FACTORS CONTROLLING THE ESTABLISHMENT OF FREMONT COTTONWOOD SEEDLINGS ON THE UPPER GREEN RIVER, USA

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ABSTRACT

Declines in cottonwood (*Populus* spp.) recruitment along alluvial reaches of large rivers in arid regions of the western United States have been attributed to modified flow regimes, lack of suitable substrate, insufficient seed rain, and increased interspecific competition. We evaluated whether and how these factors were operating during 1993–1996 to influence demographics of Fremont cottonwood (*P. deltoides* Marshall subsp. *wislizenii* (Watson) Eckenwalder) along reaches of the Green and Yampa Rivers near their confluence in northwestern Colorado. We examined seedling establishment, defined as survival through three growing seasons, at three alluvial reaches that differed primarily in the level of flow regulation: a site on the unregulated Yampa, an upper Green River site regulated by Flaming Gorge Dam, and a lower Green River site below the Green–Yampa confluence. Seed rain was abundant in all sites, and led to large numbers of germinants (first-year seedlings) appearing each year at all sites. The regulated flow in the upper Green River reach restricted germination to islands and cut banks that were later inundated or eroded; no seedlings survived there. Mortality at the lower Green River site was due largely to desiccation or substrate erosion; 23% of 1993 germinants survived their first growing season, but at most 2% survived through their second. At the Yampa River site, germinants appeared on vegetated and unvegetated surfaces up to 2.5 m above base flow stage, but survived to autumn only on bare surfaces at least 1.25 m above base flow stage, and where at least 10 of the upper 40 cm of the alluvium was fine-textured. Our studies of rooting depths and the stable isotopic composition of xylem water showed that seedlings in the most favorable locations for establishment at the Yampa site do not become phreatophytic until their third or fourth growing season. Further, the results of experimental field studies examining effects of shade and competition supported the hypothesis that insufficient soil moisture, possibly in combination with insufficient light, restricts establishment to unvegetated sites. Collectively, the demographic and experimental studies suggest that, in arid regions, soil water availability is at least as important as light level in limiting establishment of Fremont cottonwood seedlings. We hypothesize that in cases where arid land rivers experience large spring stage changes, recruitment is further constrained within bare areas to those sites that contain sufficient fine-textured alluvium, saturated during the spring flood, to provide the flood-derived soil moisture normally necessary for late-summer seedling survival. Copyright © 1999 John Wiley & Sons, Ltd.

KEY WORDS: alluvial soil; Colorado; competition; cottonwood; desiccation; *Populus*; regulated river; riparian vegetation; seedling population dynamics; tamarisk; *Tamarix*; Utah

INTRODUCTION

The structure, functioning, and dynamics of floodplain ecosystems are determined in part by stream flows and fluvial processes that influence site hydrologic and geomorphic conditions, and in part by ecological processes that influence the patterns of species colonization, competition, and succession (Johnson *et al.*, 1976; Hupp and Osterkamp, 1996). Sediment erosion and deposition during periods of high flow are of particular importance because these processes both destroy and create seedbeds, thereby linking fluvial and ecological processes (Campbell and Green, 1968; Hupp and Osterkamp, 1996; Scott *et al.*, 1996).

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In many temperate and boreal regions of North America, the primary colonizers of mineral soil surfaces exposed by receding floodwaters are species of *Populus* (cottonwood) and *Salix* (willow). The ecological significance of cottonwood is especially great in arid regions of western and southwestern North America because in most areas no native replacement tree species exists (Rood and Mahoney, 1990). Our understanding of cottonwood autecology varies among the three dominant taxa present in this region, narrow-leaf cottonwood (*P. angustifolia* James), plains cottonwood (*P. deltoides* Marshall subsp. *monilifera* (Aiton) Eckenwalder), and Fremont cottonwood (*P. deltoides* Marshall subsp. *wislizenii* (Watson) Eckenwalder), with Fremont cottonwood probably being least known (nomenclature follows Weber and Whittman, 1996). It is recognized that cottonwood recruitment involves multiple factors (Rood and Mahoney, 1993; Busch and Smith, 1995), and most likely varies with geomorphic setting and channel type (Scott *et al.*, 1996; Friedman *et al.*, 1997). Recruitment processes on free flowing river systems remain incompletely understood for even the most studied species. For example, cottonwood seedling establishment has been reported to result primarily from large, relatively infrequent floods (Everitt, 1968; Scott *et al.*, 1997). However, large floods may result in stage changes greater than 2–3 m with seedlings establishing in relatively high landscape positions (Scott *et al.*, 1997). Because seedlings are intolerant of dry soils, rapid water table declines (> 4–6 mm/day) can leave seedlings far above the late summer water table and lead to seedling death (Mahoney and Rood, 1991, 1992; Segelquist *et al.*, 1993). Thus, the mechanism of seedling establishment on rivers with large stage change is unclear.

Cottonwood seedlings are reported to be shade intolerant (Read, 1958; Braatne *et al.*, 1996; Scott *et al.*, 1996). Studies of rooted stem cuttings of eastern cohorts of plains cottonwood indicate that plants can attain approximately 80 and 60% of their maximum net photosynthetic rate (P_n) in approximately 50 and 25%, respectively, of full sun (Regehr *et al.*, 1975; Bassman and Zwier, 1991). However, physiological studies of cottonwood seedlings have not been performed and thus it is unclear if cottonwood seedlings on western rivers can attain similarly high photosynthetic rates in shaded environments. The rooted cuttings were also sensitive to soil water availability, with stomatal closure and the cessation of photosynthesis at twig xylem pressure potentials (Q_{xp}) of between -1.10 and -1.25 MPa (Regehr *et al.*, 1975; Bassman and Zwier, 1991), and 80–90% loss of xylem hydraulic conductivity occurring at Q_{xp} of -1.5 to -2.0 MPa (Tyree *et al.*, 1994). It is unclear whether reduction of sunlight or reduction of soil water availability by neighbors has a greater influence on seedling survival.

The apparent correlation between flow modification of the major rivers of interior western North America and the limited cottonwood recruitment now found along them (Colorado River: Busch and Smith, 1995; Rio Grande: Howe and Knopf, 1991; Missouri River: Johnson *et al.*, 1976; Reily and Johnson, 1982; Gila River: Fenner *et al.*, 1985; Oldman River: Rood and Mahoney, 1990; Marias River: Rood and Mahoney, 1995) strongly suggests that regulation may be a causative factor (Johnson *et al.*, 1976; Williams and Wolman, 1984; Braatne *et al.*, 1996). River regulation by high dams and water diversions typically reduces both annual maximum or peak flow (Andrews, 1986; Stanford and Ward, 1991) and sediment load (Andrews, 1986, 1991), raises annual low or base flow (Williams and Wolman, 1984), and modifies the rate of flood stage decline. Resultant modifications in hydrologic and fluvial processes could potentially affect every stage in the recruitment process, from quantity and quality of seed rain to the growth and survivorship of seedlings. They could also indirectly affect the recruitment process through direct affects on herbivore or competitor populations. The widespread invasion of a competitor, tamarisk (*Tamarix ramosissima* Ledebour), into western riparian systems further complicates establishment of cause-and-effect linkages between river regulation and declines in cottonwood recruitment (Turner, 1974).

We utilized field studies conducted at paired floodplain sites along the unregulated Yampa River and regulated Green River to examine seed rain, and the requirements for Fremont cottonwood seedling establishment (defined by us to be survival through the first three growing seasons). The rivers studied are large (typical peak annual discharges of 300–500 m³/s), have sand beds, and in their unregulated condition, feature annual stage changes of 2–3 m. The goal of this paper is to address five primary questions: (1) What are the natural patterns of seedling establishment on regulated and unregulated rivers? (2) What is the effect of shade on cottonwood seedling survival? (3) What is the effect of

competition from tamarisk on cottonwood seedling survival? (4) Is cottonwood seedling survival linked to taproots reaching the late summer water table or capillary fringe? (5) Is soil texture an important determinant of cottonwood seedling survival?

THE STUDY REACHES

Our studies were conducted on floodplains of the Green and Yampa Rivers, above and below their confluence in northwestern Colorado (Figure 1). The Green River originates in the Wind River Range in west central Wyoming and flows generally southward to its confluence with the Colorado River in Utah. The Green River is regulated by two high dams: Flaming Gorge, completed in 1962, and Fontanelle, a smaller, upstream structure completed in 1964. Releases from Flaming Gorge Reservoir, which began to
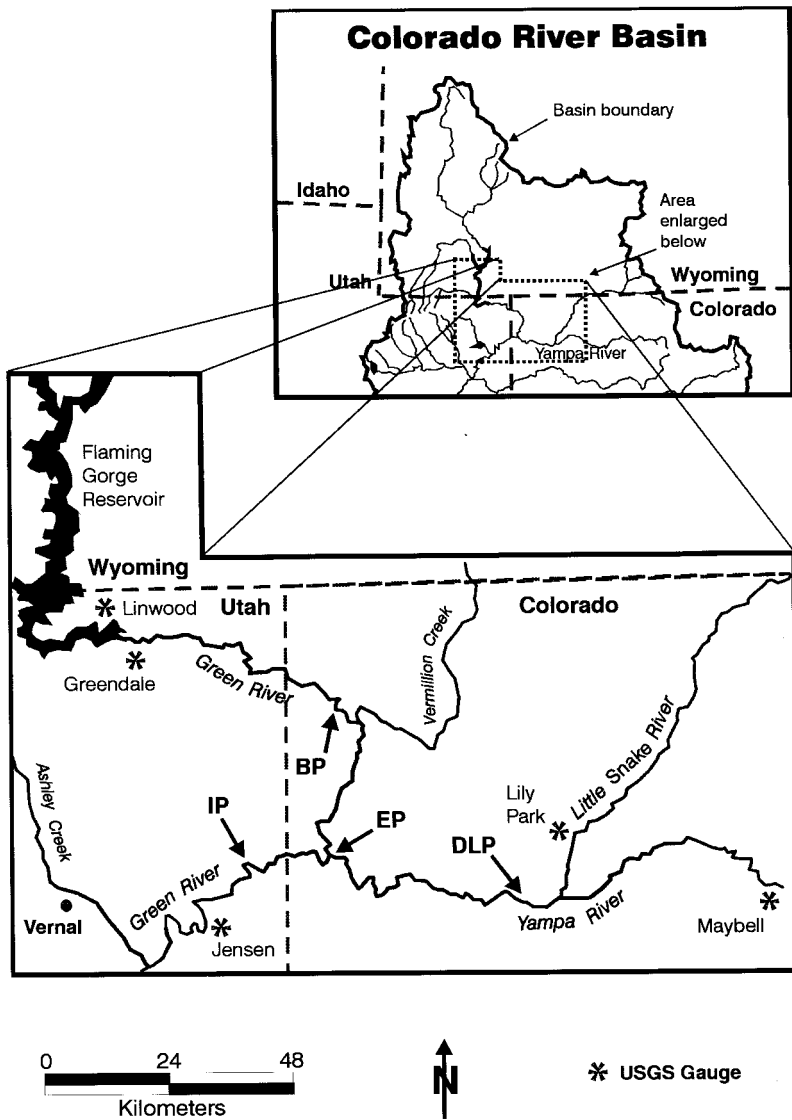

Figure 1. Locations of the three main study areas in Colorado and Utah: Island Park (IP), Deer Lodge Park (DLP), and Brown's Park (BP). Locations of USGS stream gauges used in the study are also shown, as is Echo Park (EP) at the confluence of the Yampa and Green Rivers

fill in December 1962, almost completely determine flows in the Green for 102 km, until its confluence with the Yampa River. The extent of river regulation in the Colorado River and Green River systems are reviewed by Stanford and Ward (1986) and Stanford (1993).

The Yampa River originates in the Park Range and White River Plateau in north central Colorado and is the last major tributary of the Colorado River that remains largely unregulated. There are three small headwater dams within its basin, and a total of about 10% of the annual flow is diverted for municipal or agricultural use.

Two of our three study sites, Brown's Park and Deer Lodge Park are along reaches that were quite similar in geomorphic, hydrologic, and ecological setting prior to river regulation. The Brown's Park site (BP) is in Brown's Park National Wildlife Refuge, along the highly regulated segment of the Green River, 63 km below Flaming Gorge Dam (see Figure 1). Deer Lodge Park (DLP) is on the unregulated Yampa River, 50 km above its confluence with the Green and below the last major tributary of the Yampa River, the Little Snake River. The third site, Island Park (IP) is on the Green River, 15 km below the confluence with the Yampa. The geomorphic and ecological setting at IP is similar to that of the upstream sites, but its hydrologic regime features an intermediate level of regulation. Both DLP and IP are located in Dinosaur National Monument. The elevations at DLP, BP, and IP are approximately 1705, 1630, and 1510 m, respectively. The river channel is unconfined within each study reach, meandering across thick, generally fine-textured alluvium (< 2 mm). We also worked in Echo Park (EP), at the confluence of the Yampa and Green Rivers.

Long-term discharge data for these reaches are available from USGS gauging stations (Figure 1). We used the Linwood, UT gauge (#09225500) to represent BP flows from 1929 to 1962, when this station was inundated by the filling of Flaming Gorge Reservoir. We used data from the Greendale, UT gauge (#09234500), located just below the dam, for 1963 to present. For DLP, we summed discharges of the Yampa River at Maybell, CO (gauge #09251000) and the Little Snake River at Lily Park, CO (gauge #09260000). Both of these gauges have continuous data from 1922 to present. For the combined flow of the Yampa and Green Rivers at IP, we used data from Jensen, UT (1947 to present, gauge #09261000).

The Green and Yampa Rivers both have snowmelt driven peak flows, and their hydrographs prior to 1963 were similar. Mean annual discharges on the two rivers were 54.6 and 58.1 m^3/s, respectively, and are not significantly different. Historic Green River peak flows averaged 80% of the Yampa's, and typically occurred about 2 weeks later than the Yampa peak. There was no significant difference between the mean peak annual discharge of the Yampa at DLP for the periods 1922–1962 and 1963–1995. In contrast, mean peak annual discharge of the Green River was significantly lower during the 1963–1995 post-Flaming Gorge Dam period at both BP and IP. DLP and IP had similar peaks in 1993 (498 and 566 m^3/s, respectively) and 1995 (519 and 527 m^3/s), reflecting the large contribution of the Yampa to peak discharge of the Green at IP.

Annual flow variation (calculated as peak flow divided by low flow for a given year) averaged ~ 33 in BP and ~ 100 in DLP prior to 1963. Current Green River flow variation is approximately 5–6. The two rivers have distinctive patterns of stage dynamics (Figure 2). During 1993–1995, river stage in DLP varied by 1.8–2.9 m, and occurred during the 6–8 weeks between late May and late July or early August (Figure 2). The analogous stage decline was only ~ 0.7 m in BP where peak stage was similar in both magnitude and duration (~ 1 month) each year (Figure 2). We also regularly monitored floodplain water table depth in hand-bored wells cased with slotted PVC pipe. We related water table elevation to river stage by developing rating curves using staff gauges we installed in our study areas and United States Geological Survey (USGS) daily average discharge data.

Both the Yampa River and the pre-dam Green River carried large sediment loads. The mean annual sediment load for the Yampa River at its mouth, the Green River in Brown's Park, and the Green River at the Jensen gauge (downstream from Island Park, see Figure 1) were 1.5, 3.3, and 6.3 × 10^6 tons/year, respectively, prior to 1962. Since 1963, sediment load within the BP reach has been reduced to input from a few small tributaries. The sediment load at the Jensen gauge has been decreased by 54% due to sediment retention in Flaming Gorge Reservoir (Andrews, 1986).
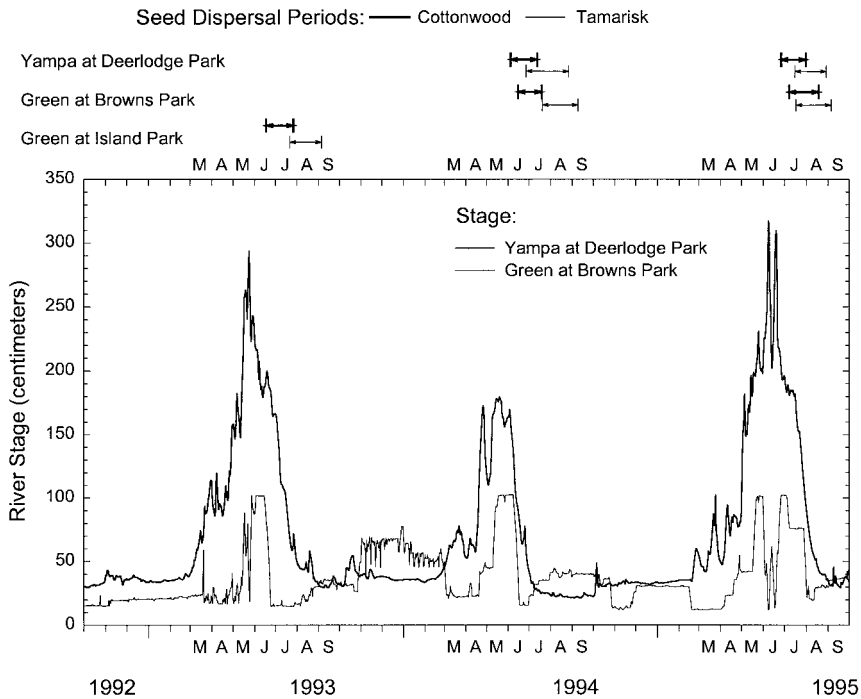
Figure 2. Daily mean stage for the period October 1993 to October 1995 for the Yampa River in Deer Lodge Park (DLP) and the Green River in Brown's Park (BP). The periods of seed rain for DLP and BP (1994 and 1995) are shown as horizontal arrows. Stage was calculated from USGS daily mean discharge data, and the rating curve generated from our stage measurements

Climatic conditions at the three sites are similar, based on daily precipitation and temperature data from US National Weather Service stations at Maybell, CO (located 20 km east of DLP), Brown's Park, CO (located ~5 km from BP), and Jensen, UT (located ~15 km southwest of IP). Long-term mean annual precipitation for Maybell, Brown's Park, and Jensen are 284, 209 and 199 mm, respectively. On the average, approximately 1/12th of the annual mean precipitation fell during each of the four growing season months (June–September). A critical dry period occurred during the summer of 1994 when less than 10 mm of rain fell during June and July (< 20% of the long-term mean), and essentially no rain fell during July.

METHODS

Patterns of Fremont cottonwood and tamarisk seedling establishment

We determined the period of cottonwood and tamarisk seed dispersal by observation during 1993 (IP) and 1994 (DLP and BP). In 1995, we quantified cottonwood seed rain in BP and DLP using eight traps in each area. The traps were oriented in two lines parallel with the river and located in areas where seedlings could potential establish. Traps were 400-cm^2 boards, coated with Tanglefoot© and mounted horizontally 1 m above the soil surface. We removed seeds and reset traps every 4–15 days from early June (prior to seed release) through mid-August, by which time all capsules had opened. We determined the period of tamarisk seed dispersal in 1995 by monitoring ten tamarisk plants in the area of the seed traps in both BP and DLP.

We evaluated the causes and magnitude of mortality among natural cohorts of Fremont cottonwood seedlings by monitoring the fates of nearly 5000 seedlings contained in 139 permanent plots, 0.25 m^2 in size, distributed among the DLP, BP and IP study areas. Plots were selected to represent the full range

of geomorphic and hydrologic conditions present in these study areas. Most (90) plots were established to monitor members of the 1993 cohort. We censused live seedlings within each plot periodically each summer during 1993–1995. No plot was protected from herbivores. Seedling survival was evaluated separately in each study area, with plots grouped by establishment date. We assigned cause of death into one of four possible categories: inundation, channel erosion, bank sloughing, and desiccation. Channel erosion or bank sloughing was determined by the loss of the plot substrate, desiccation by the presence of dead dry seedlings, and inundation, by dead seedlings in seasonally or semi-permanently saturated soils.

To evaluate the importance of stage decline rate and water table depth on the survival of cottonwood germinants, we established two 60-m long transects in DLP in 1995 (D95-1, and D95-2), running from the mature cottonwood forest edge across the topographic gradient of the unvegetated floodplain toward the river. These transects were located in the inside bend of meanders across sites with active sediment deposition. We placed permanent 10×10-cm plots at 1-m intervals along each transect and censused the live cottonwood germinants present in the plots in late July, and again in mid-September. Plot surface elevation above the late summer base flow water table and soil texture were determined by surveying and the hydrometer method, for plots ($n = 60$) containing germinants. We pooled plot data from both transects for analysis using logistic regression to model fates (death or survival) of individual germinants within each plot ($N = 774$ plants) over the monitoring period. Stepwise regression (Steinberg and Colla, 1991) was used to derive a model relating probability of death to position along the elevation gradient (variable ELEV, distance above base flow stage elevation, in centimeters), percentages of SILT and CLAY in plot surface soils (1–10 cm depth), initial plant density (JUL95), and mid-September gravimetric surface soil water content expressed as a percent (MOIST).

We tested whether cottonwood germinants rooted to the late-summer water table using morphologic (rooting depth) and topographic data (elevation above the late summer water table). We measured maximum first year rooting depths by carefully excavating 64 germinants (1995 and 1996 cohorts) from DLP sites spanning the full range of elevations and landforms where germinants had survived through early September.

Determination of xylem water sources

We directly determined the source of water used by cottonwoods from stable isotope analyses of ground water, soil water, and xylem water. Because of their greater atomic mass, water molecules containing deuterium, a stable isotope of hydrogen, are enriched in water exposed to evaporation. Thus, both unsaturated soil water and summer precipitation contain a higher relative amount of deuterium than does ground water recharged by the river, furnishing a basis for determining whole plant water sources using free water extracted from plant tissues (Flanagan and Ehleringer, 1991; Dawson 1993). We collected fully suberized stem samples from plants that were 2, 4, 8–12, 20–25, and 90+ years old in late August 1996 at DLP; age was determined by ring counts of stems sectioned just above the germination surface. No 3-year-old plants (1994 seedling cohort) occur at this site. Because stems of germinants (1996 cohort) were not yet suberized, we collected the top 5 cm of the taproot. Each sample of germinant tissue contained the taproots of 12 individuals. Unsaturated soil water was obtained from soil collected at a 10–35 cm depth at sites where plants were collected. Samples of ground water were collected by pumping from monitoring wells that were generally within 10 m of each sample location. We calculated the isotope ratio relative to that of a standard, δD, as:

$$\delta D \ (\text{‰}) = [(D/H)_{\text{sample}}/(D/H)_{\text{standard}} - 1] \times 1000,$$

using Standard Mean Ocean Water (SMOW) as our standard (Dawson, 1993). Hydrogen isotope ratios were determined by Mountain Mass Spectroscopy (Evergreen, CO), using cryogenic distillation methods with liquid nitrogen to trap water from soil and plant samples, and zinc as a catalyst in hydrogen reduction of all water samples (Ehleringer and Osmond, 1989).

The effects of competition from older cohorts on cottonwood seedling establishment

We assessed the effect of previously established cottonwoods on cottonwood germinant survivorship in a mensurative experiment using paired plots established on 36 fluvial landform features. These features, located at DLP and Echo Park (EP), represented the full range of sites where cottonwood germinants survived to mid-September during 1995 and 1996. A 1-m^2 plot containing live germinants was established at a representative location on each landform. On landforms where living or dead germinants were present both on bare soil and beneath a canopy of older cottonwoods (generally 2–15 years old), a plot was established in each area. Germinants were censused and their heights measured in early September.

We determined the surface elevation of each plot relative to the river at base flow stage, documented the underlying soil stratigraphy, and collected samples from each soil horizon for analysis of texture and water content. We determined gravimetric soil water content for each soil horizon on landforms examined in 1995, whereas both gravimetric and volumetric samples were collected during 1996 that allowed the determination of both gravimetric and volumetric water contents. Because soil samples collected in 1995 and 1996 had similar texture and gravimetric water content, the volumetric water content of 1995 samples was estimated by tabular comparison with 1996 samples. Soil matric potential for each sample was calculated from soil texture and volumetric water content using the procedures in van Genuchten *et al.* (1989).

Effects of shade on seedling establishment

Three shade experiments addressed whether a reduction of photosynthetically active radiation (PAR) would negatively and differentially affect cottonwood or tamarisk seedling survival. We shaded seedlings using screen canopies with open sides in 1993, and canopies with both screen tops and sides in 1994 and 1995. In all experiments, we measured sunlight reaching seedlings as PAR (Li-Cor Model 189) relative to that of full sun on a cloudless mid-summer day. Seedlings were grown from local seed and transplanted into the field when approximately 1 month old. The seedlings are used as phytometers (Clements, 1935) to measure the effect of shade on plants of identical age, health and stature. However, we did not control for, or measure, potential changes in air or soil temperature due to our shading; shade/temperature interactions were considered in interpretation of results.

Experiment 1. We tested for an effect of shade on the survival of cottonwood seedlings under natural field conditions using a completely randomized experimental design. We established five replicates of each of four treatments (55, 30, 17 and 4% of full sun) plus a control on 400-cm^2 plots arranged in a grid on a freshly exposed sediment bar in IP. The bar was leveled to ensure that all plots were a similar distance above the water table (~ 1 m in late summer). Twelve, 1-month-old seedlings were transplanted in a regular array in each plot in mid-July 1993, and revisited in September 1993 and in May and August 1994. We tested for a relationship between shade and the proportion of seedlings surviving to each census using logistic regression (SAS Proc GENMOD, SAS Institute, 1992).

Experiment 2. We tested for an effect of shade on cottonwood and tamarisk seedlings grown from seed *in situ* at a field site where abundant soil water was provided by sprinkler irrigation. We created 20 pairs of adjacent 400-cm^2 plots in a grid pattern on a newly exposed sediment bar in DLP and transplanted 15 cottonwood seedlings into one plot and 15 tamarisk seedlings into the other in July 1994. We randomly assigned the paired plots to generate five replicates each of three shade treatments (69, 40 and 17% of full sun) plus controls, using a completely randomized block design. All plots received water three times daily (~ 1.8 cm/day total) until mid-August, when watering was stopped. The water table was 143 cm beneath the bar surface in early September 1994. Survival in plots at the end of the watering period, and 1 month after watering ceased was determined. We analysed data as in Experiment 1.

Experiment 3. We tested for an effect of shade and intraspecific competition on naturally established cottonwood seedlings by placing shade canopies over ~ 3-week-old cottonwood germinants in DLP in late July 1995. Five replicate pairs of 400-cm^2 plots were established for each of three shade treatments (69, 40 or 17% of full sun), plus a control. We thinned one plot from each pair to a density (r) of ten seedlings/plot ($= 250$ individuals/m^2), whereas the other plot retained its original seedling density

($r = 1073$ individuals/m^2; S.D. $= 196.7$; $n = 20$). Because no location could accommodate all 40 plots, we established five sets of four plots each, one of each treatment plus a control, at different locations (LOC) within a 0.01-ha area. Plots were revisited after 1.5 months. We analysed data as in Experiment 1.

Effects of competition with tamarisk on cottonwood seedling establishment

Experiment 4. We tested the effects of an adult tamarisk overstory (2–4 m tall) on the survival of transplanted 1-month-old cottonwood seedlings. We transplanted 15 seedlings into each of fifteen 400-cm^2 plots established under tamarisk and assigned five plots to each of two treatments plus a control. Treatment A consisted of pruning the tamarisk canopy at ground level to eliminate competition for light. Treatment B consisted of canopy pruning plus trenching the plot perimeter to sever horizontal roots in the top 40 cm of soil and reduce soil water acquisition by neighboring plants. Plots were created in July 1993 and revisited in September 1993, and in May and August 1994. We tested for differences in proportions of survivors using chi-square analysis.

Experiment 5. We tested for an effect of interspecific competition from tamarisk seedlings on survival of cottonwood seedlings. The treatment consisted of transplanting 15 cottonwood seedlings (~ 1 month old) into dense beds of naturally occurring tamarisk seedlings (~ 5000 individuals/m^2), and was replicated in three plots in IP in 1993. We removed, by hand, all tamarisk seedlings in one control plot. Removal caused only slight disturbance to the soil surface and no effort was made to duplicate the soil disturbance in the treatment plots. We monitored fates of the transplanted seedlings through September 1994.

Soil stratigraphy of fluvial features supporting emergent, seedling, and established cottonwoods

We excavated trenches across each of the 36 fluvial landform features used in the analysis of cottonwood germinant survival to analyse soil stratigraphy. We used regression analysis to relate the density of germinants surviving to mid-September to the total thickness of loam-textured soil layers (sandy loam, loam and silty loam) within the rooting zone (0–45-cm depth). We also excavated a trench through an infrequently flooded terrace supporting mature Fremont cottonwood trees in order to examine soil stratigraphy and evaluate landforms on which the trees established.

RESULTS

Patterns of Fremont cottonwood and tamarisk seedling establishment

The 1993 cottonwood seed rain, which was monitored solely in IP, began in mid-June (Figure 2). In 1994, seed rain in DLP began in early June, just after the Yampa River reached peak stage, and continued through the entire period of stage decline. In 1995, seed rain in DLP began in late June (Figure 3). Seed rain began somewhat later in BP than in DLP in both 1994 and 1995 (Figures 2 and 3), but lasted a similar length of time, 4–6 weeks. The maximum mean rate of seedfall in 1995 was higher in DLP, 362 seeds/m^2/day, than that recorded in BP, 70 seeds/m^2/day (Figure 3). Seed rain generally coincided with the declining limb of the spring hydrograph at DLP and IP, but to a lesser extent at BP due to flow regulation. Seed rain in BP during 1995 began during the second stage peak of the Green River, when all river bars in BP were inundated. When stage had declined sufficiently to reveal bars (early August), cottonwood seed rain was nearly complete, although tamarisk seed dispersal was at its peak.

Tamarisk seed dispersal began after cottonwood in all sites and years (Figures 2 and 3). In 1995 tamarisk seed dispersal began in early to mid-July during the period of maximum cottonwood seed release in DLP and BP and continued until mid-September. Overlap of seed release resulted in the formation of mixed cottonwood and tamarisk seedling stands in many locations in all study areas.

During all four summers of fieldwork (1993–1996), large numbers of cottonwood germinants estab-lished on the DLP floodplain as floodwaters receded. Germinants were also common at BP and IP during those years. In BP, successful germination was restricted primarily to islands and steep cut-banks, the only areas with moist surface soils. More than 93% of the monitored 1993 cottonwood germinants at DLP and

77% of those at IP died within a few months of germination (Table I). Survivorship through the first growing season was only slightly higher at BP (88% mortality, sites pooled). Survivorship over winter 1993–1994 was high, but survivorship through the 1994 growing season was again low (0.29 for DLP, 0.12 for IP; sets pooled: Table I), which included a 5 week long mid-summer rainless period. None of the monitored members of the 1993 cohort survived through their third growing season (i.e. to September 1995) in BP, and only 4% (61 of 1251 seedlings) survived in DLP (Table I). The DLP survivors were concentrated in four plots, all of which were located on surfaces > 185 cm above river base flow stage.

The causes of seedling mortality varied among the sites. In BP, 62.5% of the seedling mortality was due to prolonged inundation during the growing season, whereas inundation caused no deaths at IP or DLP. Germinants on BP banks were killed when banks saturated by higher stage failed (18.8%), a fate uncommon at DLP (2.3%) and absent at IP, because relatively few germinants grew on banks. In DLP and IP, seedling mortality was due primarily to desiccation (51.2 and 65.4%, respectively) during the first or second growing season, or substrate erosion during high flow in the second growing season (46.5 and 34.6%, respectively).

The cohort of 1995 cottonwood germinants monitored along transects DL-1 and DL-2 at DLP emerged on sites with surface elevations that varied from 100 to 225 cm above river base flow elevation. The logistic model fit to the July-to-September survival data included soil moisture, soil texture and initial density as independent variables [Logit (probability of dying) = 3.78 + (1.33 MOIST) − (0.80 CLAY) − (0.24 SILT) − (0.03 JUL95)]. p-values for these variables were all < 0.025, and odds ratio values were all significantly different from 1.00 (MOIST, 3.8; CLAY, 0.45; SILT, 0.78; JUL95, 0.97). The overall fit of the model was satisfactory (McFadden's $\rho^2 = 0.219$). Thus, percentages of clay and silt, as well as initial
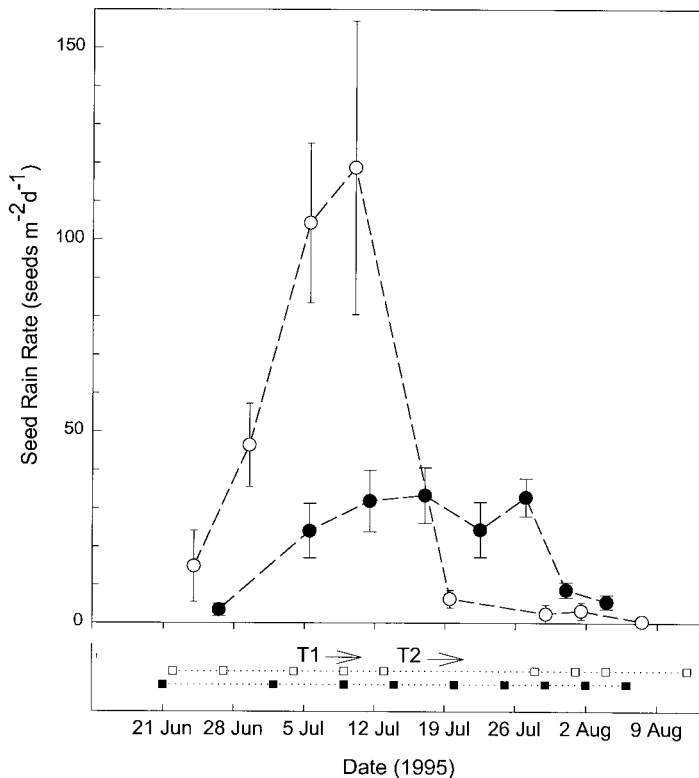

Figure 3. Density of cottonwood seed rain in Browns Park (BP, large solid circles) and Deer Lodge Park (DLP, large open circles) during 1995. Values are means of eight traps and are plotted in the middle of the period sampled; bars show ± 1 S.E. Small squares (coded as above) along the two horizontal dotted lines depict trap collection dates for each site. T1 and T2 indicate the period of tamarisk seed rain in BP and DLP, respectively

Table I. Survivorship in the 1993, 1994, and 1995 cohorts of cottonwood seedlings in Deer Lodge Park (DLP), Browns Park (BP) and Island Park (IP)

Date	DLP					BP				IP		
	1993 Cohort			1994 Cohort	1995 Cohort	1993 Cohort			1994 Cohort	1993 Cohort		
	Time 1 (n = 8)	Time 2 (n = 8)	Time 3 (n = 12)	Set A (n = 12)	Set A (n = 26)	Site A (n = 6)	Site B (n = 9)	Site C (n = 6)	Set A (n = 11)	Time 1 (n = 30)	Time 2 (n = 2)	Time 3 (n = 9)
1993												
3–8 July	151.0 (24.2)					71.3 (20.9)	76.9 (30.6)	55.3 (23.3)		196.4 (48.5)		
26–7 September	10.5 (2.1)	96.5 (21.0)				10.0 (8.5)	5.3 (2.2)	9.3 (3.4)		44.8 (20.1)	92.0 (36.0)	
1994												
18–22 May	10.5 (2.1)	69.5 (24.1)	252.0 (64.8)							18.7 (6.4)	84.0 (32.0)	68.9 (14.3)
15 June										8.6 (4.2)	84.0 (32.0)	65.3 (15.4)
6–7 July	0.0	45.5 (19.9)	174.0 (52.8)	339.7 (63.0)								
14–18 August		39.0 (17.4)	57.7 (29.2)	71.0 (41.3)		0.0	1.8 (1.8)	0.0	81.5 (18.5)	4.7 (3.8)	2.0 (2.0)	4.4 (3.5)
1995												
19 July		0.0			707.5 (121.6)							
12 August					419.7 (90.2)		0.0		0.00	—	—	—
30 September			5.1 (2.4)	—	1.3 (3.6)							

Each column represents a group of seedlings from the same cohort followed through time. The uppermost value in a column is the mean count (expressed as seedlings/m², with standard error in parentheses) of seedlings initially present in a set of 0.25-m² plots (n = number of plots) established at the same time. Subsequent values in a column are the mean number of survivors in that set at the indicated date. Dates are bracketed to indicate the period during which sets were established or revisited. Note that within the 1993 cohort, sets are differentiated by both time of establishment (DLP and IP) and by site (BP).
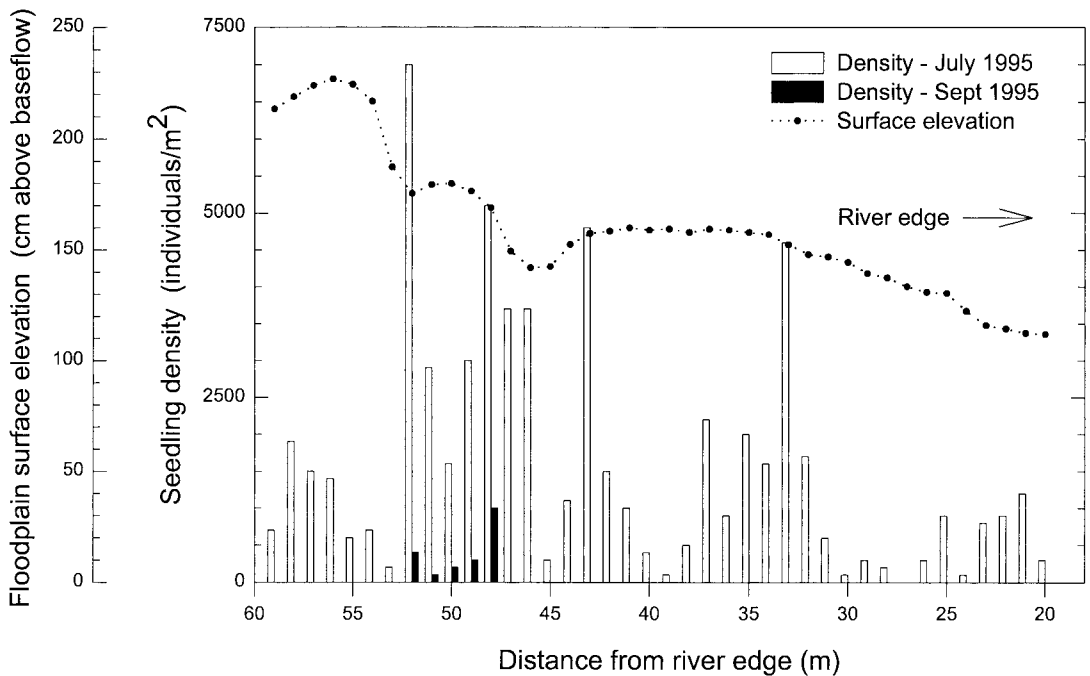
Figure 4. Densities of July germinants (open bars) and 1st-growing-season survivors (filled bars) of Fremont cottonwood seedlings along a 60-m transect, DL-1, traversing a portion of the floodplain inundated in 1995 at Deer Lodge Park. The transect was oriented perpendicular to the Yampa River, located to the right in the figure. No seedlings established at distances closer than 20 m to the river. The wavy horizontal line depicts plot surface elevation relative to river stage at base flow. Transect DL-2 featured a very similar pattern

plant density were positively associated with the proportion of germinant survival through the period. Importantly, plot elevation above ground water was not a significant determinant of survivorship probability. Germinant survival through mid-September was highest in areas 175 and 125 cm above river base flow stage along transects DL-1 and DL-2, respectively (Figure 4).

Taproot lengths of Fremont cottonwood germinants at the end of the 1995 growing season in DLP averaged 34.2 cm ($n = 64$, S.D. = 5.3). The maximum taproot length was 44.0 cm.

The stage decline rate at DLP averaged > 3 cm/day for at least a 1-month period in each of 1993, 1994, and 1995. In addition, a period of very rapid decline, > 6 cm/day for > 10 days, occurred in 1993 and 1995, and > 5 cm/day for > 14 days in 1994. Depth to the floodplain water table at DLP was tightly coupled to river stage, with the value of the regression slope close to one (e.g. Well 20: $Y = -29.267 + 1.013X$, $r^2 = 0.99$, $p = < 0.001$). Thus, the rate of ground water table decline in areas supporting germinants is nearly identical to the rate of river stage decline.

Determination of xylem water sources

There was no significant difference in the mean deuterium isotopic ratio (δD) of soil water (-91.5 ± 3.8) and sap water of either germinants (-86.7 ± 11.9) or 2-year-old seedlings (-91.5 ± 4.6) (t-tests; $p > 0.05$) (Figure 5). Germinant and 2-year-old δD sap ratios differed significantly from mean values for sap in plants > 4 years old and ground water (-114.9 ± 2.8) ($p < 0.05$). The mean ratio for stem water in plants > 4 years old was not statistically different from that for ground water ($p > 0.05$).

The effects of competition from older cohorts on seedling establishment

Germinant mortality was 100% under or immediately adjacent to older cottonwoods on bars and in backwaters. Soils beneath isolated stands of live germinants had a higher gravimetric water content than
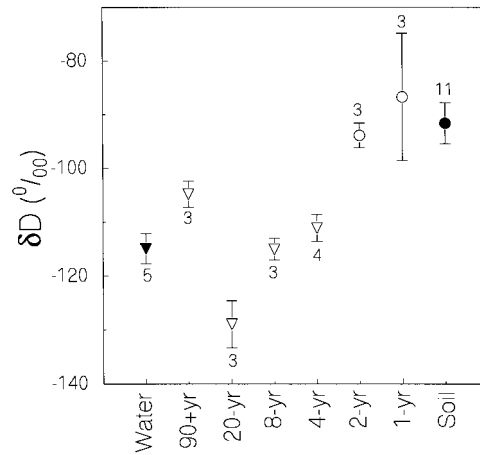
Figure 5. Isotopic ratios in stem water in cottonwood trees of various ages and in water from unsaturated soil (Soil) and from ground water (Water)

soil of similar texture collected at the same time (late August) from beneath cottonwood seedlings and saplings established in previous years (Figure 6). Coarse-textured soils (sand and loamy sand) consistently had moderately negative matric potentials and low volumetric water content, regardless of whether the sample was obtained from beneath saplings or germinants (Table II). In contrast, the matric potential and water content of sandy loam, loam and silt loam soils were significantly different beneath germinants and saplings. The highest water content occurred in fine-textured layers (sandy loam, loam, and silt loam) under germinants (Table II). Sites supporting live germinants in late summer had at least one soil layer in the rooting zone that contained plant-available water (matric potential between 0 and -1.5 MPa), whereas plant-available water was absent in the upper 45 cm of soils under saplings.
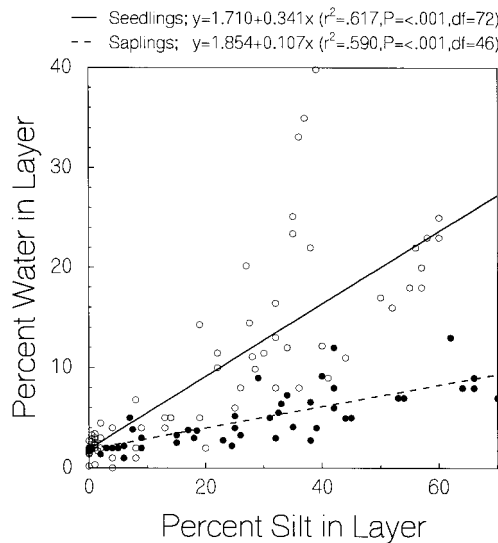

Figure 6. Regression analysis of percent gravimetric water content for each soil layer between 7- and 45-cm depth against percent silt in that layer. Open circles are for layers in plots supporting only seedlings, filled circles are for layers in plots supporting an overstory of existing woody plants

Table II. Comparison of matric potential (MPa) and volumetric water content (cm³/cm³) of like-textured soils under cottonwood seedlings and sapling stands

Soil texture	Under seedlings			Under saplings		
	n	Matric	Volumetric	n	Matric	Volumetric
Sand	32	−5.13 (17.46)[a]	3.74 (1.60)[a]	14	−8.27 (25.56)	3.44 (1.67)
Loamy sand	7	−2.76 (34.89)[b]	5.59 (2.66)[a]	5	−7.83 (8.59)	3.65 (1.85)
Sandy loam	20	−0.96 (2.27)[c]	15.99 (8.66)[c]	15	−285 (high)	5.55 (1.74)
Loam	4	−0.48 (0.31)[c]	27.33 (4.07)[c]	7	−538 (high)	7.27 (2.93)
Silt loam	9	−1.49 (0.62)[c]	14.75 (1.20)[c]	7	−1246 (high)	5.29 (2.05)

Values are means, with 1 S.D. in parentheses. Student's t-tests were used to compare matric potential and volumetric water content between seedling and sampling samples of the same soil texture.
[a] No significant difference, $p > 0.05$.
[b] Different at $p < 0.05$.
[c] Different at $p < 0.001$.

The effects of shade on intra- and interspecific competition

The probability that a transplanted cottonwood seedling would survive through the first 10 months of Experiment 1 was significantly related to the percentage of full sun (SUN) it received [logit (probability of survival) = −2.055 + (0.0178 SUN); variable SUN: $\chi^2 = 6.71$, $p = 0.01$]. The shade dependence remained significant through the August 1994 census (13 months; $\chi^2 = 8.97$, $p = 0.003$).

Shading had no detectable effect on survival of Experiment 2 transplants during the ~4 week period prior to the termination of irrigation. Survivorship was 100% in nearly all plots, including four of the five plots receiving only 17% PAR. After irrigation ended, survival dropped dramatically in all plots. The lowest values were for cottonwood (Table III).

Table III. Survivorship of cottonwood seedlings in experiments involving shade treatments (replicates pooled)

Experiment	Period	Group	Survivorship (N_f/N_o)	
		(%PAR)	Cottonwood	Tamarisk
1	July 1993–May 1994	100	26/60 = 0.43	
		55	9/60 = 0.15	
		30	23/60 = 0.38	
		17	8/60 = 0.13	
		4	2/60 = 0.03	
2	June/July 1994–August 1994 (Irrigated)	100	74/75 = 0.99	58/75 = 0.77
		69	73/75 = 0.99	60/75 = 0.80
		40	75/75 = 1.00	66/75 = 0.88
		17	69/75 = 0.92	70/75 = 0.93
	Aug 1994–September 1994 (Post-irrigation)	100	20/74 = 0.27	53/58 = 0.91
		69	22/73 = 0.30	12/60 = 0.20
		40	20/75 = 0.27	42/66 = 0.63
		17	32/69 = 0.46	53/70 = 0.76
3	July 1995–September 1995	100-Thinned	17/50 = 0.34	
		100-Unthinned	14/450 = 0.03	
		69-Thinned	33/50 = 0.66	
		69-Unthinned	40/515 = 0.08	
		40-Thinned	26/50 = 0.52	
		40-Unthinned	19/497 = 0.04	
		17-Thinned	17/50 = 0.34	
		17-Unthinned	4/503 = 0.01	

Tabulated survivorship values are given as N_f/N_o, where N_f is the final, and N_o the original population size.
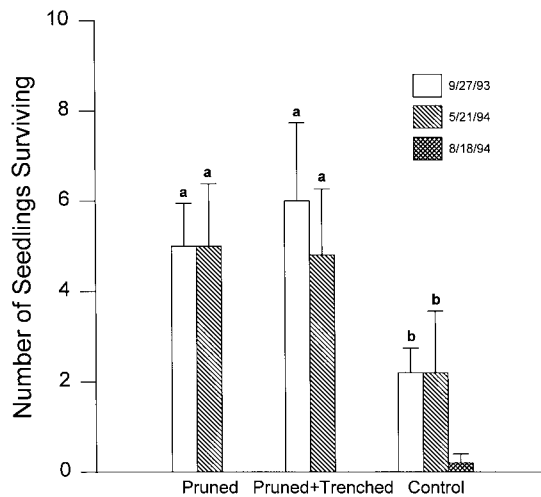
Figure 7. Mean (± 1 S.E.) number of cottonwood seedlings (out of 15 planted in July 1993) surviving under adult tamarisk in two treatments (pruned, pruned and trenched) and control. Three overlapping periods are evaluated. Means with same letter are not significantly different. Data from Experiment 5, conducted in the Island Park study area

The proportion of naturally established cottonwood seedlings surviving in unthinned plots was much lower than in thinned plots (Experiment 3; Table III); however, the number of seedlings ultimately surviving in thinned and unthinned plots was similar. The probability that a naturally growing cottonwood germinant in an unthinned plot would survive through the 6 weeks of Experiment 3 was significantly related to its location on the floodplain (categorical variable LOC), but not to the percentage of full sun (SUN) it received [logit (probability of survival) $= -2.710 + 0.0115$ SUN $- 0.438$ LOC; variable SUN: $\chi^2 = 2.1$, $p = 0.15$; variable LOC: $\chi^2 = 4.9$, $p = 0.03$]. Survivorship also appeared to be independent of shade in plots thinned to 250 seedlings/m² (variable SUN: $\chi^2 = 0.07$, $p = 0.79$).

Effects of tamarisk on seedling establishment

Cottonwood seedlings transplanted under adult tamarisk suffered higher mortality during their first summer than those similarly planted but with the tamarisk canopy removed (Experiment 4: $\chi^2 = 14.1$, df $= 2$, $p = 0.001$) (Figure 7). Canopy removal plus trenching did not significantly increase cottonwood seedling survival over canopy removal alone ($\chi^2 = 0.718$, $p = 0.40$). Although the higher survivorship was still evident in May 1994, the effect of canopy removal was eventually masked by desiccation during the drought of mid-summer 1994, which led to the death of all planted seedlings.

Cottonwood seedlings transplanted into dense beds of naturally established tamarisk seedlings had lower survivorship than the control group transplanted into a plot cleared of tamarisk seedlings (Experiment 5: $\chi^2 = 41.04$; $p < 0.001$). Through two summers (1993 and 1994), 11 of 15 (73.3%) of cottonwood seedlings in the control group survived, compared with only two of 45 (4.4%) in treatments.

Soil stratigraphy of fluvial features supporting cottonwoods

We found complex stratification of the underlying alluvial materials in all 36 fluvial features examined. A representative transverse cross section through an accreting braid bar, backwater, and channel complex in DLP is depicted in Figure 8. Braid bars are linear features formed on the channel margin where flow splits into multiple channels. The bar shown in Figure 8 was cigar-shaped and ~ 10 m long in 1995. Saplings (~ 10 years old) grew on the upstream end and a stand of 3-year-old seedlings (the only survivors of the 1993 cohort on the bar) occupied the middle section. At peak stage in 1995, floodwaters were more than 1 m deep in the backwater and covered the bar.

We sectioned the bar downstream of the 1993 cottonwoods, through a group of surviving germinants (1995 cohort). The sediment texture 0.5–1.0 m below the bar surface was sand (Figure 8). A mound of sandy loam sediment formed the core of the braid bar, most likely deposited where roughness, higher due to the presence of ∼ 10- and 3-year-old plants, allowed fine sediments to settle out of suspension. A series of vertically accreted deposits that varied in texture between loam and sand had raised the channel side of the bar, and a series of silt loam, sandy loam, and sand deposits had raised the floor of the backwater. Surface sediments on the bar were loam. Germinants had initially grown on all three of these landforms, but they survived only on bar and backwater sediments, where loam textured layers occurred.

Germinant density on these 36 landforms was significantly related to the total thickness of loam-textured soil layers (sandy loam, loam and silty loam) within the rooting zone (0–45-cm depth). Germinants survived where loam layers > 10 cm thick occurred in the upper 45 cm of soil, such as the backwater and bar illustrated in Figure 8, whereas 100% mortality occurred in the channel areas.

A trench excavated across a relatively flat terrace supporting mature cottonwoods provided insight into the long-term fate of cottonwoods established on braid bars. Floodwaters reached the top of the terrace only four times in recent decades, in 1957, 1974, 1984, and 1997. Beneath a clay surface soil, we found two well-developed braid bars composed of a 20–30 cm thick silt loam layer, separated by a channel (Figure 9). A series of sections (slabs) taken from a cottonwood tree growing next to the trench indicated that the ∼ 90-year-old tree had germinated on one of the braid bars (see right arrow on Figure 9). The germination surface was located by identifying the slab with the highest ring count (Scott *et al.*, 1997), and the lowest slab with a pith. A second cottonwood along the trench with similar morphological characteristics was not aged, but the root crown occurred at the same location on the other braid bar surface. The germination surfaces of these two trees were ∼ 150–200 cm above the current late-summer water table. The trees had survived the vertical accretion of more than 1 m of sediment, including ∼ 50 cm of loam, a thin bed of red sandy loam (probably derived from a flooding tributary), and 50 cm of clay sediments.

DISCUSSION

Seed rain

Seed rain was abundant in all 3 years at all study sites, and does not appear to be restricting the establishment of either Fremont cottonwood or tamarisk. Seeds were aerially dispersed across the full
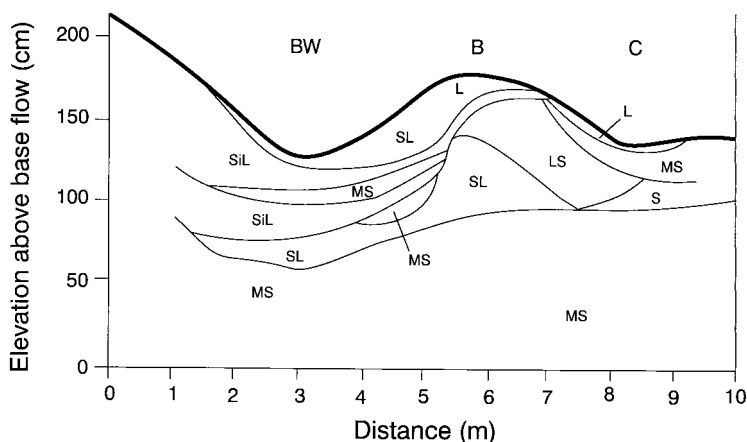

Figure 8. Transverse cross section through a braid bar (B) at Deer Lodge Park depicting sediment stratigraphy. A backwater (BW) borders the bar toward the upland, and by a channel (C) toward the river. Textures of layers are loam (L), silt loam (SiL), sandy loam (SL), medium sand (MS), and sand (S)
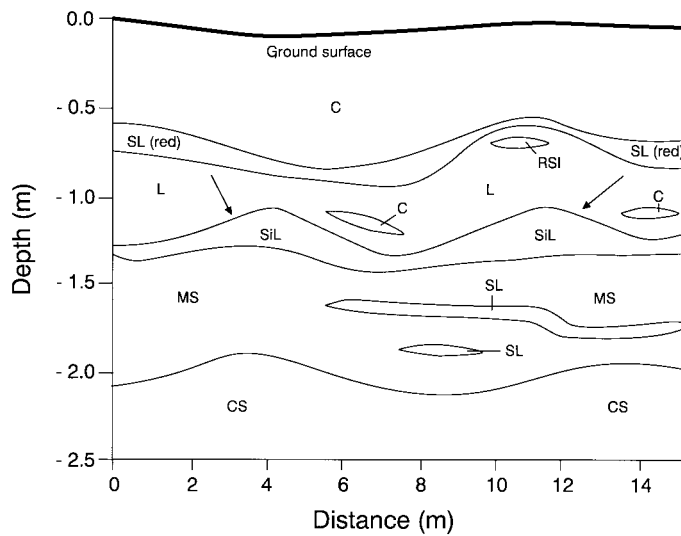
Figure 9. Stratigraphic cross section through part of a DLP terrace that currently supports mature cottonwoods. The profile was oriented perpendicular to the river channel. Soil textures of layers are clay (C), loam (L), silt loam (SiL), sandy loam (SL), medium sand (MS), and coarse sand (CS). Two cottonwoods had germinated on surfaces of well-developed braid bars, now buried, at positions marked by arrows

range of moist floodplain surfaces and elevations exposed as floodwaters receded at DLP and IP (Figure 2). The 4–5 week duration of seed dispersal we noted was similar to that reported for cottonwood along the San Pedro River in Arizona (Warren and Turner, 1975), and along the Rio Grande in New Mexico (Everitt, 1980), but slightly shorter than that reported for plains cottonwood along the Platte River, Nebraska (Johnson, 1994). The mean density of cottonwood seeds reaching the floodplain was much greater in DLP than in BP (Figure 3), a difference we attribute to the presence of dense stands of young, yet sexually mature cottonwood poles (ranging from 22 to 26 years old) at DLP. Seeds in BP are produced solely by large, old trees that are widely scattered on high floodplain surfaces. The density of seeds dispersing onto the DLP floodplain is higher than values reported for Fremont cottonwood along the Salt, Gila and San Pedro Rivers in Arizona (Horton *et al.*, 1960; Turner, 1974; Warren and Turner, 1975), but lower than values recorded for plains cottonwood along the Platte (Johnson, 1994). The majority of germinants in DLP, BP, and IP originated from aerially dispersed seed falling on moist substrate. The high densities we recorded, > 500 seedlings/m^2, have previously been associated primarily with water dispersed seed (Craig and Malanson, 1993).

Overlap in the timing of cottonwood and tamarisk seed dispersal resulted in mixed seedling beds in all study areas. However, because cottonwood seed dispersal begins earlier than tamarisk (Figure 2), the timing of peak discharge from Flaming Gorge Dam can influence the composition of seedling beds in BP: early summer peaks promote cottonwood establishment, whereas mid- to late-summer peaks promote tamarisk establishment. Fenner *et al.* (1985) and Everitt (1995) also noted the relationship of flood peak timing to seedbed composition along western US rivers.

Survival of natural seedling cohorts

Our results indicate that landscape position plays a strong role in cottonwood seedling survival. Cottonwood germinants established in large numbers in all study areas, on the wet sediments of bars, islands, backwaters, and banks, in years of low (1994) as well as high (1993 and 1995) peak discharges. Survivorship through the first growing season, however, was extremely low at DLP and IP except in previously unvegetated sites on particular landforms along the floodplain margin far from the late summer and winter channel position. Where germinants survived their first growing season in low topographic positions relative to late summer stage, they were likely to be scoured out and die as the

channel bed was mobilized during the subsequent spring flood. Cottonwood seedlings that survived their first few growing seasons at DLP, EP, or IP were located on the tops and sides of unvegetated vertically accreting bars and backwaters with fine-textured soils, but not in the channels between braid bars, or on broad point bars, a location often associated with successful establishment of plains cottonwood (Bradley and Smith, 1986). The actively accreting bars and backwaters that supported 2- and 3-year-old cottonwood in DLP and IP were absent in BP. Cottonwood germinants in BP were restricted to islands and cut banks where long-term survival was improbable given the long duration of soil saturation on islands and the instability of annually sloughing vertical banks. Thick beds of *Schoenoplectus lacustris*, *Bobloschoenus pungens* and other marsh vegetation on the islands attested to their wetland rather than riparian character (Merritt, 1997) and consistently high water table. The limited range of stage change and lack of suitable unvegetated, developing fluvial landforms in BP precluded natural cottonwood seedling establishment.

Most cottonwood seedling mortality in DLP and IP was attributable to either flood scouring or desiccation. Sacchi and Price (1992) also considered soil moisture a key to *Salix lasiolepis* seedling survival at a riparian site in northern Arizona. McBride and Strahan (1984) noted that 93% of Fremont cottonwood seedlings on gravel bars along a California stream survived through summer if they were located adjacent to surface water, whereas none survived where the late summer water table depth was > 1 m.

Fremont cottonwood seedling survival was not found to be dependent upon their maintaining contact with the ground water. In DLP, IP, and EP cottonwood germinants initially established throughout a wide elevation zone, but first summer survival occurred almost exclusively at elevations $> 125–250$ cm above base flow ground water elevations (Figure 4). Our isotopic analyses, and excavations of seedlings, indicate that only $4 +$ -year-old cottonwoods have rooted to the depth of the late summer ground water table.

Soil texture and cottonwood seedling survival

Free-flowing western rivers with large (> 2 m) annual stage changes and large fine-textured suspended sediment loads, such as the Yampa, create environmental opportunities for, and place constraints on, cottonwood establishment fundamentally different from those on (1) regulated rivers with small (< 1 m) stage changes, (2) regulated or unregulated rivers with low sediment loads, or (3) river reaches with primarily coarse-textured substrates. Large annual stage changes and a highly mobile sand bed limit seedling survival to relatively stable sites in high landscape positions. These sites are typically far from the winter channel and are unaffected by river ice flows. In contrast, the bars formed along cobble and gravel bed river reaches are more stable than sand bed channels, and offer opportunities for seedling establishment close to the channel.

The mechanisms that allow Fremont cottonwoods seedlings to survive high above the late-summer water table in DLP for the 3–4 years necessary to become phreatophytic are, (1) the presence of fluvial landforms containing layers of fine-textured sediment, (2) relatively high annual river stage, even in years with average or below average peak discharge, and (3) the predictable occurrence of at least a small amount of July and August precipitation. Our rating curve (relating discharge to stage) for DLP indicates that a flow of 270 m³/s, which occurs in 4 years out of 5 (probability of occurrence = 0.83), results in a river stage 200 cm above late summer base flow stage, a height adequate to saturate soils on most landforms supporting seedlings, even when seedlings initially establish on surfaces created during a large flood such as occurred in 1995 (peak discharge of 519 m³/s, peak stage 277 cm above base). Peak flows less than 170 m³/s, which still results in a stage 164 cm above base flow level, have occurred only three times since 1922: in 1934, 1954 and 1977.

The importance of fine-textured sediment is due to its capacity to store more plant-available water than sands (van Genuchten *et al.*, 1989). Soil moisture derived from spring floods and depleted by growing seedlings can only be replenished by summer precipitation. A drought during the mid-summer of 1994 resulted in the death of almost all seedlings planted in our 1993 experimental plots, as well as most natural seedlings of the 1993 and 1994 cohorts. Thus, during a seedlings first 3–4 years of life, it is susceptible to

drought induced mortality, regardless of landscape position. Once a seedling roots to the late summer water table depth its probability of long-term survival becomes limited by biotic rather than abiotic factors. Although erosion may have a role in survival after the 4th summer, herbivory and other biotic factors become increasingly important (Andersen and Cooper, unpublished data).

Floodplains with primarily coarse-textured substrates have low water holding capacity, limiting germinant survival to sites where they can maintain contact with the water table as stage declines (Rood and Heinze-Milne, 1989; Mahoney and Rood, 1993; Stromberg, 1993; Braatne *et al.*, 1996). Hupp and Osterkamp (1996) suggest that along such reaches in arid and semi-arid regions the spatial pattern of germination and initial seedling establishment is influenced by river surface flows (floods), whereas ground water levels greatly influence seedling survival. On rivers with large stage changes, however, germinants growing close enough to the channel elevation to reach the water table could be under >2 m of water during most subsequent stage maxima, with a low probability of surviving sediment burial or scouring (Hosner, 1957, 1960; Warren and Turner, 1975; McBride and Strahan, 1984). Everitt (1968) and Scott *et al.* (1996, 1997) documented that plains cottonwood trees had established 2 m or higher above river base flow elevation on the northern Great Plains, but neither study provided an explanation of how seedlings could have survived there. Krasny *et al.* (1988) linked willow seedling survival and the texture of the alluvial substrate on Alaskan floodplains.

Tamarisk and cottonwood seedling competition

The timing of cottonwood and tamarisk seed dispersal overlaps, resulting in mixed-species seedbeds in many areas. We found that cottonwood seedling survival was low in dense tamarisk seedling beds. Our 1994 shade experiment in DLP indicated high survival of both cottonwood and tamarisk seedlings under conditions of high soil moisture. When supplemental watering was ceased however, cottonwood survival fell below that of tamarisk. Thus, we feel that Turner's (1974) statement that tamarisk outcompetes native vegetation must be qualified. Our results support Busch and Smith's (1995) hypothesis that tamarisk, because of its higher water use efficiency, will outcompete cottonwood when water is limiting.

Our field analyses of germinants on sites with and without older cottonwoods showed that soil water was depleted under stands of saplings relative to soils supporting only germinants (Figure 6). These results suggest that competition for water is a factor restricting Fremont cottonwood seedling establishment to sites lacking existing plants. While cottonwoods >4 years old use ground water, they also likely deplete soil water.

Shade and cottonwood seedling survival

We hypothesize that both intra- and interspecific competition effects on cottonwood seedlings are manifested primarily through competition for soil water, and secondarily for light. Our experimental studies indicate that Fremont cottonwood is more shade tolerant than previously reported (Read, 1958; Strahan, 1984; Harris, 1987; Scott *et al.*, 1996). Only the greatest reduction in PAR caused a significant reduction in seedling survival in unwatered plots, and shade had no effect on survival in watered plots (Table III). Heavy shade increased cottonwood seedling mortality in (a) unwatered plots, (b) dense plots of cottonwood seedlings, and (c) plots under adult tamarisk, all situations in which competition for soil moisture is high. Further testing of this hypothesis should include an analysis of interaction effects; shade may limit root growth and reduce a seedling's ability to acquire soil water, as has been shown for *Salix lasiolepis* (Sacchi and Price, 1992) and plains cottonwood (Shafroth *et al.*, 1995). Shade also changes soil and air temperatures that could alter water use by plants.

Removal of an overstory tamarisk canopy resulted in a large increase in 1st-year cottonwood seedling survival, as did canopy removal plus trenching (Figure 7). Both treatments increased light reaching cottonwood seedlings and reduced the transpirative area, which could have increased soil water availability to seedlings. Because we did not monitor soil water in Experiment 4 we cannot reject the hypothesis that increased water availability, rather than increased light, improved seedling survival.

Synthesis and management implications

The formation of fluvial features comprised of fine-textured sediments requires a supply of fine sediment and backwater or slackwater areas for deposition of this material to occur. Obstructions to flow, such as large woody debris, bedforms, or the stems of vegetation lead to a localized reduction in stream power and the deposition of fine-textured sediment. When exposed, these fine-textured surfaces not only provide adequate sites for germination, but also enhance survival through the first growing season due to their higher water holding capacity. Our data suggest that, in the absence of older plants, soils with a thickness of at least 10–15 cm of fine-textured layers within the top 40 cm of soil have sufficient water holding capacity to support germinants through their first summer. Where seedlings persist through the following year's flood they increase hydraulic roughness, decrease velocity and result in vertical and lateral accretion (Hadley, 1961; Smith, 1976; McBride and Strahan, 1984; Strahan, 1984; Hupp, 1992; Johnson, 1994; Friedman *et al.*, 1996; Hupp and Osterkamp, 1996) forming elongated bars that build vertically and in a downstream direction. Fresh fine-textured sediment deposited in the lee of the bar each year allows additional cohorts of cottonwood and tamarisk seedlings to establish, creating a patchy landscape with small (1–20 m^2) stands of relatively even-aged plants which decrease in age in a downstream direction.

Fluvial complexes of bars, channels between bars, and backwaters develop and vertically accrete as a unit. Eventually they are inundated by only the largest floods, which deposit fine-textured sediment, burying the landforms, leveling the topography, and creating a superficially homogenous fluvial feature, as illustrated by our high floodplain excavation (Figure 9) (Schumm and Lichty, 1963; Brice, 1964; Nadler and Schumm, 1981). In our study areas, we also found areas where seedlings have established in abandoned channels (in IP). Although fine-textured bars high above base flow stage appear to be the primary sites for seedling establishment in our study sites, establishment also occurs in other areas where fines are present.

Although the design of Flaming Gorge Dam allows for releases above power plant capacity, there is no capability to restore fine-textured sediment now trapped in the reservoir to regulated reaches of the river. Currently, Green River flows are managed primarily for endangered Colorado River fish, and annual variability (including peak flow) is essentially constant from year to year. Seed bed soils are saturated for much of the summer and are unsuitable for cottonwood establishment. Prescribed high flows in the range of 185–245 m^3/s could flood sparsely vegetated or mechanically cleared fluvial deposits that were formed by pre-dam floods. These features could provide seedling beds for recruitment events, but once cottonwood or tamarisk populates these surfaces further seedling establishment is unlikely until new, open substrates become available through tree mortality, or are artificially created. Cottonwood seedlings established by controlled floods will be dependent upon subsequent high flows during their 2nd and 3rd growing seasons to provide soil moisture until taproots reach the late summer water table. A reservoir release intended to establish cottonwood seedlings should be followed the next 2 years by flows with similar peaks. Our data also suggest that dense tamarisk thickets preclude or hinder cottonwood establishment by depleting soil moisture and creating shade. Tamarisk removal prior to a controlled flood could facilitate cottonwood seedling establishment in existing tamarisk stands.

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