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Source: Arctic, Antarctic, and Alpine Research, 37(4) : 636-643

Published By: Institute of Arctic and Alpine Research (INSTAAR), University of Colorado

URL: https://doi.org/10.1657/1523-0430(2005)037[0636:HFAIWS]2.0.CO;2

Arctic, Antarctic, and Alpine Research, Vol. 37, No. 4, 2005, pp. 636–643

Hydrologic Factors Affecting Initial Willow Seedling Establishment along a Subalpine Stream, Colorado, U.S.A.

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Abstract

Willows (*Salix* spp.) are important riparian plants along high elevation streams of western North America, but the hydrologic conditions needed for initial recruitment are not well defined. A replicated plot experiment was used to determine the effects of (1) elevation above the stream (high, middle, or low), (2) soil texture (sand or gravel), (3) watering to simulate additional rainfall, and (4) an upstream water diversion on soil water content and first-year willow seedling survival along a subalpine reach of the Colorado River.

Soil water content varied with elevation ($F = 163.8$, $p < 0.001$) and soil texture ($F = 387.3$, $p < 0.001$), while the effect of the watering treatment was not statistically significant. Soil water content controlled first-year willow seedling survival ($r^2 = 0.257$, $p = 0.002$), and no seedlings were found in plots with a mean soil water content of less than 15%. Sandy sites near the river elevation provide the optimal conditions for initial establishment of willows along this and other subalpine streams in the semiarid western United States. Potential establishment sites occur along abandoned channels and in drained beaver ponds, and creation of these sites depends on the occurrence of high flows. Therefore, as at lower elevation, cottonwood-dominated systems, maintenance of a flow regime that includes periodic high flows is essential for sustaining willow establishment along subalpine streams.

The upstream diversion reduced the stream stage by up to 13 cm during the growing season, resulting in a similar decline in the water table level and a reduction of up to 15% in plot soil water content. Since seedling survival depends on the availability of soil water, water diversions may adversely affect willow establishment along subalpine streams.

Introduction

Willows (*Salix* spp.) are key components of riparian vegetation along streams and rivers throughout the northern hemisphere (Bliss, 1957; Ellenberg, 1988; Zoltai et al., 1988; Rodwell, 1991) and are the most abundant woody plants along high elevation streams in the western United States (Patten, 1998). Although many willow species are capable of asexual reproduction, establishment from seed is an important recruitment mechanism (Barnes, 1983; Nhyama, 1990; Langlade and Decamps, 1994). Willows produce abundant small seeds that are widely dispersed by wind and water in the early summer (Densmore and Zasada, 1983; Krasny et al., 1988). Germination occurs on bare, moist mineral soil surfaces (Scott et al., 1996). Seedling mortality rates during the first year are extremely high, so the initial establishment phase is an important control on recruitment (Saachi and Price, 1992). Soil water availability is a critical control on willow seedling survival in the first year, and remains an important factor until the plant root system reaches the water table. It is unclear how long willow seedlings remain dependent on soil water, but the roots of cottonwood (*Populus deltoides*) seedlings may not reach the summer water table until they are 3 to 4 years old (Cooper et al., 1999).

Riparian zone soil water availability is controlled by several factors including elevation above the river channel, soil texture, and climate. Seedlings establishing near the river elevation generally have more soil water available than those in higher positions due to seasonal flooding and a shallower summer water table. A soil's texture influences its water holding capacity, with fine sands and silts capable of retaining more water than coarse sand and gravel. This makes finer-grained soils more suitable for seedling establishment, particularly in environments with little summer rainfall and summer water tables deeper than first year seedling taproots can reach (Cooper et al., 1999). Summer rainfall may play an important role in maintaining adequate soil water availability for willow seedling survival, especially along high elevation streams where the coarse sandy and gravelly alluvial sediments have little soil water holding capacity.

Most information on seedling establishment for Salicaceae species is for *Populus deltoides*, which occurs only in lower elevation sites (e.g., Shafroth et al., 1995; Auble et al., 1997; Auble and Scott, 1998). Optimal sites for *P. deltoides* establishment are high enough above the river to be exposed during the seed rain period and protected from flood scouring in most years, but low enough for seedlings to survive summer drought (Scott et al., 1996; Mahoney and Rood, 1998). The conditions required for willow establishment are less well understood, and previous studies of *Salix* species have focused primarily on low elevation species and sites (Krasny et al., 1988; Saachi and Price, 1992; Cooper and Van Haveren, 1994; Douglas, 1995). There is little information on the factors affecting willow establishment along high elevation streams.

Initial seedling establishment may be adversely influenced by anthropogenic activities that affect streamflow (Smith et al., 1991). Water diversions, which are present along many high elevation streams in the western United States (Petsch, 1985), reduce stream flow and stage, lower alluvial water tables (Ruddy and Williams, 1991), and reduce flood frequencies and soil water availability. However, little is known about the effects of water diversions on woody plant recruitment along high elevation streams.

In this paper we use a field experiment to investigate the influence of soil water availability, as controlled by elevation, soil texture, simulated summer rainfall, and an upstream diversion on initial willow seedling establishment along a subalpine reach of the Colorado River in northern

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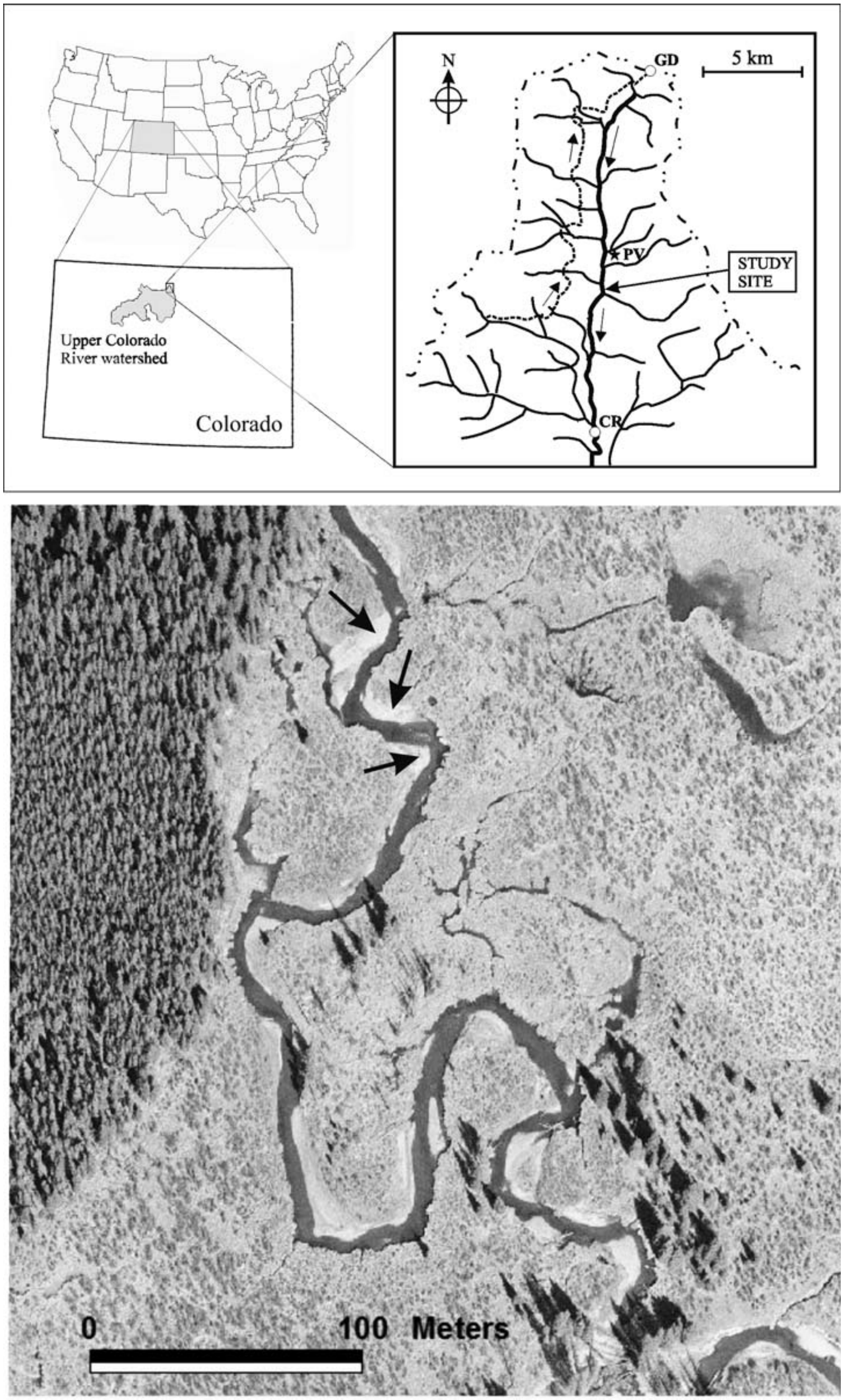

FIGURE 1. Location of study site in the upper Colorado River watershed. Inset map indicates location of study site, Phantom Valley SNOTEL site (PV), and stream gauging stations on the Grand Ditch (GD) and along the Colorado River (CR). Dot-dot-dash line denotes the watershed boundary, solid lines represent streams, and dashed line represents the Grand Ditch. Arrows indicate direction of flow in the Colorado River and Grand Ditch. Arrows on photograph indicate the three study bars.

Colorado. Few willow seedlings are establishing along this headwater section of the Colorado River, and we wanted to investigate the physical processes controlling initial willow establishment. We also investigated the possibility that establishment is influenced by the water diversion.

STUDY SITE

The study was conducted along a 100-m reach of the Colorado River at its headwaters within Rocky Mountain National Park (RMNP) in northern Colorado (Fig. 1). Here the nascent Colorado River flows within a large subalpine valley, flanked by the Never Summer Range to the west and the Front Range to the east. The Continental Divide follows the watershed boundary. The study reach has a pool-riffle channel with gravel and small cobbles in riffles and sand and gravel in pools. The Colorado River floodplain supports extensive willow communities that are dominated by *Salix geyeriana* (Geyer's willow) and *S. monticola* (mountain willow). Plant species nomenclature follows Weber and Whittmann (1996). These two species, which dominate montane and subalpine riparian willow communities throughout the southern Rocky Mountains, occupy similar niches, have relatively similar tolerances for flooding and water stress, and both disperse seeds in the early summer (Law et al., 2000; Peinetti et al., 2001; Carsey et al., 2003). Recent work elsewhere in RMNP indicates that *S. geyeriana* and *S. monticola* reproduce almost entirely by seed (Dickens, 2004). Willows dominate the riparian area and much of the valley floor, but there is little evidence of recent recruitment. Since the study site is within RMNP, the only grazing is by native ungulates.

Mean annual precipitation at the Phantom Valley SNOTEL station (PV on Fig. 1), located ~2 km from the study site at ~2900 m elevation, is 640 mm with a standard deviation of 121 mm (period of record 1981–2002). Precipitation is distributed evenly throughout the year, but the driest months are June and September. From October through April most precipitation accumulates as snow. High intensity thunderstorms, driven by monsoon airflow, occur from late July through August. The growing season extends from late May through mid-September.

More than 80% of the annual Colorado River flow at the U.S. Geological Survey (USGS) gauging station at Baker Gulch (USGS gage no. 09010500, CR on Fig. 1), located 6.5 km downstream from the study reach, occurs during the snowmelt period of May, June, and July. Mean annual peak flow is 17 $m^3\ s^{-1}$ and typically occurs in early June. Base flow conditions predominate from mid-July through October, although summer storms can cause short-term flow increases.

The Grand Ditch, constructed in the late 1800s, intercepts the flow of 13 headwater tributaries of the Colorado River, 10 of which are upstream from the study reach. The Grand Ditch diversion removes a mean of 29% of the annual Colorado River watershed runoff (above the USGS gage), and reduces both peak flows and summer base flows by up to 50% (Woods, 2000).

Methods

EXPERIMENTAL DESIGN

A replicated split–split plot experiment was conducted on gravel bars along the study reach in the summer of 1999 to test the effects of elevation above the stream, soil texture, and simulated rainfall additions on soil water availability and willow seedling establishment. There were five replicates of the design, with two replicates on each of two large gravel bars and one replicate on a third bar. Each replicate consisted of four 0.25 m^2 plots at each of three elevations: high (H), middle (M), and low (L). Plot elevations encompassed the range of exposed bar surface elevations in early summer. The high and middle elevation plots were approximately 30 cm and 15 cm higher than the low plots, which were installed in early July, at the onset of the willow seed rain period on the lowest exposed part of each bar. A monitoring well constructed from slotted 2.5-cm-diameter PVC pipe was installed at each elevation to measure the water table depth. A staff gage was installed in the stream channel adjacent to each bar to measure river stage. Water table depth and stream stage were measured every 7 to 10 days in the early summer, and every 3 to 5 days from mid-July through August.

The effect of soil texture on soil water content and seedling establishment was determined by replacing the top 20 cm of native soil in each plot with either fine gravel (G) or medium sand (S). There were two plots each of the gravel and sand treatments at each elevation. In the study area, fine gravel is the dominant soil type on point bars, while medium sand is abundant on higher parts of the floodplain and in other depositional environments with lower stream power. The median grain size (D_{50}) for each plot was obtained from a sieve analysis of samples collected from the plots (Gee and Bauder, 1986). The D_{50} of the gravel plots ranged from 1.4 mm to 3.2 mm, with a mean of 1.8 mm (standard deviation (SD) = 0.13 mm). The D_{50} of the fraction less than 2 mm diameter in the gravel plots ranged from 0.65 mm to 0.99 mm with

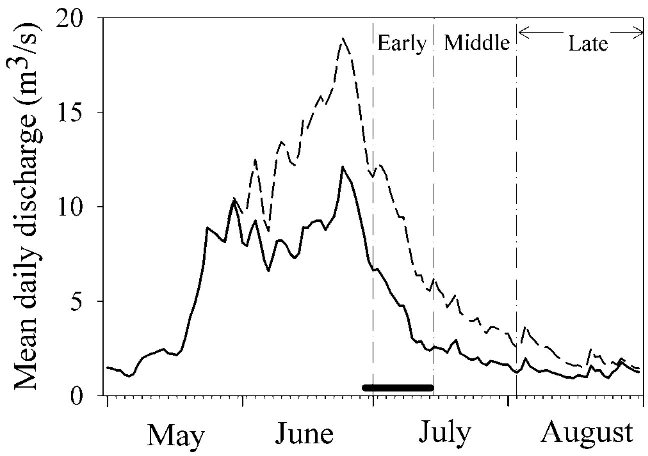

FIGURE 2. Mean daily discharge of the Colorado River at U.S. Geological Survey (USGS) gage no. 09010500 (solid line), and sum of mean daily discharges of the Colorado River at USGS gage no. 09010500 and the Grand Ditch at La Poudre Pass (dashed line) for 1 May to 31 August 1999. Dot-dash lines separate early, middle, and late periods of study, as described in text. Thick solid line indicates period of observed willow seed rain.

a mean of 0.81 mm (SD = 0.03 mm). The D_{50} of the sand plots ranged from 0.36 to 0.57 mm, with a mean of 0.42 mm (SD = 0.01 mm). None of the particles in the sand soils was greater than 2 mm in diameter. The mean D_{50} values for the fraction <2 mm in the gravel and the sand plots were significantly different ($p < 0.0001$).

The effect of rainfall on soil water content and seedling establishment was investigated by applying a watering treatment to one sand and one gravel plot in each elevation treatment. One cm of water was applied every 7 to 10 days in the early part of the study, and every 3 to 5 days from mid-July through August using a watering can. A fine nylon mesh was placed over the plot during watering to reduce water-drop impacts. The water was applied slowly so that it infiltrated the soil. The two remaining plots at each elevation received only natural rainfall.

The soil water content in the top 15 cm of each plot was measured immediately prior to each watering treatment using a Moisture Point time domain reflectometry (TDR) unit with custom-made 3-mm-diameter probes (Environmental Sensors Inc., Victoria, B.C., Canada). Soil water content was recorded as the mean of three measurements randomly located within each plot. Water content was not measured immediately after the watering treatment because we wanted to test the influence of the watering treatment at an approximately weekly scale.

Seed rain at each site was measured using seed traps, 225 cm^2 plywood squares mounted approximately 1 m above the soil surface, and coated with Tanglefoot®, adjacent to the middle and high elevation plots. Willow seeds, which are easily identified by their size and cottony web, were counted, and Tanglefoot® was reapplied weekly during the period of seed rain, mid-June through mid-July.

Willow seedlings in each plot were counted in mid-July and mid-September 1999, immediately after seed rain and prior to the first frost, respectively. Willow seedlings were distinguished by leaf shape and stem color. Since the seedlings were very small (<25 mm), it was not possible to discriminate between species. Percent seedling survival was based on the ratio of seedlings present in September to those present in July. If there were more seedlings present in September than in July, the survival rate was assumed to be 100%.

DATA ANALYSIS

The study was divided into three periods based upon the hydrologic conditions (Fig. 2). The early period included the steep

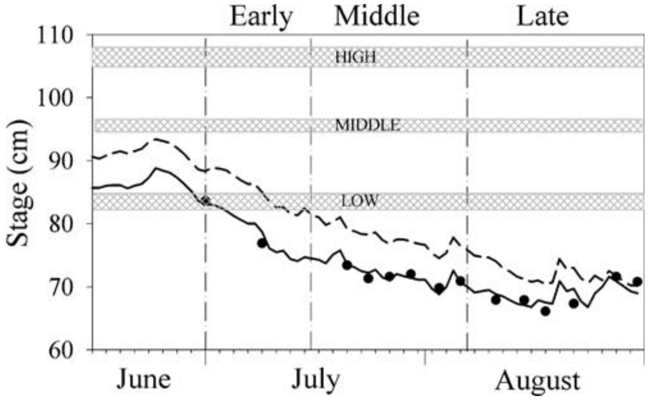

FIGURE 3. Observed stage (black dots), simulated stage with diversion (solid line), and simulated stage without diversion (dashed line) in the Colorado River adjacent to study plots on upstream bar, June through August 1999. Gray shaded rectangles indicate range of elevations for high, middle, and low plots. Dot-dash lines separate early, middle, and late study periods.

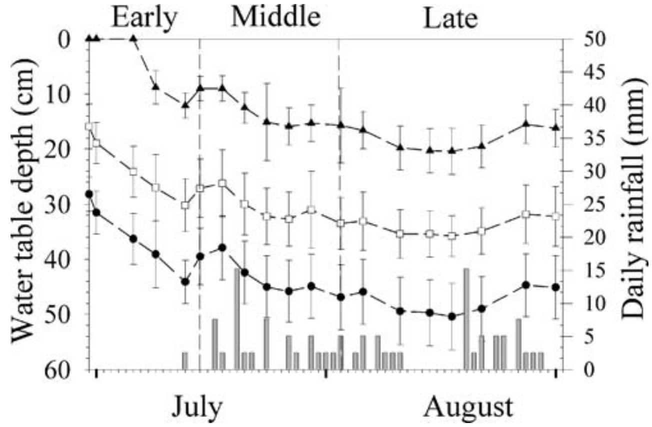

FIGURE 4. Mean water table depths in high, middle, and low elevation plots and daily precipitation at Phantom Valley SNOTEL site, 1 July to 31 August 2003. Low, middle, and high plot mean water table depths are denoted by solid triangles, open squares, and solid circles, respectively. Bars around each point indicate one standard deviation. Bar graph indicates daily rainfall totals (mm).

recession limb of the snowmelt hydrograph. The middle period included the initiation of summer low flows and the dry early summer. The late period began with the onset of monsoon rain and ended in early September.

The reduction in river stage due to the Grand Ditch diversion was determined by relating the observed stage (h) at each of the bars to the corresponding mean daily discharge (Q) in the Colorado River at the USGS gage using the following power function,

$$h = h_0 + aQ^b, \qquad (1)$$

where h_0 is the stage when Q is 0, and a and b are constants. An estimate of the undiverted discharge record was then developed by summing the daily mean discharges of the Grand Ditch at La Poudre Pass (Colorado Division of Water Resources gage, GD on Fig. 1), and the Colorado River at the USGS gage. Using the stage-discharge relationship for each bar and the estimated undiverted flow record, the undiverted stage record was calculated and compared to the observed stage values. These relationships were also used to determine the change in the duration of inundation for each of the study plots.

Linear regression was used to relate the measured water table depth at each well to the stage measured at each bar. These linear regression relationships and the calculated undiverted stage records were used to estimate the water table depth under the plots if the Grand Ditch had not been operating.

Multivariate repeated measures analysis of variance (MANOVA) was used to test for (1) differences between water table levels in the three elevation treatments, and (2) differences in soil water content between all treatments. We followed the methods outlined in Potvin et al. (1990) and von Ende (1993) to meet the assumptions of MANOVA. A univariate ANOVA was used to test for differences in seedling survival between treatments. Multiple comparisons (Ott, 1993) were used to determine which treatments were significantly different, and the Bonferroni adjustment was used to control the experiment-wise error rate at an alpha level of 0.05 (Ott, 1993). All analyses were performed using the SPSS Version 10.0.5 statistical software (SPSS Inc., 1999).

Results

PRECIPITATION

Precipitation was above average throughout the study period; monthly precipitation totals at the Phantom Valley SNOTEL station for June (63 mm), July (56 mm), and August 1999 (76 mm) were 179%, 110%, and 143% of average, respectively. The highest 24-h rainfall total was 15 mm on both 20 July and 20 August. The longest period without rainfall was 23 days, from 20 June until 12 July.

STREAMFLOW

The 1999 instantaneous annual peak flow in the Colorado River at the USGS gage at Baker Gulch of 13.9 $m^3 s^{-1}$ occurred on 23 June, and had a recurrence interval of approximately 1.5 years. The low study plots were inundated during peak stage and were exposed by the first week of July. The high and middle plots were never inundated. Flows declined throughout the summer, and reached a low of 0.93 $m^3 s^{-1}$ in mid-August (Fig. 2).

The Grand Ditch diverted water from 28 May through 3 September, and Colorado River daily mean flows at the USGS gage at Baker Gulch were reduced by up to 59%. Between 1 June and 31 August, the Grand Ditch captured 2.4×10^7 m^3 or 41% of the total Colorado River runoff upstream from the USGS gage. These values are close to the 45-year means of 2.0×10^7 m^3 and 39% of the total runoff. The diversion reduced stream stage by 5 to 10 cm during the early and middle study periods (Fig. 3). The calculated undiverted peak stage in late June would not have been high enough to inundate middle or high plots. However, low plots would have been inundated for an additional 9 to 11 days. The maximum daily stage reduction was 13 cm in mid-July. By the end of August, river stage was less than 1 cm below the calculated undiverted stage.

WATER TABLE DEPTHS

The highest water table in all plots occurred during the period of highest stream flow in late June (Fig. 4). Mean water table depths in all plots during the early period ranged from 2.8 to 36.9 cm below the soil surface, and the mean water table decline was 6.0 mm/day. Water table depths in the middle period ranged from 8.5 to 50.8 cm below the soil surface, and the water table declined at a mean rate of 3.8 mm/day. The water table continued to decline at a rate similar to the middle period during the first two weeks of the late period, and the lowest water tables occurred in mid-August (Fig. 4). Mean water table depths during the late period ranged from 12.2 to 55.6 cm below the soil surface.

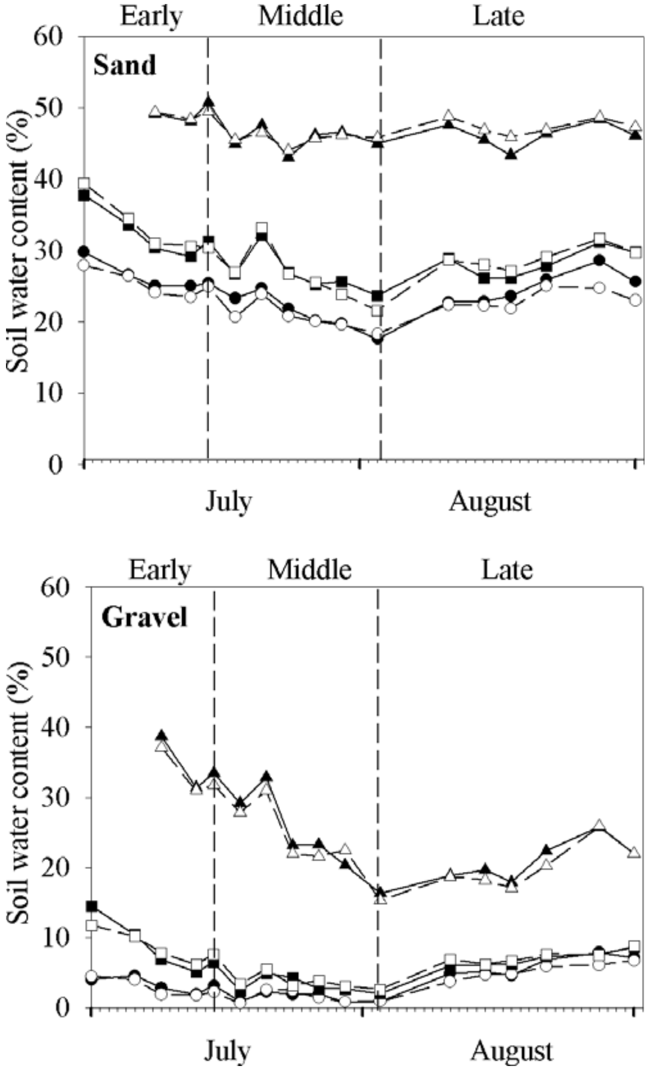

FIGURE 5. Mean volumetric soil water contents (%) in sand and gravel plots. Low, middle, and high plots are represented by triangles, squares, and circles, respectively. Solid symbols represent watered plots, and open symbols represent unwatered plots.

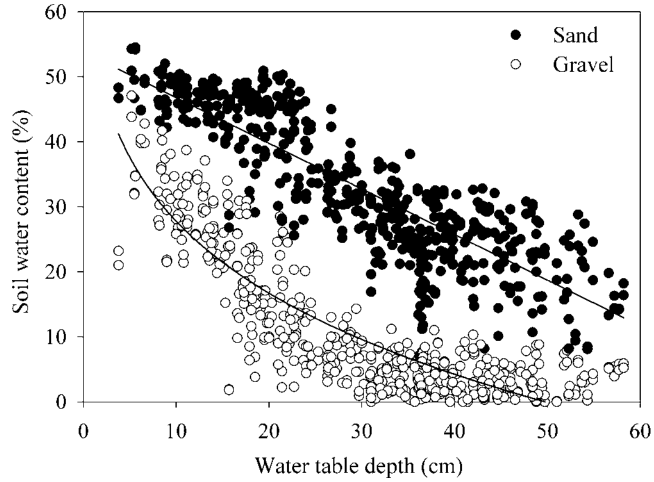

FIGURE 6. Volumetric soil water content (%) vs. water table depth in sand and gravel plots. Solid lines indicate regression relationships as described in text.

Repeated measures MANOVA of water table depth over time indicated a significant between-subject effect for elevation (MS [mean squares] = 20710, $F = 55.84$, $df = 2$). Multiple comparisons indicated that water table depths in all three of the elevation treatments were significantly different ($p < 0.002$).

Throughout the study period, water table depths in all wells, except one middle elevation well, were highly correlated with river stage ($r^2 > 0.90$, $p < 0.001$). Water levels in the atypical middle well closely tracked stream stage in the early period, but remained almost constant in the middle and late periods, suggesting that the well screen had become blocked. Data from this well were omitted from analyses of Grand Ditch effects on river stage and water table depths.

Regression analyses between river stage and water table levels indicated that the Grand Ditch diversion reduced ground water levels beneath the plots by up to 15 cm in the early and middle periods. However, by the end of the late period the calculated undiverted water table depths were nearly identical to the measured water table depths.

SOIL WATER CONTENT

The highest soil water content in most plots occurred in early July, and the lowest in early August. Soil water content ranged from 18% to 40% in the high and middle elevation sand-texture plots, and from 44% to 52% in the low sand-texture plots. The high and middle elevation gravel-texture plots generally had soil water content <10%, while in the low plots it ranged from 16% to 39% (Fig. 5).

Soil water content in all plots declined through the middle period. In late July it ranged from <5% in high elevation gravel-texture plots to >20% in low elevation sand-texture plots. Soil water content increased slightly during the late period, apparently due to rain recharge. The increases ranged from <3% in low elevation sand plots to >7% in low elevation gravel plots (Fig. 5).

Repeated measures MANOVA of soil water content indicated significant between-subject effects for elevation (MS = 43939, $F = 163.8$, $df = 2$) and soil texture (MS = 103870, $F = 387.3$, $df = 1$), but not for the watering treatment (MS = 11.4, $F = 0.043$, $df = 1$). Multiple comparisons indicated that the three elevation treatments were all significantly different in soil water content ($p < 0.022$). None of the interactions between elevation, soil texture, or watering was significant. The within-subject effects of time (Wilks $\lambda = 0.03$; $F = 81.053$, error $df = 35$, $p < 0.0001$), time × elevation (Wilks $\lambda = 0.057$; $F = 7.985$, error $df = 70$, $p < 0.0001$), time × soil (Wilks $\lambda = 0.503$; $F = 2.474$, error $df = 35$, $p = 0.015$) and time × elevation × soil (Wilks $\lambda = 0.081$; $F = 6.280$, error $df = 70$, $p < 0.0001$) were all highly significant. These results indicate that soil moisture varied with elevation and soil texture, and that soil moisture over time varied according to elevation, soil texture, and elevation × soil texture.

Soil water content was inversely related to water table depth for both sand ($r^2 = 0.73$, $p < 0.0001$) and gravel ($r^2 = 0.75$, $p < 0.0001$) plots (Fig. 6). The soil water content of most sand plots remained >15% even as the water table dropped to >50 cm depth. In contrast, the soil water content of most of the gravel plots was always <15% when the water table was more than 20 cm below the soil surface.

SEED RAIN AND SEEDLING DENSITY IN PLOTS

Willow seed dispersal began immediately after the peak Colorado River flow in late June and lasted approximately 2 weeks (Fig. 2). The highest seed density recorded, 133 seeds m^{-2}, is considerably less than reported elsewhere in the Colorado River drainage for cottonwoods (Cooper et al., 1999) or willows (Gage and Cooper, 2005), which can average more than 2000 seeds m^{-2}.

July seedling density ranged from zero in all of the middle and high gravel plots to a mean of 31.2 m^{-2} in the watered low sand plots

TABLE 1

Mean (and standard deviation) of seedling density (m^{-2}) in plots in July and September 1999, and percent survival between the two sampling dates.

Elevation	Soil Texture	Watering	Seedling density July	Seedling density September	Percent survival
High	Sand	Watered	8.0 (11.7)	3.2 (7.2)	10.0 (10.8)
		Unwatered	7.2 (5.2)	0.8 (1.8)	
	Gravel	Watered	0	0	—
		Unwatered	0	0	
Middle	Sand	Watered	15.2 (11.5)	5.6 (4.6)	31.9 (10.8)
		Unwatered	25.6 (16.1)	6.4 (7.8)	
	Gravel	Watered	0	0	—
		Unwatered	0	0	
Low	Sand	Watered	22.4 (17.1)	20.8 (12.1)	72.0 (11.7)
		Unwatered	31.2 (19.0)	19.2 (8.7)	
	Gravel	Watered	8.8 (7.2)	7.2 (5.2)	44.3 (14.0)
		Unwatered	10.5 (14.0)	8.8 (8.2)	

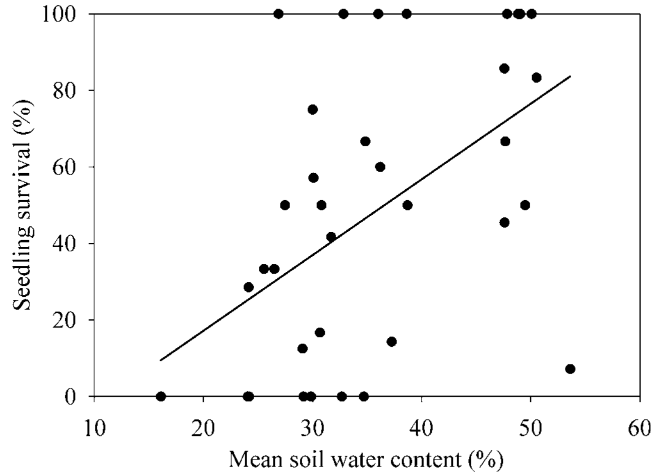

FIGURE 7. Seedling density vs. early season mean volumetric soil water content (%). Solid line was generated using linear regression ($r^2 = 0.257$, $p = 0.002$).

(Table 1). Univariate ANOVA of July seedling density indicated significant between-treatment effects for elevation (MS = 953.9, $F = 8.90$, $p = 0.001$) and soil texture (MS = 3588.3, $F = 34.7$, $p < 0.001$), but the watering treatment effect was not statistically significant ($p = 0.278$). Multiple comparisons indicated that only the high and low elevation treatments were significantly different ($p < 0.001$).

The overall distribution of seedlings among treatments in early September was similar to July, but the mean seedling density decreased, ranging from zero to 20.0 seedlings m^{-2} (Table 1). As for the July results, univariate ANOVA indicated that seedling density varied with elevation (MS = 980.0, $F = 23.13$, $p < 0.0001$) and soil texture (MS = 666.7, $F = 15.7$, $p < 0.001$), but watering had no significant effect ($p = 0.875$). Seedling density in the low elevation treatments was significantly different from both the high and medium elevation treatments ($p < 0.001$ for both). None of the interactions between elevation, soil texture, and watering treatment was significant in either July or September.

Due to the non-significant effect of the watering treatment, data from watered and unwatered plots were combined when calculating seedling survival rates. Mean survival rates from July to September ranged from 10% in the high sand plots to 72% in the low sand plots (Table 1). Percent seedling survival was significantly correlated with the mean plot soil water content for all dates throughout the season ($r^2 = 0.128$, $p = 0.032$, SE = 35.9) and in the early period ($r^2 = 0.257$, $p = 0.002$, SE = 33.16, Fig. 7), but not for the middle or late season periods ($p = 0.059$ and 0.081, respectively).

The study plots were revisited periodically in the second year of the study. All seedlings in the low and middle elevation plots were killed during the 2000 spring flood. Seedlings in the high plots survived the spring flood, but all died later that summer.

Discussion

SOIL WATER AVAILABILITY AND SEEDLING ESTABLISHMENT

Soil water availability controlled first year willow seedling survival in our experiment. This is consistent with results from a northern Arizona stream where nearly 100% of *Salix lasiolepis* Benth. seedlings died in unwatered plots in the first year, while many seedlings lived in watered plots (Saachi and Price, 1992). In interior Alaska, *Salix interior* Rowlee and *S. alaxensis* (Anderss.) Cov. germination rates were positively correlated with soil water availability along the Tanana River (Krasny et al., 1988), while supplemental watering increased survival rates of *S. alaxensis* seedlings on placer-mine tailings along Birch Creek (Cooper and Van Haveren, 1994). Although the Arizona site has higher summer temperatures than our Colorado River study area, the Alaskan sites are comparable in both temperature and precipitation. In our study, seedling survival was more highly correlated with early season soil water content than with middle or late season values, suggesting that the conditions during and immediately following germination are most critical for willow seedling survival in the first year.

Soil water availability and seedling survival rates varied with elevation and soil texture, and the highest seedling survival rates were in low-elevation, sand plots. Similarly, germination and initial seedling establishment of *Salix hindsiana* Benth. and *S. laevigata* Bebb occurred primarily on lower elevation, sandy as opposed to gravelly sites along Dry Creek in California (McBride and Strahan, 1984). No seedlings were found in any of our plots that had mean July and August soil water content below 15%, suggesting that this may be a threshold for first year seedling survival.

We did not identify willow seedlings to the species level, so it is not possible to determine whether both of the dominant species in the study area—*Salix geyeriana* and *S. monticola*—were represented in the plots. However, these two species occur under very similar hydrologic conditions on montane and subalpine floodplains in the Rocky Mountain region (Law et al., 2000; Peinetti et al., 2001), suggesting that the 15% threshold for first year willow seedling survival applies to both species.

Soil water content in the gravel-texture plots was typically below 15% if the water table was more than 20 cm below the ground surface (Fig. 6). Since the middle and high elevation plots in our study had water table depths greater than 20 cm for most of the summer, it suggests that gravel bars in our study reach are unsuitable for willow seedling establishment in most years. In contrast, sand-texture plots generally retained more than 15% soil water content even after the water table depth exceeded 50 cm (Fig. 6). Since most portions of the Colorado River floodplain in our study area had a water table within 50 cm of the soil surface during the growing season, any sandy site is potentially suitable for initial establishment.

Willow seedling survival rates generally increase after the first year, as the root system grows long enough to reach the late summer water table (Saachi and Price, 1992; Douglas, 1995). Factors other than soil moisture availability, such as vulnerability to flood scour and the effects of grazing, play increasingly important roles in determining seedling survival beyond the first year. Due to limitations on initial establishment caused by soil water availability, longer-term survival is likely only on sandy sites in our study area. Most low elevation sites are vulnerable to flood scour, and high sites are prone to desiccation. Therefore, the optimal conditions for longer-term establishment will occur on sandy sites close to the river elevation but in locations sheltered from scour. Along the subalpine upper Colorado River, these sites occur along abandoned channels and in drained beaver ponds. Because channel abandonment and breaching of beaver ponds occurs primarily during high flows, maintaining a flow regime that includes periodic high flows is essential for the formation of many willow establishment sites along western U.S. subalpine streams.

Surprisingly, our watering treatment had no measurable effect on soil water content or seedling survival. This may be due to our TDR probe averaging water content in the top 15 cm of soil, while our watering treatment may have increased soil water content only near the soil surface. In addition, the high hydraulic conductivity and low water holding capacity of the alluvial soils in the study area would result in rapid drainage with limited water retained in the upper soil profile. However, soil water content increased in all plots during August while the water table dropped, suggesting that the unusually high summer precipitation was sufficient to recharge soil water content in all plots. Had we conducted this experiment in a drier summer, we may have measured a significant watering treatment effect. Summer rainfall may increase first year seedling survival in certain years, as Douglas (1995) found for *Salix setchelliana* along glacial rivers in Alaska.

EFFECT OF FLOW DIVERSION ON WILLOW SEEDLING ESTABLISHMENT

The Grand Ditch diversion reduced the peak stage of the Colorado River in the study reach by ~10 cm in 1999, a year with a below-average peak flow. The higher natural stage would not have been sufficient to flood either the middle or high elevation plots, and little additional soil water recharge would have occurred. However, river stage during July and August was reduced by up to 13 cm, causing reductions in the water table level. Since plot soil water content is inversely related to elevation above the water table, the decline in summer river stage resulted in mean soil water declines ranging from less than 4% in high elevation sand plots to about 15% in low elevation gravel plots. Based on the positive correlation between mean soil water content and seedling survival, these decreases could adversely affect willow establishment rates. Similarly, Smith et al. (1991) concluded that flow diversions could adversely affect the recruitment of *Populus fremontii*, *P. trichocarpa*, and *Betula occidentalis* along streams in the eastern Sierra Nevada.

Conclusions

First-year establishment of willow seedlings along this and other subalpine streams in the semiarid western United States is limited by soil water availability. Soil water availability is controlled primarily by soil texture and elevation above the floodplain water table, with sheltered, sandy sites near the river elevation providing the optimal conditions for establishment. Along subalpine streams, these sites occur along abandoned channels and in drained beaver ponds. Channel abandonment depends on the periodic occurrence of high flows, as does the breaching of beaver dams. Therefore, as in lower elevation streams and rivers with cottonwood-dominated riparian vegetation (Johnson, 1992; Rood and Mahoney, 1990, 1995; Rood et al., 1995; Scott et al., 1997), maintenance of a flow regime that includes periodic high flows is essential for the formation of potential willow establishment sites along western U.S. subalpine streams. Water diversions have the potential to adversely affect willow recruitment by reducing soil water availability in potential establishment sites.

Acknowledgments

The U.S. Department of Interior National Park Service provided financial and logistical support for this study, which was completed while the first author was a graduate student in the Department of Earth Resources at Colorado State University. The National Science Foundation provided funding to enable Jamie Miller to participate in the study through the Research Experience for Undergraduates (REU) program. Dr. Lee MacDonald and two anonymous reviewers provided helpful review and comments on earlier drafts of the paper.

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Revised ms submitted January 2005