

RESEARCH ARTICLE

Riparian Seedling Mortality from Simulated Water Table Recession, and the Design of Sustainable Flow Regimes on Regulated Rivers

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Abstract

Seasonal water limitation exerts a strong ecological filter on stream communities in semiarid regions. For first-year riparian willow and poplar tree seedlings, desiccation from rapidly declining river flows can limit reproduction, especially on rivers in which flow regulation and land conversion have limited the amount of area available for recruitment. We investigated survivorship of first-year riparian seedlings to simulated river stage declines, focusing on the three dominant species in California's heavily regulated San Joaquin Basin: Fremont cottonwood, Goodding's black willow, and sandbar willow. Seedlings grown in mesocosms were subjected to water table decline rates typical in spring on unregulated and regulated rivers. We compared species' differences in survival time and fit the empirical data to accelerated failure time models that predicted time until death as a function of drawdown rate,

initial seedling size, and maternal line. We used Akaike information criteria to select the best model for each species. Water table decline rates ≥ 6 cm/day were lethal to all species. At an intermediate rate (3 cm/day) survival varied most among species (12–38%) and was highest for Goodding's black willow. Failure time models indicated no maternal effects on survival but that initial seedling size was important for cottonwood. Using these models, we simulated survivable flow scenarios on the Tuolumne River (CA) and assessed the survivability of actual flow releases in two representative years. This modeling approach shows promise for optimizing flow releases to restore pioneer riparian habitat on regulated rivers in some of the world's most water-limited regions.

Key words: environmental flow, *Populus*, river regulation, Salicaceae, *Salix*, seedling establishment, survival analysis, water table decline.

Introduction

For riparian plants in Mediterranean-climate ecosystems, water supply is a strong ecological filter on plant life history (Gasith & Resh 1999; O'Connor 2001; Stella 2005). This is particularly the case for willow and poplar trees (family Salicaceae), which are dominant species in many semiarid riparian ecosystems (Patten 1998). Given that seedling recruitment is dependent on floods and the availability of open seedbeds (Hughes et al. 2001), this life stage is the major demographic bottleneck for these species (Stromberg et al. 1991; Lytle & Merritt 2004). However, river regulation throughout the world's drought-prone regions has profoundly changed the natural flow regime

(Poff et al. 1997), resulting in reduced recruitment opportunities for native riparian species that, together, tend to favor species that are nonnative, xeric-adapted, and/or less tolerant to disturbance (Hughes 1990; Friedman et al. 1998; Johnson 1998; Shafroth et al. 2002; Sher et al. 2002). In light of projected increases in drought and human water demand in the world's Mediterranean-climate regions (Vorosmarty et al. 2000; Wetherald & Manabe 2002), understanding the specific processes governing the establishment of riparian seedlings is critical for forecasting the future of streamside forests in these areas and for designing flow regimes that minimize the disruption of natural recruitment processes (Patten 1998; Jenkins & Boulton 2007; Valladares & Gianoli 2007; Palmer et al. 2008; Rood et al. 2008).

Water table manipulation experiments have been used to simulate dynamic riverine environments in order to study the effects of seasonal moisture stress on seedling survival and growth (Mahoney & Rood 1992; Segelquist et al. 1993; Hughes et al. 1997; Horton & Clark 2001). However, most studies to date focused on measuring riparian seedling survival under a given moisture regime for a fixed period of time. A more relevant question to ask is "What is the cumulative impact of water drawdown on survival time?" Furthermore,

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few studies evaluate how flow regimes differentially affect survival of native species within the same community, which has the potential to shift composition and dominance over time (but see Dixon 2003; Francis et al. 2005; Renofalt et al. 2007).

In this study, we quantified survival of riparian tree seedlings across a range of simulated flow recession rates typical of both free-flowing and regulated rivers in California's San Joaquin Basin, a Mediterranean-climate region in which the natural discharge on all major rivers is dominated by spring snowmelt (Peterson et al. 2000). Our research focused on the three most common native pioneer species that dominate riparian woodlands throughout California and much of the semiarid western United States: *Populus fremontii* (POFR) S. Watson ssp. *fremontii*, (Fremont cottonwood); *Salix gooddingii* (SAGO) C. Ball (Goodding's black willow); and *Salix exigua* (SAEX) Nutt., (sandbar willow). POFR and SAGO are trees, and SAEX generally grows as a shrub. As the largest, fastest growing, and most cosmopolitan riparian plants, they are foundational species (sensu Ellison et al. 2005) for terrestrial and in-stream ecosystems, yet they are also vulnerable to long-term changes to flow regime (Scott et al. 1999; Rood et al. 2003a; Williams & Cooper 2005). Our approach in this study was to measure seedling survival in open-air mesocosms where the rate of soil moisture decline was experimentally modulated. Our goal was to evaluate regulated flow regimes on seedling survival potential and to design flow release scenarios that maximized survival for the three species. To accomplish this goal we sought to: (1) establish baseline differences in survival among the dominant woody species of a riparian ecosystem; (2) compare species' responses to imposed drought stress; (3) fit the empirical data to accelerated failure time (AFT) models that predicted time until death as a function of drawdown rate and individual covariates including initial seedling size and maternal line; and (4) use the models to design environmental flow prescriptions beneficial to seedling establishment.

Methods

Study Environment and Experimental Design

The study was conducted outdoors at the University of California's Russell Research Station in Lafayette, CA (37°55'03.77" N, 122°09'28.76" W) in late summer 2002. The region averages 52 cm annual rainfall occurring almost exclusively from late October through April; no precipitation occurred during the study. Temperature during the study period averaged 18°C (range 4–44°C); mean midday (10 AM–2 PM) vapor pressure deficit was 3.02 kPa. The plants used in the study were grown from seed collected in early summer from 7 to 10 females per species along the lower Tuolumne and San Joaquin rivers in California. Seed trees were distributed among three sites per species and at distances that ensured that none were clones of each other. Seeds were separated from catkins and refrigerated with desiccant until planting. The substrate used in the study was excavated from a sandbar on the Tuolumne River representative of those on San Joaquin Basin alluvial rivers.



Figure 1. The experimental setup consisted of 20 tanks with seedlings grown in PVC tubes suspended within each tank (inset). Four tanks were randomly assigned to each of five drawdown treatments. Each tank contained individuals of all species tested.

The substrate median particle size was 0.6 mm and 85% of the sample was classified as medium or coarse sand (0.25–1 mm).

The experimental mesocosms consisted of 20 steel, cylindrical tanks with open tops and a drain outlet at the bottom (Fig. 1). Each tank was plumbed with a flexible discharge tube that was elevated and lowered to effect changes in the tank's water level. Four tanks were randomly assigned each to one of five drawdown treatments (1, 3, 6, and 9 cm/day and a stable water table, referred to as the control) that spanned a wide range of spring water surface changes observed along rivers in the San Joaquin Basin and other semiarid regions (Shafroth et al. 1998; Stella 2005). Each treatment tank contained 32–41 seedlings with roughly equal numbers of all three species, except for the 9-cm/day tanks, which contained 20–25 seedlings. No SAEX seedlings were assigned to the 9-cm/day treatment due to a shortage of viable plants. Sample sizes for all species and treatment combinations ranged from 47 to 58 seedlings ($n = 663$ for the overall survival analysis). During planting, seedlings from the various seed trees were distributed as evenly as possible among the tanks and treatments in order to eliminate confounding effects and to allow testing for maternal influence on survival.

Seedlings were grown individually in polyvinyl chloride tubes, 125-cm long by 3.2 cm diameter, packed with sand and suspended within the tanks, which were 125-cm deep by 61 cm diameter (Fig. 1). Growth tubes were spaced in an approximately 8 × 8-cm grid to prevent light competition with neighbors and thereby maintained treatment effects independent of plant density. In late July, seeds were planted in the growth tubes and for 3 weeks, tubes were shaded with 30% shade cloth and water levels were maintained at 10 cm below the soil surface to facilitate germination. Drawdown began on August 22; this is referred to as day 0 of the experiment. Tank water levels for the control groups remained at 10 cm below the soil surface, and water levels for all treatment groups decreased from this datum. Water was added as necessary to compensate for daily evaporation. When water level treatments dropped below the depth of the tank, the drain tubes were cut to ensure that there was no residual moisture available. This event occurred on days 39, 20, and 13, respectively, for the 3, 6, and 9-cm/day treatments. To evaluate the availability of moisture from the unsaturated zone, we measured the capillary fringe height in 20 tubes at the beginning of the experiment.

Data Collection

For 50 days, we examined seedlings daily and recorded the ones that had died (indicated by brown leaves and brittle stems). At days 18 and 49 during the experiment, 109 seedlings (total, distributed among all experimental groups) were randomly selected and harvested to provide intermediate measures of biomass and physiological function (Stella 2005). The harvested plants were considered censored individuals in the survival models (see below). To control for unintended effects of seedling size on mortality, we tested differences among treatment groups in seedling height just prior to drawdown using analysis of variance. There were no significant height differences among groups ($p > 0.05$ in all cases) or nested tank effects prior to treatment.

Seedling Survival and Baseline Hazard Analysis

We used the daily mortality records to analyze the differences in seedling survival between species and treatment groups. Survivorship over time was calculated for each group using Kaplan–Meier nonparametric estimations to account for censored observations (Parmar & Machin 1995). From these distributions, we calculated final percent survival and median survival time in days with confidence limits for the medians using the Greenwood method (Parmar & Machin 1995). Differences between survival distributions were tested using the Mantel–Haenszel log-rank test (Lee & Wang 2003). All statistical tests were conducted in S-PLUS (Version 6.1, Insightful Corporation, Seattle, WA, U.S.A.). In order to evaluate changes in mortality rate over time, we plotted the hazard rate for all seedling species and treatment groups. The hazard rate is defined as the change in instantaneous death rate for seedlings alive at any specific time (Zens & Peart 2003) and was derived from the empirical seedling survival data.

AFT Model

We analyzed predictors of density-independent mortality of the seedlings using a parametric AFT model (Kalbfleisch & Prentice 2002). The AFT model accounts for censored data (e.g. missing individuals and unobserved deaths) and is particularly useful for predicting when a cumulative stress (such as drawdown rate) results in mortality, not just whether mortality occurs over a fixed interval. Survival time distributions were specified for each species using fits to the data and graphical analysis of the empirical hazard functions (Harrell 2001).

We used the AFT model to determine the effect of drawdown rate on seedling survival time, as well as to account for potential influence from two biological covariates: seedling size at start of drawdown and maternal line (because seedlings were grown from a limited number of female seed trees). For model selection, we took an information-theoretic approach, using Akaike information criterion (AIC) to compare a suite of competing models (Burnham & Anderson 2002). The best models were selected using the lowest AIC values in a candidate set, and alternate models were assessed using differences from the minimum AIC (AIC_{diff}) and associated Akaike weights (w_i). The Akaike weight for model i is calculated

$$w_i = \frac{e^{-0.5 \times AIC_{diff_i}}}{\sum_{p=1}^n e^{-0.5 \times AIC_{diff_p}}}$$

Because all w_i sum to unity, each represents an approximate probability that a candidate model is the best of all those being compared (Burnham & Anderson 2002).

For each species, eight AFT models were considered: a null model with only intercept and scale parameters; single factor models each for drawdown rate (as a continuous variable), initial seedling height and maternal line; additive models for each binary combination of factors; and a model with all three factors. AIC values and Akaike weights were computed for all alternatives and compared to select the minimum adequate model. We analyzed parameter estimates for all models in which AIC difference values were less than 2 in order to determine whether model-weighted averaging of parameter estimates was warranted (Burnham & Anderson 2002).

For the best model for each species (i.e. those with the lowest AIC values), we generated response surfaces of seedling survival time as a function of drawdown rate and duration. As a check on our models, we compared the model projections to the empirical survival times estimated from Kaplan–Meier nonparametric distributions for specific survival quantiles.

Analysis of Flow Regime Effects on Survival

We used the results from the mesocosm experiment to evaluate regulated versus unregulated flow regimes within the San Joaquin River with regard to potential effects on first-year seedling survival. As a case study, we used the lower Tuolumne River near Modesto, in the reach containing the

source trees for the mesocosm experiment. To compare regulated and unregulated regimes, we obtained daily discharge data for the LaGrange gauge (USGS #11289650) downstream of New Don Pedro Dam and reconstructed unimpaired daily flow modeled for that location based on reservoir inflows (Turlock Irrigation District).

We analyzed the two discharge series for the effects of flow regulation on three hydrologic characteristics important for willow and cottonwood establishment: seasonal streamflow timing, snowmelt runoff volume, and rate of spring flow recession. Flow regulation effects on streamflow timing were assessed using the temporal centroid of streamflow (CT) (Stewart et al. 2004), which is the annual date when 50% of a water year's cumulative volumetric streamflow has been exceeded. Changes in timing were quantified as the difference in days between regulated and unregulated CT. Modification of the snowmelt runoff volume was calculated as the ratio of the regulated-to-unregulated total daily runoff from April 1 to August 31.

To assess the changes in the spring stage recession rate, we compared the rates of stage decline between regulated and unregulated conditions in the six highest flow years between 1971 and 2004: 1982, 1983, 1986, 1995, 1996, and 1998. We used high flow years in our scenarios because high flows create the environmental conditions for widespread, successful seedling recruitment, including survival from subsequent floods (Stromberg et al. 1993; Rood et al. 1998). The regulated and computed unregulated discharge for the six high-flow years were converted to elevation above summer baseflow using the stage–discharge relationship at Modesto, CA (USGS gauge #11290000, California Data Exchange Center). Change due to regulation was calculated as the ratio of the regulated to unregulated recession rates for the final extended (i.e. ≥ 9 days in duration) flow decline of spring.

In order to illustrate how the AFT model can be applied to design regulated flow regimes that are survivable for seedling cohorts, we designed spring hydrographs for the Tuolumne River in two water years (2004, a low-to-normal flow year and 2006, a high-flow year). In these designs, we maintained the same seasonal flow volume but modified the onset date and rate of flow recession. Using the best AFT models developed

for each species, we calculated the steepest recession rate that would still allow survival of 25% of the cohort after 60 days, a typical recession period under unregulated conditions. Daily flow rates were computed using the following criteria: (1) the total spring discharge volume (March 1 to July 10) was set equal to actual releases in each year; (2) flow recession was synchronized with the start of seed release as observed on in the field from 2002 to 2004 (Stella et al. 2006); (3) river stage declined monotonically at the AFT-modeled rates to summer baseflow levels (i.e. mean annual stage from July 11 to September 11); and (4) all conversions between river stage and discharge used the USGS Modesto rating curve.

Results

Seedling Survival

Drawdown rate had a strong influence on seedling mortality. Final survival was close to zero for all seedlings subjected to rates ≥ 6 cm/day. Among the three species, final survival ranged 12–38% for the 3-cm/day group, 64–68% in the 1-cm/day group, and 66–72% in the control groups (Table 1; Fig. 2). Mantel–Haenzel log-rank tests for differences between the control and 1-cm/day rate indicated no difference for any species.

Of the three species, SAGO had consistently higher survival across the drought gradient (Table 1; Fig. 2). Cohort survival at day 50 was 10–20% greater for SAGO than the other species in the control, 1- and 3-cm/day groups, corresponding to a 5–10 day increase in seedling survival time. Significant differences in survival time at 3 cm/day for POFR (34 days) and SAGO (45 days) were indicated by nonoverlap of 95% confidence intervals. SAEX median survival at this drawdown rate (35 days) was not significantly different from either of the other species.

The hazard rate, the instantaneous probability of dying, was relatively constant throughout the study for the control and 1 cm/day rates (Fig. 3a). However, for the three more stressful treatments, the hazard rate increased abruptly early in the experiment (Fig. 3b–d). Though temporal patterns in the hazard rate were similar among species, the onset of high mortality

Table 1. Final seedling survival (proportion of original cohort) and median survival time (days) for all species and treatment groups estimated using the Kaplan–Meier method for censored data.

Drawdown Rate (cm/day)	50-Day Survival, Proportion of Initial Cohort			Median Survival, days (95% Confidence Limits) ^a		
	POFR	SAGO	SAEX	POFR	SAGO	SAEX
0	0.72	0.88	0.66	NA	NA	NA
1	0.68	0.84	0.64	NA	NA	NA
3	0.12	0.38	0.26	34 (32–37)	45 (41–NA ^b)	35 (21–42)
6	0	0.05	0.02	29 (21–31)	34 (29–35)	25 (21–34)
9	0.03	0	Not tested	19 (16–22)	21 (18–28)	Not tested

^a Median survival time are shown for groups with final survival ≤ 0.5 ; median survival was not calculable for survival rates greater than 0.5. Simultaneous 95% confidence intervals were calculated using the Greenwood variance method; survival times are significantly different from each other if the confidence limits do not overlap. SAEX was not tested at the 9-cm/day rate.

^b Indicates that the upper confidence limit includes the end of the experiment period (day 50).

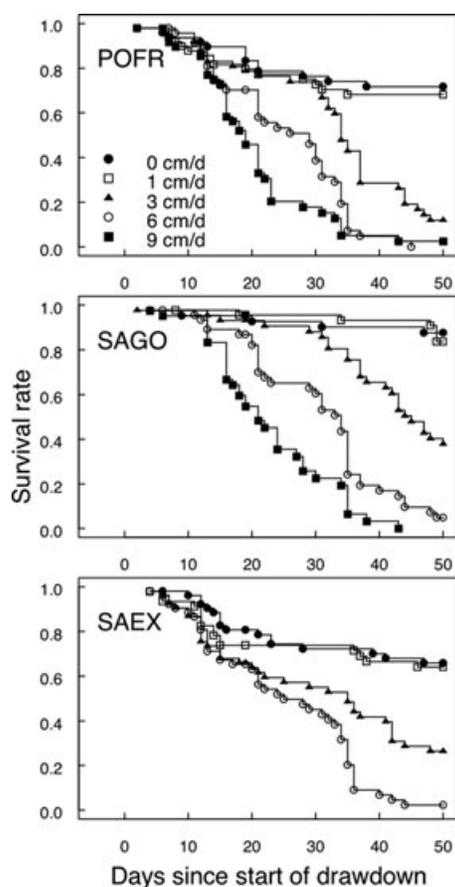


Figure 2. Seedling survival by species and treatment level. Survival was estimated for censored data using the Kaplan–Meier method.

was steeper and occurred sooner for POFR than the willows, indicating an increased sensitivity to drought stress. SAGO was the most drought-tolerant, showing a milder and later response across the stress gradient. The onset of high mortality did not have a consistent relationship to when the water levels reached the bottom of the tanks and the drain tubes were cut (Fig. 2). The height of the capillary fringe measured at the beginning of the experiment was 43.5 ± 3.8 cm (mean \pm 1 SE) above the saturated zone; therefore, plants had access to residual moisture for some time after the tanks were drained.

Survival Modeling

For all species, the empirical survival data were robustly approximated using an AFT regression model with the distribution of seedling mortality dates described by a Weibull function (Kalbfleisch & Prentice 2002). Drawdown rate was a factor in all the best models, which were those with the lowest AIC value (Table 2). Initial shoot height was also important and included in the best model for POFR, and second-best models for SAGO and SAEX. Maternal origin was not a factor in any of the top models, indicating a negligible effect on mortality. Parameter estimates for the best models (Table 3) were used to develop response surface plots (Fig. 4). Differences in

parameter estimates among the top ranked models were negligible, precluding the need for model averaging (Burnham & Anderson 2002).

Response surface plots of the AFT models illustrate different species' mortality patterns (Fig. 4). The SAGO surface has the slowest mortality response to drawdown rate ≤ 3 cm/day, with sharp increases in mortality at higher drawdown rates. Modeled mortality quantiles were in good accordance with Kaplan–Meier point estimates for the drawdown rates tested, particularly for SAGO. For all species, the 95% confidence limits bounding the median mortality point estimates contained the AFT-modeled median quantile. Simulations using the best-fit AFT model for each species predict that 25% survival after 60 days of drawdown is achievable at a rate of 2.25 cm/day for POFR, 3.5 cm/day for SAGO, and 2.75 cm/day for SAEX.

Influence of Flow Regime on Survival

Based on our comparison, regulation on the Tuolumne River had led to a shift to earlier flow releases, a substantial reduction in spring runoff volume, and an increase in the final spring flow recession rate. Since closure of New Don Pedro Dam in 1971, the Tuolumne River's annual spring–summer runoff volume was reduced 85% (median; range 34–91%) compared to unregulated inflow, and the CT shifted earlier by 62 ± 43 days (mean \pm SD). Currently, half of the annual regulated runoff occurs by February 25, compared to April 28 under a natural flow regime. In all years except 1998, spring regulated discharge dropped to baseflow levels (approximately $25 \text{ m}^3/\text{s}$) by mid-May, compared to mid-July in the unregulated flow case. In the six highest flow years, regulated river stage declines were $211 \pm 188\%$ (mean \pm SD) steeper than under-unregulated reference conditions (Fig. 5). Modifications from the reference conditions ranged from a 415% steeper in 1982 to -26% in 1998, the only year with a slightly more gradual rate compared to reference conditions.

The AFT model simulations indicate that in 2004, the spring flow recession from reservoir releases was gradual enough to support $\geq 25\%$ survivorship of the seedling cohort for all three species (Fig. 6a). In that year, stage declines were approximately 2.20 cm/day between April 14 and June 10; these were all less than the lowest modeled rate (2.25 cm/day for POFR). In 2006, the spring flow pulse attenuated much more quickly (averaging 6.23 cm/day between May 18 and July 18) and included a period of high stage fluctuations in June (Fig. 6b). Flow stage declined an average of 11.65 cm/day during the last 4 weeks of this period, far exceeding the survival threshold for any species (Fig. 2). The total stage drop during the spring recession was approximately 1.7 m in 2004 and 4.5 m in 2006. It is important to note that these absolute estimates of stage change are based on a single stage–discharge relationship established at a flow gauge, and that stage changes experienced in the field will vary with geomorphic setting.

Field surveys in these two years showed large interannual differences in seedling density and composition among the three riparian species. In both years, a series of transects were surveyed on 8–11 sandbars at the end of summer to

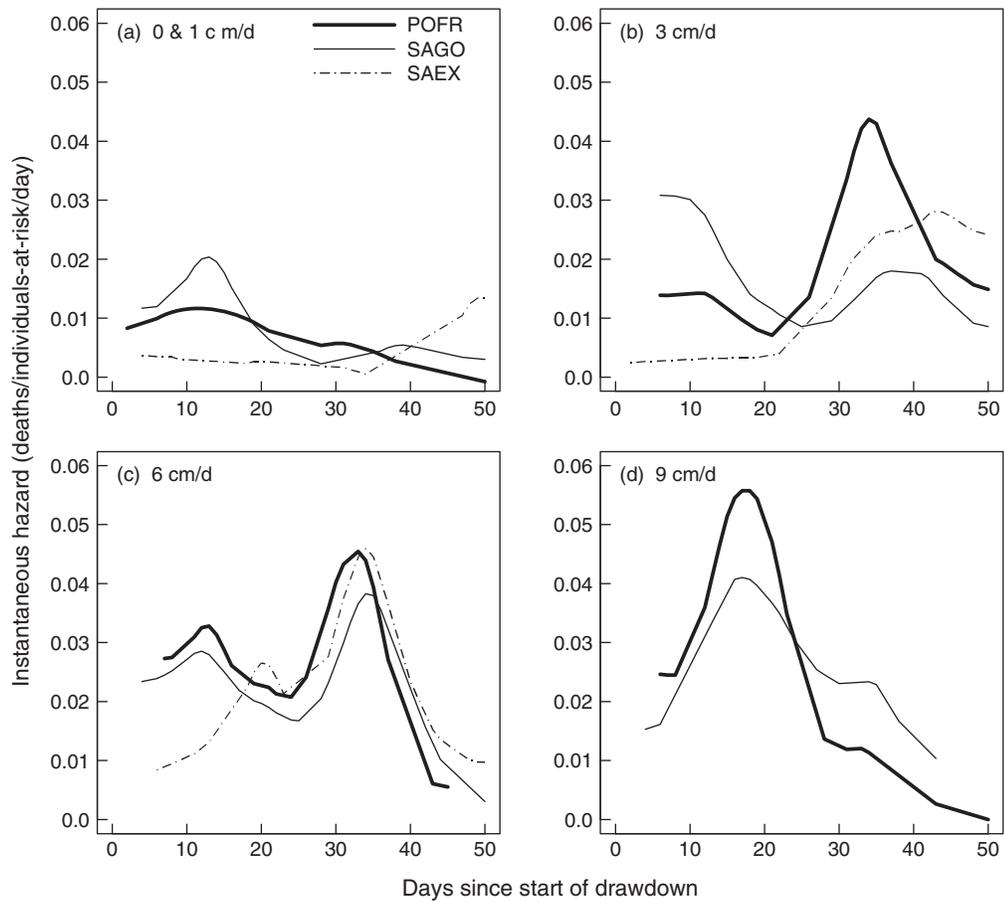


Figure 3. Hazard rate, or per capita daily mortality risk for live seedlings, by species and experimental drawdown rate. Panels indicate different experimental drawdown rates: (a) 0 and 1 cm/day groups pooled (a); (b) 3 cm/day; (c) 6 cm/day; and (d) 9 cm/day. Curves were plotted using a cubic-B spline smoothing function applied to the negative slope of the Kaplan - Meier survival curves (predict.smooth.spline function, Splus). The timing of the peak mortality pulse varies for each group and decreases once many of the susceptible seedlings are dead.

Table 2. Selection criteria for AFT models of seedling mortality as a function of drawdown rate and plant initial size and maternal line. Eight models were considered for each species; the three best models (i.e., those with the lowest AIC values) are presented. Models with AIC difference (AIC_{diff}) values less than 2 are equally parsimonious as the best models.

Species ^a	Model Rank	K^b	AIC ^c	AIC_{diff}^c	AIC Weights ^c	Model Factors ^d
POFR	1	4	1,336.06	0	0.96	rate + shoot.init
(N=239)	2	10	1,343.53	6.67	0.03	rate + shoot.init + mother
[87]	3	3	1,350.08	14.09	0.00	rate
SAGO	1	3	996.40	0	0.72	rate
(N=219)	2	4	998.41	1.93	0.27	rate + shoot.init
[107]	3	10	1,008.58	11.23	0.00	rate + mother
SAEX	1	3	1,090.50	0	0.59	rate
(N=202)	2	4	1,091.30	0.72	0.41	rate + shoot.init
[88]	3	12	1,104.56	12.53	0.00	rate + mother

^a Total number of observations are in parentheses, and number of censored observations are in brackets.

^b K , number of model parameters. In addition to the parameters listed in the last column, each model includes estimates for the intercept and Weibull scale parameters.

^c AIC, Akaike information criteria; see text for explanation of AIC difference values (AIC_{diff}) and AIC weights.

^d Model factor codes: "rate," drawdown rate; "shoot.init," initial shoot height; "mother," maternal line.

quantify seedling density and composition (Stella 2005). For both 2004 and 2006, approximately 12% of the 1-m² plots surveyed (744 in 2004 and 1,320 in 2006) contained three or more seedlings of POFR, SAGO, or SAEX. In 2004, a

total of 25,747 seedlings were found or 35/m² searched. Of these, 16% (4,171) were POFR and 86% (21,517) were SAGO. In 2006, the year with the much steeper water table decline, 7,139 seedlings were found or 5.4/m² searched. The 30 POFR

Table 3. AFT model coefficients. The models predict the logarithm of seedling survival time (in days) as a function of drawdown rate and, for some models, initial shoot height (in mm). Models include an intercept (or location) parameter and a scale parameter for the Weibull distribution. For SAGO and SAEX, coefficient values for the best respective model (model 1) are very similar to the second best (model 2). Values in parentheses are lower and upper 95% confidence intervals for the parameter estimates.

Species	Model Rank ^a	AIC Weight	Intercept ^b	Rate Slope ^b	Shoot Height Slope ^b	Scale Parameter ^c
POFR	1	0.96	3.79 (3.53–4.05)	-0.13(-0.16 to -0.11)	0.030 (0.015–0.046)	0.51
SAGO	1	0.72	4.51 (4.34–4.68)	-0.15(-0.17 to -0.12)	NA	0.38
	2	0.27	4.49 (4.29–4.70)	-0.15(-0.17 to -0.13)	0.0028 (-0.019 to 0.024)	0.38
SAEX	1	0.59	4.41 (4.18–4.64)	-0.19(-0.24 to -0.14)	NA	0.66
	2	0.41	4.30 (4.02–4.59)	-0.19(-0.25 to -0.14)	0.048 (-0.038 to 0.13)	0.66

^a Model rank referenced from Table 2.

^b Parameter estimate with lower and upper 95% confidence limits in parentheses.

^c The scale parameter is estimated for the Weibull distribution of failure times.

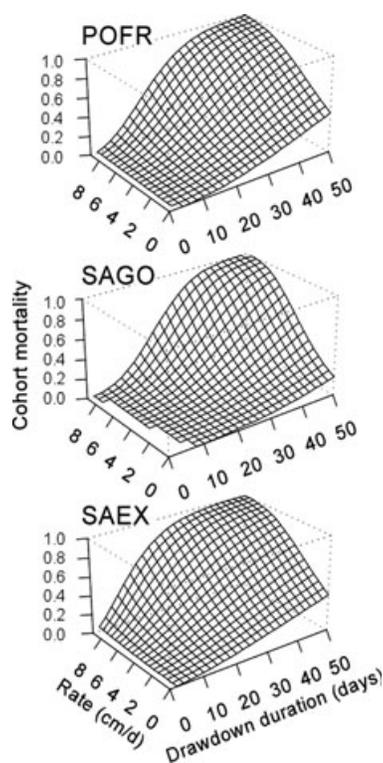


Figure 4. Seedling mortality predictions generated using a parametric AFT regression model with a Weibull hazard distribution. The predicted response surface is a function of rate and duration of groundwater stage decline.

seedlings found in all the surveys that year comprised less than 1% of the total. The 2006 cohort was composed of 96% SAGO and 3.8% SAEX. The 7-fold difference in interannual seedling density is consistent with the analysis of flow suitability for recruitment (Fig. 6), as is the lack of successful recruitment in 2006 by POFR, which is the species with the lowest tolerance for water table recession.

Discussion

In this study, simulated river flow recession exerted a strong control on riparian seedling survival. Across the treatment

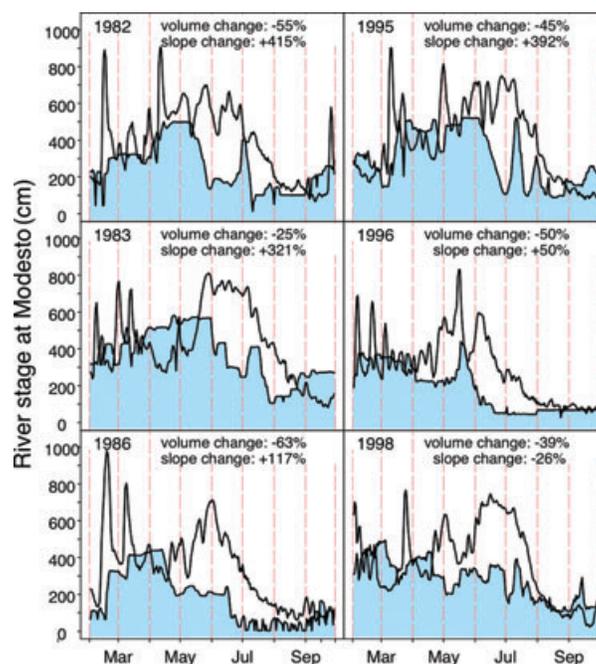


Figure 5. Computed river stage for the lower Tuolumne River in the six years between 1971 and 1994 with highest spring runoff volumes.

Regulated stage (blue polygons) was derived from USGS flow data (gauge #11289650); unregulated stage (black lines) uses reconstructed unimpaired flow from the Turlock Irrigation District. River stage was calculated using the stage–discharge relationship at Modesto (USGS #11290000). “Volume change” indicates the difference in spring runoff volume (April 1 to August 31) between regulated and unregulated flow series; “slope change” indicates the difference in stage recession rates for the final flow decline in spring.

gradient, there was a marked shift in the impact of water table recession on seedling survival, from no increase above controls for ≤ 1 cm/day to full mortality at ≥ 6 cm/day. Intermediate rates yielded the most varied response among species, with SAGO survivorship 50% greater than SAEX and more than 300% greater than POFR. These results imply that some river drawdown scenarios, whether under natural or regulated flow conditions, will induce species-level differences in recruitment success. If imposed for sufficient duration and/or frequency,

these regimes have the potential to influence community structure.

Experimental Versus Field Conditions

In general, the absolute rates of survival observed in this mesocosm study were higher than reported in field studies (Stromberg 1997; Sher et al. 2002; Stella 2005). Admittedly, the experimental setup greatly simplified field conditions in important ways, including the protected and somewhat later germination period, the monotonically decreasing water table compared to real rivers, differences in water quality, and the absence of other mortality sources such as herbivory and post-establishment flow scour. Perhaps the largest difference is the absence of inter- and intraspecific competition; however, excluding the confounding effects of competition was a specific objective of the experiment.

Working against these presumably protective experimental factors, the limited mesocosm depth (125 cm) may have induced somewhat higher mortality than imposed by field conditions. Because the water table reached the bottom of the tanks at days 39, 20, and 13 for the 3, 6 and 9-cm/day groups, respectively, this would presumably dry out the approximately 40-cm deep capillary zone prematurely compared to field conditions. However, the timing of greatest mortality, as noted by a sharp increase in the hazard rate, occurred after the drain tubes were severed only for the 6-cm/day treatment. For the 3 and 9-cm/day treatments, peak mortality had either already occurred or was well underway when the tanks dried out. The peaks in seedling mortality, therefore, imply threshold events driven primarily by other factors, such as the decoupling of root growth from the capillary fringe and/or decreased physiological function under sustained summer vapor pressure deficits (Stella 2005).

Species-Level Differences and Community Implications

Despite differences between the mesocosm experiment and field conditions, we would expect relative differences in survival to be maintained in the field because all three species were tested similarly. In this experiment, a moderate draw-down rate of 3 cm/day resulted in the largest survival differences between species (SAGO = 38% vs. POFR = 12%). As a result, river level changes near this rate (2–4 cm/day) during spring may have the largest effect on species composition and distribution in riparian zones, favoring willow establishment over POFR. Greater SAGO survivorship was somewhat unexpected given that results from previous studies (van Splunder et al. 1996; Amlin & Rood 2002) found consistently higher survival of *Populus* seedlings relative to *Salix* along experimental water stress gradients. In field settings, however, some studies indicate higher vulnerability of POFR seedlings to water stress. Sher et al. (Sher et al. 2002) found summer mortality of POFR to be greater than SAEX on the Rio Grande in New Mexico. In a study of seedling demography following flooding on the Hassayampa River, AZ (Stromberg 1997), mortality for POFR was greater than SAGO, though

initial densities were higher as well. The field surveys we conducted in 2004 and 2006 are consistent with a higher vulnerability by POFR, because relative densities of this species were less than 1% in 2006, the year with the steeper flow recession (Stella 2005). Factors other than flow recession rate may have contributed as well; for example, the large flow increase in June 2006 that followed an initial May decline may have scoured POFR seedlings that had established previously.

Some physiological studies also support the case that particular tree-form willows are more drought-tolerant than POFR. Physiological research done in conjunction with this study showed higher seasonal water use efficiency by SAGO seedlings compared to POFR (Stella 2005). In another study, mature SAGO trees had better physiological recovery than POFR to drought stress caused by seasonal water table variation (Horton et al. 2001). Busch and Smith (1995) found that on the Colorado River, *Salix* trees had greater water- and salinity stress tolerance than POFR; they also noted a corresponding preponderance of senescent *Populus*, but not *Salix*, individuals along that river. This greater sensitivity to drought by POFR may partly explain why it is a less dominant component of riparian communities in California's San Joaquin Basin, where precipitation is lower and summer vapor pressure deficits higher than in the Sacramento River Basin to the north (Griffen & Critchfield 1972).

Considerations for River Management and Habitat Restoration

Management of rivers in the San Joaquin Basin for flood control, irrigation, and hydropower has a disproportionately large impact on spring snowmelt runoff, the critical period for recruitment of pioneer trees (Mahoney & Rood 1998; Stella et al. 2006). Since the completion of the New Don Pedro Dam on the Tuolumne River in 1971, spring flow volume has been drastically reduced and the timing of bulk flow has been shifted to earlier in the year. Furthermore, controlled releases result in more rapid river stage drops in high-flow years compared to unregulated flow, which greatly exceeds tolerable levels by new germinants. Taken together, conditions for successful initiation of willow and cottonwood cohorts are less frequent and more perilous. Critically, these high-flow years present the best opportunities for seedling recruitment both ecologically and from a river management perspective, because runoff exceeds human irrigation demand and is available for streamflow-driven natural processes (e.g. "environmental flow releases" for sediment transport, salmonid rearing, and/or tree recruitment).

The results of the present study are directly applicable to designing flow releases in the San Joaquin Basin and along other regulated rivers in semiarid regions to promote large-scale habitat restoration and influence plant community dynamics (Bovee & Scott 2002; Rood et al. 2003b). For example, we would expect POFR mortality to be high at all but mild rates of water table decline, whereas SAGO seedlings would be more successful under more dynamic hydrologic conditions (Busch & Smith 1995). Given this region's dry climate, a sustained rate of 2.5 cm/day, commonly cited as

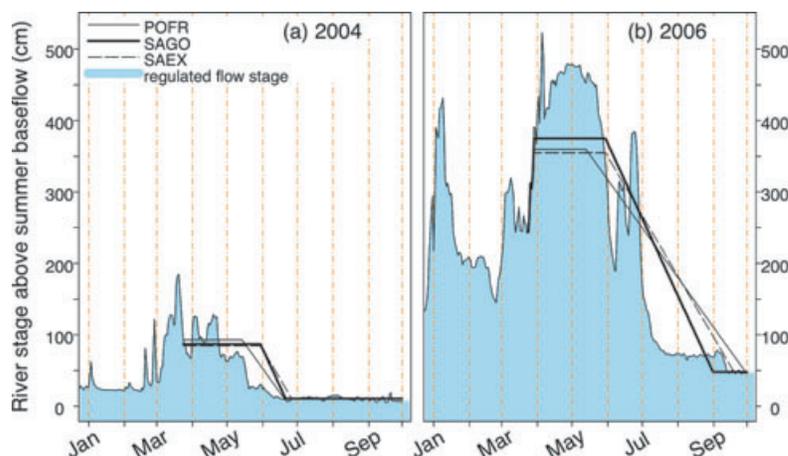


Figure 6. River stage and synthetic hydrographs for the Tuolumne River, CA (Modesto gauge, USGS #11290000) in (a) 2004, a low-to-normal flow year; and (b) 2006, a high-flow year. Daily average gauge height data were translated into river stage above summer baseflow, which was computed annually as average flow from July 11 to September 11. Sloped lines indicate stage declines maintained at each species' 25% survival rate (see text). Stage declines begin during the peak seed release for each species (Stella et al. 2006) and attenuate at summer baseflow levels. The total discharge volumes from March 1 to July 10 for all curves are equal within each year.

ideal for poplar species (Mahoney & Rood 1998), may be too high for POFR trees, whose seedlings have lower survivorship than willow. However, the threshold responses noted in the mortality data and the failure time model results suggest that shorter (approximately 1 week) periods of rapid drawdown may be sustainable if followed by stable flows that allow recharge of the capillary fringe.

Our survival modeling approach can be adapted to other semiarid regions, which are under severe water demand worldwide by both the ecosystem and human users (Gasith & Resh 1999; Arthington et al. 2006). Regeneration of pioneer woody plants with similar life history requirements to those in the present study is a restoration or management issue in riparian zones in southern Europe (Hughes et al. 2001; Dufour & Piegay 2008), Australia (Stokes & Cunningham 2006), and Southern Africa (Hughes 1990; Pettit & Naiman 2006), among other regions. Flow releases for ecosystem rehabilitation in semiarid regions will need to consider the limiting factors for sensitive organisms (Gasith & Resh 1999; Jenkins & Boulton 2007; Valladares & Gianoli 2007), increasing human water demand and climate change projections of reduced precipitation in the subtropics (Vorosmarty et al. 2000). To ensure more frequent and widespread establishment of riparian trees, flow prescriptions need to occur at the right time to coincide with dispersal and at an appropriate rate of change to ensure seedling survival. Projections of stage changes will need to consider both the biological thresholds of target species and the variation in channel morphology (and therefore stage–discharge relationships) within geomorphically active reaches where seedlings typically establish; these are generally dissimilar to USGS gauge locations (as used in the present study), which are selected for their relative stability. Where extractive water demands are high, relaxing the operational constraints on flow timing without increasing overall volume may be the most feasible

option. Wet years such as 2006 represent best-case scenarios for environmental flow releases; the proportion of runoff diverted for irrigation in dry years is typically much greater. Altering releases may pose challenges to a water management infrastructure that is already taxed with multiple goals (e.g. flood control, irrigation, hydropower), and that will experience further operational constraints with projected reductions in snowpack volume and higher runoff earlier in winter (Vicuna et al. 2007; Cayan et al. 2008). However, determining the critical needs of foundational species in these water-limited ecosystems is an important step toward making conservation efforts technically and economically feasible for the long term.

Implications for Practice

- Seasonal water table recession in semiarid regions can limit the success of riparian trees, particularly for first-year willow and poplar seedlings that require flooding to germinate but are vulnerable to desiccation during prolonged or rapid flow recession in late spring.
- Mesocosm experiments that test flow recession effects on seedling survival are useful in controlling for potentially confounding mortality agents such as resource competition, herbivory, or scour. Regional or reach-specific factors such as local species, substrate size, and climate need to be considered in the design of experiments.
- Abrupt drops in flow stage (≥ 6 cm/day sustained over several weeks) are generally lethal to willow and poplar species, including those native to California's Central Valley. Regulated flow regimes in this region increase the rate of flow recession beyond this threshold, greatly reduce overall runoff volume, and constrain higher releases to winter and early spring, prior to seed dispersal.

- Experimental data can be extended via survival and failure time models adapted from engineering applications to set restoration targets (e.g., 25% survival after 60 days) for designing ecologically beneficial flow releases. This approach results in quantifiable predictions, including error estimates, which can be used to gauge the cost of designing effective ecological flow regimes and to measure the success of specific restoration actions.

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