

ESTABLISHMENT, GROWTH, AND EARLY SURVIVAL OF WOODY RIPARIAN SPECIES AT A COLORADO GRAVEL PIT

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ABSTRACT.—Presence of a wetted edge during the period of seedfall was an effective predictor of suitable establishment (defined as germination and survival to the 1st autumn) locations for *Populus deltoides* subsp. *monilifera*, *Salix amygdaloides*, *S. exigua*, and *Tamarix ramosissima* seedlings during 3 successive years of a gravel pit revegetation project in Fort Collins, Colorado. At locations predicted to be suitable for establishment, position within the pit (possibly reflecting additional moisture provided by seepage) was a significant factor in determining whether establishment actually occurred. Cover of herbaceous species, which became established at the same time as, or after, woody seedlings, was positively related to probability of establishment for 8 of 11 species-year combinations, probably reflecting more favorable moisture conditions at certain locations. Herbaceous cover also was positively related to seedling height at the end of the 1st summer of growth for 9 of 11 species-year combinations. Neither establishment nor 1st-summer growth was consistently related to overall decline in the water table as estimated by the drop in surface-water level during the growing season. Flooding in the 1st spring after establishment was negatively related to subsequent survival for 5 of 8 species-year combinations. The 4 species established at different elevations in the pit, depending on location of the wetted edge during the period of seedfall, and there was no evidence that differential mortality subsequently altered their distribution along the elevation gradient. However, the primary objective in this study was to restore native woody species, and we attempted to maintain conditions conducive to meeting this objective. Differential postestablishment mortality may be more important in structuring the riparian community in more rigorous riverine environments.

Key words: seedlings, survival, *Populus*, *Salix*, *Tamarix*, drawdown, herbaceous cover, flooding.

Riparian areas in the western United States, often dominated by members of the willow family (*Salicaceae*), are widely recognized as providing important wildlife habitat and significant benefits to society. Trees and shrubs composing western riparian communities are structurally complex compared to the surrounding landscape and support diverse assemblages of mammals, birds, reptiles, and amphibians (Stevens et al. 1977, Brode and Bury 1984, Knopf 1985, Finch and Ruggiero 1993). Recent years have seen increasing concern about a variety of impacts to these communities, much of which has focused on alteration of stream flow patterns by dams and diversions and resulting detrimental effects on riparian vegetation, particularly cottonwoods (*Populus* spp.; Bradley and Smith 1986, Rood and Heinze-Milne 1989, Rood and Mahoney 1990).

Cottonwoods produce abundant wind- and water-borne seeds adapted to germinate on bare, moist soils in full sunlight. In the western U.S., seed release is in spring or early summer, depending on latitude and elevation,

and is timed to coincide with recession of flood flows following snowmelt (Scott et al. 1993). Reworking and deposition of alluvial sediments by floods historically provided ideal conditions for cottonwood germination and establishment, at least in some years (Stromberg et al. 1991, Friedman et al. 1997, Stromberg 1997). However, dams and diversions have significantly altered flow patterns of many western streams, particularly by reducing spring flood peaks. Suitable germination sites that are high enough to provide security from scouring by floods and ice, yet low enough to allow roots to establish contact with the subsurface water table, are produced less frequently (Bradley and Smith 1986, Scott et al. 1997). As a result, recruitment can no longer keep pace with mortality in many areas.

A number of authors have expressed this relationship in the form of conceptual or quantitative models designed to predict where (relative to stream elevation) cottonwood establishment will occur during a particular sequence of hydrologic events (Bradley and Smith 1986,

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Friedman et al. 1997, Auble and Scott 1998, Mahoney and Rood 1998, Shafroth et al. 1998). The central component of these models is the location of a disturbed and wetted edge, produced by declining stream stage, during the period when germinable seeds are present. The period of seed germinability is usually taken as the period of seed release, either observed directly or estimated from general phenological information. An additional interval during which seeds are likely to remain germinable under natural conditions is sometimes added to the end of the period of seed release. Elevation of the wetted edge at a particular site is usually estimated from stream flow records and stage-discharge relations, sometimes in association with visible clues such as debris lines.

Various models differ in their treatment of mortality factors that may be important following germination. For example, Mahoney and Rood (1998) limited both the upper and lower bounds of the predicted establishment zone. They argued that there is an upper elevational limit to establishment, above which seedling roots will not be able to grow deep enough to establish contact with the subsurface water table in the initial growing season, and a lower limit, below which subsequent scouring by stream flow and ice are likely to remove seedlings. Rate of water table decline was also a component of their model, reflecting the fact that there is a limit to how fast seedling roots can grow and thus maintain contact with subsurface water as stream stage declines.

The efficacy of such models in predicting establishment of cottonwoods and other woody riparian species is of obvious interest in understanding and assessing the impacts of both past and future stream flow alterations. In this article, using data from a riparian revegetation project at an abandoned gravel mine (the WREN Pit) in Fort Collins, Colorado, we examine the importance of factors included in such models relative to establishment, growth, and survival of seedlings of *Populus deltoides* Marshall subsp. *monilifera* (Aiton) Eckenwalder, *Salix amygdaloides* Andersson, *S. exigua* Nuttall, and the exotic *Tamarix ramosissima* Ledebour (Great Plains Flora Association 1986). Information regarding distribution of the 4 species along an elevational gradient is also presented.

METHODS

Field Sampling

The overall objective at the WREN Pit was to test the feasibility of restoring a former gravel pit to woody riparian forest through natural seedfall and hydrologic manipulation. Details of water manipulations and vegetation sampling methods can be found in Roelle and Gladwin (1999). Briefly, the WREN Pit resembles a flat-bottomed bowl with 2 islands in the middle. The bottom of the pit, which lies below the elevation of the adjacent Cache la Poudre River, was graded to slope toward the southeast corner, where a drain pipe and screw gate allowed control of the outflow (Fig. 1). Grading removed nearly all vegetation in the pit, leaving a bare, heterogeneous surface of clay, overburden, sand, gravel, and cobble. In the spring of 1994, we filled the pit with water and then allowed the water to drain slowly to provide a gradually receding fringe of moist soil suitable for germination of wind- and water-borne seeds produced by mature *Populus* and *Salix* along the Cache la Poudre River. Though not desirable from a restoration perspective, *Tamarix* seed was also supplied by several stands within about 1 km of the pit. For all 4 species, we also monitored the timing of seed release.

When water in the pit was at its highest level, we randomly located 67 points 2 m (measured on the ground surface) above the water's edge. Following drawdown, we established a transect extending from each of these starting points to the new water's edge, located a 0.5-m² sample plot every 2 m along each transect, and counted seedlings of the 4 species in each plot. We also estimated surface cover (0–25%, 25–50%, 50–75%, or 75–100%) at each plot and measured the height of up to 5 seedlings of each species. If more than 5 individuals were present, we measured those closest to the center of the plot. Following seedling counts, plot locations and elevations were surveyed using a total station.

The drawdown process was repeated in 1995 and 1996 at successively lower elevation intervals. Each year we began the drawdown at approximately the lowest elevation where there had been significant establishment of cottonwoods and willows in the previous year and extended the sampling transects down to the new water's edge. In all 3 years water levels

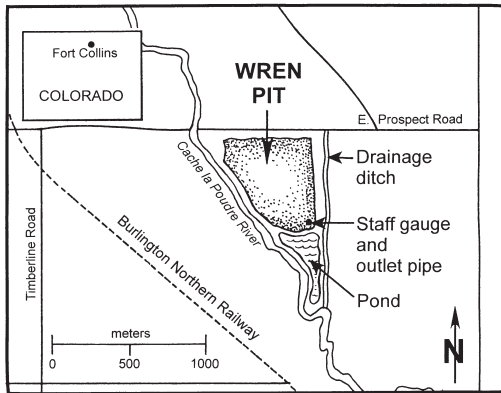


Fig. 1. Location of the WREN Pit.

as determined by a staff gauge were recorded 4–5 times each week. Drawdowns and water level monitoring were terminated after the 1996 census. We conducted a final census in 1997 to calculate survival of seedlings established in previous years. The 1997 census was restricted to *P. deltoides* and *S. exigua* made it difficult to identify individuals, a prerequisite for calculating survival. Control measures applied to *T. ramosissima* in 1997 prevented survival calculations for this species.

Analysis

Information obtained in field sampling was used to test 4 hypotheses.

H1₀: Location and rate of seedling establishment are unrelated to the presence of a wetted edge during seedfall. For each year and species, we assigned plots to 1 of 3 elevation zones. Zone 1 included all plots above the highest water level that occurred during the period of seedfall. Zone 2 included all plots inundated by the highest water level and subsequently exposed (by the drawdown) during the seedfall period. Zone 3 included all plots below zone 2 (i.e., exposed after the period of seedfall). Because of differences in the timing of seedfall, zones were specific to a species; for example, a given plot in a particular year might be in zone 2 for *P. deltoides* and zone 1 for *S. exigua*. For each species we tested for differences in presence/absence among the zones at the end of the 1st growing season using a chi-square statistic. A negative binomial generalized linear model was used to estimate standard errors and to test for differences in

mean seedling density among zones (Roelle and Gladwin 1999).

H2₀: Location of seedling establishment is unrelated to position within the pit, presence of herbaceous cover, or magnitude of the drawdown. On plots that have a wetted edge during the period of seedfall, other factors may be important in determining whether establishment actually occurs. We used logistic regression to examine the effects of position within the pit, herbaceous cover, and total drawdown on presence or absence of seedlings on plots in zone 2 at the end of the 1st growing season. Plots were assigned to 1 of 4 cover classes as described above, total drawdown was calculated as the plot elevation minus the lowest water level recorded during the growing season (assumed to end on 15 October), and surveyed x,y (easting, northing) plot locations were used to represent position within the pit. In these regressions we did not use a model selection procedure (i.e., all independent variables were included in all models, regardless of significance).

H3₀: Growth of seedlings in the summer of establishment is unrelated to position within the pit, presence of herbaceous cover, or magnitude of drawdown. Experimental studies have shown that the rate of water table decline can affect growth of *Populus* seedlings (Mahoney and Rood 1991, 1992, Segelquist et al. 1993). We used ordinary least-squares regression to examine the impact of total drawdown on plant height in the setting of our revegetation project. Herbaceous cover and position were also included as covariates. For these analyses we used all plots where establishment occurred, not just those in zone 2. As in the logistic regressions described above, all independent variables were entered into each of these least-squares regressions. Inspection of residuals from these regressions revealed a pattern of increasing variance (larger residuals) at higher values for predicted height. In an attempt to reduce heteroscedasticity, we regressed the absolute values of these residuals against predicted height and used the inverse square of predicted values as weights in a least-squares regression.

H4₀: Seedling survival in the 1st year following establishment (autumn to autumn) is unrelated to position within the pit, presence of herbaceous cover, or duration of flooding in the spring. We calculated 1st-, 2nd-, and 3rd-year

survival rates for all plots (regardless of draw-down zone) in which seedling age was known with certainty (i.e., we eliminated those plots where establishment occurred in >1 year). These rates represent survival from one autumn to the next; thus 1st-year survival represents seedlings that live from the 1st autumn following establishment to the next autumn. For these calculations and all subsequent analyses, survival rates were truncated at 1.0. Flooding is known to be an important mortality factor for seedlings under some circumstances (Gladwin and Roelle 1998). Each year our lowest plots were reflooded for an indefinite period in the autumn in an attempt to eradicate *T. ramosissima* seedlings. These and additional plots were also flooded in the spring following establishment as we raised the water level to begin a new drawdown. Ordinary least-squares regression was used to examine relationships between survival and days inundated in the spring following establishment. Position and cover (in the 2nd summer) were also included as covariates in these analyses. We compared alternate regression models in a generalized linear modeling context; based on comparison of residual deviances and partial residual plots, none was preferable to the linear least-squares model. Finally, we graphically examined the relative position of surviving cohorts along the elevation gradient.

Because of the multiplicity of estimates in the above regression models, some adjustment to P -values for a family of simultaneous estimates may be appropriate. We considered the parameter estimates for a given species in an individual year to be the family of comparisons for simultaneous inference. Using Sidak's method for simultaneous inference (Westfall and Young 1993:44–45), adjusted probabilities given k simultaneous estimates with unadjusted probabilities are $P_{\text{adj}} = 1 - (1 - P_{\text{unadj}})^k$. Thus, the unadjusted probabilities reported here can be referenced to the following adjusted probabilities given $k = 5$ simultaneous parameter estimates: $P_{\text{unadj}} = 0.0102$ has $P_{\text{adj}} = 0.0500$, $P_{\text{unadj}} = 0.0020$ has $P_{\text{adj}} = 0.0100$, and $P_{\text{unadj}} = 0.0002$ has $P_{\text{adj}} = 0.0010$.

RESULTS

Establishment

Because of a failure of the seed crop (probably due to winter dieback of mature plants),

we were unable to specify elevation zones for *T. ramosissima* in 1996. Thus, we have information regarding establishment for 11 species-year combinations. Chi-square analyses indicate that presence/absence differed among the 3 elevation zones for all 11 combinations (Table 1). Percent occurrence was highest in zone 2, where a wetted edge was present during the period of seedfall, for 9 of 11 combinations. In the 2 cases that do not fit this pattern (*P. deltooides* and *S. amygdaloides* in 1994), percent occurrence was highest in zone 1. Tests using a negative binomial model also indicated that mean seedling densities differed among zones for all 11 species-year combinations (Table 1). Mean densities were always highest in zone 2, but in 1994 mean densities of *P. deltooides* and *S. amygdaloides* in zone 1 were similar to those in zone 2.

For plots in zone 2, logistic regression models incorporating position within the pit (east-west, north-south), cover, and total drawdown accounted for a maximum of 30% of total variability in establishment ($0.06 \leq \text{Rho} \leq 0.30$; $P \leq 0.0037$). Regression coefficients for easting and northing were always negative (indicating a lower probability of establishment to the east and north), and coefficients for both position variables differed from zero for 10 of 11 species-year combinations (Fig. 2). Cover and probability of establishment were positively related in 8 of 11 regressions (Fig. 2). Cases where coefficients for cover did not differ from zero all occurred in 1994 (*P. deltooides*, *S. amygdaloides*, and *T. ramosissima*). Total drawdown ranged from 4 cm to 67 cm for various combinations of species and year (Table 2) and tended to be greater for those species (*P. deltooides*, *S. amygdaloides*) that establish earlier in the year. The relationship between total drawdown and probability of establishment was less clear than for other covariates (Fig. 2). *Populus deltooides* and *S. amygdaloides* each had a negative relationship in 1995 and 1996, as did *T. ramosissima* in 1995. For *S. exigua*, total drawdown was not related to probability of establishment in any of the 3 years.

Growth

First-year growth of seedlings generally reflected the phenology of seed production (Table 3); seedlings of *P. deltooides* and *S. amygdaloides*, the earliest seed producers, were tallest, followed by those of *S. exigua* and *T. ramosissima*.

TABLE 1. Percent occurrence and mean density (number · m⁻²) of seedlings in the 3 zones defined by presence or absence of a wetted edge during the period of seedfall. *N* is the number of plots. Deviance is from a negative binomial generalized linear model.

Year/ Zone	<i>N</i>	% present	Chi-square (df)	<i>P</i> > chi- square	Mean density ± <i>s</i> _{\bar{x}}	Deviance (df)	<i>P</i> > chi- square
<i>Populus deltoides</i> subsp. <i>monilifera</i>							
1994							
1	94	9.6			0.21 ± 0.115		
2	325	8.6	13.65 (2)	0.0012	0.29 ± 0.064	7.45 (2)	0.0241
3	194	1.0			0.02 ± 0.073		
1995							
1	722	7.8			0.81 ± 0.089		
2	599	50.6	301.78 (2)	<0.0001	7.78 ± 0.410	539.15 (2)	<0.0001
3	166	34.3			3.60 ± 0.424		
1996							
1	1295	4.5			0.67 ± 0.064		
2	553	47.6	501.50 (2)	<0.0001	15.47 ± 0.817	1484.84 (1)	<0.0001
3	1	0.0					

<i>Salix amygdaloides</i>							
1994							
1	94	16.0			2.49 ± 0.433		
2	315	15.9	26.45 (2)	<0.0001	2.65 ± 0.246	107.65 (2)	<0.0001
3	204	2.0			0.04 ± 0.106		
1995							
1	722	3.9			0.26 ± 0.055		
2	599	22.0	100.34 (2)	<0.0001	1.93 ± 0.116	208.98 (2)	<0.0001
3	166	15.7			0.77 ± 0.149		
1996							
1	1295	0.1			0.00 ± 0.033		
2	553	16.3	217.33 (2)	<0.0001	1.75 ± 0.101	431.87 (1)	<0.0001
3	1	0.0					

<i>Salix exigua</i>							
1994							
1	218	11.9			0.51 ± 0.139		
2	340	32.4	46.61 (2)	<0.0001	4.99 ± 0.377	186.17 (2)	<0.0001
3	55	1.8			0.04 ± 0.205		
1995							
1	1213	6.3			0.63 ± 0.059		
2	240	50.0	329.29 (2)	<0.0001	15.66 ± 1.104	1289.78 (2)	<0.0001
3	34	11.8			0.35 ± 0.306		
1996							
1	1484	0.1			0.00 ± 0.029		
2	364	21.7	330.60 (2)	<0.0001	2.22 ± 0.128	559.51 (1)	<0.0001
3	1	0.0					

<i>Tamarix ramosissima</i>							
1994							
1	324	8.6			0.39 ± 0.094		
2	284	34.9	64.65 (2)	<0.0001	2.89 ± 0.233	131.32 (1)	<0.0001
3	5	0.0					
1995							
1	1321	1.3			0.06 ± 0.034		
2	161	63.4	746.17 (2)	<0.0001	14.15 ± 0.834	2335.91 (2)	<0.0001
3	5	20.0			0.40 ± 0.667		

Least-squares regressions using the covariates position, cover, and total drawdown explained 19–40% of the variance in mean seedling height at the end of the 1st growing season ($0.19 \leq R^2 \leq 0.40$; $P \leq 0.041$). In contrast to its relationship to the probability of establishment, the covariate easting (x location) was positively related to mean plant height (i.e., seedling height increased to the east) in 6 of 11 species-year combinations (Fig. 3). On the other hand, the relationship between the covariate northing (y location) and mean plant height was negative for 6 of 11 combinations of species and year. Cover was positively related to mean plant height in 9 of 11 cases, the only exceptions being *P. deltoides* in 1996 and *T. ramosissima* in 1994. As with probability of establishment, the relationship between drawdown and mean plant height was variable, with 4 of 11 coefficients being positive and 4 negative.

Survival

Truncation of survival rates to 1.0 affected 101 of 1631 (6.2%) species-plot combinations used in calculating 1st-year survival rates, 39 of 469 (8.3%) used in calculating 2nd-year survival rates, and 0 of 32 (0.0%) used in calculating 3rd-year survival rates. First-year survival rates ranged from a low of 0.14 for *T. ramosissima* in 1996 to a high of 0.55 for *S. exigua* in 1996 (Table 4). With the exception of *T. ramosissima*, 1st-year survival rates were highest in 1996 and lowest in 1995. All species showed increased survival in the 2nd year, as did *P. deltoides* and *S. amygdaloides* in the 3rd year. Second-year survival for *S. exigua* may be overestimated due to vegetative reproduction.

Least-squares regressions relating position, cover (in the 2nd summer after establishment), and days flooded (in the spring after establishment) to 1st-year survival were significant ($P \leq 0.0356$) for 7 of 8 species-year combinations, the lone exception being *P. deltoides* in 1995. Again, however, proportion of variance explained by these models was low ($0.04 \leq R^2 \leq 0.29$). Regression analysis showed no consistent relationships between 1st-year survival and the covariates position and cover (Fig. 4). Number of days that a plot was inundated in the spring following establishment, however, tended to be negatively related to survival, with 5 of 8 species-year combinations having regression coefficients differing from

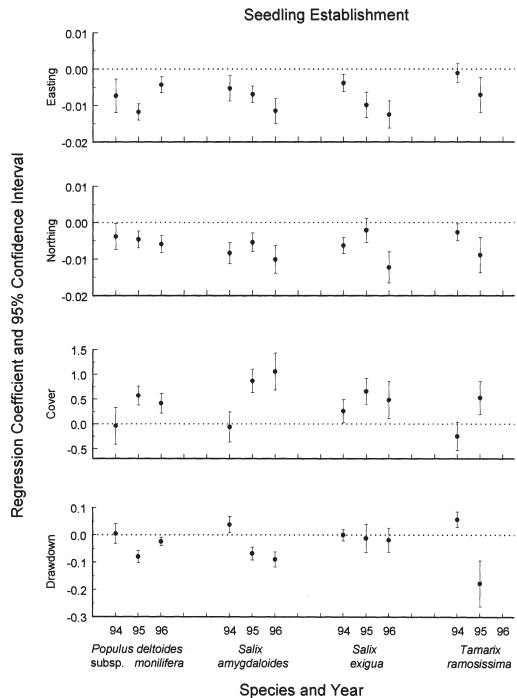


Fig. 2. Logistic regression coefficients and 95% confidence intervals for relations between seedling establishment and the covariates position (easting, northing), cover, and drawdown. Sample sizes (number of plots) are as in Table 2, zone 2.

zero. The maximum number of days inundated was greater in 1995 for all species (Table 5), but this did not result in a stronger effect of flooding in that year (Fig. 4).

Distribution of plots with surviving seedlings along the elevation gradient of the WREN Pit did not change substantially through the 4 years in which censuses were conducted (Fig. 5). Surviving *P. deltoides* and *S. amygdaloides* were at the highest elevations for cohorts established in a particular year, with *S. exigua* and *T. ramosissima* at lower elevations. The lower end of the distribution for several cohorts was “trimmed,” probably by both autumn and spring flooding. This effect is particularly noticeable for *T. ramosissima* established in 1994 (Fig. 5).

DISCUSSION

Establishment

Presence of a bare, wetted edge was a good predictor of establishment for all 4 species

TABLE 2. Range of total drawdown (cm) experienced by seedlings on sample plots.

Year	<i>Populus deltoides</i> subsp. <i>monilifera</i>	<i>Salix</i> <i>amygdaloides</i>	<i>Salix exigua</i>	<i>Tamarix</i> <i>ramosissima</i>
1994	27–67	28–67	11–5	4–39
1995	23–59	23–59	9–32	4–23
1996	9–67	9–67	9–51	—

TABLE 3. Mean (cm) ± $s_{\bar{x}}$ of seedling heights averaged by plot. Number of plots is in parentheses.

Year	<i>Populus deltoides</i> subsp. <i>monilifera</i>	<i>Salix</i> <i>amygdaloides</i>	<i>Salix exigua</i>	<i>Tamarix</i> <i>ramosissima</i>
1994	11.0 ± 1.20 (39)	11.8 ± 1.19 (69)	5.2 ± 0.39 (137)	3.8 ± 0.22 (127)
1995	11.2 ± 0.42 (416)	18.6 ± 0.94 (186)	7.0 ± 0.50 (200)	3.3 ± 0.16 (120)
1996	10.6 ± 0.43 (321)	15.1 ± 0.88 (91)	7.8 ± 0.58 (80)	—

studied. Several other investigators have reported comparable results. For example, Auble et al. (1997), working on Boulder Creek in Colorado, found that establishment of *Populus deltoides* subsp. *monilifera* was limited to bare, moist surfaces created by spring flooding. Shafroth et al. (1998) obtained similar results for *Populus fremontii*, *Salix gooddingii*, *Baccharis salicifolia*, and *Tamarix ramosissima* along the Bill Williams River in Arizona.

Inaccuracies in estimating whether or not a plot was moist during the period of seedfall likely accounted for many of the prediction errors in our study, particularly at the upper ends of the establishment zones. For example, establishment of *P. deltoides* and *S. amygdaloides* was similar in zones 1 and 2 in 1994 (Table 1). Of 24 species-plot combinations in which establishment of *P. deltoides* or *S. amygdaloides* occurred in zone 1 in 1994, all plot elevations were within 9 cm of the top of zone 2 (i.e., the water level at the start of drawdown, as measured by a staff gauge), and 22 were within 2 cm. Plots this close to surface water level at the start of drawdown could easily have been moist due to capillary rise. A component to account for capillary rise might improve predictions; in the case of the WREN Pit, however, capillary rise would likely have to be estimated separately for each plot because of the variability of the substrate. Water standing in perched depressions at the start of seedfall could account for additional inaccuracies in predictions at the upper ends of establishment zones. At the lower ends of establishment zones, predictions might be improved by adding a (species-specific) period to account

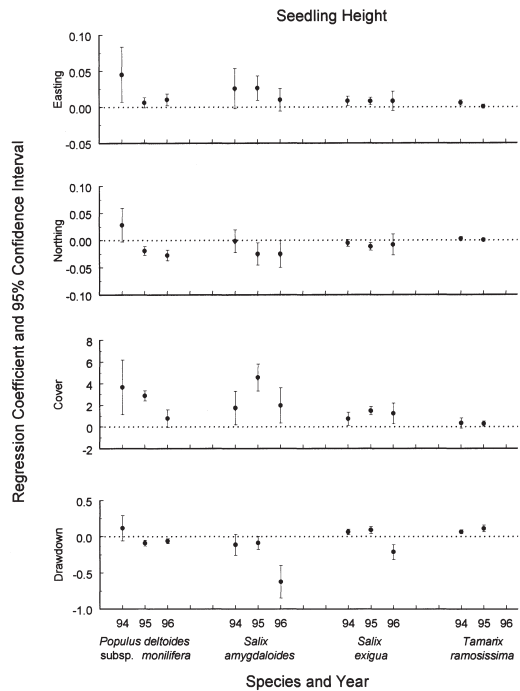


Fig. 3. Least-squares regression coefficients and 95% confidence intervals for relations between 1st-year seedling height and the covariates position (easting, northing), cover, and drawdown. Sample sizes (number of plots) are as in Table 3.

for the time that seeds remain germinable after they are released. The period of germinability has been estimated at about 1 week for *Salix* spp. (Ware and Penfound 1949, Densmore and Zasada 1983), 1–2 weeks for *Populus* spp. (Moss 1938, Ware and Penfound 1949),

TABLE 4. Mean $\pm s_{\bar{x}}$ of plot survival rates. Number of plots is in parentheses. Survival rates >1.0 were truncated to 1.0.

Year	1st-year rate	2nd-year rate	3rd-year rate
<i>Populus deltoides</i> subsp. <i>monilifera</i>			
1995	0.21 \pm 0.060 (35)	—	—
1996	0.41 \pm 0.019 (414)	0.58 \pm 0.149 (12)	—
1997	0.33 \pm 0.020 (276)	0.81 \pm 0.020 (230)	0.83 \pm 0.126 (8)
<i>Salix amygdaloides</i>			
1995	0.30 \pm 0.048 (67)	—	—
1996	0.38 \pm 0.030 (183)	0.46 \pm 0.078 (31)	—
1997	0.37 \pm 0.039 (89)	0.58 \pm 0.043 (102)	0.69 \pm 0.082 (24)
<i>Salix exigua</i>			
1995	0.35 \pm 0.037 (130)	—	—
1996	0.55 \pm 0.031 (190)	0.77 \pm 0.049 (60)	—
1997	—	—	—
<i>Tamarix ramosissima</i>			
1995	0.19 \pm 0.031 (127)	—	—
1996	0.14 \pm 0.025 (120)	0.67 \pm 0.069 (34)	—
1997	—	—	—

and 8 weeks for *Tamarix* spp. (Horton et al. 1960). In most of these trials, however, seeds were stored in the laboratory rather than under field conditions.

Position

We initially included x- and y-coordinates in our regression analyses of other factors affecting establishment, growth, and survival of seedlings to account for any variability due to position before examining the effects of cover, drawdown, and flooding. We were somewhat surprised to find a consistent effect of position on establishment, which tended to decrease to the north and east for all species and years. The most likely explanation for this effect is that seepage from the Cache la Poudre River and a pond (Fig. 1) often provided additional moisture to the west and south banks of the pit, thus resulting in conditions more favorable for establishment. Reasons for the generally positive relationships between easting (y location) and seedling height remain unclear. Other factors that may be important in position effects include soil texture, chemistry, and water relations; location of seed sources and the target area relative to wind patterns; and depth to groundwater.

Cover

Previous studies have shown that herbaceous cover or leaf litter present during the period of cottonwood and willow seedfall can

inhibit germination and growth. Friedman et al. (1995), for example, found that removing sod to expose bare mineral soil significantly enhanced establishment of *Populus deltoides* subsp. *monilifera* and *Salix amygdaloides*. Stromberg et al. (1991) found that densities of *Populus fremontii* and *Baccharis salicifolia* were negatively related to herbaceous cover, a result they attributed to the difficulty of seeds penetrating vegetation to make contact with the soil. They also reported that seedlings grow better (in spring and summer of establishment) on less densely vegetated plots. Johnson et al. (1976) and Walker et al. (1986) found similar negative effects of leaf litter on cottonwood and willow establishment, though other factors (e.g., reduced light, reduced soil temperatures) may also be important under an existing forest canopy.

In cases where herbaceous cover establishes simultaneously with or after seedlings, interactions may be more complicated. Stromberg (1997) found that *Tamarix chinensis* seedlings were sparsely distributed in plots with $>50\%$ cover of sweet clover (*Melilotus* spp.) but were abundant in plots with $<50\%$ sweet clover cover. Densities of *Populus fremontii* seedlings, on the other hand, were not affected by the presence of sweet clover. Their explanation of this pattern was that *T. chinensis* seedfall occurred after sweet clover had germinated and expanded to cover much of the ground, whereas *P. fremontii* seedlings established

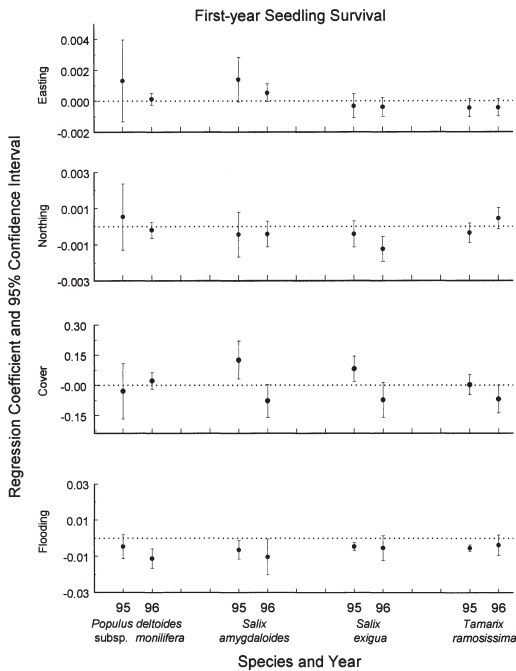


Fig. 4. Least-squares regression coefficients and 95% confidence intervals for relations between 1st-year seedling survival and the covariates position (easting, northing), cover, and flooding. Sample sizes are as in Table 4.

before sweet clover. Even though *P. fremontii* seedlings were overtopped by sweet clover in early summer, they were subsequently exposed to full sunlight as sweet clover senesced and therefore survived well. Shafroth et al. (1998) reported that plots in which woody riparian seedlings established tended to have greater herbaceous cover than those without establishment. They also found a correlation between herbaceous cover and lower, wetter sites and hypothesized either that these sites were simply more favorable for plant growth in the arid environment of Arizona or that herbaceous cover became established after seedlings.

In our study it is clear that herbaceous cover generally developed either simultaneously with or after woody seedlings because site preparation resulted in bare substrate throughout most of the pit, and flooding prevented establishment of any vegetation prior to drawdown. Thus, in zone 2, where we examined effects of factors such as cover on establishment, there was little cover to interfere with seed deposition on most plots. We suspect that positive relations between woody seedling establish-

ment and herbaceous cover (Fig. 2) are an indication that both herbs and woody seedlings established better on wetter sites. The 3 species-year combinations for which the relationship between herbaceous cover and establishment was nonsignificant (Fig. 2) all occurred in 1994, the 1st year in which we conducted a drawdown. In 1994 surface water in some parts of the pit extended into areas where site preparation had not removed existing vegetation. Such vegetation may have interfered with seed deposition and resulted in different relationships between cover and establishment than in other years. The hypothesis that plots with greater herbaceous cover are simply favorable sites where both herbs and woody seedlings may thrive is perhaps further supported by the positive relationships between cover and woody seedling height in the 1st summer (Fig. 3). However, we did not find consistent relationships between 1st-year survival (from the autumn following establishment to the next autumn) and herbaceous cover during the 2nd summer of growth (Fig. 4). This may indicate that cover was dense enough on some plots in the 2nd summer to result in significant competition for light, water, and nutrients.

Drawdown

Tolerance of woody riparian seedlings, particularly *Populus* spp., to drawdown or water table decline has been examined in both laboratory and field studies. Laboratory investigations have generally involved measuring plant response to controlled drawdown rates. Mahoney and Rood (1991), for example, reported that rates of water table decline ≥ 4 cm \cdot day $^{-1}$ limited survival of seedlings of a natural poplar hybrid (*Populus deltoides* \times *P. balsamifera*) through the 1st growing season (which is equivalent to establishment as defined for our study), and that a decline of 1 cm \cdot day $^{-1}$ resulted in maximum root elongation. In a similar study of *Populus deltoides* subsp. *monilifera* seedlings, Segelquist et al. (1993) found that drawdown rates ≥ 0.7 cm \cdot day $^{-1}$ affected establishment and that shoot height, shoot biomass, root length, root biomass, and total biomass were greatest at a rate of 0.4 cm \cdot day $^{-1}$.

The approach in field studies has generally been to measure the elevation of established seedlings relative to elevation of the adjacent

TABLE 5. Flooding characteristics of the plots for which 1st-year survival could be calculated.

Year	Flooding characteristic	<i>Populus deltoides</i> subsp. <i>monilifera</i>	<i>Salix amygdaloides</i>	<i>Salix exigua</i>	<i>Tamarix ramosissima</i>
1995	Range (days)	0–83	0–84	0–94	0–89
	Mean (days)	13.8	11.2	38.6	51.1
	Percent of plots flooded	57.1	58.2	87.7	94.5
1996	Range (days)	0–35	0–25	0–35	0–42
	Mean (days)	3.3	3.0	8.0	21.4
	Percent of plots flooded	23.4	25.7	46.3	90.8

stream at some reference flow (usually late summer or autumn), the difference representing overall water table decline or drawdown experienced by the seedlings. The assumptions in this approach are that seedlings become established at the wetted edge as flood flows recede and that the subsurface water table roughly parallels water level in the stream. While subsurface water levels have rarely been measured in studies of this nature, Mahoney and Rood (1998) argued that it is reasonable to assume a horizontal water table in the generally coarse alluvial substrates adjacent to most western streams. Mahoney and Rood (1998) recently summarized information from these kinds of studies in the context of their "Recruitment Box" model, concluding that *Populus* establishment is most likely to occur at elevations 60–150 cm above the growing season "base flow." Above 150 cm, seedlings are likely to die from desiccation (i.e., their roots are not able to grow fast enough to maintain contact with the subsurface water table, even taking into account capillary rise). Below 60 cm, the probability of surviving future scouring by stream flow or ice is low. Mahoney and Rood (1998) also incorporated a maximum drawdown rate of $2.5 \text{ cm} \cdot \text{day}^{-1}$ as part of their recruitment model.

While generalizations from these kinds of studies are difficult (Shafroth et al. 1998), we established a target drawdown rate of $1.0 \text{ cm} \cdot \text{day}^{-1}$ for our work at the WREN Pit. Our overall objective was to test the utility of natural seedfall and hydrologic manipulation as a revegetation technique, and we viewed $1.0 \text{ cm} \cdot \text{day}^{-1}$ as a conservative choice that would prevent seedlings from becoming hydrologically stranded but still promote root elongation. Thus, it is perhaps not surprising that there was no consistent relationship between drawdown and establishment (Fig. 2) or growth in the 1st summer (Fig. 3). In addition, the lower

bound (60 cm) suggested by Mahoney and Rood (1998) is probably not applicable in the context of the WREN Pit, where we attempted to maintain winter water levels low enough that established seedlings would not be affected by ice, and where scouring by stream flow is not a problem. Finally, subsurface water relationships in the WREN Pit are probably more complicated than in most floodplain situations, due to the fact that most alluvial sand and gravel was removed.

Flooding

Several authors have reported that inundation by standing water can be a significant mortality factor for some riparian seedlings (Gladwin and Roelle 1998). *Populus* and *Tamarix* have been best studied in this regard, and, in general, results indicate that susceptibility to inundation decreases significantly after the 1st year. Gladwin and Roelle (1998) found significant mortality of both *P. deltoides* and *T. ramosissima* seedlings inundated for 25 days in autumn (15 September through 10 October) following establishment, but no significant effect of inundation for 28 days in the following spring (21 May through 18 June). In the current study, however, spring flooding (as we raised the water level in the pit to begin the new drawdown) had a consistent negative effect on 1st-year survival (Fig. 4), although regression coefficients were significant for only 5 of 8 species-year combinations.

Reasons for this apparent difference in the effects of spring flooding are unclear. In 1995 many seedlings were flooded earlier (beginning April 1) and longer (up to 94 days) than those in the study reported by Gladwin and Roelle (1998). In 1996, however, starting date (11–26 May, depending on species) and duration (up to 42 days) of flooding were more similar to those reported by Gladwin and Roelle

Elevation of Plots with Surviving Seedlings

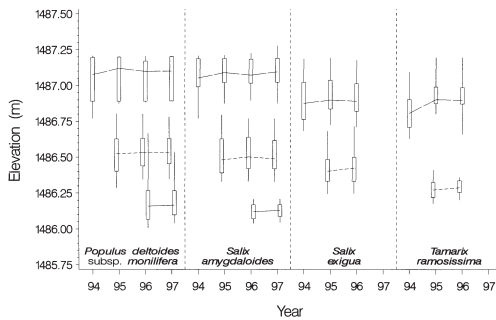


Fig. 5. Distribution of plots with surviving seedlings along the elevation gradient of the WREN Pit. Boxes represent 25th–75th percentiles; whiskers extend to 5th and 95th percentiles. Long-dash horizontal lines connect medians for cohorts established in 1994, short-dash lines for cohorts established in 1995, and solid lines for cohorts established in 1996.

(1998). It is possible that date of initiation and duration of flooding relative to the precise phenology of plant growth are important determinants of vulnerability, especially for relatively young seedlings just emerging from their 1st dormant season. However, given that there were no consistent differences in the results in 1995 compared with 1996, it seems unlikely that date of initiation or duration of flooding was primarily responsible for the fact that results in the current study were different from those of Gladwin and Roelle (1998). Interpretation is further complicated by the fact that some plots were flooded for a period of unknown duration each autumn as we attempted to control *T. ramosissima*.

The hypothesis that survival over the 1st winter is positively related to seedling size was also considered. If seedlings at lower elevations were smaller (due to later germination) and if smaller seedlings had poorer survival than larger ones, then the apparent flooding effect could be an artifact, because smaller (lower) seedlings were more likely to be flooded. However, we found no consistent relationship between seedling size and elevation in the current study. Furthermore, *P. deltoides* seedlings in the current study were somewhat taller (Table 3) at the end of the 1st summer than those used by Gladwin and Roelle (1998; Table 1), and *T. ramosissima* seedlings were about the same size.

Physical and chemical characteristics of flood water are also known to influence plant response (Whitlow and Harris 1979), and any number of differences in such parameters may have existed between the WREN Pit and the pond in which Gladwin and Roelle (1998) did their spring treatment. Detailed study of the response of seedlings to flood waters differing with respect to factors such as salinity and dissolved oxygen is warranted.

Seedling Distribution

A temporal pattern in seed production by various species of *Populus*, *Salix*, and *Tamarix* has been reported by several authors. With some variation due to species and geographic location, *Populus* usually produces seed earliest in the growing season and for a relatively short time, followed by *Salix* (often for a somewhat longer time) and then *Tamarix*, which usually has the longest and latest period of seed production (Warren and Turner 1975, Stromberg 1997, Shafroth et al. 1998, Roelle and Gladwin 1999). If the common mode of establishment of these species is seed germination on bare, moist surfaces remaining as stream flows recede following spring or early summer floods, then the median establishment elevation for *Populus* should be highest, followed by *Salix* and then *Tamarix*, usually with some overlap between species. For any given year, this is exactly the pattern observed at the WREN Pit (Fig. 5).

In contrast, several investigators have found different patterns in juvenile and mature stands of these same species (Stromberg et al. 1996, Allred and Schmidt 1999, Shafroth 1999), with *Tamarix* occupying relatively higher positions than in the establishment pattern described above. There are 2 possible explanations for such differences in distribution between seedlings and older plants. First, the various species might have been established in different flood events, perhaps in different years (i.e., the establishment pattern described above did not apply to a particular site). For example, a relatively large flood in late summer (when only *Tamarix* is producing seed) might lead to establishment of *Tamarix* above *Populus* and *Salix* that established during smaller flood events. Second, and perhaps more likely, differential mortality among species might have altered their relative distribution through

time. Many factors that have been proposed to account for the invasive success of *Tamarix* (e.g., high tolerance of drought, inundation, and salinity; vigorous resprouting after fire; lack of herbivory) might be responsible for such differential mortality (Smith et al. 1998).

Thus far, there is no evidence of differential mortality at the WREN Pit sufficient to alter the distribution of established seedlings (Fig. 5). This is perhaps not surprising, however, in that the basic objective of our work at the WREN Pit was restoration of native woody species. To this end, we attempted to provide conditions suitable for *Populus* and *Salix*, and these conditions appear also to be conducive to *Tamarix* establishment and growth. Conditions at the WREN Pit were thus relatively benign (e.g., slow drawdown, shallow groundwater, lack of scouring) compared to most riverine situations, where differential mortality following establishment may be much more important in structuring the riparian community.

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