. 1992,

¹Department of Plant Biology, Arizona State University, Tempe, AZ 85287-1601.

²Present address: United States Geological Survey, Midcontinent Ecological Science Center, Fort Collins, CO 80525-3400.

Tyree et al. 1994, Smith et al. 1998, Scott et al. 1999). *Tamarix* is reported to be more tolerant of water stress than *Populus* or *Salix* (Busch and Smith 1995, Cleverly et al. 1997, Devitt et al. 1997, Smith et al. 1998), and therefore it should be able to survive where water tables are relatively deep. There are also likely critical water table depths beyond which given sized individuals of a given species cannot survive (Graf 1982).

Despite the importance of alluvial water table conditions to riparian vegetation, little is known about how established plants respond to different magnitudes, rates, and durations of groundwater decline. Quantifying plant response to changing water table conditions may result in identification of stress or mortality thresholds and hence aid efforts to manage land use and stream flow in ways that minimize impacts to groundwater and promote survival of desirable riparian species. Few studies in western riparian ecosystems have reported a plant response to measured water table declines (Condra 1944, Judd et al. 1971, Stromberg et al. 1992, Devitt et al. 1997, Scott et al. 1999). The objective of our study was to add to this sparse database by quantifying the response of 3 woody riparian species to different water table dynamics and to clarify factors that are likely to be important in determining plant response. We examined growth and survival of saplings of *Populus fremontii*, *Salix goodingii*, and *Tamarix ramosissima* at 3 sites with different groundwater regimes over a 3-yr period along the Bill Williams River in western Arizona.

STUDY AREA

The Bill Williams River drains approximately 13,700 km², with headwaters in the Central Highlands region of central Arizona at approximately 1830 m, and downstream reaches in the Sonoran Basin and Range Province in west central Arizona. Beginning at the confluence of the Big Sandy and Santa Maria rivers, the Bill Williams River flows for approximately 70 km. The upstream-most 6.5 km now consists of waters impounded behind Alamo Dam, which was completed in 1968. Downstream of the dam the Bill Williams River flows 63 km to its confluence with the Colorado River (now Lake Havasu) at an elevation of 137 m. Variation in the depth of alluvium results in a mix of reaches with perennial and seasonally intermittent

flow. Average annual precipitation along the river ranges from approximately 22 cm near Alamo Dam (National Climatic Data Center stations; Alamo Dam 6ESE and Alamo Dam) to 13 cm near the Colorado River (National Climatic Data Center station; Parker 6NE). Mean annual flow in the Bill Williams River is approximately 3.5 m³ s⁻¹ (1941–1996; U.S. Geological Survey Gaging Station #09426000). Flow regulation by Alamo Dam has dramatically reduced flood peaks and in recent years has increased low flows (Shafroth et al. 1998). Riparian vegetation along the Bill Williams River is dominated by several woody species common to low-elevation southwestern riparian ecosystems, including *Populus fremontii* S. Watson (Fremont cottonwood), *Salix goodingii* Ball (Goodding willow), *Tamarix ramosissima* Ledebour (saltcedar), *Baccharis salicifolia* (R. & P.) Pers. (seep willow), and *Prosopis* spp. (mesquite).

METHODS

In April 1995 we selected 8 sites along the Bill Williams River as part of a larger study (Shafroth et al. 1998). The sites were subjectively selected to represent a range of geomorphologic and vegetative conditions. For the present study we examined 3 of these sites (BW1, BW5, BW7). At each site a cross-valley transect was established perpendicular to the stream channel, and different patches of vegetation were identified along the transect based on a combination of overstory dominance and geomorphologic setting. For this study we examined patches that contained seedlings and saplings of *Populus*, *Salix*, and *Tamarix* that became established between 1993 and 1995 (age determined by counts of annual rings; Shafroth et al. 1998). Seedling patches were those containing plants that became established in 1995, saplings in 1993–94. The number of seedling and sapling patches per transect was variable and included 2 patches along BW1 and 4 patches along BW5 and BW7. Within each patch we randomly located a 5 × 20-m quadrat and in January 1996 measured the diameter of all saplings in the quadrat. During summer 1996, wilting, chlorosis, and apparent shoot mortality of woody plants were observed at 1 of the sites (BW5). To quantify the response, we resampled stem densities in the 2 sapling quadrats at BW5 in October

1996. In December 1997 these sapling quadrats were again resampled and 2 quadrats containing 1995 cohorts were also sampled. In December 1997 quadrats with plants of the same age as those at BW5 were also resampled at 2 other sites (BW1, BW7) that had groundwater dynamics different from those at BW5. At each site a representative *Populus fremontii* sapling was excavated in December 1997, its root distribution sketched, and the soil stratigraphy of the excavated pit described.

Sandpoint wells were installed at each site in April 1995 and used to measure the depth to groundwater approximately monthly through October 1997. To obtain relative elevations of the quadrats and monitoring wells, we surveyed the topography of each transect in January 1996. Soil samples were collected from 2 depths at each quadrat: 0–30 cm and 30–60 cm below ground surface. The proportion of each sample in 5 particle size classes was determined by (1) visual estimation in the field for particles >2 cm median dimension, (2) sieving for particles >2 mm and <2 cm, and (3) hydrometer method for sand, silt, and clay (Day 1965). Electrical conductivity (dS m⁻¹) of the filtered solution from a 1:1 soil:water slurry was determined with a Beckman Instruments conductivity probe.

Groundwater level measurements were summarized as follows: measured depths through time, maximum depth to the water table for each year, and difference between the deepest water table level in 1995 and deepest levels in 1996 and 1997. Changes in stem density and basal area between January 1996 and December 1997 were calculated and expressed as percentages of the January 1996 measurements. To assess correlations between plant response and groundwater level change, we conducted simple linear regression analysis with change in stem density and basal area for both *Populus/Salix* and *Tamarix* as dependent variables and change in groundwater level as the independent variable.

RESULTS

At site BW1 the water table had regular intra-annual fluctuations, with observed differences between annual high and low water tables ranging from 1.51 to 2.10 m (Fig. 1a). The maximum depth to water where saplings at BW1 survived was -2.91 m. The lowest

water table levels in 1996 (-2.55) and 1997 (-2.91) were 0.44 and 0.80 m deeper than the lowest water table level in 1995. Soil texture at BW1 ranged from strata containing principally coarse and medium sands to strata with large quantities of organic material and silt (Fig. 1b). Electrical conductivity ranged from 0.7 to 1.6 dS m⁻¹. At BW1 the 1997 rooting depth was approximately -1.40 m, where a flare of roots spread atop a soil layer rich in organic material and silt (Fig. 1b). Coarse roots also occurred at other locations throughout the soil column. Because of large fluctuations in the water table, most roots were inundated for part of the year and were well above the water table at other times.

At BW1 *Populus* and *Salix* sapling densities declined 88–89% between January 1996 and December 1997. However, basal area of these species increased 110–160% over the same period. *Tamarix* stem density at BW1 decreased 50%, while its basal area increased 16%. In December 1997 the mean $\pm s_{\bar{x}}$ density of *Populus/Salix* and *Tamarix* was 70 ± 55 and 28 ± 23 stems 100 m⁻², respectively ($n = 2$). The mean $\pm s_{\bar{x}}$ basal area was 3.46 ± 2.64 cm² 100 m⁻² for *Populus/Salix* and 3.23 ± 3.07 cm² 100 m⁻² for *Tamarix* ($n = 2$).

At site BW5 the water table was relatively high and stable throughout 1995 (ca -0.80 m), but the lowest water tables in 1996 and 1997 were 1.11 and 2.28 m deeper than in 1995 (Fig. 2a). Quadrats containing saplings at this site were 1.55–1.97 m and 2.72–3.14 m above the lowest water table in 1996 and 1997, respectively. Soils at BW5 primarily comprised sands and secondarily gravels (Fig. 2b); electrical conductivity ranged from 0.3 to 1.5 dS m⁻¹. At BW5 the excavated sapling was rooted to a depth of -0.65 m in 1997, and the majority of root biomass was distributed between -0.45 and -0.60 m (Fig. 2b), or 0.14–0.41 m above the high water tables observed between 1995 and 1997.

Populus and *Salix* saplings at BW5 experienced a 92–100% reduction in stem density between January and October 1996. By December 1997 no *Populus* or *Salix* individuals were alive in the quadrats, and only scattered, older trees survived in the transect vicinity. In the 2 sapling quadrats at BW5, *Tamarix* stem density declined 0–13% by October 1996. By December 1997 stem density in 1 quadrat increased by 105%, while in the other it

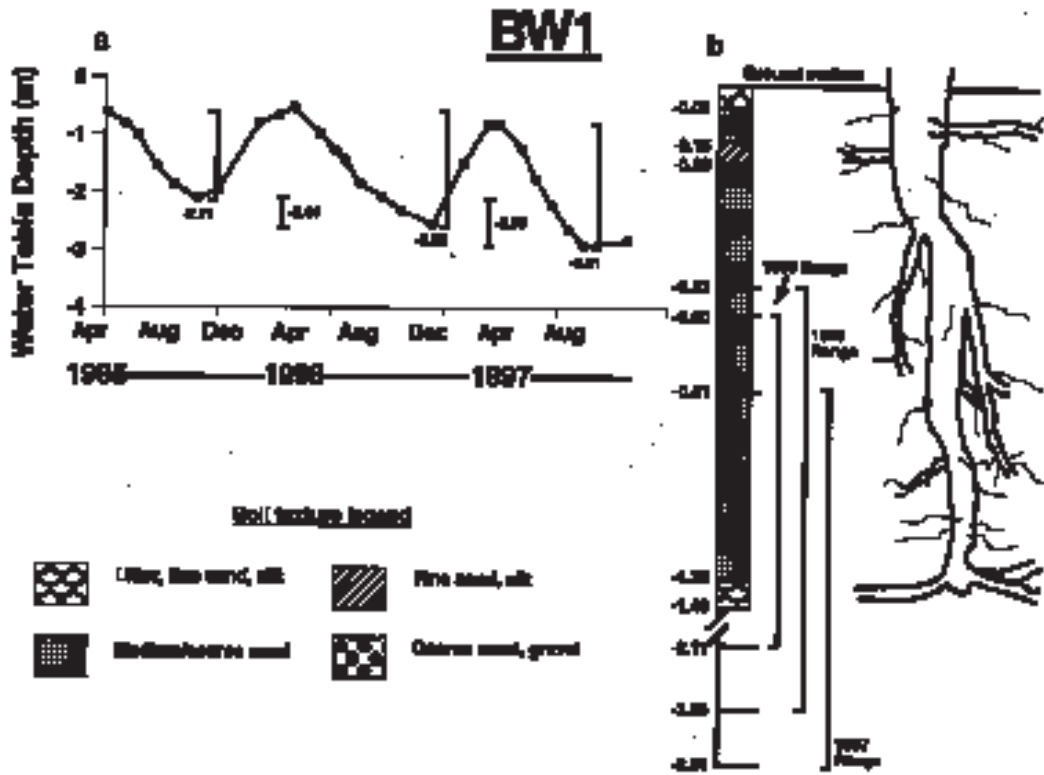


Fig. 1. Groundwater dynamics and *Populus fremontii* sapling root architecture at site BW1, Bill Williams River, Arizona: a, BW1 water table levels, measured approximately monthly from April 1995 through October 1997. Solid vertical bars depict annual water table level range, with lowest observed water table depth noted below the bar. Hashed vertical bars depict water table decline, defined as the difference between lowest observed water table depth in 1995 and lowest observed in 1996 and 1997. b, Root architecture of a *Populus fremontii* sapling at site BW1. Annual water table level range is shown for years 1995–1997. Also shown is the soil profile where the sapling was excavated.

decreased to 48% of the January 1996 level. Basal area of *Tamarix* in 1997 increased 300% in 1 quadrat and decreased 33% in the other, though the absolute changes were small. By December 1997 only *Tamarix* survived at relatively low stem densities and basal area. Its mean $\pm s_{\bar{x}}$ density was 55 ± 39 stems 100 m^{-2} , and mean $\pm s_{\bar{x}}$ basal area was $0.57 \pm 0.48 \text{ cm}^2 100 \text{ m}^{-2}$ ($n = 4$).

The water table at site BW7 was high and stable throughout the study period (ca -0.40 m), except for a decline of 0.66 m in June and July 1997 (Fig. 3a). Even with this drop, the water table was relatively high and was only 0.44 m lower than the lowest water table in 1995 (-0.38 m) and no more than 0.82 m below the ground surface of a quadrat containing saplings. Soil texture at BW7 was the coarsest, with the proportion of gravel almost

equal to that of sand in most samples. Soil electrical conductivity ranged from 0.2 to 0.5 dS m^{-1} . At BW7 roots were much shallower, reaching a depth of only -0.20 m (Fig. 3b), always within 0.12 m of the annual high water table level. Where excavated, these roots were of large diameter and had spread laterally.

At BW7 only *Salix* and *Tamarix* were present in the sapling quadrats. Stem density of *Salix* decreased 57%, while *Tamarix* stem density varied from a 48% decrease to a 400% increase. *Salix* basal area increased 201%, while *Tamarix* basal area increased 43–78%. The December 1997 mean $\pm s_{\bar{x}}$ density of *Salix* and *Tamarix* was 27 ± 18 and 176 ± 83 stems 100 m^{-2} , respectively ($n = 4$). For *Salix* the mean $\pm s_{\bar{x}}$ basal area was $10.58 \pm 4.94 \text{ cm}^2 100 \text{ m}^{-2}$ and for *Tamarix* it was $2.87 \pm 1.14 \text{ cm}^2 100 \text{ m}^{-2}$.

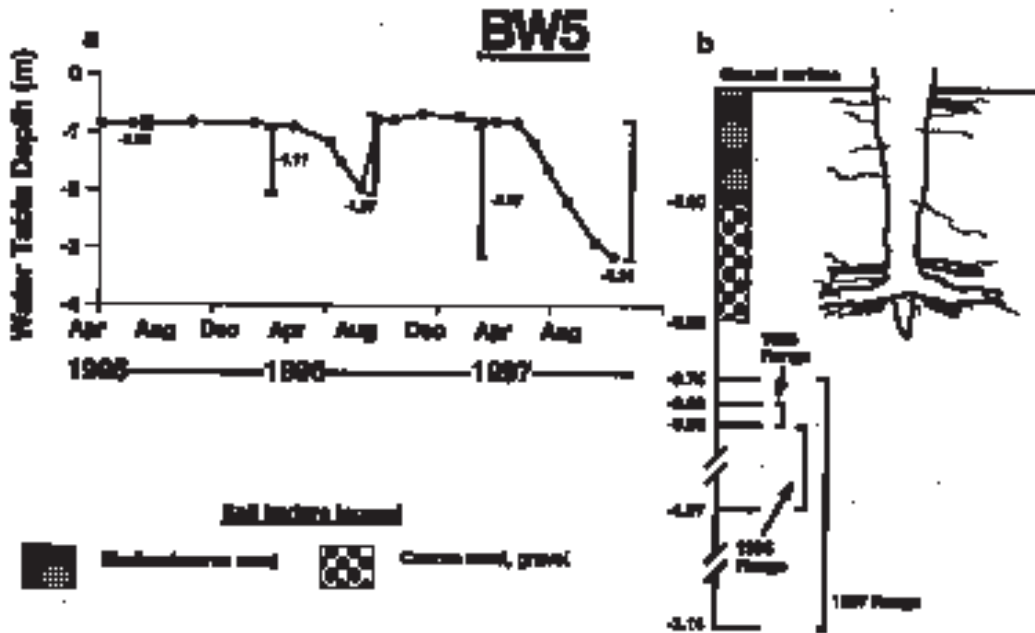


Fig. 2. Groundwater dynamics and *Populus fremontii* sapling root architecture at site BW5, Bill Williams River, Arizona. Details of a and b are as described in Figure 1.

Change in stem density between sampling dates decreased in linear fashion with the change in water table depth (defined as the maximum annual decline from the lowest water table level observed in 1995) for *Populus* and *Salix* (Fig. 4a, $r^2 = 0.65$, $P = 0.05$, df error = 4), but not for *Tamarix* (Fig. 4c, $r^2 = 0.04$, $P = 0.74$, df error = 3). Stem density of *Populus* and *Salix* decreased in all sampled quadrats (Fig. 4a), whereas *Tamarix* stem density increased in some quadrats (Fig. 4c). Change in basal area was also negatively correlated with change in water table depth for *Populus* and *Salix* (Fig. 4b, $r^2 = 0.99$, $P < .01$, df error = 4), but not for *Tamarix* (Fig. 4d, $r^2 = 0.12$, $P = 0.56$, df error = 3). Basal area of *Populus* and *Salix* increased between January 1996 and December 1997, except at BW5 where all plants died (Fig. 4b). Basal area of *Tamarix* increased in 4 of 5 measured quadrats between January 1996 and December 1997 (Fig. 4d).

DISCUSSION

Almost complete mortality of *Populus* and *Salix* saplings was observed following a groundwater decline of 1.11 m (from lowest level in 1995 to lowest level in 1996) in soils

composed largely of sand and gravel, and complete mortality followed a decline of 2.28 m in the subsequent year (from lowest level in 1995 to lowest level in 1997; site BW5). Where groundwater declines were smaller, decreases in *Populus* and *Salix* density were smaller and basal area increased. In contrast to *Populus* and *Salix*, some *Tamarix* individuals survived under all conditions and basal area increased in 80% of the measured quadrats. Decreases in stem density are typical as a stand of young trees ages and, except where complete mortality is observed, should be interpreted in conjunction with basal area measurements. For example, where plots were subjected to a groundwater change of 0.44–0.80 m, *Populus* and *Salix* density decreased 52–89% but basal area increased 200–300% (Figs. 4a, 4c).

These results are consistent with previous studies that documented lethal effects of groundwater declines on *Populus*, but not on *Tamarix*. Scott et al. (1999) observed high mortality of mature *Populus deltoides* ssp. *monilifera* trees in eastern Colorado following a sustained groundwater decline of 1.12 m, and reduced branch growth where water tables declined by 0.47 m. Condra (1944) reported mortality of shallow-rooted *Populus*, *Fraxinus*,

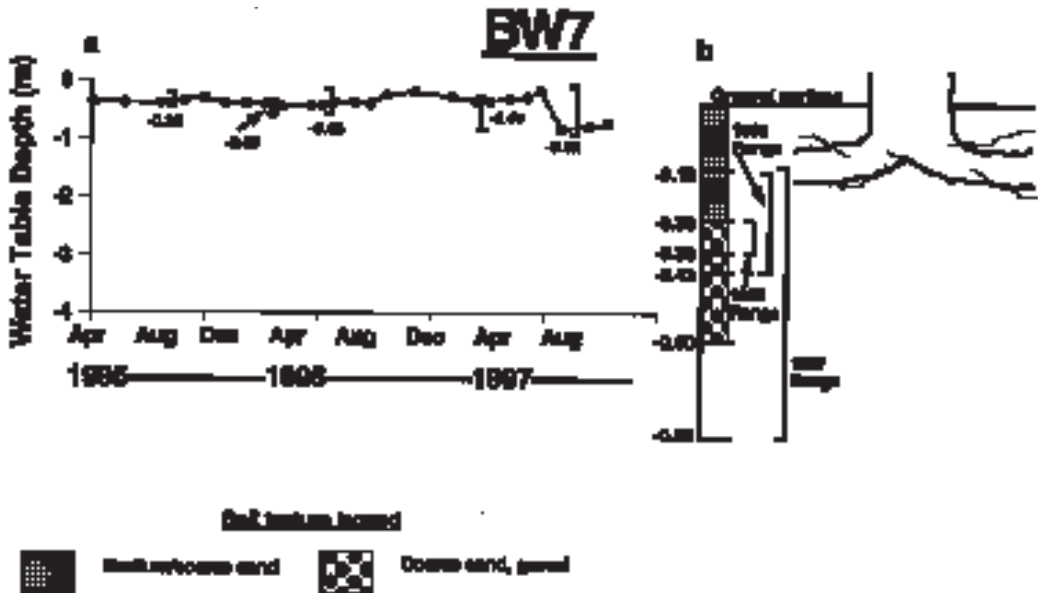


Fig. 3. Groundwater dynamics and *Populus fremontii* sapling root architecture at site BW7, Bill Williams River, Arizona. Details of a and b are as described in Figure 1.

and *Acer negundo* trees along the Platte River following water table declines of 0.61–0.91 m in coarse soils. Two-year-old *Tamarix* survived a water table decline (0.9 m) that stranded roots above moist soil for 30 d; roots resumed growth immediately following rewetting (Devitt et al. 1997). Differential survival of *Tamarix* vs. *Populus/Salix* at site BW5 corroborates reports that greater tolerance of water stress can lead to *Tamarix* dominance on relatively dry, riparian sites (Smith et al. 1998, Stromberg 1998).

Results of this study suggest the importance of *change* in groundwater depth relative to a previous condition or pattern as opposed to the absolute depth to the water table. For example, saplings at site BW1 survived where the depth to the alluvial water table was –2.91 m and their basal area increased, whereas almost no saplings at site BW5 survived at water table depths of –1.55 to –1.97 m (1996), and none survived where water table depths were –2.72 to –3.14 m (1997). By contrast, the change in water table was 1.11 m (1996) and 2.38 m (1997) at BW5 vs. 0.48 m (1996) and 0.8 m (1997) at BW1. Water content of *Tamarix* cladophylls did not vary on plants growing at sites with different depths to the water table in New Mexico (range of ca 1–3 m; Wilkinson

1972). However, studies of *Prosopis velutina* in southwestern riparian ecosystems suggest that the absolute water table depth may effectively determine the expression of various physiological and morphological traits (Stromberg et al. 1992). At 2 sites along the Bill Williams River, Busch and Smith (1995) reported that leaf number, leaf area, specific leaf area, and stem elongation of *Populus fremontii* were greater at the site with relatively high and stable water tables.

We propose that the importance of change from a previous groundwater depth is due to the influence of groundwater history on root architecture. Root architecture has been shown to be a function of soil moisture conditions and water table depth in *Populus* and *Salix* in Nebraska (Sprackling and Read 1979) and *Tamarix* in Arizona (Gary 1963). At site BW1, where relatively large fluctuations in groundwater levels are the norm, *Populus* saplings were rooted relatively deeply, with a somewhat broad depth distribution of coarse roots. At sites BW5 and BW7, roots were distributed largely in a flare above, but near, the annual high water table, suggesting that water tables were stable in the early years of plant growth. When groundwater levels dropped in 1996 and

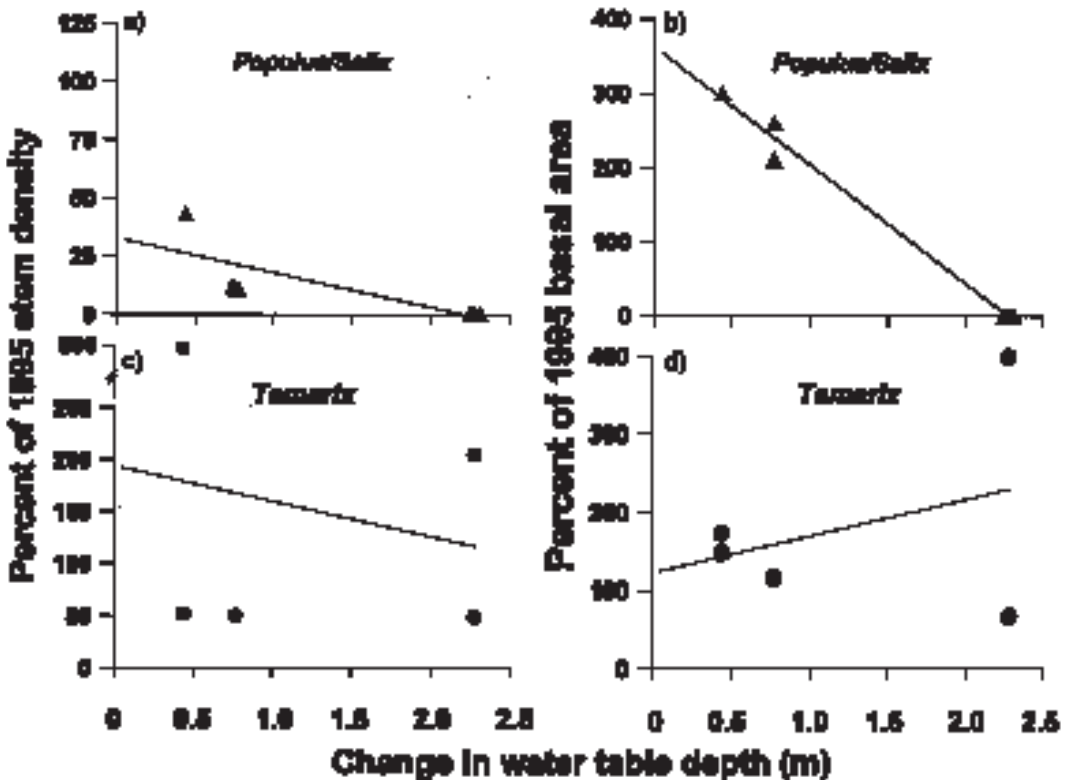


Fig. 4. Change in stem density and basal area of stands of saplings as a function of change in annual low water table level. Lines are from linear regression analysis: a, stem density of *Populus* and *Salix*; density change = $32.8 - 14.9^*$ (water table change; $r^2 = 0.65$, $P = 0.05$, df error = 4); b, basal area of *Populus* and *Salix*; basal area change = $362.6 - 159.2^*$ (water table change; $r^2 = 0.99$, $P < .01$, df error = 4); c, stem density of *Tamarix*; density change = $194.0 - 33.9^*$ (water table change; $r^2 = 0.04$, $P = 0.74$, df error = 3); d, basal area of *Tamarix*; basal area change = $122.5 + 46.8$ (water table change; $r^2 = 0.12$, $P = 0.56$, df error = 3).

1997 at BW5, roots apparently were stranded well above the water table, resulting in shock to the plants.

Plant response to water table level change is mediated by soil water retention, which is largely a function of soil texture and stratigraphy. Trees growing in finer-textured soils may survive greater water table changes than trees growing in coarser soils (Condra 1944). Cooper et al. (1999) have noted the importance of fine-textured soils for the survival of *Populus* seedlings that have not yet tapped the alluvial water table. Stratification of the soil profile may result in retention of significant quantities of water where a finer-textured layer lies above a coarse layer (Brady 1990). This effect may explain how saplings at site BW1 survived with their deepest roots more than 1.5 m above the lowest water table, as many of

these roots are located at a layer of fine sediments and organic matter which likely retains excess water even when the water table has dropped to a lower level (Fig. 1). Water retained above a clay lens at a site in the Carmel River valley, California, apparently enabled trees to maintain relatively vigorous growth, despite a groundwater change in excess of 2.5 m (J.G. Williams personal communication; Fig. 5). Relatively little water can be retained in coarser soils found at BW5, which likely contributed to mortality observed there. Textural differences alone do not determine water availability, however, and better estimates can be obtained with measures of soil water potential.

Species differences in morphological and physiological above- and belowground adjustments to reduced soil moisture should result

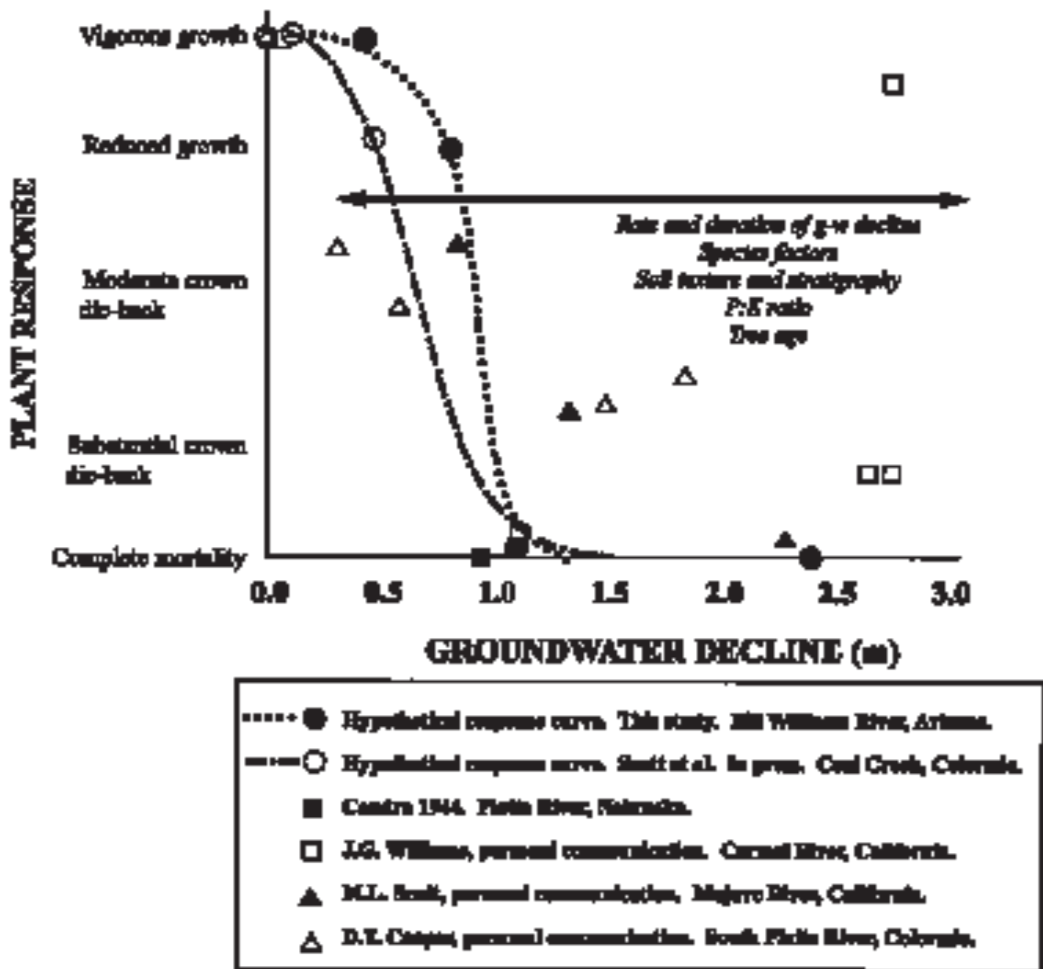


Fig. 5. Conceptual model of woody riparian plant response to water table decline. Plant response (y -axis) scale is semi-quantitative and represents a gradient of growth and morphological responses. Position of plotted points on y -axis is estimated. Groundwater decline (x -axis) refers to a change in groundwater from a previous, presumably consistent, condition or dynamic. All plotted points are responses of either *Populus* or *Salix* spp. Lines are hypothetical response curves for data from this study and another. In this conceptual model hypothetical response curves would shift position along the x -axis and their slopes could be altered, depending on different combinations of groundwater decline rate and duration, species, soil texture, precipitation:evaporation ratio, and tree age.

in differential survival or growth following a groundwater decline. At site BW5, some *Tamarix* individuals survived and increased in size, whereas all *Populus* and *Salix* died. Devitt et al. (1997) reported *Tamarix* survival following a depth and duration of water table decline similar to that observed at BW5. *Tamarix* has been shown to have greater water-use efficiency than *Populus* or *Salix* and can maintain high rates of photosynthesis at relatively low water potentials (Busch and Smith 1995, Cle-

erly et al. 1997), whereas *Populus* is vulnerable to cavitation at relatively high water potentials (Tyree et al. 1994). Additionally, whereas *Populus* and *Salix* may reduce leaf area in response to dry conditions (Smith et al. 1991, Busch and Smith 1995), *Tamarix* can maintain high leaf areas under these conditions (Sala et al. 1996, Cleverly et al. 1997). The ability of plants to grow new roots to respond to groundwater declines is not well understood but would likely be effective only where water table changes

are gradual (Groeneveld and Griepentrog 1985, Mahoney and Rood 1991, Segelquist et al. 1993).

Species differences in dependence on groundwater may influence response to water table declines. Plants that rely on precipitation-derived soil water for some of their water supply (facultative phreatophytes) may experience a reduction only in leaf area or crown volume in some situations that are lethal to plants that must maintain root contact with the groundwater or capillary fringe (obligate phreatophytes). Similarly, facultative phreatophytes should be able to survive a given water table decline for a longer duration than obligate phreatophytes. There appears to be mixed evidence in the literature for the phreatophytic status of *Populus*, *Salix*, and *Tamarix*. There is some evidence that *Tamarix* is a facultative phreatophyte (Busch et al. 1992), although it has been observed to use only groundwater where this was readily available (McQueen and Miller 1972). *Populus fremontii* on the Bill Williams River has been shown to be dependent on groundwater (Busch et al. 1992), though it may be considered a facultative phreatophyte when including the full range of its growing sites (McQueen and Miller 1972, Snyder et al. 1998). *Salix gooddingii* has been reported to be an obligate phreatophyte (McQueen and Miller 1972, Busch et al. 1992), although it is apparently more drought tolerant than *P. fremontii* (Busch and Smith 1995).

Climatic variables such as precipitation, temperature, and humidity will also influence plant response to water table decline. The degree to which plants use precipitation-derived soil water depends in part on reliability and quantity of precipitation and is therefore probably more common in regions or at elevations with higher precipitation. Detrimental effects of water table declines may be mitigated where precipitation occurs and plants have roots near the surface. Climatic factors are also important determinants of transpirational demand (via temperature, humidity). Consequently, in especially hot and dry settings such as low-elevation sites in western Arizona, the lethal duration of water table decline of a given magnitude is likely to be much shorter than at sites where plants can utilize precipitation and where lower temperatures

and more humid conditions result in lower transpirational demand.

CONCLUSIONS

The impact of a particular water table decline depends on several interacting factors that influence both water uptake and water demand. These factors include magnitude of groundwater decline relative to the pre-decline distribution of roots, rate of decline, duration of decline, ability of soil to retain water following the decline, ability of the plant to grow new roots to adjust to lowered water table, ability of the plant to adjust water demand (e.g., via physiological and morphological adaptations), plant age and size, transpirational demand, and importance of other sources of water (e.g., precipitation) to the overall plant water supply. We synthesize these variables into a conceptual model of woody riparian plant response to water table decline in Figure 5. We have drawn hypothetical response curves for our data and another study (Scott et al. 1999) that span the plant response range from vigorous growth to complete mortality. The basic shape of these curves may apply to other situations and species, but the position on the x-axis and the slope of the response curves may vary depending upon the particular combination of rate and duration of groundwater decline, species attributes, soil texture and stratigraphy, climate and tree age (Fig. 5).

Future research incorporating more of the variables discussed above would provide a better understanding of how particular magnitudes, rates, and durations of alluvial groundwater decline will influence woody riparian vegetation in arid and semiarid regions. Such research could have important management implications. For example, on the Bill Williams River, flows from Alamo Dam upstream of our sites could be managed to promote survival of desirable species. This could be accomplished by intentionally varying flows in early years following an establishment event to promote deeper root growth and hence less vulnerability to lower water tables during inevitable dry periods. Another stream flow management option would be to release a mid- to late-summer pulse to resaturate the soil column and raise water tables. Such summer pulses commonly occurred prior to the construction of Alamo Dam in association with monsoonal

precipitation, but they have been virtually eliminated since completion of the dam. Other human activities that impact alluvial water table levels throughout western North America such as groundwater pumping and sand and gravel mining could be managed to ensure that water tables do not fall at rates and magnitudes likely to kill existing stands of riparian vegetation.

ACKNOWLEDGMENTS

This manuscript benefited from reviews by G.T. Auble, D.E. Busch, J.M. Friedman, T.E. Kolb, J.L. Horton, M.L. Scott, S.D. Smith, and an anonymous reviewer.

LITERATURE CITED

- BRADY, N.C. 1990. The nature and properties of soils. 10th edition. MacMillan, New York.
- BRYAN, K. 1928. Change in plant associations by change in ground water level. *Ecology* 9:474–478.
- BUSCH, D.E., N.L. INGRAHAM, AND S.D. SMITH. 1992. Water uptake in woody riparian phreatophytes of the southwestern United States: a stable isotope study. *Ecological Applications* 2:450–459.
- BUSCH, D.E., AND S.D. SMITH. 1995. Mechanisms associated with decline of woody species in riparian ecosystems of the southwestern U.S. *Ecological Monographs* 65:347–370.
- CLEVERLY, J.R., S.D. SMITH, A. SALA, AND D.A. DEVITT. 1997. Invasive capacity of *Tamarix ramosissima* in a Mojave Desert floodplain: the role of drought. *Oecologia* 111:12–18.
- CONDRA, G.E. 1944. Drought, its effects and measures of control in Nebraska. *Nebraska Conservation Bulletin* 25. Lincoln, NE. 43 pp.
- COOPER, D.J., D.M. MERRITT, D.C. ANDERSEN, AND R.A. CHIMNER. 1999. Factors controlling the establishment of Fremont cottonwood seedlings on the upper Green River, USA. *Regulated Rivers* 15:419–440.
- DAY, P.R. 1965. Particle fractionation and particle-size analysis. Pages 545–568 in C.A. Black, editor, *Methods of soil analysis*. American Society of Agronomy, Madison, WI.
- DEVITT, D.A., J.M. PIORKOWSKI, S.D. SMITH, J.R. CLEVERLY, AND A. SALA. 1997. Plant water relations of *Tamarix ramosissima* in response to the imposition and alleviation of soil moisture stress. *Journal of Arid Environments* 36:527–540.
- GARY, H.L. 1963. Root distribution of five-stamen tamarisk, seepwillow, and arrowweed. *Forest Science* 9: 311–314.
- GRAF, W.L. 1982. *Tamarix* and river channel management. *Environmental Management* 6:283–296.
- GROENEVELD, D.P., AND T.E. GRIEPENTROG. 1985. Interdependence of groundwater, riparian vegetation, and streambank stability: a case study. USDA Forest Service, General Technical Report RM-120:44–48.
- JUDD, J.B., J.M. LAUGHLIN, H.R. GUENTHER, AND R. HANDEGRADE. 1971. The lethal decline of mesquite on the Casa Grande National Monument. *Great Basin Naturalist* 31:153–159.
- KOLB, T.E., S.C. HART, AND R. AMUNDSON. 1997. Boxelder water sources and physiology at perennial and ephemeral stream sites in Arizona. *Tree Physiology* 17:151–160.
- KONDOLE, G.M. 1997. Hungry water: effects of dams and gravel mining on river channels. *Environmental Management* 21:533–551.
- MAHONEY, J.M., AND S.B. ROOD. 1991. A device for studying the influence of declining water table on poplar growth and survival. *Tree Physiology* 8:305–314.
- _____. 1992. Response of a hybrid poplar to water table decline in different substrates. *Forest Ecology and Management* 54:141–156.
- _____. 1998. Streamflow requirements for cottonwood seedling recruitment—an integrative model. *Wetlands* 18:634–645.
- MCQUEEN, I.S., AND R.F. MILLER. 1972. Soil-moisture and energy relationships associated with riparian vegetation near San Carlos, Arizona. Professional Paper 655-E. United States Geological Survey, Washington, DC.
- ROBINSON, T.W. 1958. Phreatophytes. United States Geological Survey Water-supply Paper 1423. Washington, DC.
- SALA, A., D.A. DEVITT, AND S.D. SMITH. 1996. Water use by *Tamarix ramosissima* and associated phreatophytes in a Mojave Desert floodplain. *Ecological Applications* 6:888–898.
- SCOTT, M.L., J.M. FRIEDMAN, AND G.T. AUBLE. 1996. Fluvial process and the establishment of bottomland trees. *Geomorphology* 14:327–340.
- SCOTT, M.L., P.B. SHAFROTH, AND G.T. AUBLE. 1999. Responses of riparian cottonwoods to alluvial water table declines. *Environmental Management* 23: 347–358.
- SEGELQUIST, C.A., M.L. SCOTT, AND G.T. AUBLE. 1993. Establishment of *Populus deltoides* under simulated alluvial groundwater declines. *American Midland Naturalist* 130:274–285.
- SHAFROTH, P.B., G.T. AUBLE, J.C. STROMBERG, AND D.T. PATTEN. 1998. Establishment of woody riparian vegetation in relation to annual patterns of streamflow, Bill Williams River, Arizona. *Wetlands* 18:577–590.
- SMITH, S.D., D.A. DEVITT, A. SALA, J.R. CLEVERLY, AND D.E. BUSCH. 1998. Water relations of riparian plants from warm desert regions. *Wetlands* 18:687–696.
- SMITH, S.D., A.B. WELLINGTON, J.L. NACHLINGER, AND C.A. FOX. 1991. Functional responses of riparian vegetation to streamflow diversion in the eastern Sierra Nevada. *Ecological Applications* 1:89–97.
- SNYDER, K.A., D.G. WILLIAMS, AND V.L. GEMPKO. 1998. Water source determination in cottonwood/willow and mesquite forests on the San Pedro River in Arizona. Pages 185–188 in E.F. Wood, editor, *Proceedings of the American Meteorological Society Special Symposium on Hydrology*. 78th Annual Meeting, Phoenix, AZ.
- SPRACKLING, J.A., AND R.A. READ. 1979. Tree root systems in eastern Nebraska. *Nebraska Conservation Bulletin* 37. Lincoln, NE. 73 pp.
- STROMBERG, J. 1998. Dynamics of Fremont cottonwood (*Populus fremontii*) and saltcedar (*Tamarix chinensis*) populations along the San Pedro River, Arizona. *Journal of Arid Environments* 40:133–155.
- STROMBERG, J.C., AND D.T. PATTEN. 1996. Instream flow and cottonwood growth in the eastern Sierra Nevada of California, USA. *Regulated Rivers* 12:1–12.

- STROMBERG, J.C., B.D. RICHTER, D.T. PATTEN, AND L.G. WOLDEN. 1993. Response of a Sonoran riparian forest to a 10-year return flood. *Great Basin Naturalist* 53:118–130.
- STROMBERG, J.C., R. TILLER, AND B. RICHTER. 1996. Effects of groundwater decline on riparian vegetation of semiarid regions: the San Pedro, Arizona. *Ecological Applications* 6:113–131.
- STROMBERG, J.C., J.A. TRESS, S.D. WILKINS, AND S.D. CLARK. 1992. Response of velvet mesquite to groundwater decline. *Journal of Arid Environments* 23: 45–58.
- TYREE, M.T., K.J. KOLB, S.B. ROOD, AND S. PATIÑO. 1994. Vulnerability to drought-induced cavitation of riparian cottonwoods in Alberta: a possible factor in the decline of the ecosystem? *Tree Physiology* 14: 455–466.
- WILKINSON, R.E. 1972. Water stress in salt cedar. *Botanical Gazette* 133:73–77.

Received 5 October 1998
Accepted 19 February 1999