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PHYSIOLOGICAL ECOLOGY - ORIGINAL PAPER

# How do riparian woody seedlings survive seasonal drought?

**John C. Stella · John J. Battles**

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**Abstract** In semi-arid regions, a major population limitation for riparian trees is seedling desiccation during the dry season that follows annual spring floods. We investigated the stress response of first-year pioneer riparian seedlings to experimental water table declines (0, 1 and 3 cm day$^{-1}$), focusing on the three dominant cottonwood and willows (family Salicaceae) in California's San Joaquin Basin. We analyzed growth and belowground allocation response to water stress, and used logistic regression to determine if these traits had an influence on individual survival. The models indicate that high root growth (>3 mm day$^{-1}$) and low shoot:root ratios (<1.5 g g$^{-1}$) strongly predicted survival, but there was no evidence that plants increased belowground allocation in response to drawdown. Leaf $\delta^{13}$C values shifted most for the best-surviving species (net change of +3.5 per mil from −30.0 ± 0.3 control values for Goodding's willow, *Salix gooddingii*), implying an important role of increased water-use efficiency for surviving water stress. Both *S. gooddingii* and sandbar willow (*S. exigua*) reduced leaf size from controls, whereas Fremont cottonwood (*Populus fremontii*) sustained a 29% reduction in specific leaf area (from 13.4 to 9.6 m$^2$ kg$^{-1}$). The functional responses exhibited by Goodding's willow, the more drought-tolerant species, may play a role in its greater relative abundance in dry regions such as the San Joaquin Basin. This study highlights the potential for a shift in riparian forest composition. Under a future drier climate regime or under reduced regulated river flows, our results suggest that willow establishment will be favored over cottonwood.

**Keywords** Ecophysiology · Cottonwood and willow · Water use efficiency · River regulation · Drought stress

## Introduction

Riparian corridors in dry regions provide important ecosystem services, where abundant water—a limiting resource in the surrounding upland landscape—promotes a local community with typically high plant density, biomass, diversity and structural complexity (Naiman and Decamps 1997; Patten 1998; Scott and Auble 2002). Commonly, the stream channel feeds a perennial, shallow groundwater table that supports floodplain forest stands, including those of fast-growing, generally drought-intolerant pioneer species such as willows and poplars (family Salicaceae). However, in many arid and semi-arid regions, these trees must contend with decreased soil moisture during a portion of the year, particularly in Mediterranean climates where the dry season may extend for several months (Gasith and Resh 1999). Seasonal drought is one reason why abiotic conditions are primary drivers structuring riparian plant communities in arid and semi-arid regions (Hughes et al. 2001; Scott et al. 1999).

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J. C. Stella (✉)
Department of Forest and Natural Resource Management,
State University of New York College of Environmental
Science and Forestry (SUNY-ESF), One Forestry Drive,
Syracuse, NY 13210-2788, USA
e-mail: stella@esf.edu

J. J. Battles
Department of Environmental Science, Policy,
and Management, University of California at Berkeley,
137 Mulford Hall, Berkeley, CA 94720-3114, USA

Willows and poplars comprise a functional group well-adapted to riverine systems (Lytle and Poff 2004; Rood et al. 2003), because they employ a strategy of abundant seed production, wind dispersal, and fast growth to colonize newly created habitats (mineral sediments on bars and banks). However, the life-history tradeoffs include demand for abundant soil moisture and intolerance to drought. Survival of seedlings in particular is a challenge. Seasonally fluctuating water tables and severe vapor pressure deficits can dramatically reduce water availability during the critical establishment stage (Donovan and Ehleringer 1991; Horton and Clark 2001; Hughes et al. 2001; Rood et al. 2003). On snowmelt-dominated rivers, such as in California's Central Valley, extended flow and groundwater declines typically occur in late spring and early summer as the snowpack melts (Peterson et al. 2000). First-year seedlings are particularly vulnerable because they have neither the deep roots to tap a fast-receding water table nor the extensive root system to access a large soil volume. This chronic water shortage, along with other stressors in the riparian zone (e.g., scour, herbivory, competition with herbaceous species), makes seedling establishment a limiting step in riparian tree population dynamics (Lytle and Merritt 2004; Scott et al. 1996; Stromberg et al. 1991). Along regulated rivers in the semi-arid San Joaquin Basin in California, long-term alterations in flow magnitude, timing, and recession rate have exacerbated this demographic bottleneck, and threaten to further reduce the extent of riparian woodlands over time (Stella 2005).

Despite their vulnerability to drought, pioneer riparian seedlings demonstrate some mitigating morphological and physiological traits. In particular, rapid root extension and small shoot:root biomass ratios are adaptations that potentially reduce stresses related to seasonally variable water tables (Rood et al. 2003). Other morphological responses to water stress include reduction in specific leaf area (SLA) (Busch and Smith 1995), crown dieback (Scott et al. 1999; Stromberg and Patten 1992), branch abscission (Rood et al. 2000), and reduced diameter growth (Stromberg and Patten 1996). Studies of physiological function in adults indicate that these species are generally intolerant of drought and have low xylem cavitation thresholds (Amlin and Rood 2003; Cooper et al. 2003; Leffler et al. 2000; Tyree et al. 1994). Water table manipulations in controlled mesocosms have been used to simulate dynamic riverine environments in order to study the effects of seasonal moisture stress on plant survival and growth (e.g., Cordes et al. 1997; Horton and Clark 2001; Mahoney and Rood 1992; Segelquist et al. 1993; Stella et al. 2010). However, few studies on riparian seedlings in arid climates have linked survival and growth to morphological and physiological traits that may either reflect or mitigate the effects of water stress. In California's Central Valley, river regulation has greatly altered the annual hydrologic balance, and climate change is expected to further shift the system toward earlier snowmelt and a longer summer drought (Dettinger and Cayan 1995; Knowles et al. 2006; Maurer et al. 2007). Understanding these effects on native species is critical for predicting community shifts and for designing mitigation strategies.

In this study, we quantified growth and physiological function 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. This study builds on previous work in which we analyzed species survival patterns and established that SAGO seedlings had approximately 20% greater survivorship among the three species across a moderate range of drawdown, 0–3 cm day$^{-1}$ ("Electronic Supplementary Material;" Stella et al. 2010). Here we link the seedlings' demography to their underlying morphological and physiological responses to water table decline. Our objectives were to: (1) quantify differences in growth and functional traits among the dominant woody species of a riparian ecosystem; (2) analyze how growth and functional responses shifted in response to imposed drought stress; (3) understand which plant traits were associated with increased individual survival; and (4) infer how differences in drought tolerance may affect species abundance under changing climate and river flow conditions. We focused on the three native pioneer tree species that dominate riparian zones throughout California's San Joaquin Basin as well as much of the semi-arid southwestern US (Griffen and Critchfield 1972): Fremont cottonwood (*Populus fremontii* S. Watson ssp. *fremontii*, referred herein as POFR), Gooding's black willow (*Salix gooddingii* C. Ball, SAGO), and sandbar willow (*Salix exigua* Nutt., SAEX). As the largest, fastest-growing, and most widely distributed riparian trees, these are foundational species (sensu Ellison et al. 2005) for the terrestrial and instream ecosystems (Bangert et al. 2008; Schweitzer et al. 2004; Whitham et al. 2008), yet they are also vulnerable to long-term changes in the flow regime (Scott et al. 1999; Williams and Cooper 2005).

## Materials and methods

### Study environment and experimental design

The study was conducted outdoors at the University of California's Russell Research Station in Lafayette, CA, USA (37°55′03.77″N, 122°09′28.76″W) in late summer 2002. During the study, no precipitation occurred, and air temperature averaged 18°C (range 4–44°C). The mean midday (10 a.m.–2 p.m.) vapor pressure deficit was

3.0 ± 0.2 kPa (mean ± SE) throughout the study, and averaged 2.7 ± 0.3 kPa during the latter half. The plants used in the study were grown from seed collected in early summer from 7–10 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 >15 m apart to avoid the sampling of clones. Seeds were separated from catkins and refrigerated with desiccant until planting.

The experimental mesocosms consisted of steel, cylindrical tanks (125 cm deep × 61 cm diameter) with open tops, a bottom drain, and a flexible discharge tube that was elevated and lowered to effect changes in the tank's water level; this system was the same as reported in Stella et al. (2010). Four tanks were randomly assigned each to one of three drawdown treatments that imposed a range of water stress: a 1 cm day$^{-1}$ drawdown, a mild rate compared to actual river regimes; 3 cm day$^{-1}$, which is well within the range of snowmelt recessions on unregulated rivers; and a control group with a stable water table. Each treatment tank contained 32–41 seedlings with equal proportions of all three species. Seed sources were distributed evenly among tanks to eliminate confounding maternal effects. Sample sizes for all species by treatment combinations ranged from 48 to 58 seedlings (overall $N = 473$).

Seedlings were germinated and grown in individual PVC tubes, 125 cm long × 3.2 cm diameter, packed with sand and suspended within the tanks. The substrate used in the study was excavated from a sandbar on the Tuolumne River; median particle size was 0.6 mm and 85% of the sample was classified as medium or coarse sand (0.25–1 mm). Individual 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 three weeks the tubes were shaded with a 30% shade cloth and water levels were maintained at 10 cm below the soil surface to facilitate germination. Drawdown began on 22 August; 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 baseline. Water was added as necessary to compensate for daily evaporation. For the 3 cm day$^{-1}$ group, the water level reached the bottom of the tank on day 39.

## Data collection

We monitored the seedlings daily to record mortality and measured the height and length of the longest leaf weekly throughout the study. At days 0, 18 and 49, 4–8 live seedlings from each experimental group were randomly selected and harvested to measure root length and total biomass; all remaining seedlings were harvested at day 62. Immediately following harvest or natural death, seedlings were removed from their tubes, their longest root measured, and all tissue was oven-dried at 60°C and weighed. For all harvested individuals (those that were alive until sampled), we conducted leaf tissue analyses. Note that we did not include foliar chemistry results from plants that died naturally during the study because of potential changes in foliar chemistry due to decomposition. From each plant we sampled the terminal 2–3 leaves, the last ones formed, in order to assess the cumulative stress response to the treatment. Measures included SLA, carbon-to-nitrogen (C:N) ratio, and stable carbon isotope ratio ($\delta^{13}$C). To calculate SLA, the ratio of leaf area to mass (m$^2$ kg$^{-1}$), we used an analytical balance and an LI-3100C leaf area meter (Li-Cor Biosciences, Lincoln, NE, USA). The $\delta^{13}$C ratio was sampled to assess patterns in seasonal water use efficiency across the treatment gradient (Farquhar et al. 1989). The $\delta^{13}$C ratio was determined using a PDZ Europa Scientific 20/20 mass spectrometer with a continuous-flow CN elemental analyzer at the Center for Isotope Biogeochemistry at the University of California at Berkeley. Peachleaf working standards calibrated to the PDB Vienna standard (Craig 1957) were used for every four samples, and the long-term precision (standard deviation) for the instrument is ±0.15‰. Output data were corrected for instrument drift and nonlinear mass bias (P. Brooks, Univ. of California, Berkeley, unpublished data). The C:N ratio was calculated from the elemental data.

## Data analysis

To ensure that growth differences for these seedlings were due to treatment effects rather than prior conditions, we used analysis of variance (ANOVA) to test seedling size differences between treatment groups of each species at the start of the drawdown experiment. There were no significant treatment differences in initial seedling height, length of longest leaf, or nested tank effects, except for POFR leaf length (ANOVA: $F_{5,253} = 5.5$, $p < 0.0001$). Because of this difference, we excluded raw measures of leaf length from the rest of the analyses, and used change in leaf length from initial conditions instead.

### Analyzing species-level differences in growth and physiological function

For the seedlings that survived the study, we wanted to know how the three dominant species differed in growth and allocation, and their responses to sublethal effects of drawdown. We therefore conducted two separate analyses: (1) species-level differences in growth, biomass allocation, and physiological traits; and (2) species-specific responses of these factors to drawdown. For the first case, we used one-way ANOVA to test baseline differences among species, defining baseline as the control groups with a constant water table ($N = 72$). Factors analyzed were final shoot height, root length, total biomass, shoot-to-root mass ratio (SRR), SLA, leaf C:N mass ratio, and stable carbon isotope ratio ($\delta^{13}$C). Log transformations were used for length, biomass, and shoot:root ratio data to satisfy residual distribution assumptions. Post hoc, pairwise species differences were tested using simultaneous 95% confidence intervals calculated by the Tukey method (Zar 1999).

We evaluated the treatment effect on these traits using analysis of covariance (ANCOVA) with species as a categorical factor and drawdown rate as a continuous covariate. This analysis used surviving seedlings from the three treatment groups ($N = 166$). The magnitude and significance level of the drawdown rate slope coefficient indicated the treatment effect. For response variables in which only particular species were sensitive (i.e., the ANCOVA interaction term was significant at the $P < 0.05$ level), we used linear regression to isolate the treatment influence for each species.

### Influence of growth and allocation on survival

We used the trait data to quantify how well growth and biomass allocation patterns predicted individual seedling survival throughout the experiment. We tested the survival effects of seedling growth rate, biomass allocation, and their interaction using a logistic regression model with binary survival response and lifetime-averaged values of growth and biomass for each seedling as model predictors. For these individual survival models, potential explanatory variables were constrained to seedling size measurements (e.g., shoot length, root length and biomass), because chemical and ecophysiological leaf trait data were not available for plants that died during the course of the experiment. A more general consideration of the full suite of traits on cohort (rather than individual) survival is provided in the "Discussion."

In the logistic survival models, each species was modeled separately, and the drawdown treatment was included as a continuous factor. Plants harvested prior to the end were excluded from these models because their ultimate fates were not known. Biomass allocation was represented as the shoot-to-root ratio, which was calculated from dry weights after death. We used root elongation rate (mm day$^{-1}$) to represent growth rate. Root elongation was highly correlated with biomass and shoot growth (Pearson's $r = 0.55$–$0.68$); but, unlike these other measures, root growth was linear over time. Therefore, the lifetime-average root growth rate was independent of the seedlings' time of death.

For each species, five logistic survival models were considered, all of which contained drawdown rate as a factor: a base model with only drawdown rate, two-factor models each for root growth and shoot:root ratio, a three-factor model with all variables, and all variables plus the interaction of root growth and shoot:root ratio. For model development and selection we adopted an information theoretic approach using Akaike's information criterion (AIC; Burnham and Anderson 2002). AIC values and Akaike weights were computed for all alternatives and compared to select the minimum adequate model. We calculated variance inflation factors (VIF) for each species' best logistic model to evaluate multicollinearity between variables and centered data values about their means (Hosmer and Lemeshow 2000). We also used receiver operating characteristic (ROC) analysis to evaluate how well the final logistic models discriminated between predictions of live and dead seedlings (Fielding and Bell 1997). For the best model of each species (those with the highest Akaike weights), odds ratios were calculated from the parameter estimates to interpret the influence of the model factors on predicted survival (Hosmer and Lemeshow 2000).

## Results

### Drawdown effects on growth and biomass allocation

In addition to higher survivorship (Stella et al. 2010), SAGO seedlings sustained the highest rates of shoot and root elongation (Fig. 1). SAGO plants in the control group were 40% taller than POFR and 89% taller than SAEX (ANOVA: $F_{2,69} = 27.7, p < 0.0001$, Table 1). The longest SAGO root was on average 118% longer than POFR and 51% longer than SAEX (ANOVA: $F_{2,69} = 19.3$, $p < 0.0001$, Table 1). SAGO dry biomass was also higher than the other two species (Table 1), but only significantly greater than SAEX (ANOVA: $F_{2,69} = 7.06$, $p = 0.002$). The shoot:root ratio was highest for POFR (Table 1) and significantly greater than the willows (ANOVA: $F_{2,68} = 7.80$, $p < 0.001$).

Water table recession had a strong negative influence on plant growth (Fig. 1). Whereas mortality was greater only for plants subjected to drawdown rates $\geq 3$ cm day$^{-1}$ ("Electronic Supplementary Material;" Stella et al. 2010), growth decreased from controls for all groups across the treatment gradient (Fig. 1). All species showed a strongly negative response of drawdown rate to shoot height (ANCOVA: slope = $-0.30$, $F_{1,162} = 78.9$, $p < 0.0001$) and root length (ANCOVA: slope = $-0.28$, $F_{1,161} = 53.6$, $p < 0.0001$). In contrast, the responses of net change in leaf length, seedling biomass, and shoot:root ratio varied by

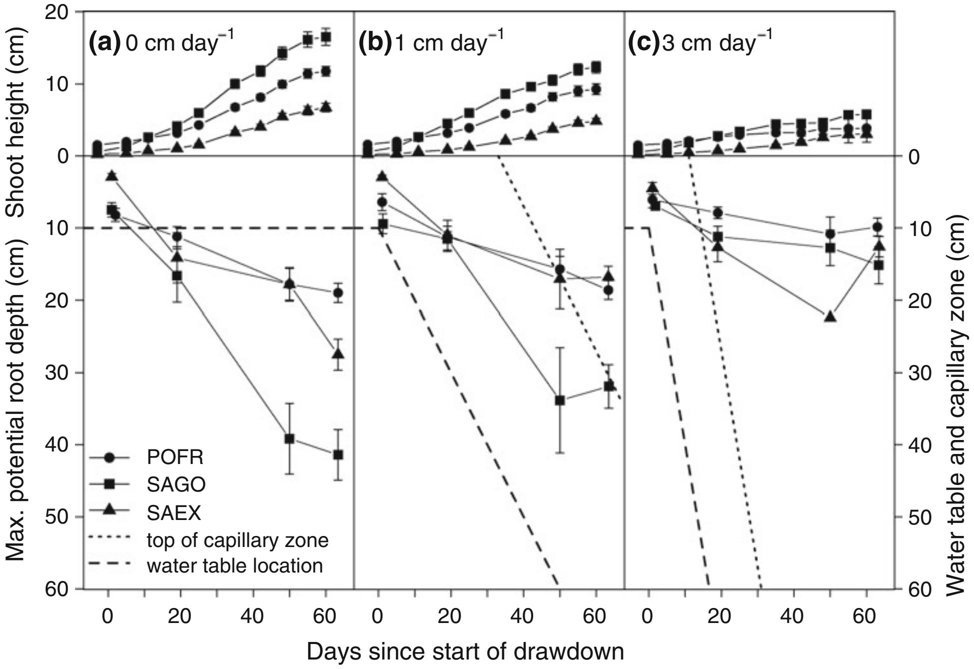

**Fig. 1** Seedling shoot height and maximum potential root depth (mean ± SE) over the experiment period for all species: **a** 0 cm day$^{-1}$, control group; **b** 1 cm day$^{-1}$, drawdown group; and **c** 3 cm day$^{-1}$, drawdown group. Shoot heights were the means of all live plants at each sampling interval. Root depth was calculated as the mean longest root of all plants harvested at days 0, 18, 49 and 60. The location of the water table and estimated top of the capillary zone are shown on the right vertical axis

**Table 1** Summary of baseline size, morphological and physiological characteristics for seedlings in the control group (constant water table) that survived the experiment period

| Response | Group means (±SE)[a] | | |
|---|---|---|---|
| | POFR ($n$ = 19–22) | SAGO ($n$ = 25–28) | SAEX ($n$ = 22) |
| Shoot height (mm) | 118 (±7)$^{a}$ | 165 (±12)$^{b}$ | 67 (±6)$^{c}$ |
| Root length (mm) | 190 (±13)$^{a}$ | 414 (±35)$^{b}$ | 275 (±21)$^{c}$ |
| Leaf elongation (mm) | 8.4 (±1.1)$^{a}$ | 24.7(±1.5)$^{b}$ | 21.4 (±1.4)$^{b}$ |
| Total dry biomass (g) | 0.29 (±0.02)$^{ab}$ | 0.40 (±0.04)$^{a}$ | 0.22 (±0.02)$^{b}$ |
| Shoot-to-root mass ratio (g g$^{-1}$) | 1.61 (±0.12)$^{a}$ | 1.32 (±0.17)$^{ab}$ | 1.06 (±0.06)$^{b}$ |
| Specific leaf area (m$^2$ kg$^{-1}$) | 13.42 (±0.41)$^{a}$ | 10.1 (±0.48)$^{b}$ | 8.54 (±0.34)$^{c}$ |
| C:N mass ratio (g g$^{-1}$) | 23.6 (±1.0)$^{a}$ | 17.0 (±0.9)$^{b}$ | 19.9 (±0.6)$^{c}$ |
| Carbon isotope ratio, $\delta^{13}$C (‰) | −30.01 (±0.19)$^{a}$ | −29.95 (±0.26)$^{a}$ | −28.54 (±0.21)$^{b}$ |

[a] Sample sizes varied because some parameters were not available for all plants. *Superscript letters* indicate post hoc ANOVA significant pairwise species differences using 95% simultaneous confidence intervals for specified linear combinations, by the Tukey method. Log values were used in ANOVA models for shoot height, root length, biomass, and shoot-to-root ratio to satisfy residual assumptions

species (Fig. 2). Net change in leaf increment (Fig. 2a) was negatively correlated with drawdown rate for both willows (SAGO: slope = −0.26, $F_{1,64} = 17.09$, $p < 0.0001$; SAEX: slope = −0.18, $F_{1,51} = 14.25.0$, $p < 0.001$) but not for POFR (slope = 0.23, $F_{1,44} = 2.95$, $p = 0.09$). Similarly, reduction in total biomass (Fig. 2b) was strong across treatment levels for the willows (SAGO: slope = −0.46, $F_{1,65} = 46.6$, $p < 0.0001$; SAEX: slope = −0.33, $F_{1,51} = 41.0$, $p < 0.0001$), but not for POFR (slope = −0.16, $F_{1,44} = 2.3$, $p = 0.14$). The shoot:root ratio (Fig. 2c) was unchanged across treatments for POFR (slope = 0.12, $F_{1,43} = 0.37$, $p = 0.55$) and SAGO (slope = 0.11, $F_{1,64} = 1.48$, $p = 0.23$), but increased for SAEX (slope = 0.13, $F_{1,51} = 6.44$, $p = 0.01$).

## Drawdown effects on foliar morphology and chemistry

The three traits measured on leaf tissue of surviving plants were C:N ratio, SLA, and carbon isotope ratio (Fig. 2d–f). Among the control groups, there were species-level differences in SLA (ANOVA: $F_{2,68} = 32.4$, $p < 0.0001$) and C:N ratio (ANOVA: $F_{2,63} = 14.6$, $p < 0.0001$; Table 1). For both metrics, POFR had the highest values and SAEX the lowest, and all pairwise comparisons were significant (Table 1). The C:N ratio (Fig. 2d) decreased proportionally for all species with increasing drawdown rate (ANCOVA: slope = −1.81, $F_{1,153} = 32.8$, $p < 0.0001$). The largest decrease in C:N ratio occurred between the 0 and 1 cm day$^{-1}$ groups. SLA (Fig. 2e) decreased 29% from

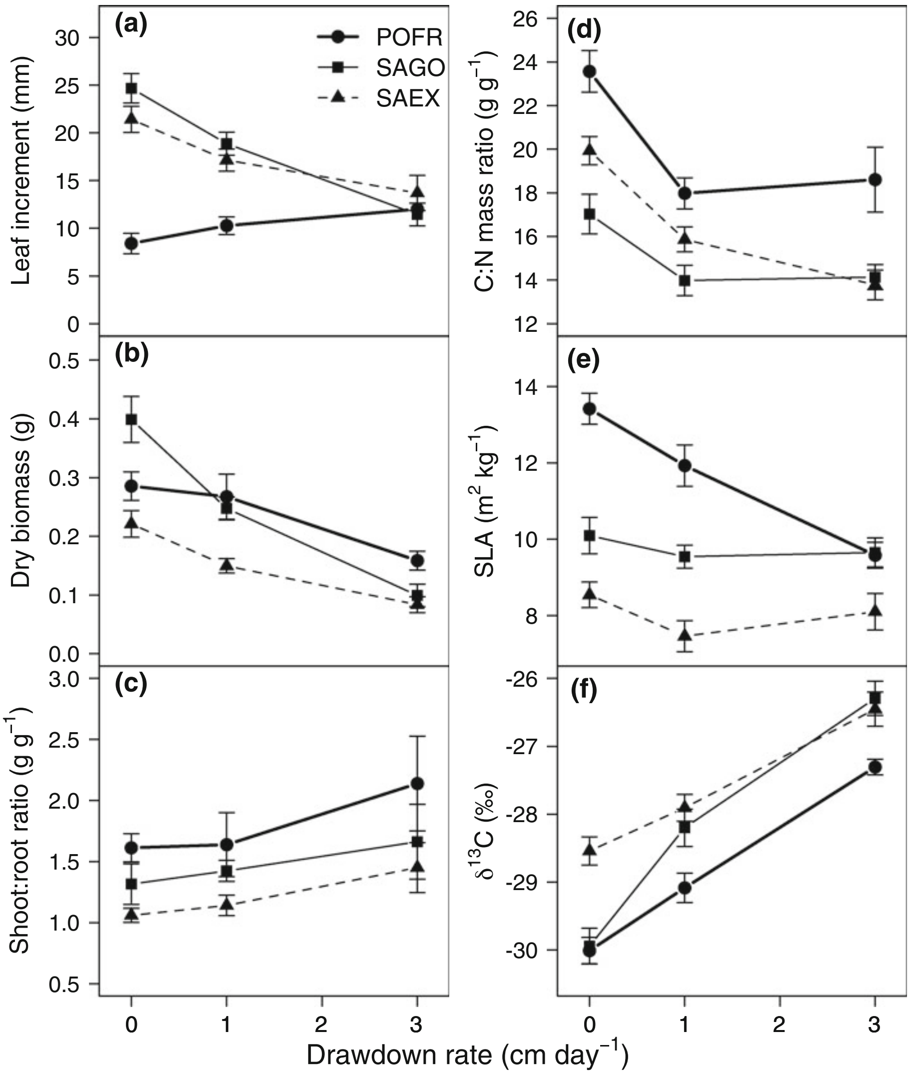

**Fig. 2** Growth, biomass allocation, and foliar trait responses (mean ±1 SE) of surviving seedlings for the 0, 1, and 3 cm day$^{-1}$ drawdown treatments: **a** leaf growth increment, **b** total dry biomass, **c** shoot:root ratio, **d** carbon:nitrogen ratio, **e** specific leaf area, and **f** $\delta^{13}$C. *Lines* are plotted to distinguish species patterns across treatment groups

control values (13.4–9.58 m$^2$ kg$^{-1}$) for water-stressed POFR plants (slope = −1.36, $F_{1,44} = 8.71$, $p < 0.01$) but remained constant for both willow species (SAGO: slope = −0.17, $F_{1,64} = 0.48$, $p = 0.49$; SAEX: slope = −0.16, $F_{1,51} = 0.53$, $p = 0.47$).

Carbon isotope values ($\delta^{13}$C) for the surviving seedlings showed clear species differences (ANOVA: $F_{2,63} = 12.7$, $p < 0.0001$; Table 1) and treatment effects (ANCOVA: $F_{1,151} = 105.6$, $p < 0.0001$; Fig. 2f). Control group means were equivalent for POFR and SAGO, approximately −30 ± 0.2‰, and significantly enriched (less negative) for SAEX, −28.54 ± 0.21‰ (Table 1). With increased drawdown rate, mean $\delta^{13}$C was higher (less negative) for all species, indicating decreased $^{13}$C discrimination and higher seasonal water-use efficiency compared to controls (Fig. 2f). The reduction in $^{13}$C discrimination between groups was greatest for SAGO, approximately 3.5‰ across the drawdown gradient, than for the other two species, which ranged 2–2.5‰. At the 3 cm day$^{-1}$ drawdown rate, SAGO and SAEX $\delta^{13}$C values were equivalent, approximately −26.4 ± 0.25‰, and higher than that of POFR (−27.3 ± 0.12‰). These results indicate that although SAEX had the highest baseline water-use efficiency, SAGO seedlings had the greatest change at high rates of drawdown.

### Influence of growth, allocation, and physiology on survival

In the logistic models of individual plant survival, both root growth and shoot:root ratio were good predictors of survival for all species. In all control and treatment groups, seedlings that survived the experiment had greater rates of root elongation and lower shoot:root biomass ratios compared to those that died. The best logistic regression survival model (i.e., that with the lowest AIC value) for POFR and SAGO included terms for both root growth and shoot:root ratio, and the best model for SAEX included both of these variables plus the interaction term (Table 2). The Akaike weights of the best models ranged 0.65–0.99 among species, indicating strong predictor variables, and ROC values ranged from 0.92 to 0.94, indicating excellent model discrimination between actual live and dead individuals (Table 2). Multicollinearity between variables in the models was low; VIF values for all factors without interaction terms were $\leq 1.5$ ("Electronic Supplementary Material"), much lower than the values $\geq 10$ that are considered problematic for parameter estimation (Neter et al. 1996).

We fit response surfaces for individual seedling survival using the best logistic model for each species (Fig. 3). For all three species, survival decreased with increased drawdown rate, decreased root growth and increased shoot:root ratio. Though both root elongation and biomass allocation were important for all species, coefficient estimates and their corresponding odds ratios indicate that root growth was the strongest determinant of plant survival for POFR, and shoot:root ratio was most important for the willows ("Electronic Supplementary Material"). For example, a drawdown rate of 3 cm day$^{-1}$ is survivable for POFR seedlings that can sustain root growth >4 mm day$^{-1}$, whereas a low shoot:root ratio has little impact. In contrast, SAEX survival at all drawdown rates is largely determined by maintaining a shoot:root ratio of <2, regardless of root growth (Fig. 3). Odds ratios, which were calculated by exponentiating the coefficient estimates (Hosmer and Lemeshow 2000), quantify precisely the difference in survival due to an incremental change in a model parameter. The odds ratio for root growth in POFR is 4.1 ("Electronic Supplementary Material"), indicating that survival is more than four times as likely for a seedling growing 1 mm day$^{-1}$ more than another. The odds ratio for SAGO root growth is 1.7, indicating a 70% greater survival rate from a 1 mm day$^{-1}$ greater growth rate. A unit decrease in shoot:root ratio (e.g., comparing seedlings with ratios of 3 versus 2 g g$^{-1}$) confers an approximate twofold survival advantage for both species (odds ratios 1.8 for POFR and 2.5 for SAGO). For SAEX, odds ratios for each factor varied as a function of the other because of the interaction term; therefore, the survival advantage of incremental changes in the factors is not static. However, as noted above, odds ratios for shoot:root ratio are much higher than for root growth, indicating that biomass allocation is the major driver of individual plant survival.

**Table 2** Top candidate models for logistic regression models of seedling survival as a function of drawdown rate, root growth and shoot:root mass ratio

| Model | Residual deviance | *K* | AIC | AIC$_{\text{diff}}$ | $w_i$ | ROC | Parameters |
|---|---|---|---|---|---|---|---|
| POFR | | | | | | | |
| **1** | **73.99** | **4** | **81.99** | **0.00** | **0.65** | **0.92** | **rate + root + srr** |
| 2 | 73.53 | 5 | 83.53 | 1.54 | 0.30 | 0.92 | rate + root + srr + root × srr |
| 3 | 81.39 | 3 | 87.39 | 5.40 | 0.04 | 0.90 | rate + srr |
| 4 | 84.81 | 3 | 90.81 | 8.82 | 0.01 | 0.90 | rate + root |
| 5 | 114.51 | 2 | 118.51 | 36.52 | 0.00 | 0.76 | rate |
| SAGO | | | | | | | |
| **1** | **74.16** | **4** | **82.16** | **0.00** | **0.60** | **0.92** | **rate + root + srr** |
| 2 | 74.05 | 5 | 84.05 | 1.89 | 0.23 | 0.92 | rate + root + srr + root × srr |
| 3 | 78.65 | 3 | 84.65 | 2.49 | 0.17 | 0.90 | rate + srr |
| 4 | 87.68 | 3 | 93.68 | 11.52 | 0.00 | 0.87 | rate + root |
| 5 | 102.11 | 2 | 106.11 | 23.95 | 0.00 | 0.79 | rate |
| SAEX | | | | | | | |
| **1** | **72.94** | **5** | **82.94** | **0.00** | **0.99** | **0.94** | **rate + root + srr + root × srr** |
| 2 | 83.63 | 4 | 91.63 | 8.69 | 0.01 | 0.93 | rate + root + srr |
| 3 | 93.09 | 3 | 99.09 | 16.15 | 0.00 | 0.91 | rate + srr |
| 4 | 115.72 | 3 | 121.72 | 38.78 | 0.00 | 0.87 | rate + root |
| 5 | 156.47 | 2 | 160.47 | 77.53 | 0.00 | 0.66 | rate |

Information reported for each model includes number of model parameters (*K*), Akaike information criterion (*AIC*), relative difference (*AIC*$_{\text{diff}}$), Akaike weights ($w_i$), and discrimination (receiver operating characteristic curve, *ROC*). Models are ranked by Akaike weight, which indicates each model's likelihood given the candidate model set

Significance tests for the best models (in bold) were conducted using model likelihood ratio tests. Resulting chi-square statistics (with degrees of freedom and sample size in parentheses) were $\chi^2$ (3, $N = 108$) = 72.72, $p < 0.0001$ for POFR; $\chi^2$ (3, $N = 103$) = 60.35, $p < 0.0001$ for SAGO; and $\chi^2$ (4, $N = 123$) = 95.22, $p < 0.0001$ for SAEX

*rate* drawdown rate (cm day$^{-1}$); *root* lifetime mean root growth (mm day$^{-1}$); *srr* shoot:root mass ratio (g g$^{-1}$)

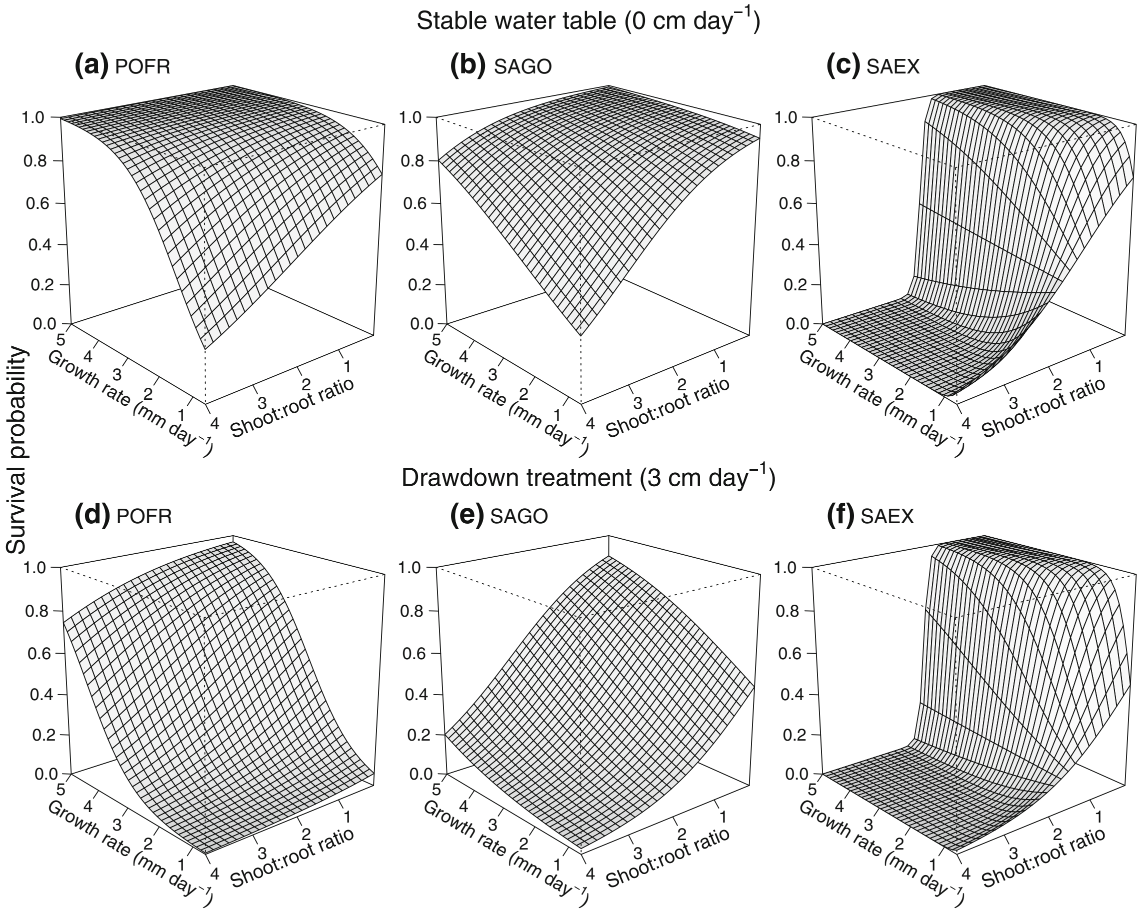

**Fig. 3** Response surfaces for logistic regression models of survival probability as a function of lifetime-average shoot:root ratio (g g$^{-1}$) and root growth rate (mm day$^{-1}$). Plots **a**–**c** show each species' response when grown with a stable water table (0 cm day$^{-1}$); **d**–**f** show the responses when grown at a rate of drawdown of 3 cm day$^{-1}$

## Discussion

Simulated river flow recession had profound effects on riparian seedling growth, morphology, and foliar chemistry. Though mild water-table recession (1 cm day$^{-1}$) had no effect on seedling mortality compared to controls (Stella et al. 2010), all recession rates induced reduction in biomass, stem, root and leaf elongation (Figs. 1, 2a, b), and changes in shoot:root ratio, C:N ratio, SLA, and $\delta^{13}$C (Fig. 2c–f). With the exception of C:N ratio, all of these changes became more pronounced with increasing drawdown rate, indicating that at sublethal rates of water stress, seedling growth and physiological function were nevertheless impaired.

For all species, individual seedling survival was correlated positively with root growth and negatively with shoot-to-root ratio (Fig. 3), suggesting that both absolute and relative growth in roots are important for survival. As drawdown rate increased, seedling water use efficiency increased (indicated by higher $\delta^{13}$C values), particularly for SAGO, which also had the highest survival ("Electronic Supplementary Material"). These results suggest that all three species used stomatal closure to maintain high internal water potential, and that SAGO was the most effective species in this regard.

### Species-level responses to water stress

Despite the general intolerance of riparian willows and poplars to drought (Braatne et al. 1996; Rood et al. 2003), the three species demonstrated distinct differences in the suite of survival, growth, and morphological responses to increased water table drawdown (Fig. 2). Contrary to our expectations based on the reported drought intolerance of other willow species (Amlin and Rood 2002; van Splunder et al. 1996), SAGO seedlings in this study survived better (Stella et al. 2010) and grew faster than POFR seedlings at all experimental rates (Fig. 1). Compared to SAEX, which is a shrub, SAGO is more similar to POFR in growth form, and the traits that best explain SAGO's better performance were water use efficiency combined with high absolute rates of root growth. Higher water use efficiency, as indicated by higher $\delta^{13}$C values, is a common response of water-stressed plants (Smedley et al. 1991), and has been observed for riparian seedlings under experimental drought (Zhang et al. 2004) and adult natural populations between wet and dry years (Leffler and Evans 1999). In our study, both willow species had higher $\delta^{13}$C values than POFR, and SAGO seedlings had the greatest change in $\delta^{13}$C from controls to stressed plants (Fig. 2f). Sparks and Ehleringer (1997) found similar patterns among adult plants. In their study, SAEX shrubs had higher seasonal water use efficiency than POFR trees. However, other studies evaluating leaf isotope values along a gradient of groundwater depth found no differences between POFR and SAGO trees at the same sites (Busch and Smith 1995; Horton et al. 2001). Instantaneous measures of plant water status do generally show better drought tolerance of willow relative to POFR in terms of leaf gas exchange, relative water content and xylem water potential at the turgor loss point for both seedlings (McBride et al. 1989) and adults (Busch and Smith 1995).

The shift toward more enriched $^{13}$C in leaf tissue between control and stressed groups indicates longer periods of stomatal closure during the growing season in response to high vapor pressure deficits, resulting in a suboptimal $c_i/c_a$ ratio for photosynthesis. Consequently, the stressed willows, particularly SAGO, demonstrated a greater reduction in overall growth from control values (Figs. 1, 2a, b) compared to surviving POFR plants that did not reduce gas exchange as much. However, SAGO's greater reduction in biomass under drought conditions was offset at all treatment levels by faster absolute root growth (Fig. 1) and a higher relative allocation to roots (i.e., lower overall shoot:root ratio) compared to the other species (Fig. 2c). Therefore, it appears that the combination of inherently fast growth (evident in the control groups, Table 2), and better stomatal control (resulting in steep growth reductions) allowed SAGO among the three species to best maintain a balance of sufficiently high internal water status, adequate root elongation, and fine root development under drought conditions.

Drought stress also induced morphological changes at the leaf level. Both willows reduced the rate of leaf elongation with increased drought stress (Fig. 2a), and SAGO seedlings had higher rates of leaf abscission than the other species, up to 70% of all plants (Stella 2005). These results are consistent with a strategy of reducing transpiring area by controlling leaf area. POFR seedlings, in contrast, exhibited no change in leaf increment or abscission rates; however, it sustained large reductions in SLA (Fig. 2e). Whereas the willows appear to reduce water demand under stress by reducing leaf area, POFR's reduction in SLA suggests that it can increase carbon assimilation per unit transpiring leaf area, particularly under high-light conditions (Poorter and Nagel 2000). POFR also have appreciable transpiration from stomata on both upper and lower leaf surfaces compared to willow species (McBride et al. 1989); therefore, reducing its SLA may especially benefit POFR. Busch and Smith (1995) found significant decreases in SLA in POFR at dry sites compared to SAGO, and concluded that SAGO may rely more on stomatal regulation than morphological adaptations to mitigate effects of drought.

General relationships between survivorship and the larger group of plant functional traits are illustrated in Fig. 4. These pairplots differ from the logistic individual survival models (Fig. 3) because survival is modeled as a proportion of the entire cohort and traits are from the mean of the surviving individuals. This approach, while lacking the specificity of the individual survival models, considers a wider range of explanatory traits that could not be measured for dead plants in the logistic models. Survivorship was calculated as Kaplan–Meier estimates (Parmar and Machin 1995) of the experimental seedling survival times ("Electronic Supplementary Material;" Stella et al. 2010). Trait means (±SE) of the surviving individuals in each group are the same as in Fig. 2. Plotting all treatment groups from controls (open symbols) to stressed (3 cm day$^{-1}$, closed symbols) demonstrates the collinearities of survival with plant trait shifts across the water stress gradient (Valladares and Sanchez-Gomez 2006). For a trait to have an effect on survival, two patterns should be evident: (1) shifts in mean trait values should occur over the treatment gradient; and (2) plotted relationships between trait values and species survival should be strongest for the most stressed groups (i.e., a linear plot of species for the 3 cm day$^{-1}$ group). In our study, these patterns are most evident for final root length and $\delta^{13}$C, both of which increased with species-level survival, and shoot:root ratio, which decreased with survival (Fig. 4a–c). In contrast, shoot length, dry biomass, and SLA (Fig. 4d–f) show no correlation with species-level survival for the stressed groups.

## Root growth and biomass allocation

The logistic models show clear survival advantages for all species of fast root growth and high relative allocation to root biomass (Table 2; Fig. 3). Other studies report that at sublethal rates of drawdown ($\leq$2 cm day$^{-1}$), seedling root growth increases and/or shoot:root ratio decreases relative to those grown with stable water tables (Amlin and Rood 2002; Horton and Clark 2001; Hughes et al. 1997; Kranjcec et al. 1998; Mahoney and Rood 1992; Segelquist et al. 1993). However, seedlings in the present study did not show these responses. Root growth monotonically decreased (Fig. 1) and shoot:root ratios increased (Fig. 2)

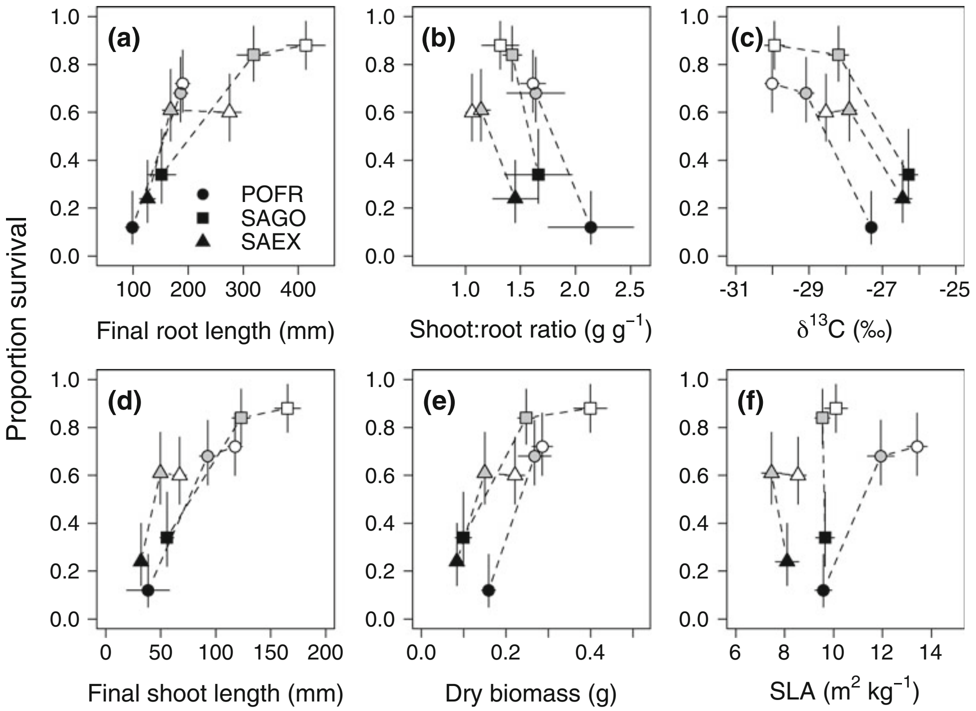

**Fig. 4** Treatment group survivorship (Kaplan–Meier estimates ± SE) plotted against plant traits of the surviving individuals for each treatment group (mean ± SE). In each panel, *open symbols* represent the control (0 cm day$^{-1}$) groups, *gray-filled symbols* represent 1 cm day$^{-1}$ groups, and *black filled symbols* represent 3 cm day$^{-1}$ groups. Plant traits plotted: **a** final root length, **b** shoot:root ratio, **c** $\delta^{13}$C, **d** final shoot height, **e** total dry biomass, and **f** specific leaf area. *Lines* are plotted to distinguish species patterns across treatment groups

across the drawdown gradient for all species. Nevertheless, the logistic models indicate that individual seedlings with intrinsically high rates of root elongation survive much better (Fig. 3).

Rapid root elongation in particular is considered an important survival trait for obligate phreatophyte species living in environments with seasonally variable water tables (Mahoney and Rood 1998). Root growth rates for the seedlings in the present study ranged from 1.1 to 2.2 mm day$^{-1}$ for POFR, 0.7 to 4.6 mm day$^{-1}$ for SAGO, and 1.4 to 3.1 mm day$^{-1}$ for SAEX. Studies done on first-year plants grown from seed report similar values, between 1 and 6 mm day$^{-1}$ (Horton and Clark 2001; Mahoney and Rood 1991; Segelquist et al. 1993), whereas root growth for older seedlings or plants grown from cuttings is generally higher, ranging up to 13 mm day$^{-1}$ (Amlin and Rood 2002; Kranjcec et al. 1998; Mahoney and Rood 1992; McBride et al. 1989). Cuttings and older seedlings likely offer a growth advantage over first-year plants because of stored carbon in roots and stems.

## Community-level implications along regulated rivers

The greater root elongation and greater physiological adjustment to drought conditions by SAGO compared to POFR reinforce our earlier results of superior survivorship under simulated conditions of river level decline (Stella et al. 2010). Taken together, these results suggest that SAGO is a better competitor than POFR in riparian zones with dynamic water tables. As a result, river level changes during the spring seedling establishment period may have a large effect on species composition and distribution in riparian zones. Current river management practices in the San Joaquin Basin have a disproportionately large impact on spring snowmelt runoff, the critical period for recruitment of pioneer trees (Stella et al. 2006), due to widespread reductions in peak flows, earlier seasonal releases, impoundment of spring pulse flows for summer irrigation, and more rapid stage declines during the growing season (Stella et al. 2010). Furthermore, regional climate models project reductions in snowpack volume and higher runoff earlier in winter from climate change (Vicuna et al. 2007). If physiological differences do drive differences in seedling mortality on a large scale, we would expect the hydrological trends to contribute to eventual reductions in Fremont cottonwood abundance throughout the San Joaquin Basin, with increased dominance of pioneer habitats by Goodding's willow or other more drought-tolerant species.

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