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Inundation depth, duration, and temperature influence Fremon cottonwood (*Populus fremontii*) seedling growth and survival

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Perennial plant species of semiarid riparian ecosystems must tolerate a wide range of water conditions ranging from complete submergence to drought. Under natural conditions semiarid riparian zones usually experience inundation early in spring followed by gradual soil drainage and a decline of the water table during the summer (Brinson et al. 1981, Kozlowski 2002, Stella et al. 2006). Early high-river stage and the beginning of recession coincide with seed dispersal and germination of riparian trees and shrubs on exposed sediments. The regeneration of riparian forests depends first on the ability of the seedlings to extract sufficient water from root-zone sediments. It also depends on their ability to keep up with a declining water table associated with the recession stage of the river hydrograph (Stromberg

INUNDATION DEPTH, DURATION, AND TEMPERATURE INFLUENCE FREMONT COTTONWOOD (POPULUS FREMONTII) SEEDLING GROWTH AND SURVIVAL

L.C. Auchincloss1,4, J.H. Richards1, C.A. Young2, and M.K. Tansey3

ABSTRACT.—Fremont cottonwood (Populus fremontii) is an early successional foundation species found in riparian forest ecosystems in the North American Southwest. Along rivers, the upper limit of the seedling establishment zone depends on the proximity of seedling roots to the declining water table. The lower limit is a function of the maximum elevation of inundation or scour. Fremont cottonwood seedlings are likely to experience short-term (1- to 5-week) inundation during their first year of growth under both natural and human-influenced hydrologic regimes. Previous studies show that inundation can account for more than 70% of seedling mortality during this time. Using controlled inundation experiments, we found that seedlings of Fremont cottonwood have high tolerance of inundation to the soil surface and a reasonable tolerance of complete shoot submergence for a duration of 1 or 2 weeks (22% and 50% mortality, respectively). Mortality increased linearly with days of complete submergence (mortality percentage = 4.6 + (2.5 × days of submergence)). Warm water temperature (25/18 °C day/night) during complete submergence adversely affected seedling biomass and survival, resulting in 64% mortality versus 39% with cooler water temperatures (18/11 °C day/night). Our results indicate that establishment of new Fremont cottonwood populations in the riparian corridor will be more successful when flows do not completely cover the shoots of seedlings for more than 2 weeks and if water temperatures during inundation are cool. From the perspective of the management of river flows for cottonwood recruitment, deep, prolonged, late-season (warm water) inundations are the most detrimental.

RESUMEN.—El álamo negro (Populus fremontii) es una especie de sucesión temprana en los ecosistemas de bosques ribereños, en el suroeste norteamericano. A lo largo de los ríos, el límite superior de la zona de establecimiento de plántulas depende de la proximidad de las raíces de las plántulas al nivel freático decreciente. El límite inferior es una función de la elevación máxima de inundación o abrasión. Es posible que las plántulas de álamo negro experimenten una inundación de corto plazo (de 1 a 5 semanas) durante sus primeros años de crecimiento en sistemas hidrológicos naturales y con influencia humana. Estudios anteriores revelaron que la inundación puede explicar más del 70% de la mortalidad de las plántulas durante este tiempo. Mediante experimentos de inundación controlada, encontramos que las plántulas de álamo negro poseen una elevada tolerancia a la inundación de la superficie del suelo y una tolerancia razonable a la inmersión completa del tallo durante una o dos semanas (22% y 50% de mortalidad respectivamente). La mortalidad aumentó en forma lineal con los días de inmersión completa (porcentaje de mortalidad = 4.6 + (2.5 × días de inmersión)). La temperatura caliente del agua (25/18 °C día/noche) durante la inmersión completa afectó de manera adversa la biomasa y la supervivencia de las plántulas, lo que resultó en un 64% de mortalidad contra el 39% en temperaturas más frías (18/11 °C día/noche). Nuestros resultados indican que el establecimiento de nuevas poblaciones de álamos negros en el corredor ribereño tendrá mayor éxito cuando los caudales no cubran por completo los tallos de las plántulas por más de dos semanas, y si la temperatura del agua es fría durante la inundación. Desde la perspectiva del manejo de los caudales de los ríos para el reclutamiento de álamos negros, las inundaciones profundas, prolongadas y en temporada tardía son las más perjudiciales.

Perennial plant species of semiarid riparian ecosystems must tolerate a wide range of water conditions ranging from complete submergence to drought. Under natural conditions semiarid riparian zones usually experience inundation early in spring followed by gradual soil drainage and a decline of the water table during the summer (Brinson et al. 1981, Kozlowski 2002, Stella et al. 2006). Early high-river stage and the beginning of recession coincide with seed dispersal and germination of riparian trees and shrubs on exposed sediments. The regeneration of riparian forests depends first on the ability of the seedlings to extract sufficient water from root-zone sediments. It also depends on their ability to keep up with a declining water table associated with the recession stage of the river hydrograph (Stromberg

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et al. 1991, Mahoney and Rood 1992, 1998, Scott et al. 1997, Kranjcec et al. 1998, Rood et al. 2003). However, depending on the timing of precipitation, snowmelt rate, dam releases, and other conditions, seedlings growing along rivers in spring and summer may be subject to short-term flooding (Mahoney and Rood 1998, Amlin and Rood 2001). Thus, regeneration of riparian forests depends also on the ability of seedlings to survive temporary inundation. This study examines the effects of floodwater conditions and plant age on the growth and survival of Fremont cottonwood (*Populus fremontii* S. Watson ssp. *fremontii*) seedlings.

Riparian Fremont cottonwood occurs from western Texas through New Mexico, Arizona, California, Nevada, and Utah. In mature riparian forests, it is a foundation species, making up a large portion of the biomass and influencing the overall productivity of the ecosystem (McBratney and Strahan 1984, Warner and Hendrix 1984, Stromberg 1993, Rood et al. 2003). Along the Sacramento River, California, Fremont cottonwood disperses seed that germinates within 2 days on exposed substrates in April–May. This seed dispersal is coincident with monthly average peak flows (prior to dam regulation) of the river’s major tributaries, the Feather and American rivers (USGS 2010a, 2010b). Because Fremont cottonwood establishes close to the river’s edge on exposed point bars and germinates early in spring, the seedlings are likely to experience brief inundation due to either natural or human-induced hydrologic changes. In some years, inundation has accounted for more than 70% of seedling mortality during the first year of growth along the Sacramento River (Morgan 2005).

Flood events can cause damage to establishing seedlings through several processes, including substrate saturation and root hypoxia, inhibition of photosynthetic carbohydrate generation, erosion of sediments or plants, and burial by sediments. Physiological damage during inundation includes suppressed shoot and root growth, delayed leaf formation, accelerated senescence, and root decay (Kozlowski 2002). These stresses become more pronounced as the duration of inundation increases (Neuman et al. 1996). Complete inundation of shoots inhibits photosynthesis, and warm water temperature during inundation increases respiration rate and depletion of carbohydrates. After submergence ends and seedlings are reexposed to high light, the potential for oxidative damage to their leaves is high (Parolin 2009). Thus, physiological stress may occur both during and after inundation and can lead to plant mortality or decreased productivity. Damage and stress can result in plant death up to 2 weeks postinundation (Banach et al. 2009).

Considering the stresses and plant acclimation potential, the severity of physiological effects of inundation on cottonwood seedlings depends on several environmental factors: duration of inundation, depth of inundation, developmental age of the plant, and water temperature during inundation. Hosner (1958, 1960) observed that complete submergence for 16 days negatively impacted the survival of cottonwood seedlings (among other riparian species). Short-term shoot submergence of 2–4 days led to partial leaf death, whereas 8-day submergence required complete renewal of the leaf canopy. Sixteen-day submergence led to death of all seedlings of plains cottonwood (*Populus deltoides*; Hosner 1958). A later study from Amlin and Rood (2001) showed that cuttings of 3 cottonwood species (*P. angustifolia*, *P. balsamifera*, and *P. deltoides*) survived more than 7 weeks of inundation to the soil surface, although dry weight was lower in inundated treatments compared to controls.

Although these studies examined flooding for different durations, they did not compare the effects of inundation to the soil surface and complete shoot submergence. Complete inundation of the shoot is expected to be more damaging than partial inundation of the soil and stem base. This is because an inundated shoot has little or no access to the atmosphere, a condition that hinders internal oxygen transport and inhibits photosynthesis (Kozlowski 2002). Also, the described experiments were conducted with warm, still water and may not be representative of inundation by cool, flowing river waters that contain higher dissolved oxygen concentrations. It is important to reinvestigate this topic, as inundation with warm, stagnant water decreased growth of some riparian species to a much greater extent than inundation with cool, flowing water (Brink 1954, Kozlowski 2002).

Most work on inundation of cottonwood has been done with cuttings (e.g., Amlin and Rood 2001). To study establishment of new populations we need to consider the effect of
inundation on seedlings because of their small size, younger developmental age, and lack of nutrient and carbohydrate reserves. Plant age affects stem and taproot size, which affects the potential amount of stored nutrients and carbohydrates and, thus, affects the plant’s ability to withstand long inundation duration. Seedling establishment is particularly important in natural ecosystems that are subject to flooding stress. Thus, it is important to investigate the specific tolerance of *P. fremontii* seedlings to inundation, considering that the species is a foundation species along many western waterways. Large differences in flood response physiology and growth rate are known to exist among 13 hybrid poplar genotypes resulting from crosses between *P. trichocarpa, P. nigra, P. deltoides,* and *P. euramericana* (Guo et al. 2011). Because large differences existed among these hybrids, differences in flooding tolerance may vary significantly among species, and we cannot necessarily apply results from examination of other species to *P. fremontii.*

In this experiment, we examined the effects of water temperature, duration of inundation, and depth of inundation on Fremont cottonwood seedlings of 2 ages. We tested the hypothesis that warmer inundations of longer duration and greater depth would result in decreased growth and survival of seedlings. We also examined 2 ages of Fremont cottonwood seedlings to test the hypothesis that more-developed plants, presumably with greater nutrient and carbohydrate stores, are better able to withstand inundation. The results from this study provide characterization of multiple water conditions important for cottonwood seedling survival of inundation and hence for the establishment of new populations and maintenance of semiarid riparian ecosystems.

**Methods**

**Seedling Germination and Plant Growth**

In May 2008, catkins were collected from 13 trees between river mile (RM) 190 and 220, elevation 33–52 m asl, of the Sacramento River, California. Seeds were cleaned and stored with desiccant at 4 °C, similar to Segelquist et al. (1993). Germination tests were conducted on moistened filter paper at approximately 20 °C. A commercially available sandy soil (Schwartzgruber plaster mix mined from a tributary of the Sacramento River, Cache Creek, Yolo County, CA) was used. This soil was a good match to previous particle size and soil profile data from a point bar at RM 192.5 on the Sacramento River where Fremont cottonwood establishment occurs. Seeds from 11 high-germination (78%–100%) trees were sown on the sandy soil in 240 large, approximately 650-mL Deepots® (Stuewe & Sons, Inc., Tangent, OR) on 18 June 2008; 5 seeds were sown per pot. After germination, seedlings were thinned to one seedling per pot. Seedlings were maintained outdoors on the University of California, Davis (UC Davis) campus, elevation 16 m asl, with a constant water table 10–15 cm below the soil surface, and they were fertilized daily by top watering with 5% modified Hoagland's solution (Epstein and Bloom 2005) until treatments commenced. One month later seed was sown in 240 small, approximately 165-mL Conetainers® (Stuewe & Sons, Inc., Tangent, OR), and seedlings were grown with the same procedures described above. The 2 sowing dates provided seedlings of different age at the beginning of the experimental treatments.

**Experimental Design and Treatments**

Three pairs (blocks) of insulated galvanized steel stock tanks (0.6 × 0.6 × 1.2 m, 432 L) were filled with deionized water. Racks holding the plants were placed at different depths to allow complete submergence of the plant shoots or submergence just to the soil surface. Control plants blocked with each pair of tanks were grown with a constant water table 12.5 cm below the soil surface. We used a thermostatically controlled cooling unit to regulate the temperature of the cool treatment tanks. Cool treatment tanks (one from each pair) were set to oscillate between 11 °C at night and 18 °C during the day. This regime approximated Sacramento River water temperature during summer 2004–2006. Warm tanks oscillated naturally with diurnal temperature change from 18 °C at night to 24 °C during the day. Water was circulated within each tank via a submersible pump to simulate flowing river water, to maintain water oxygenation, and to maintain uniform temperature throughout.

The experimental design was a split-split-plot randomized complete block. Within the 3 blocks, plants were randomly assigned to treatments with 4 (occasionally 2–3) plants per treatment per block (Table 1). Control plants
were paired with treatment plants for final harvests and for some intermediate harvests. The variables for each treatment were (A) age of the plant: 6 or 10 weeks old at time of inundation; (B) temperature of inundation: cool or warm; (C) duration of inundation: 1 week (6-week-old plants only), 2 weeks, or 4 weeks; and (D) depth of inundation: soil surface, complete submergence (all aerial portions of the plant covered), or no inundation (control with constant water table 12.5 cm below the soil surface). The main plot was temperature with plant age randomized as a subplot and depth and duration randomized as sub-subplots. Each plant was placed in an inundation tank corresponding to its block and its inundation temperature treatment assignment. Inundation tanks were outdoors at the UC Davis campus and received full morning and midday sunlight for approximately 10 h and afternoon shade for 4 h. Inundation treatments commenced on 26 August 2008, and the experiment ended 8 weeks later.

Harvests and Measurements

At the end of each inundation period, 1 plant (occasionally 2 plants) from each treatment and block was harvested, and 2 or 3 were elevated to the level of controls and allowed to recover for 4 weeks prior to final harvest. Plants within treatment combinations within blocks were subsamples. At each harvest, plant containers were removed from treatments and allowed to drain. Plant shoots were cut at the root collar and placed in deionized water in a zipper-lock plastic bag. The pot, soil, and plant roots were also sealed in plastic bags, and all samples were stored at 4 °C until processed.

Total leaf area and stem length for each plant were determined by scanning all leaves and stems within 3 days of harvest. Scans were analyzed using custom macros in Image J (National Institutes of Health; http://rsb.info.nih.gov/ij/). Roots were dissected from the soil to best maintain overall root structure. Root samples from each plant were washed with deionized water, placed in vials, and stored in a refrigerator until they could be scanned. Roots were scanned and measurements of total root length and average diameter were made using standard procedures for the program WinRhizo 2003B (Regent Instruments, Inc., Nepean, Ontario, Canada). The roots, leaves, and stem of each plant were dried at 45 °C for 3 days, and dry weights were recorded.

Statistical Analyses

Contingency table analyses of survival were performed using total levels of mortality after inundation and recovery (Glantz 2002). This cumulative survival analysis provided a realistic assessment of the effect of inundation. If a
The plant was alive immediately after inundation but had been damaged or stressed so that it could not recover; it was inferred that inundation caused mortality, as no control plants died during the 4-week recovery period. Regression analysis using SigmaPlot (Systat Software, Inc., San Jose, CA) was performed to assess plant mortality over time. ANOVA analyses using SAS (SAS Institute, Inc., Cary, North Carolina) were performed for the split-split-plot design using Proc GLM. Factors associated with higher-level plots (main plots and subplots as opposed to subplots and sub-subplots, respectively) generally have higher levels of variance and must be tested using larger error terms. Thus, analysis of the main plot, temperature, was performed with the larger error term \( \text{block} \times \text{temperature} \) and the analysis of subplots with \( \text{block} \times \text{temperature} \times \text{age} \). The analysis of the effect of the sub-subplot inundation level used the smallest error term \( \text{block} \times \text{inundation level} \times \text{temperature} \times \text{age} \). By specifying these error terms, we could compare the effects of temperature, age, depth of inundation, and the interactions among these factors using Proc GLM in SAS 9.2.

**Results**

**Mortality**

Contingency table analyses of cumulative mortality of Fremont cottonwood seedlings during the inundation and 4-week recovery period provided a clear assessment of the overall effects of inundation. These analyses showed that seedling death varied with depth of inundation, inundation water temperature, and duration of inundation. Across all treatments, completely submerged plants suffered approximately 5-fold greater mortality (51%) than noninundated control plants and plants inundated to the soil surface (plants in both treatments experienced <10% mortality; \( P < 0.00001 \); Fig. 1a). Plants inundated to the soil surface suffered little mortality and did not differ from controls (\( P = 0.98 \)). Within the complete submergence treatment, plants in warm water had significantly greater mortality than plants in cool water across all treatments (\( P = 0.02 \); Fig. 1b). Both young and old seedlings had high mortality in the complete submergence treatment across all durations of inundation (\( P = 0.38 \); Fig. 1c).
Mortality was linearly related to duration of inundation (% mortality = 4.60 + [2.54 × days of submergence]; $P = 0.024$, Adj. $R^2 = 0.93$; Fig. 2), consistent with results of contingency table comparisons among the specific treatments. Plants completely submerged for 4 weeks showed significantly greater mortality (71%) than plants inundated for either 1 week (22%, $P = 0.001$) or 2 weeks (50%, $P = 0.02$). All plants suffering mortality after complete submergence for 4 weeks were dead upon removal from inundation, with the exception of 2 plants that died within 5 days during the recovery period. Approximately 75% of plants that died as a result of 2 weeks of complete submergence were dead upon removal from inundation. The other 25% of plants died within a week of removal. Within young plants exposed to complete submergence for 1 week, approximately half of the plants suffering
mortality were dead upon removal from inundation and half died within a week of removal. Among young plants only, no statistical difference in mortality was observed when they were completely submerged for 1 week or 2 weeks ($P = 0.20$).

**Biomass of Surviving Plants**

Biomass measurements were analyzed only for living individuals that survived both the inundation and recovery periods. After inundation and recovery, both younger and older seedlings that were completely submerged had less than one-third the biomass of comparable control, noninundated plants. They also were smaller than plants in the soil-surface inundation treatment ($P < 0.0001$; Fig. 3a, 3d). However, plants inundated to the soil surface and controls did not show a significant difference in biomass ($P = 0.83$). Neither older nor younger plants were different in biomass among treatment durations within the complete submergence treatment (Fig. 3b, 3e). Also, cool water temperature resulted in much higher average biomass after complete submergence and recovery; however, very few plants surviving for this analysis meant $P = 0.11$. (Fig. 3c, 3f).

**Root Characteristics Immediately After Inundation**

Few differences were observed in root length per plant and average root diameter immediately after the 2-week inundation period, when surviving plants of different ages exposed to different inundation durations (Fig. 4a, 4c) were compared. Younger plants subject to complete submergence had approximately half the average root length compared to plants subject to control conditions or soil-surface inundation; this difference was nearly significant but the test had low power because of limited survival
in this treatment \((P = 0.075, \text{ power } = 0.354; \text{ Fig. 4a})\). After the 4-week inundation period, larger and significant differences were observed, despite small numbers of surviving plants. Both younger and older plants displayed a consistent pattern of greatly reduced root length and increased average diameter, indicating more fine-root loss for complete inundation plants compared to controls (Fig. 4b, 4d) or soil-surface inundated plants.

**DISCUSSION**

This study aimed to characterize multiple water conditions important for Fremont cottonwood seedling survival of inundation and hence for establishment of new populations along the Sacramento River and other watercourses. We evaluated the relative importance of the key environmental factors: inundation depth, inundation duration, and water temperature. Differences in response to these factors were relatively small among first-year seedlings of different age. Inundation depth, duration, and water temperature all significantly affected survival and health of Fremont cottonwood seedlings. The combination of environmental factors most detrimental to seedling health was complete submergence of seedlings in warm water for long duration (4 weeks). Negative effects of this treatment combination were apparent as reduced survival (Fig. 1) and, for surviving plants, reduced biomass and root length (Figs. 3, 4).

**Complete Inundation**

Consistent with results from Hosner’s (1958) experiment examining cottonwood seedlings, complete submergence of the shoot was deleterious for Fremont cottonwood seedling survival and growth over all ages, temperatures, and durations. Energy limitation via inhibition of photosynthesis, depletion of carbohydrates, accumulation of toxic compounds, and subsequent root decay may all have contributed to the mortality, as well as to the reduced growth of surviving plants of Fremont cottonwood under complete submergence (Roberts et al. 1984, Neuman et al. 1996, Borman and Larson 2002, Kozlowski 2002, Banach et al. 2009). With the shoot completely submerged, photosynthesis and growth are inhibited, and oxygen limitation requires all tissues of the plant to use anaerobic respiration. Anaerobic respiration is only about 20% as efficient as aerobic respiration and produces toxic compounds, which can damage tissues (Roberts et al. 1984, Neuman et al. 1996, Kozlowski 2002). Also, when stored carbohydrate supplies become limited, the plant no longer has resources to maintain organs, especially fine roots, which then die and decompose. This compromises the ability of the root system to absorb nutrients and water not only during inundation but after the shoot is reexposed to the atmosphere (Borman and Larson 2002, Kozlowski 2002, Banach et al. 2009). Lower root length per plant and higher average root diameter in the complete submergence treatment immediately after the 4-week inundation period are consistent with the hypothesis that fine roots die and decompose during 2- and 4-week inundation periods (Fig. 4). The death of the fine roots would increase average diameter. Likewise, both growth inhibition of roots and death of fine roots would decrease overall root length.

Longer duration of complete submergence resulted in a linear increase in plant mortality (Fig. 2). This again is consistent with the hypothesis that waning carbohydrate stores and accumulation of toxic compounds contributed to seedling death, since we would expect stored carbohydrates to be broken down over time as they are used to support respiration. Once carbohydrate stores are depleted, plants are unable to maintain normal metabolic activity and growth, eventually leading to plant death (Roberts et al. 1984, Neuman et al. 1996, Kozlowski 2002). It is unclear whether shorter inundation periods of 1 and 2 weeks showed a difference in mortality. Fine-scale determination of the effects of short-term submergence will require larger sample sizes.

Adding to previous knowledge of cottonwood inundation response, we found that survival, growth, and recovery of seedlings were adversely affected by warm water (Figs. 1, 3). Higher mortality with warm water inundation and lower mortality with cool water suggests that the slope of the average relationship given in Fig. 2 could be adjusted to model effects of different water temperatures. The detrimental effect of complete warm water inundation was likely due to higher respiration rates, which would have depleted carbohydrate stores faster than the lower respiration rates in cool water.
An alternative hypothesis of post-inundation stress caused by reexposure of leaves to high light conditions (Parolin 2009) is not consistent with the observations in our experiment. Most plants that did not survive were dead at the beginning of the recovery period; if post-inundation stress was important, mortality should have occurred later. Furthermore, results for root length per plant and average diameter (Fig. 4) suggest effects during and not after inundation. These results support the hypothesis that fine-root death and decay occurred during the inundation period. Nevertheless, analyses of soluble carbohydrates before and after inundation would be needed to fully assess the carbohydrate depletion hypothesis.

Inundation to the Soil Surface

Inundation to only the soil surface did not affect Fremont cottonwood seedling survival or biomass accumulation after recovery in this experiment. These results are consistent with Amlin and Rood's (2001) investigation of Populus cuttings, which found reasonable tolerance of 3 cottonwood species to 7-week soil inundation. Our results indicate that seedlings are likely to survive soil-surface inundation periods longer than 4 weeks, similar to cuttings, because we saw no significant detrimental effects to biomass of seedlings inundated to the soil surface compared to controls. Because the shoot system was still in contact with the atmosphere, the plants in our study were able to continue growth during the 4-week inundation period, with the result that their ending biomass was not significantly different from control plants (Fig. 3). Mature cottonwoods form shallow adventitious roots and lenticels along the stem to facilitate oxygen exchange under partially or fully inundated soil conditions (Pereira and Kozlowski 1977, Nilsen and Orcutt 1996). Although the seedlings in our experiment were too small to form lenticels, development of shallow root systems and aerenchyma in roots may have contributed to survival and growth maintenance of roots despite the soil-surface inundation. Future experiments could examine longer inundation periods for seedlings to determine if they have the same tolerance to flooding as the cuttings examined in Amlin and Rood's study (2001). They could also quantify the length of time seedlings can be exposed to soil-surface flooding without deleterious effects.

Applications

These findings can be used in developing river management strategies and riparian forest restoration plans. The results suggest that only seedlings with partial or complete shoot system submergence will show negative effects after short-term (2- to 4-week) inundation. Therefore, restoration efforts and river management should aim to develop new populations of Fremont cottonwood seedlings in areas that will experience only abbreviated shallow inundation. To the extent river stage can be managed, flow regimes that minimize inundation when seedling shoots are short and more vulnerable would promote survival. Inundation of longer than 2 weeks should be avoided to ensure good seedling survival, especially when warmer water temperatures prevail. The cool temperature treatment in this experiment approximated the in-stream summer temperatures of the Sacramento River in the reach between Red Bluff and Colusa. For this reach, water temperature is influenced mainly by daily air temperature. However, water temperature in other riparian systems may be significantly impacted by human activities or upstream riparian vegetation.

In other riparian systems, releases of warm water from reservoirs, as well as embayments that reduce flow rate, can result in warming of river water temperatures. Likewise, water withdrawals and channel engineering can warm river waters by reducing the assimilative capacity of the river for heat and by reducing the potential for groundwater buffering of temperature (Poole and Berman 2001). Riparian forests themselves can contribute to maintaining cooler water by providing shade or slowing heat exchange, thus reducing temperatures of the surface and groundwater adjacent to the stream (Larson and Larson 1997, Poole and Berman 2001). However, this temperature regulation is lessened as stream channels widen with increased sediment erosion from surrounding land and decreased flow power from damming, water diversion, and channel engineering. Wider channels cannot be as well shaded and insulated as narrower channels, and wide channels have less capacity for temperature buffering (Poole and Berman 2001). On the basis of our results, significant changes to water regime could increase water temperatures and potentially decrease seedling survival. If riparian forests
die and fail to regenerate, water temperatures could further increase. This negative feedback condition would not only accelerate riparian forest decline but also contribute to detrimental effects on associated aquatic communities (Baltz and Moyle 1984, Barton et al. 1985, Allan 1995, Poole and Berman 2001).

Results from this study, along with other field observations and laboratory experiments (Richards et al. unpublished data), have been used by the United States Bureau of Reclamation (USBR 2009) to evaluate potential riparian habitat establishment and river management strategies in this reach of the Sacramento River. Managers with the USBR have also applied similar modeling to assess riparian habitats for the San Joaquin River restoration program.

Conclusion

This study provides perspective on the ability of Fremont cottonwood seedlings to withstand short-term inundation, indicating that they have a reasonable tolerance for 1- and 2-week shoot inundation, especially in cool waters. Fremont cottonwood seedlings also appear remarkably resilient when river flows do not cover the aerial portion of the plant. Fremont cottonwood is instrumental as an early successional species, and its successful establishment provides a robust foundation for a healthy riparian ecosystem. Our examination of how Fremont cottonwood responds to several key characteristics of inundation provides useful insight and potential application to modeling semiarid riparian ecosystem processes and specifically ecosystem regeneration.

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