RESEARCH
Restoration of Riparian Forest Using Irrigation, Artificial Disturbance, and Natural Seedfall

JONATHAN M. FRIEDMAN*
MICHAEL L. SCOTT
National Biological Service
Midcontinent Ecological Science Center
4512 McMurry Avenue
Fort Collins, Colorado 80525-3400, USA

WILLIAM M. LEWIS, JR
Department of Environmental, Population, and Organismic Biology
Campus Box 334
University of Colorado
Boulder, Colorado 80309, USA

ABSTRACT / In interior western North America, many riparian forests dominated by cottonwood and willow are failing to reproduce downstream of dams. We tested the hypothesis that establishment is now prevented by absence of the bare, moist substrate formerly provided by floods and channel movement. Along Boulder Creek, a dammed stream in the Colorado plains, we tested the effects of disturbance (sod removal), irrigation, and addition of seed on the establishment of seedlings of plains cottonwood (*Populus deltoides* subsp. *monilifera*) and peachleaf willow (*Salix amygdaloides*). In unirrigated, undisturbed plots, mean cottonwood density was 0.03 seedlings/m^2. Irrigation or disturbance alone produced mean cottonwood densities of 0.39 and 0.75 seedlings/m^2. Plots that were both irrigated and disturbed produced a mean cottonwood density of 10.3 seedlings/m^2. The effects of irrigation and disturbance on cottonwood establishment were significant ($P < 0.005$); added seed had no significant effect ($P = 0.78$). The few cottonwood seedlings in unirrigated plots were in low positions susceptible to scour by future moderate flows. We conclude that cottonwood establishment along Boulder Creek is limited by the scarcity of bare, moist sites safe from future scour. Establishment of peachleaf willow was significantly affected only by disturbance; daily sprinkler irrigation did not provide sufficient moisture to increase survival of this species. Our results demonstrate the feasibility of restoring plains cottonwood forests using natural seedfall, even where only widely scattered adult trees are present. Because use of natural seedfall conserves the genetic makeup of the local population, this method may be preferable to the use of imported cuttings.

In relatively arid regions of interior western North America, riparian ecosystems are dominated by members of the willow family (Salicaceae) including both cottonwoods (*Populus*) and willows (*Salix*). Especially where uplands are too dry to support trees, the riparian forests provide important habitat for mammals and birds (Knopf 1985, Brinson and others 1981). These forests have been greatly altered by upstream dam construction.

Cottonwood and willow seedlings are sensitive to drought (Moss 1938, Burns and Honkala 1990) and intolerant of shade (Johnson and others 1976, Scott and others 1993); therefore, they are usually found on moist, recently deposited sediment. Dams typically decrease downstream peak flows and sediment load.

KEY WORDS: Disturbance; Flood; Natural seedfall; Peachleaf willow; Plains cottonwood; Restoration; Riparian; Seedling establishment

*Author to whom correspondence should be addressed

Where dams have been constructed along wide braided channels, the result has often been channel narrowing by as much as an order of magnitude (Williams and Wolman 1984, Johnson 1994). In this situation there has usually been a transient increase in cottonwood and willow establishment on the bare, moist, areas of former channel bed (Johnson 1994, Friedman and others 1995, Scott and others 1995). Where dams have been constructed along meandering channels, which have a relatively low ratio of width to depth, little narrowing has occurred, but the channels have often responded by greatly reducing the rate of lateral migration. In this situation, reproduction of cottonwood and willow has been reduced or eliminated (Johnson and others 1976, Bradley and Smith 1986, Scott and others 1995). The present study addresses the reason for these failures of regeneration, which have been observed as far north as Alberta (Rood and Mahoney 1990) and as far south as Arizona (Ohmart and others 1988).

Several authors have argued that decline of cottonwood and willow downstream of dams on meandering channels results from the decreased rate of formation of moist open sites suitable for seedling establishment (Bradley and Smith 1986, Rood and Mahoney 1990, Johnson 1992, Friedman 1993, Scott and others 1995). This hypothesis has never been tested. Other possible explanations for a decline of cottonwood and willow include decreases in vigor of adults, leading to decreased seed production, changes in patterns of grazing and fire, and competition from exotic species. If, indeed, reproduction is limited by a shortage of bare, moist sites, it should be possible to restore stands of cottonwood and willow using natural seedfall in artificially disturbed, irrigated locations.

We used an experimental approach to test this hypothesis along Boulder Creek, a dammed, formerly meandering stream in the plains of Colorado, USA. Our study focused on plains cottonwood [*Populus deltoides* Marshall subsp. *monilifera* (Aiton) Eckenwalder] and peachleaf willow (*Salix amygdaloides* Andersson). These two species are the dominant native trees in bottomlands of the Colorado plains and are important components of bottomland forests throughout the Great Plains (Great Plains Flora Association 1986). We hypothesized that seedling establishment could be increased by increasing the abundance of sites that are both moist and free of litter and competing vegetation. A corollary of this hypothesis is that there are enough naturally dispersed, viable seeds to populate sites that are physically suitable.

Study Area

Boulder Creek is a perennial stream flowing east from the Indian Peaks of the Rocky Mountains into Saint Vrain Creek, a tributary of the South Platte River. The study site is the north bank of a 1-km reach east of Boulder, Colorado, 15 km east of the mountain front, and 38 km downstream of Barker Reservoir. This reach has an elevation of 1650 m and a gradient of 0.003. The study site is at latitude 40° 3′ north and longitude 105° 8′ west in the Colorado Piedmont Section of the Great Plains Physiographic Province (Madole 1991). The climate is continental and temperate, with long warm summers and cold winters. The average number of days between the last spring frost and the first fall frost is 154 (Colorado Climate Center 1992a). Mean annual precipitation is 46.9 cm (Colorado Climate Center 1992b). Discharge at the study site ranged from 0.65 to 12 m^3/sec between 1 February and 30 September 1992 (James Disinger, City of Boulder, personal communication).

Former channels apparent in aerial photographs of Boulder Creek indicate that the stream once migrated across a valley more than 1 km wide. However, as a result of flow regulation and channel stabilization, the channel is now relatively static. The Boulder Creek bottomland is dominated by a broad terrace 1–2 m above the channel thalweg. Between the terrace and the stream is a slope 5–30 m wide.

The bottomland vegetation of the study site is typical of perennial streams in eastern Colorado. Cobbly terraces are dominated by grasses, especially the exotics intermediate wheatgrass (*Agropyron intermedium*) and smooth brome (*Bromus inermis*) and the native saltgrass (*Distichlis spicata*). Silty and sandy terrace sediments are dominated by tall exotic herbs including pigweed (*Amaranthus retroflexus*), canada thistle (*Cirsium arvense*), peppergrass (*Lepidium latifolium*), saltbush (*Atriplex heterosperma*), lamb's quarters (*Chenopodium album*), and teasel (*Dipsacus fullonum*). Depressions subject to anaerobiosis are dominated by native graminoids, especially the sedges *Carex emoryi*, *C. lanuginosa*, and spikerush (*Eleocharis macrostachya*). Areas wet throughout much of the growing season but without anaerobic sediments are dominated by the exotic reed canary grass (*Phalaris arundinacea*).

The terrace supports widely scattered old trees, including six female plains cottonwoods, three female peachleaf willows, and several female crack willows (*Salix* × *rubens*) an exotic hybrid. On slopes between the terrace and the channel, there are scattered thickets of the native shrub sandbar willow (*Salix exigua*) that include many female clones. Two channel islands support young cottonwood and willow trees; elsewhere on the bottomland the only evidence of tree reproduction in the last few decades is one small crack willow and two apparent cottonwood root sprouts. The site is not grazed at present but has probably been heavily grazed in the past. Taxonomy follows Great Plains Flora Association (1986) except for crack willow (*Salix* × *rubens*: Shafroth and others 1994).

Methods

We carried out a three-way factorial experiment with two levels for each treatment. The three pairs of contrasting treatments were irrigation vs no irrigation, sod removal vs no sod removal, and addition of seeds vs no addition of seeds. In 1992 we tested all possible combinations of these variables using the design shown in Figure 1. This design was replicated in three blocks along the study reach. Each of the eight treatment combinations within a block occupied a plot 2 m wide extending from the water's edge to the terrace; this plot shape integrated the effects of the treatments over the entire elevational gradient in the Boul-

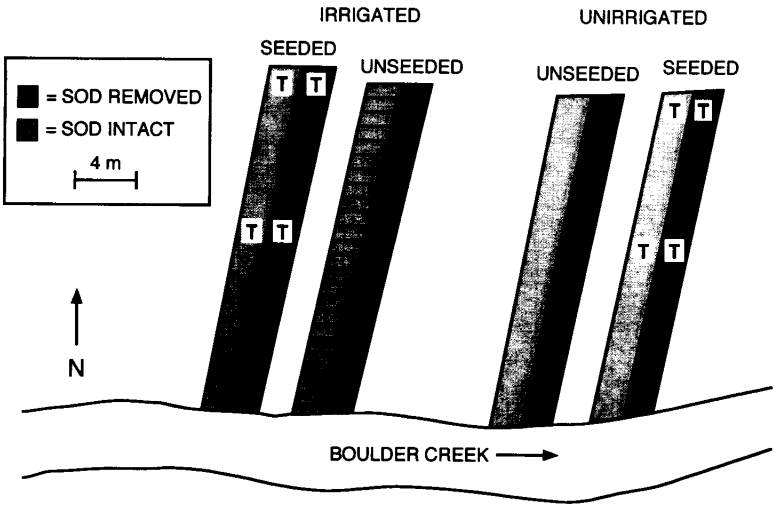

Figure 1. Design of block 2 of the establishment experiment for plains cottonwood and peachleaf willow along Boulder Creek, Colorado. Each of the eight plots was divided into 1 × 2-m subplots as illustrated in the third plot from the left. Locations of tensiometer nests are indicated by the letter T. Elevations of the eight tensiometer nests at the ground surface were (clockwise from upper left) 0.66, 0.56, 0.58, 0.50, 0.11, 0.23, 0.26, and 0.39 m relative to the water surface on 6 August 1992.

der Creek bottomland. Plots varied in length from 19 to 30 m. Depth to water table measured in 12 shallow wells ranged from 0 to 113 cm.

Within a block, all four irrigated plots were located together to prevent inadvertent irrigation of nontarget plots and to simplify the irrigation system. Within the irrigated and unirrigated groups, plots with added seed were segregated from those without to minimize transport of added seed by wind to the wrong plots. Plots to receive added seed were determined by coin toss. A plot from which sod was removed was always immediately adjacent to and downstream of a plot with intact sod.

Sod was removed using a track-mounted excavator on 19 May 1992. This operation lowered the surface elevation by an average of 16.5 cm. The technique was based on the work of Johnson (1965), who reported that stands of eastern cottonwood (*Populus deltoides* subsp. *deltoides*) can be established in Mississippi bottomlands using natural seedfall without irrigation in bulldozed strips. By August, growth of herbs had decreased the difference in vegetative cover between undisturbed plots and those from which sod had been removed. Therefore, on 26 August, we used a gasoline-powered weed-trimmer to mow to a height of 50 cm all plots from which sod had been removed.

The irrigation treatment consisted of sets of three sprinklers per block; sprinklers were mounted 1.5 m above the ground. Streamwater was supplied to each set of sprinklers by pump. Plots were irrigated once daily from 30 May to 23 July. Thereafter plots were irrigated approximately every third day until 15 August. Irrigation was curtailed beginning in late July to promote downward root growth and to reduce establishment of competing species. Each irrigation event lasted 2.5 h and delivered an average of 0.98 cm of water to the soil surface; the range in water delivery was 0.5–1.5 cm. Shallow wells in each block showed no detectable groundwater mounding beneath the irrigated area.

We collected local seeds of plains cottonwood and peachleaf willow by picking catkins containing capsules that had begun to open. After allowing the capsules to open more completely in a paper bag for two to seven days, we cleaned the seeds by shaking the capsules in a set of soil sieves. For cottonwoods, we accelerated this process by directing air from a vacuum cleaner through the sieves (Schreiner 1974). We stored the cleaned seeds in airtight containers at 4°C for no more than 26 days. On 17 June, we combined all cottonwood seeds in one batch and all peachleaf willow seeds in another, and then sprinkled the seeds onto the plots using plastic containers with perforated tops. We planted cottonwood at a density of 146 seeds/m^2 and willow at a density of 364 seeds/m^2. In order to determine whether seed handling and storage had decreased viability, we tested the remaining seeds for viability on 18 June. We placed 100 seeds of each species on moistened filter paper in Petri dishes and counted the number of individuals with expanded cotyledons after 96 h at 20°C. Because seed mass can affect survival, we determined the mean mass of seeds of plains cottonwood and peachleaf willow by weighing 30 lots of 100 seeds of each species. Because seeds of cottonwood and willow remain viable for only a few weeks under field conditions (Ware and Penfound 1949), it was necessary to coordinate the timing of the experiment with the timing of seed release. We determined the period of seed release for all Salicaceae at Boulder Creek by making observations on 14 different days from 11 May to 31 August.

In block 2 we measured soil–water potential in four plots representing all four combinations of the irrigation and sod-removal treatments. In each of the four plots, we installed three tensiometers at depths of 10.2, 45.7, and 61.0 cm at the end of the plot farthest from the stream, and two tensiometers at depths of 10.2 and 45.7 cm in the center of the plot (Figure 1). We recorded the tensiometer readings on 38 occasions throughout the summer. We used a combination of the hydrometer and sieve methods (Gee and Bauder 1986) to analyze sediment particle size in the top 50 cm at one location in each of the three blocks.

Between 15 and 25 September 1992 we counted all woody seedlings in all 24 plots. We carried out an analysis of variance for each species on the whole-plot data using a blocked three-way factorial model (Wilkinson 1989). For the purposes of this analysis, we transformed the seedling density as follows: $y_{tr} = \ln(y + k)$, where y is the seedling density in a plot, y_{tr} is the transformed value, and the constant, k, is the smallest non-zero seedling density. This transformation counteracted a positive correlation between analysis of variance model estimates and the variance of residuals.

In order to determine the influence of elevation and inundation on seedling establishment, we divided each plot into 1 × 2-m subplots (Figure 1) and determined the density of seedlings of each species in each subplot during the 1992 sampling. Using a rod and level, we measured the elevations of the subplots relative to the water surface on 6 August 1992. We used staff gauges to relate stage at each of the three blocks to mean daily discharge in the study reach (James Disinger, personal communication). Because these relations were similar, they were lumped to produce one overall relation between discharge and stage. This relation was combined with the record of mean daily discharge between 1 May and 25 September 1992 to determine the elevations of 0 and 50% inundation duration (the elevation of the highest mean daily discharge and the elevation inundated half of the time).

On 16 September 1993 we again counted all cottonwoods and willows in all 24 plots. There had been no irrigation in 1993. Therefore, this second count enabled us to determine whether one growing season of irrigation was sufficient to allow roots of plains cottonwood and peachleaf willow to reach the water table.

Results

The peak periods of seed release were the last two weeks of May for peachleaf willow and the first two weeks of June for plains cottonwood. We observed

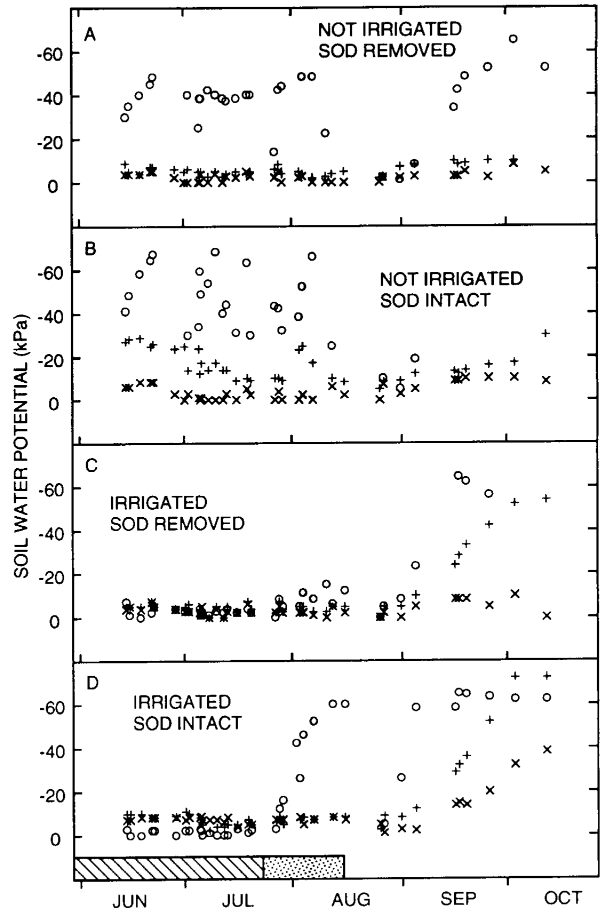

Figure 2. Tensiometer readings in experimental plots at Boulder Creek, Colorado, in 1992. Depths below ground surface are: ○ = 10.2 cm, + = 45.7 cm, and x = 61.0 cm. ▨ = daily irrigation, and ▩ = irrigation every three days.

cotton of both plains cottonwood and peachleaf willow falling on the experimental plots. As reported by Engstrom (1948), the timing of seed release varies greatly among individuals of the same population. The peak day of seed release by the six female cottonwood trees in the study reach varied from 30 May to 27 June.

Seeds of cottonwood had a mean mass of 6.4×10^{-4} g ($N = 3000$). This is essentially the same as the value of 6.5×10^{-4} g determined by Bessey (1904) in Nebraska. Seeds of peachleaf willow had a mean mass of 4.0×10^{-5} g ($N = 3000$). The viability of the sown seeds was 71% for plains cottonwood and 49% for peachleaf willow.

The soil–water potentials at the high (north) end of plots in block 2 (Figure 1) ranged from −72 to 0 kPa (Figure 2). In dry, coarse substrate, some tensiometers quickly lost their fluid, and a reading was not possible. Note, for example, the missing data in Sep-

Table 1. Temperature and rainfall in Boulder, Colorado[a]

	April	May	June	July	August	September	October
Mean temperature (°C) 1992	12.4	15.1	17.2	20.2	19.1	18.0	12.3
Mean temperature (°C) 1993	8.6	14.2	18.1	20.8	19.7	14.8	9.2
Mean temperature (°C) 1961–1990	9.6	14.4	19.6	22.8	21.7	16.9	11.6
Monthly precipitation (mm) 1992	11.7	43.2	24.4	28.7	78.2	0.5	20.1
Monthly precipitation (mm) 1993	65.0	43.9	85.9	35.6	26.4	84.3	61.5
Mean monthly precipitation (mm) 1961–1990	54.9	76.2	56.4	48.8	31.8	46.7	32.8

[a]Data are from the National Oceanic and Atmospheric Administration (1992) Colorado Climate Center (1992a,b).

tember in the unirrigated plot with sod intact at 10.2 cm (Figure 2B). In the unirrigated treatments, the surface sediment was dry most of the time. At a depth of 10.2 cm, the water potential was less than −30 kPa throughout the period of record except after rain (Figure 2A and B). In the irrigated plots, the soil surface was moist through the end of daily irrigation on 23 July (Figure 2C and D). During the period when irrigation occurred once every three days, a shallow, dry horizon developed in the plot with intact sod (Figure 2D). The eight tensiometers in the center of plots in block 2 all measured water potentials greater than or equal to −13 kPa throughout the experiment (data not shown). These locations were relatively low and remained moist because of their shallow water table.

The growing season in 1992 was cool and dry. August was the only month with above-average precipitation (Table 1). The cessation of irrigation in August and the absence of appreciable rain in September resulted in some mortality of seedlings in irrigated plots. Thus, if irrigation had continued longer, the seedling densities in irrigated plots would have been higher. In 1993, temperature was below average and precipitation was close to the mean (Table 1).

In September 1992, we counted totals of 3097 seedlings of plains cottonwood, 200 of peachleaf willow, 11 of sandbar willow, and 8 of crack willow in the 24 plots, an area of 1184 m^2. There were no older individuals of any of these species in any of the plots. In unirrigated plots with sod intact, seedlings of plains cottonwood were absent in September 1992, except on a few frequently inundated bars below the lower limit of perennial vegetation (Table 2A, Figure 3). Outside our experimental plots, such bars were the only locations in the study area where cottonwood seedlings were observed. In irrigated plots with intact sod, cottonwood seedlings were restricted to the high and low extremes of the elevation gradient, where low moisture or frequent scour limited the cover of preexisting vegetation (Table 2A, Figure 3). In unirrigated plots without sod, cottonwood seedlings did not occur higher than 20 cm above the elevation of 0% inundation duration (Table 2A, Figure 3). When irrigation was added to plots without sod, high densities of cottonwood became established, especially above the elevation of 0% inundation, where seedlings were not subject to removal by flowing water or anaerobiosis (Table 2A, Figure 3).

Table 2. Density of plains cottonwood and peachleaf willow in plots at end of first growing season, 15–25 September 1992

	Density (seedlings/m^2)			
	Unirrigated		Irrigated	
	Unseeded	Seeded	Unseeded	Seeded
A. Plains cottonwood				
Sod intact				
Block 1	0.00	0.00	1.41	0.12
Block 2	0.00	0.00	0.02	0.00
Block 3	0.08	0.07	0.37	0.40
Sod removed				
Block 1	0.00	0.00	15.67	35.60
Block 2	1.02	1.71	1.44	2.93
Block 3	1.58	0.21	2.10	4.27
B. Peachleaf willow				
Sod intact				
Block 1	0.00	0.00	0.02	0.00
Block 2	0.00	0.00	0.00	0.00
Block 3	0.02	0.00	0.00	0.00
Sod removed				
Block 1	0.00	0.00	0.12	0.17
Block 2	0.62	0.11	0.02	0.52
Block 3	0.03	0.00	0.05	2.03

Irrigation and sod removal had significant positive effects on establishment of plains cottonwood (Table 3A). In irrigated plots without sod, addition of seeds appeared to increase the number of cottonwoods es-

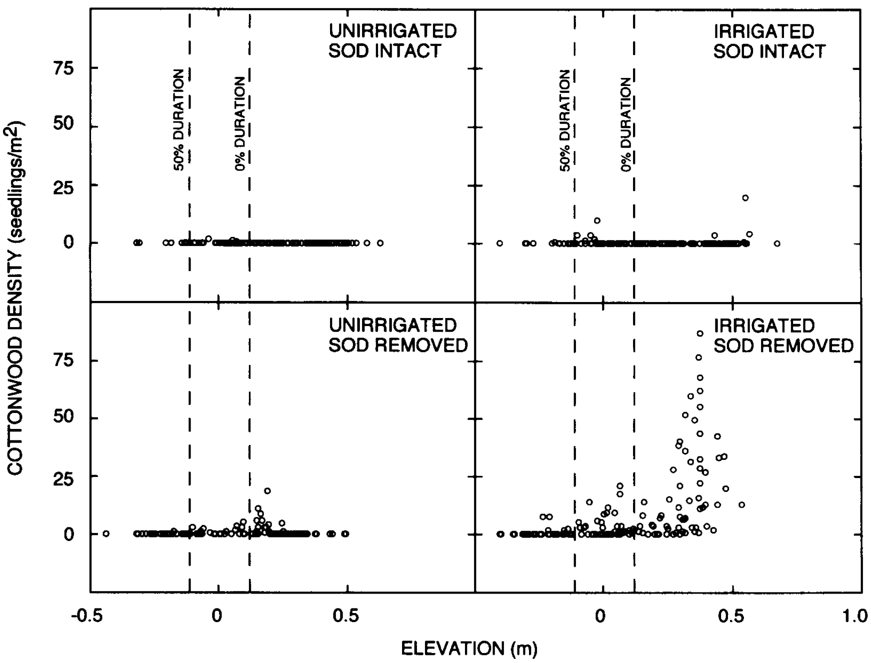

Figure 3. Density of cottonwood seedlings in 1 × 2-m subplots as a function of elevation for four treatment combinations along Boulder Creek, Colorado, 1992. Elevations are relative to the water surface on 6 August 1992. The dashed lines indicate the elevations of 0 and 50% inundation duration.

Table 3. Blocked, three-way analysis of variance of effects of irrigation, sod removal, and addition of seed on density of seedlings of plains cottonwood and peachleaf willow along Boulder Creek, Colorado, 1992

Source of variation	Sum of squares	Degrees of freedom	Mean square	*F* ratio	Probability
A. Plains cottonwood					
Irrigation	33.20	1	33.20	11.61	0.004
Sod removal	45.03	1	45.03	15.74	0.001
Addition of seed	0.23	1	0.23	0.08	0.78
Block	4.08	2	2.04	0.71	0.51
Irrigation × sod removal	2.98	1	2.98	1.04	0.33
Irrigation × seed	0.03	1	0.03	0.01	0.92
Sod removal × seed	0.63	1	0.63	0.22	0.65
Irrigation × sod removal × seed	1.75	1	1.75	0.61	0.45
Error	40.05	14	2.86		
B. Peachleaf willow					
Irrigation	2.93	1	2.93	3.21	0.10
Sod removal	16.66	1	16.66	18.23	0.001
Addition of seed	0.18	1	0.18	0.20	0.66
Block	1.28	2	0.64	0.70	0.51
Irrigation × sod removal	2.67	1	2.67	2.92	0.11
Irrigation × seed	3.31	1	3.31	3.62	0.08
Sod removal × seed	1.13	1	1.13	1.23	0.29
Irrigation × sod removal × seed	3.60	1	3.60	3.94	0.07
Error	12.79	14	0.91		

tablished (Table 2A); however, this effect was not observed in other treatment combinations and the overall effect of seed addition was not significant (Table 3A). The effects of block and interactions among treatments were also not significant (Table 3A).

There were not enough degrees of freedom to test for interactions between block and the three treatments; however, these interactions may be important. In irrigated plots without sod, block 1 had the highest densities of cottonwood seedlings (Table 2A) for two reasons. First, block 1 had a relatively coarse substrate

(Table 4). Second, block 1 included a large proportion of subplots at high elevations where seedling establishment was greatest (Figure 3); median elevations of subplots in blocks 1, 2, and 3 were 0.34, 0.20, and −0.01 m. High elevation and coarse substrate apparently caused Block 1 to be relatively xeric and low in nutrients. The dominant vegetation consisted of sparse, shallowly rooted grasses that were eliminated by sod removal. Blocks 2 and 3 were dominated by tall, competitive (Grime 1977) herbs that quickly became reestablished following sod removal. The perennials Canada thistle and peppergrass sprouted from deep rhizomes; the annuals pigweed, saltbush, and lamb's quarters, and the biennial teasel, apparently became established from seed dispersed from outside the plots. Compared to cottonwood seedlings in block 1, seedlings in blocks 2 and 3 were generally small and etiolated. Midseason counts in subsamples of plots in blocks 2 and 3 revealed high densities of cottonwood seedlings that were apparently killed by shade before the September census. In summary, the relatively high elevation and coarse substrate of block 1 led to high cottonwood densities in irrigated plots without sod. On the other hand, these same characteristics apparently made unirrigated plots in block 1 too dry for cottonwood establishment (Table 2A).

Seedlings of peachleaf willow were fewer and more erratically distributed than those of plains cottonwood (Table 2B). The only significant effect on establishment of peachleaf willow was that of sod removal (Table 3B). Seedlings that survived were mostly in low-lying areas kept wet by a shallow water table. This species was relatively scarce throughout the summer. Therefore, most seeds of peachleaf willow must have failed to germinate or died soon after germination.

The overall density of cottonwoods in September 1993 after a year without irrigation (data not shown) was 21% of that in September 1992 (Table 2A). All of the individuals counted in 1993 had become established in 1992, and their distribution with respect to the blocks and treatments was similar in the two years. Most of the surviving cottonwoods had grown more than 100% in height in 1993 and showed no sign of drought stress at the time of sampling. No new seedlings were established in 1993, even though seed set in the area was normal. Only eight peachleaf willows (4%) survived in the plots to September 1993.

Discussion

Reasons for Decrease in Cottonwood Reproduction Downstream of Dams

The failure of cottonwood reproduction along this dammed, channelized stream results from scarcity of bare, moist surfaces suitable for seedling establishment. Creation of such sites greatly increased seedling establishment, and sufficient viable seeds were delivered by natural seedfall to colonize the created sites (Table 2A). Adding seed to supplement natural seedfall had no significant effect (Table 3A). Considering the small number of degrees of freedom in the experimental design, the lack of significant effect of seed addition should not be interpreted as an indication that all physically suitable microsites were saturated with viable seeds. However, at Boulder Creek the scarcity of bare moist sites plays a greater role than seed abundance in limiting cottonwood establishment.

Recruitment of plains cottonwood is essentially restricted to sites that are not only moist and open enough for seedling establishment but also free from lethal scour during subsequent higher flows (Everitt 1968, Bradley and Smith 1986, Segelquist and others 1993, Friedman 1993, Scott and others 1995). Along meandering streams, seedlings become established on moist, open point bars; then sediment accretion and channel migration gradually decrease the shear stress experienced by the young trees during higher flows (Everitt 1968, Scott and others 1995). In addition, successful recruitment may occur on higher surfaces when an exceptional flood clears and wets areas that are high enough to avoid subsequent scour for several years (Scott and others 1995). Along Boulder Creek and many other streams below dams, flow regulation has reduced peak flows, thus decreasing the meandering rate and eliminating the occasional formation of open patches high above the bed (Bradley and Smith 1986, Rood and Mahoney 1990, Johnson 1992). As a result, the only sites bare and moist enough for establishment are low, scour-prone surfaces unsuitable for long-term survival (Asplund and Gooch 1988). Both within and outside of our plots, such bars were the only sites of seedling establishment in the absence of irrigation and sod removal (Figure 3). The rarity of young trees larger than seedlings indicates that these seedlings in low positions are almost always removed by higher flows and ice scour.

Table 4. Percent sand, silt, and clay in top 50 cm of sediment at three locations along Boulder Creek, Colorado[a]

	Sand	Silt	Clay
Block 1	86	11	3
Block 2	61	35	4
Block 3	65	28	6

[a]Sand = 0.05–2 mm; silt = 0.002–0.05 mm; clay < 0.002 mm.

Effect of Sod Removal

Sod and litter removal can promote seedling establishment by removing propagules of competitors, by increasing availability of light, by removing plant inhibitory compounds, by altering water balance, and by removing physical barriers to seedfall and seedling growth (Facelli and Pickett 1991). In a floodplain forest in interior Alaska, Walker and others (1986) found that litter removal increased initial establishment of poplar and willow. However, all poplar and willow seedlings under the forest canopy died by the end of the second growing season because of reduced light, reduced soil temperatures, and increased competition. In the present study, litter and sod removal were performed in the absence of a forest canopy, and many cottonwood seedlings survived the second growing season.

In this experiment the effect of sod removal was confounded to some extent with that of irrigation. Sod removal skimmed off an average of 16.5 cm of sediment. The resulting concave surface may have trapped some surface runoff, and the bottom of the plot was closer to subsurface moisture than were neighboring surfaces with intact sod. In addition, removal of the plants in the sod decreased evapotranspiration. Compared to plots without sod, plots with intact sod had more negative soil–water potentials at the surface, and the zone of moisture deficit extended deeper into the soil (Figure 2).

Survival of Boulder Creek Cottonwoods in the Second Year

Because light and moisture are critical factors controlling survival of cottonwood, the probability of long-term survival should increase as shoots grow above competitors and roots extend to the water table (McLeod and Mcpherson 1973, Sacchi and Price 1992, Friedman 1993). First-year seedlings in unirrigated plots were generally unable to use abundant subsurface moisture (Figure 2, Table 2A). However, after one season of growth, 21% of cottonwoods were able to survive a growing season without irrigation, indicating that roots of many seedlings were near the water table by summer of the second year. At Boulder Creek, the depth to water table varies between 0 and 1 m. We were unable to excavate intact roots of seedlings. However, root growth of 1 m by the middle of the second growing season is consistent with results reported by others (Ware and Penfound 1949, Fenner and others 1984, Segelquist and others 1993).

Differences Between Cottonwood and Peachleaf Willow

In a study of seedling establishment along the Tanana River in interior Alaska four species of poplar (*Populus*) and willow (*Salix*) had similar germination requirements (Krasny and others 1988). The investigators concluded that differences in patterns of occurrence of these species resulted from differences in their ability to spread by vegetative means. However, in our experiment, plains cottonwood responded much more strongly to irrigation than did peachleaf willow. Therefore, in this system, differences in seedling moisture requirements could play an important role in differences in distribution of adults.

The low densities of peachleaf willow (Table 2B), the insignificant effect of irrigation on its establishment (Table 3B), and the limitation of this species to low-lying sites indicate that the irrigation regime did not increase seedling survival. There were three possible shortcomings of the irrigation system for peachleaf willow. First, daily irrigation may not have been enough to prevent lethally dry conditions. In an Arizona study, mortality of *Salix lasiolepis* was much higher under once-daily irrigation than under continuous drip irrigation (Sacchi and Price 1992). Second, the impact of water droplets from the sprinklers and of a hailstorm on June 19 may have killed many seedlings. Plantations of cottonwood seedlings can be destroyed by heavy rain in the first ten days (Engstrom 1948). Because of their small size, peachleaf willow seedlings should be even more susceptible to such physical damage. Third, irrigation did not begin until 30 May, after most seeds of this species had been dispersed. Many of the seeds dispersed earlier may have germinated and died. However, if a shortage of naturally dispersed seeds had been important, then a large effect of added seeds would have been observed (Table 2B).

Seedlings of most species of cottonwood and willow are intolerant of low moisture (Moss 1938, McLeod and McPherson 1973, Krasny and others 1988). The smaller the seedling, the smaller the volume of sediment from which water can be obtained. Thus the 16-fold difference in seed mass between plains cottonwood and peachleaf willow may render the latter more susceptible to fluctuations in moisture availability during the first month after germination. This consideration suggests that peachleaf willow seedlings are more susceptible than those of plains cottonwood to the fluctuations in water availability that occur with sprinkler irrigation.

Restoration of Cottonwood Stands

Our experiment demonstrates that plains cottonwood can be established by natural seedfall in irrigated, disturbed plots. Therefore, the methods presented here may be suitable for regeneration of cottonwood stands along regulated streams where channel migration and flood disturbance no longer occur. This approach may also be suitable for regeneration of other riparian pioneer species that produce dependable crops of abundant, immediately germinable seeds capable of becoming established on a mineral substrate. In North America such pioneers include many members of the willow family (Salicaceae) as well as silver maple (*Acer saccharinum*) and river birch (*Betula nigra*) (White 1979). In humid regions, regeneration of pioneer trees from natural seedfall on artificially disturbed sites can sometimes be accomplished without irrigation (Johnson 1965).

In comparison to the use of cuttings, the principal advantage of regeneration using natural seedfall is the elimination of the need to collect and plant propagules. The principal disadvantage is the smaller initial size of individuals, which may increase the need for irrigation and weed control. When there is no nearby source of cuttings, use of natural seedfall could allow regeneration of the local population without altering the gene pool.

The techniques described here could be modified to increase seedling yield and decrease costs. First, to minimize competition from tall, deep-rooted herbs, a site with a grass cover, coarse soil texture, and low organic matter content should be chosen. Second, establishment sites should be high enough to avoid annual scour by water or ice. In areas subject to frequent scour, cuttings may be more likely to survive than seedlings. Plots as large as those in our experiment are appropriate for producing a plantation as a source of local material for cuttings; however, if the seedlings are to be grown to adulthood on site, large plots are inefficient because intraspecific competition will eventually kill almost all individuals. For establishment of a stand of adults, it would be better to dig many small widely spaced shallow depressions 2 m in diameter, and 30 cm deep in the center, sloping gradually up to ground level at the edges. The concave depressions would reduce the frequency and magnitude of irrigation necessary to keep the trees alive. After seedling establishment, intraspecific competition or thinning would reduce density to one or two adult trees per depression. The small size and wide spacing of depressions would minimize the work and physical disturbance necessary to reforest a large area. It should be kept in mind that cottonwood seedlings are intolerant of shade, and therefore unlikely to thrive in partially shaded clearings beneath existing trees (Johnson and others 1976).

In many riparian areas, an upstream dam and reservoir allow prescription of moderately high flows to moisten surfaces at a designated time, but residential and industrial development prevent the use of higher flows powerful enough to form new bare surfaces. In this situation, cottonwood forest may be established by artificially disturbing a site with a backhoe or bulldozer, flooding the area before seed dispersal, and then preventing high flows destructive to young trees during the next few years.

Establishment of forest is often desired as part of restoration of a former gravel mine or construction site. Our experiment suggests that cottonwoods can be established at low cost in such sites by creating a gradual slope and controlling drainage. The water table should be at the ground surface until seed dispersal and then gradually lowered a total of about 1 m during the first growing season. The volunteer cottonwoods often observed at gravel mines and construction sites are evidence of the feasibility of this approach.

Succession

Plains cottonwood and peachleaf willow are pioneer species; their abundant mobile seeds and ability to grow on mineral substrate in full sun enable them to colonize recently deposited alluvium. On the other hand, the small seed energy reserves and high light requirement put these species at a disadvantage on stable, fertile sites where competition is greater. As a result, cottonwood and willow seedlings rarely become established under existing trees (Johnson and others 1976). Flood control and channel stabilization decrease riverine disturbance (Bradley and Smith 1986) and over the long term cause a decrease in the area of cottonwood or willow forest and an increase in the area of later successional communities. In relatively humid regions, cottonwoods and willows are replaced by more shade-tolerant tree species (Bravard and others 1986, Johnson 1992). In more arid regions, including eastern Colorado, shade-tolerant trees are often absent, and the cottonwood or willow forests are replaced by grassland or by a shrub assemblage dominated by exotic species (Lindauer 1983, Ohmart and others 1988).

Where drastic reductions in riverine disturbance have stopped reproduction of cottonwood or willow forest, active management is probably necessary to maintain the community. Succession can be influenced by altering site availability, differential species availability, or species performance (Luken 1990). Our proposed method uses all three of these strategies: sod removal creates new establishment sites, synchronizing activities with the peak of cottonwood and willow seed release ensures a large number of seeds relative to other species, and irrigation increases survival and growth of cottonwood seedlings.

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