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Synchrony of Seed Dispersal, Hydrology and Local Climate in a Semi-arid River Reach in California

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ABSTRACT

The temporal availability of propagules is a critical factor in sustaining pioneer riparian tree populations along snowmelt-driven rivers because seedling establishment is strongly linked to seasonal hydrology. River regulation in semi-arid regions threatens to decouple seed development and dispersal from the discharge regime to which they evolved. Using the lower Tuolumne River as a model system, we quantified and modeled propagule availability for *Populus fremontii* (POFR), *Salix gooddingii* (SAGO), and *Salix exigua* (SAEX), the tree and shrub species that dominate near-channel riparian stands in the San Joaquin Basin, CA. A degree-day model was fit to field data of seasonal seed density and local temperature from three sites in 2002–2004 to predict the onset of the peak dispersal period. To evaluate historical synchrony of seed dispersal and seasonal river hydrology, we compared peak spring runoff timing to modeled peak seed release periods for the last 75 years. The peak seed release period began on May 15 for POFR (range April 23–June 10), May 30 for SAGO (range May 19–June 11) and May 31 for SAEX (range May 8–June 30). Degree-day models for the onset of seed release reduced prediction error by 40–67% over day-of-year means; the models predicted best the interannual, versus site-to-site, variation in timing. The historical analysis suggests that POFR seed release coincided with peak runoff in almost all years, whereas SAGO and SAEX dispersal occurred during the spring flood recession. The degree-day modeling approach reduce uncertainty in dispersal timing and shows potential for guiding flow releases on regulated rivers to increase riparian tree recruitment at the lowest water cost.

Key words: phenology; seed dispersal; degree-day model; seed longevity; germination; *Populus; Salix;* seedling recruitment; riparian habitat restoration; flow regulation; California central-valley.

INTRODUCTION

For organisms that inhabit river floodplain ecosystems, disturbance is a major driver of population and community dynamics (Resh and others 1988). The frequency, size, and predictability of inundation in ''flood-prone'' zones can drive the selection of life history traits that avoid or exploit these disturbances (Townsend and Hildrew 1994; Lytle and Poff 2004). Consequently, disturbance-adapted organisms are vulnerable to human-caused changes in the disturbance regime (Bunn and Arthington 2002).

Pioneer riparian tree species that inhabit the riparian zones of snowmelt-driven rivers are classic disturbance-adapted organisms (Rood and others 2003). Seed dispersal and seedling establishment are broadly synchronized with the end of the annual snowmelt flow pulse (Scott and others 1997; Cooper and others 1999; Karrenberg and others 2002). Under this disturbance regime, propagule release and dispersal must coincide with the short-

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lived availability of viable seedbeds, for reproduction to be successful in any year (Farmer and Bonner 1967; Willson and Traveset 2000). Thus the temporal availability of propagules is an important constraint for sustaining pioneer riparian plant populations (van Splunder and others 1995; Mahoney and Rood 1998; Cooper and others 1999).

In riparian zones throughout the San Joaquin Basin of California, the dominant pioneer species are Fremont cottonwood (*Populus fremontii* S. Watson ssp. *fremontii*), Goodding's black willow (*Salix gooddingii* C. Ball), and narrow-leaved willow (*Salix exigua* Nutt.), which we refer to as POFR, SAGO, and SAEX, respectively. POFR and SAGO are trees, whereas SAEX grows typically as a shrub in this region. These species' high seed output, effective dispersal and fast growth rates ensure vigorous establishment under favorable conditions (Braatne and others 1996; Karrenberg and others 2002), but their transient seed viability, intolerance to shade and drought, and short adult life spans make them vulnerable to long-term changes in the flow regime (Scott and others 1999; Williams and Cooper 2005). In the San Joaquin Basin, almost all major streams are dammed and regulated so that current flow regimes bear little resemblance to natural ones. As a consequence, riparian tree species do not establish cohorts with the same frequency as under natural flow regimes (Scott and others 1996). One potential reason is that the timing of seed release no longer coincides with a spring snowmelt pulse.

Declines in the riparian forest community have important ramifications for the function of the San Joaquin riverine ecosystem. As the first plants to colonize bare substrates deposited by floods, cottonwoods and willows stabilize banks, add energy and biomass, and build habitat complexity (Gregory and others 1991; Naiman and Decamps 1997). Thus it is important both to identify bottlenecks to population growth and to develop mitigation strategies.

Spring snowmelt runoff is broadly coordinated across river basins in the Sierra Nevada (Peterson and others 2000), but timing can vary interannually by many weeks (Cayan and others 2001). Seed release timing is also highly variable between years (van Splunder and others 1995; Cooper and others 1999). It is unlikely that elevated river flow directly triggers seed release in a given year, but because snowmelt is a function of climate patterns coordinated over large spatial scales, we suggest that temperature provides one common cue that drives the two processes. In this paper, we explore the coordination between propagule availability of the dominant riparian tree species and spring snowmelt runoff in the lower Tuolumne River, a major river in the San Joaquin Basin. Our specific objectives were: (1) to quantify the temporal pattern of propagule availability for the San Joaquin Basin based on measurements of seed release timing and seed longevity; (2) to reduce the uncertainty in predicting seed release along the lower Tuolumne River corridor in any given year using a climate-based model; and (3) to compare the long-term coordination between seed release timing in the Tuolumne River corridor and the unregulated spring snowmelt flow pulse.

METHODS

Study Area

The San Joaquin Basin covers 35,000 km^2 in California's Central Valley (Figure 1). The lower basin (below the Sierra Nevada foothills) experiences a Mediterranean climate with an average of 30 cm of precipitation falling primarily between October and April, followed by a prolonged summer drought (USACE 2002). The Tuolumne River is the largest of three major tributaries to the San Joaquin River; its basin covers 4,900 km^2 (McBain & Trush Inc. 2000). The species in our study inhabit the lowland alluvial floodplains (<200 m elevation) of the San Joaquin River and its tributaries. These ecosystems are characterized by dynamic fluxes of water, sediment and nutrients, and a structurally complex and patchy riparian zone. These reaches are also the most heavily regulated, with major dams and reservoirs at the transition between Sierra Nevada foothills and valley floor that impound water for irrigation, flood control, and hydropower.

From 2002 through 2004, we collected data on seed viability, seed release timing, stand characteristics, and local climate at three floodplain sites along the lower Tuolumne River, which extends 52 km downstream from the New Don Pedro Dam to the confluence of the San Joaquin River. Preliminary studies at these three sites confirmed our assumption that none of the species maintains a seed bank from one year to the next (Stella 2005). We also monitored seed release timing at three sites along the San Joaquin River in 2003 as part of a larger study on riparian seedling recruitment dynamics.

Field Data Collection

We collected field data on seed release patterns and local temperature to develop a predictive model. At each site, we selected ten dominant female trees of

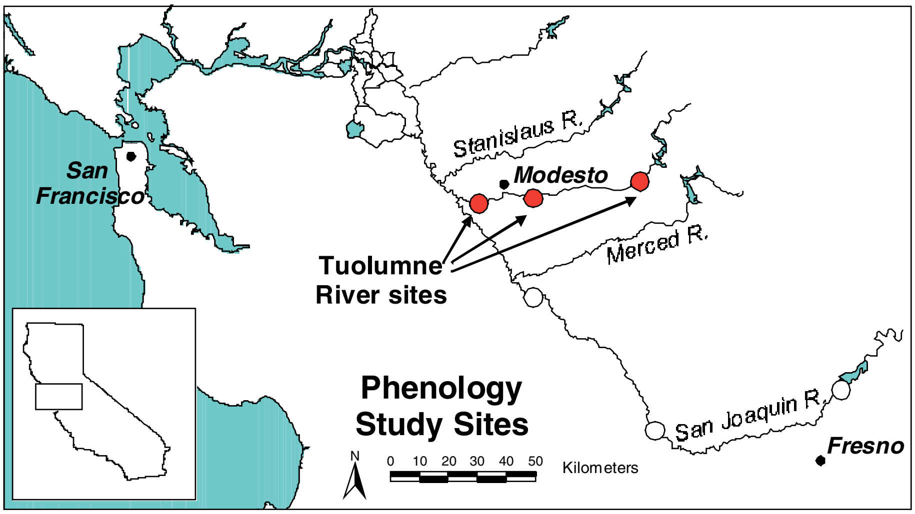

Figure 1. Phenology sampling sites in the San Joaquin Basin. *Filled circles* indicate location of Tuolumne River sites sampled in 2002–2004. *Open circles* denote San Joaquin River sites where auxiliary data were collected in 2003.

each species, which we surveyed 13–20 times during each growing season, from April through September. During each survey, seed density was quantified for each tree using 20-s counts of open catkins from each of the top, middle, and bottom thirds of the visible canopy. Our index of seed density was calculated as the sum of the three counts. Observations were conducted using a 25× binocular magnification from a fixed point. We conducted repeat samples (approximately 5% of all surveys), as well as inter-observer trials to assess observer precision. In addition to seasonal seed density, we characterized the POFR and SAGO phenology study trees in regard to their age, size, and growth rates. We measured tree height and diameter at breast height (DBH, 1.37 m), and determined minimum tree age and growth rate from increment cores using a sliding stage micrometer. SAEX were not sampled because their shrub growth form was not conducive to quantification using these methods. At all field sites, air temperature was continuously recorded using HOBO Pro sensors (Onset Computer Corporation, Pocasset, MA, USA) mounted inside weather shelters approximately 1 m above the ground surface, which was covered with unirrigated herbaceous vegetation (Snyder and others 2001).

Seed Longevity and Viability

To assess seed viability and longevity, we collected mature catkins between May and July 2002 from ten individuals of each species at the riparian phenology sites. For logistical reasons collections were limited to low branches (<5 m). Seed lot collections were distributed throughout each species' dispersal period to assess seasonal variation in seed condition (Guillot-Froget and others 2002).

Following collection in the field, we allowed the capsules to dehisce naturally, separated seeds from their seedcoat hairs, and stored them in dry paper envelopes at room temperature (van Splunder and others 1995). The first germination trial was conducted within 5 days after field collection. Subsequent trials were conducted at 13 to 15 day intervals for a maximum of five trials per seed lot. Seeds were placed on 100 mm filter paper saturated with distilled water in covered Petri dishes (van Splunder and others 1995). Germinants were counted every 2–3 days up to 10 days after imbibation (Young and Clements 2003a, b). A seed was considered germinated once the radicle had split the seed coat and began elongation (Bewley 1997). Each trial consisted of 10 replicate dishes of 15 seeds from each seed lot.

We calculated initial seed viability as the proportion of seeds that germinated within the 10-day observation window during the first trial per seed lot. Initial viability was calculated for all replicate dishes and averaged by species. We also measured seed longevity, which was defined as the storage time that reduces seed viability to 50% (Zasada and Densmore 1977; Karrenberg and others 2002). These values were calculated for each seed lot using a local linear interpolation of batch viability and storage time. For each species, seed longevity was reported as the mean (± 1 SE) longevity of all seed lots. Analysis of variance (ANOVA) was used to test differences in seed longevity between species (main effects) and between sites (sites nested within species). Given the unbalanced sampling design, we used Type III sum of squares to calculate F-ratios (Neter and others 1996). We also measured the germination delay associated with seed storage using the median response time, which is the period after trial initiation required to achieve 50% germination (Scott and others 1984).

Analyses of Tree Data and Seed Release Timing

Tree vital data were summarized by species and site to evaluate the influence of site factors on tree size, growth and fecundity. Tree age estimates are minimum values because the center of many trees contained heart rot where rings could not be identified. We used average ring increment for the last 3 years to represent current growth. Individual tree fecundity was calculated as the mean catkin count per survey over the 3 year sampling period.

To quantify seed release timing, we pooled catkin counts from the phenology trees to calculate a species-specific, site-level index of seasonal seed output. The site fecundity index was calculated as the mean of all catkin counts surveyed for all trees of a particular species at each survey date. This index of seed production and timing is the most relevant measure of seed availability in this study given the large variation in fecundity between trees, their clumped distribution and high seed dispersal ability, and the broad geographic scope of the study. Resampled catkin count observations indicate that the field methods are sufficiently precise at the site scale. The relative root mean square error (rRMSE), which was calculated using each pair of repeat field observations (approximately 5% of all observations), was ± 10% when aggregated by site.

We summed the site-based catkin counts as cumulative distributions to estimate when the majority of seeds were released, and defined the temporal boundaries of this window using quantiles of the cumulative distribution (Sokal and Rohlf 1995). Our relevant metrics for defining peak seed release were the days of the year corresponding to the 20th and 80th cumulative quantiles (referred hereafter to DY_{20} and DY_{80}), which capture the middle 60% of the seed density distribution. The 20th quantile date was chosen as an appropriate target for several reasons. Like traditional measures of phenology such as first flower and fruiting, it assumes that a physiological threshold underlies the onset of annual life stages (Fenner 1998; Trudgill and others 2005). Unlike measures of first occurrence; however, an intermediate quantile such as the 20th is not temporally sensitive to the tails of the distribution (Sokal and Rohlf 1995), nor does it require daily observations. The 20th quantile provides a robust measure of the onset of the peak seed release period and a logical management target for timing restoration flows to coincide with highest propagule density.

We tested differences in seed release timing (DY_{20}) and peak duration (number of days between DY_{20} and DY_{80}) using ANOVA for the data pooled for each Tuolumne River site in 2002–2004. Species, site and year were tested as main factors; interaction terms were not tested due to the limited degrees of freedom resulting from the site-averaging ($N = 18$). Instead, interaction plots were used to assess whether factor interactions were present.

Degree-day Modeling

To improve the accuracy of predicting the beginning of the peak seed release window (that is, DY_{20}), we developed a degree-day model using the seed release observations and continuous temperature records from the Tuolumne River sites. The baseline for comparing model performance was the average observed date of occurrence (that is, mean day of year) across all sites and years ($N = 9$) for each species. A degree-day model expresses annual plant development stages such as onset of vegetative and reproductive growth as a cumulative daily heat load above a specific threshold temperature (Snyder and others 1999; Bonhomme 2000). These models are well developed for annual cropping systems and integrative pest management (for example, Arnold 1959; Angus and others 1981), but are applied less frequently to natural systems (for example, Cenci and Ceschia 2000) or to long-lived woody species (for example, Bowers and Dimmitt 1994). A separate model was developed for each species because they exhibit unique timing patterns. Each degree-day model was optimized by empirically calculating the heat load that best predicts the observed onset of peak seed release (DY_{20obs}) for each site and year (Bowers and Dimmitt 1994; Cenci and Ceschia 2000).

In addition to seed release data, the degree-day model requires a complete and accurate local temperature record. Temperature data from the site HOBO sensors were cross-calibrated and corrected for bias, and gaps in the data record were modeled using linear fits to the nearest continuous temperature sensor in the California Irrigation Management Information System (CIMIS 2005). All model fits had r^2 values of 0.93 or greater.

The degree-day model has two parameters: a degree-day threshold corresponding to initiation of seed release, and a base temperature that represents a lower thermal limit to plant development

(Trudgill and others 2005). Both parameters were generated empirically because experimental phenological data for riparian tree species are not available. The basic unit of the model is the degree-day, which was calculated using daily time steps (Snyder and others 1999):

$$D_d = T_d - \theta$$

D_d represents daily degree-days, T_d is the mean daily air temperature from a field site and θ is the model base temperature. By definition, when T_d is less than θ, D_d equals 0.

For all sites in all years, we calculated the cumulative degree-days corresponding to DY_{20obs}, the date of observed 20th quantile of cumulative seed release. Because information on dormancy-breaking mechanisms was not available for these species, we began calculating the heat sums (denoted DD_{20obs}) on January 1 (Snyder and others 1999), which is approximately when mean daily temperature is at its annual minimum (NCDC 2005). We optimized the model base temperature, θ, for each species by calculating heat sums over all integer bases between 0–20°C and selecting the model base that resulted in the lowest RMSE of predicted minus observed seed release, $DY_{20pred} - DY_{20obs}$ (Cesaraccio and others 2001).

We evaluated the degree-day model several ways. First, we quantified each species' model fit by comparing the degree-day model mean square error (MSE) of predicted minus observed seed release initiation dates ($DY_{20pred} - DY_{20obs}$) to a null model MSE of observed dates (DY_{20obs}). The ratio of these two error estimates indicates how much environmental variation is explained by the model. Secondly, we evaluated whether the predicted dates of seed release initiation (DY_{20pred}) were reasonable estimators of observed dates (DY_{20obs}) using linear regression (Bowers and Dimmitt 1994). In a good model, a plot of predicted versus observed dates would closely fit a line with an intercept = 0 and a slope = 1. We specified a linear model using the ordinary-least-squares (OLS) bisector method (Isobe and others 1990) because functional relationships between variables and the error structure of the predicted values (which are derived from the empirical degree-day model) violate conventional OLS assumptions (Schmid and others 2000). Confidence limits were calculated using the bootstrap method with 1,000 replicates to estimate slope and intercept parameters (Feigelson and Babu 1992). All statistical analyses, model fitting, and optimizations were conducted in S-Plus (Version 6.1, Insightful Corp., Seattle, WA, USA).

Lastly, we used paired ANOVA models to evaluate the effects of site and year on two quantities, the annual date of peak seed release initiation (DY_{20obs}), and the heat sums that correspond to those dates (DD_{20obs}). We hypothesized that if site and year are significant factors in explaining variation in observed timing, a universally predictive heat sum relationship would render all factors insignificant in a corresponding ANOVA model of observed degree-days. The ANOVA model of DY_{20obs} values establishes the baseline factor influence on seed release timing; in contrast, the ANOVA model of DD_{20obs} values tests the factor effects on residual variation in timing not explained by temperature. Each species was analyzed separately, because the degree-day values were dependent on the base temperature used in each species' optimal degree-day model (Trudgill and others 2005).

Assessing Synchrony of Peak Runoff and Seed Release

If a heat sum model predicts seed release for riparian trees, we hypothesized that it should also predict to some extent the interannual variation in snowmelt runoff. To that end, we modeled annual seed release periods for the past 75 years and compared runoff timing for the same period. The date of peak flow during the spring snowmelt period was selected as the appropriate snowmelt timing parameter (Scott and others 1997). Peak flow determines the annual vertical limit of bank and floodplain inundation, and consequently the area of potential seedbeds (Mahoney and Rood 1998; Lytle and Merritt 2004). The snowmelt peak flow was calculated by constraining the temporal window after April 18 and using a 15-day running mean filter to exclude extended winter and spring rainstorms (Peterson and others 2000). We used USGS daily flow gauge data from the Tuolumne River at La Grange for the pre-dam period (1895–1970; gauge #11289650) and computed unimpaired flow for the post-dam period (1971–2004) from the Turlock Irrigation District and the California Data Exchange Center (gauges TLG and MIL).

For comparing peak seed availability with peak flow timing, we modeled annual seed release periods from 1928–2003 using the optimal degree-day model for each species. In addition to the base model parameters that predict the DY_{20} (Table 2), we calculated the degree-day threshold corresponding the end of the peak seed release period (that is, DY_{80}) at the same optimal base

Table 1. Tree Data and Seed Release Timing for Tuolumne River Sites

Site	N	Age[1], median and range (years)	DBH[2], mean ± 1 SE (cm)	Radial Growth[3], mean ± 1 SE (mm year^{-1})	Tree Fecundity[4] mean ± 1 SE (catkins survey^{-1})	Seed Release Initiation[5]			Peak Period[7]
						2002 (DY[6])	2003 (DY[6])	2004 (DY[6])	All years mean ± 1 SE (days)
POFR									
TR1-Ott	11	18 (12–29)	69.7 (± 9.4)	10.4 (± 1.3)	27.5 (± 3)	148	161	137	43 (±5)
TR2-Lakewood	11	15 (10–19)	75.4 (± 12.7)	10.2 (± 1.8)	14.3 (± 2.7)	132	133	113	30 (± 2)
TR3-Basso	10	44 (20–55)	86.7 (± 7.9)	4.1 (± 0.9)	13.2 (±2)	127	142	119	24 (± 1)
SAGO									
TR1-Ott	10	10 (7–15)	34.8 (± 6.2)	9.7 (± 1.2)	36.6 (± 4.3)	161	162	145	49 (± 2)
TR2-Lakewood	10	7 (4–16)	15.7 (± 2.5)	8.7 (± 1.8)	26.8 (± 3.4)	145	149	139	43 (± 5)
TR3-Basso	11	18 (9–67)	44 (± 6.8)	4.8 (± 1.2)	18.7 (± 3)	154	154	143	46 (± 3)
SAEX									
TR1-Ott	10	–	–	–	7.6 (± 1.8)	181	173	145	25 (± 3)
TR2-Lakewood	9	–	–	–	13.7 (± 2.8)	128	158	134	59 (± 8)
TR3-Basso	10	–	–	–	22.2 (± 2.7)	142	156	136	41 (± 6)

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[1] *Minimum age estimates, since some trees had rotten centers.*
[2] *Diameter at breast height, 1.37 m above the ground.*
[3] *Mean of last 3 years of radial growth increment.*
[4] *Calculated for each tree as the average catkin count per survey, 2002–2004.*
[5] *Peak seed release initiation is defined as the* DY_{20obs} *, the day corresponding to the 20th quantile of cumulative catkin counts (see text).*
[6] *Day-of-year conversions: 91 = April 1; 121 = May 1; 152 = June 1; 182 = July 1; 213 = August 1.*
[7] *Defined as the period bracketed by the 20th and 80th quantiles of cumulative catkin counts (*DY_{20obs} *to* DY_{80obs}*). Interannual differences in peak period were small, therefore all years are averaged.*

temperature for each species. Historical projections were generated ('hindcasted') for the $\text{DY}_{20\text{pred}}$ and $\text{DY}_{80\text{pred}}$ using mean daily temperature data from Modesto airport (National Climate Data Center cooperating station #45738), the longest local temperature record.

RESULTS

Seed Longevity, Viability, and Germination Delay

Results of the seed germination trials indicate that all species have very high initial seed viability but differ in rates of seed longevity (Figure 2). Mean initial seed viability was high for all seed batches collected early in the growing season. Average germination rates ranged from 87–97% among species. Batches collected late in the season had close to zero viability for all species. In the longevity trials, seed viability was negatively correlated with storage time, decreasing from the high initial viability values to below 50% for POFR and to less than 10% for SAGO and SAEX (Figure 2A–C). Seed longevity, or storage time corresponding to 50% germination, differed significantly by species (ANOVA $F_{2,20} = 4.98$, $P < 0.02$). POFR had the highest seed longevity (54 mean ± 6 SE days), followed by SAEX (44 ± 3 days) and SAGO (31 ± 3 days). Between sites there was more variation in POFR seed batch longevity than the other species; site means ranged from 32 days (SE ± 4 days) to 71 days (SE ± 3 days). SAGO and SAEX seed longevity values were more uniform across all sites.

For all species, maximum germination generally occurred within 2 days of the beginning of the trial, but storage times longer than several weeks substantially delayed germination (Figure 2D). Longer storage periods increased the median germination time, or the time until 50% of the seeds germinate, up to 10 days for the longest-stored POFR batches. Because seed longevity was lowest for SAGO, most long-stored batches failed to attain 50% germination; thus median germination time was not calculable for these batches.

Stand Characteristics and Seed Release Patterns

The sites used in our phenology study are broadly representative of remnant riparian stands in the San Joaquin Basin (Table 1). These riparian forest neighborhoods have a typically open canopy structure with the occasional patch of dense regeneration along river and slough channels. All of the trees sampled (which did not include SAEX)

Table 2. Summary of Degree-day Models Predicting Initiation of Seed Release

	POFR	SAGO	SAEX
Degree-day model summary			
Model base, θ (degrees C)	16	15	14
Model threshold, DD_{20pred} (degree-days)	56.7	169.1	216.9
Degree-day model MSE ($days^2$)	93.6	19.3	175
Null model MSE ($days^2$)	189.9	58.2	291.5
MSE ratio (model/null)	0.49	0.33	0.60
Degree-Day Model Fit			
(Regression of Predicted versus observed DY_{20})			
Intercept estimate (± 1SD)	−46.8 (±34.6)	−18.3 (±26.9)	−181.2 (±65.7)
Intercept 95% confidence limits	−211.9 – 20.3	−161.7 – 50.9	−888.0 – −45.1
Slope estimate (± 1 SD)	1.34 (±0.26)	1.13 (±0.18)	2.19 (±0.43)
Slope 95% confidence limits	0.91 – 2.72	0.67 – 2.03	1.28 – 6.36

Upper panel: parameters and mean square error estimates for optimized models. Model MSE is calculated for predicted minus observed DY_{20} for each site and year (N = 9 for each species). Null Model MSE is the MSE of the observed DY_{20} values. Values <1 for the MSE ratio indicate better model fits over the null model. Lower panel: evaluation of the degree-day model using OLS bisector linear regression of predicted seed release initiation date versus observed dates (see Figure 2).

were less than 70 years old; because of missing ring problems, these represent minimum estimates of actual tree age. POFR trees were typically older and larger than SAGO. Most of the variation observed in tree age and size was among sites, rather than between trees within a site. POFR cohorts were typically 7–10 years older than the SAGO trees at each site. Among sites, the per-tree fecundity index ranged between 13 and 28 catkins $tree^{-1}$ $survey^{-1}$ for POFR, 19 and 37 catkins $tree^{-1}$ $survey^{-1}$ for SAGO, and 8 and 22 catkins $tree^{-1}$ $survey^{-1}$ for SAEX (Table 1).

Seed release for POFR preceded SAGO in all years at all sites along the Tuolumne River, and POFR preceded SAEX in all cases but one (Table 1; Figure 3). The mean start date for the peak seed release period (that is, the DY_{20obs} metric using site-pooled data) was May 15 (range April 23–June 10). The mean DY_{20} for SAGO and SAEX were roughly the same, May 30 and 31 respectively, but the range in SAEX start dates (May 8–June 30) was greater than for SAGO (May 19–June 11). In 2004, a year with an unusually warm spring, seed release occurred substantially earlier at all sites for all species compared to 2002 and 2003 (Table 1; Figure 3). Seed release was coordinated among trees at each site, though groups of trees at some sites consistently released seeds earlier than others.

Initiation of peak seed release was significantly different between species (ANOVA, $F_{2,20} = 13.7$, $P < 0.0002$), sites ($F_{2,20} = 18.6$, $P < 0.0001$) and years ($F_{2,20} = 16.2$, $P < 0.0001$). Bi-plots of the main effects indicated no strong factor interactions. The variation in the duration of peak seed release (the period from DY_{20} to DY_{80}) was neither significant for species ($F_{2,20} = 2.9$, $P = 0.08$), site ($F_{2,20} = 0.69$, $P = 0.52$), nor year ($F_{2,20} = 0.35$, $P = 0.71$). Peak seed release lasted 24–43 days for

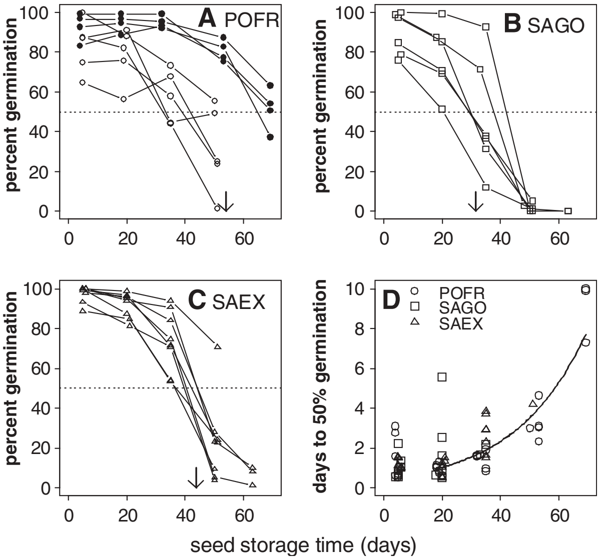

Figure 2. Seed longevity and germination rate as a function of storage time for all seed batches. Longevity is defined as the storage time corresponding to a reduction of germination rate to 50%. *Arrows* indicate mean seed longevity for **A**) POFR (54 days), **B**) SAGO (31 days) and **C**) SAEX (44 days). POFR had large site-based differences in longevity. *Solid symbols* in panel **A**) are for trees at the TR1-Ott site; *open symbols* are for trees from all other sites. Panel **D**) plots the observed delay in germination associated with seed storage time. Data points are number of days required to reach 50% germination for each seed batch; batches with less than 50% final germination are not shown. The *fitted line* illustrates an exponential increase in germination delay with storage time after approximately 3 weeks; data from the three species are pooled.

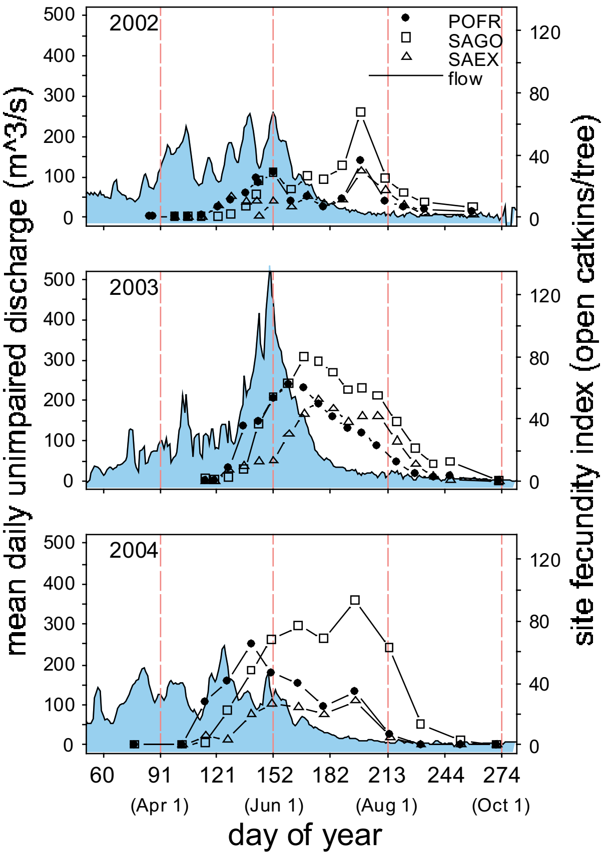

Figure 3. Patterns of seed release and unimpaired flow along the Tuolumne River. For all species, the annual fecundity index is calculated as mean per-tree open catkin count for all surveys; data from all sites are pooled. The hydrograph is computed unimpaired discharge at La Grange Dam (California Data Exchange Center, gauge TLG). *Day-of-year axis labels* indicate the first day of each month.

POFR, 43–49 days for SAGO and 25–59 days for SAEX (Table 1). When the data were pooled across all sites to evaluate basin-wide patterns, peak seed release coincided with the end of the unimpaired Tuolumne River snowmelt runoff period, with POFR seed density reaching a maximum 2–4 weeks earlier than SAGO and SAEX (Figure 3).

Degree-day Model Evaluation

We used the degree-day model to evaluate the influence of local temperature on the observed variation in seed release initiation for each species. For the Tuolumne River data, the optimized degree-day model predicts DY_{20obs} better for all species than the null model, which was specified as the mean day of occurrence (Table 2). The heat sum thresholds (DD_{20pred}) and optimal base temperature (θ) of the best fitted model were 56.7 degree-days (θ = 16°C) for POFR, 169.1 degree-days (θ = 15°C) for SAGO, and 216.9 degree-days (θ = 14°C) for SAEX (Table 2). Predictions of seed release initiation dates (DY_{20pred}) based on unique temperature records for each site and year resulted in a lower MSE ($DY_{20pred} - DY_{20obs}$) than the comparable null model MSE for all species. The MSE ratio, which is a goodness-of-fit measure for the degree-day model (Cesaraccio and others 2001), was 0.49 for POFR, 0.33 for SAGO, and 0.60 for SAEX; lower values indicate better model fits. These ratios indicate that the degree-day model reduced the error in predicting the onset of seed release by 51% for POFR, 67% for SAGO, and 40% for SAEX (Table 2). Sensitivity analysis of the base temperature model parameter indicated that for POFR, all bases between 0 and 20°C resulted in better models than simple day-of-year averages; for SAGO and SAEX, all models with base parameter values between 0 and 18°C were better (Figure 4).

A plot of seed release initiation dates generated by the model (DY_{20pred}) versus the observed values (DY_{20obs}) indicates that most points fall along the 1:1 line for POFR and SAGO; in general, SAEX predictions were less accurate (Figure 5). Using the OLS bisector regression method (Isobe and others 1990), we generated linear parameter estimates and compared them to the hypothesized parameters (intercept = 0 and slope = 1). The 95% confidence intervals for the OLS bisector parameters contained the hypothesized parameters for POFR and SAGO, but not for SAEX (Table 2). Slope estimates were 1.34 for POFR, 1.13 for SAGO and 2.19 for SAEX. Slope estimates greater than 1 indicate that the range of observed values is greater than the range of predicted values; this situation is particularly evident for SAEX.

The paired ANOVA models testing site and year effects on the peak seed release initiation dates (DY_{20obs}) and the corresponding degree-day sums (DD_{20obs}) indicate that annual and site-to-site differences in heat sums preceding seed release were generally smaller than differences in timing due to those factors (Table 3). In the baseline ANOVA models predicting the $DY_{20obs,}$ site and year factors were significant at the P less than 0.05 level for both POFR and SAGO. Plot traces for site and year did not cross in either species model, indicating no strong factor interactions. In the matching ANOVA models testing DD_{20obs}, the year effect was removed for both POFR and SAGO, and the site effect was removed as well for SAGO; these factors were not significant at the P less than 0.05 level. For

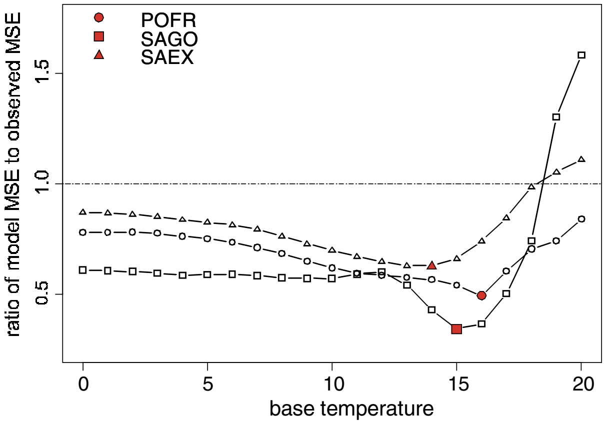

Figure 4. Sensitivity analysis of the base temperature parameter for species-specific degree-day models predicting the onset of peak seed release. The ordinate axis is the ratio of the degree-day model MSE (see text) to the MSE of the observed values (DY_{20obs}). Values less than 1 for the MSE ratio indicate better degree-day model fit over the null model. Solid symbols indicate the optimal base temperature for each species.

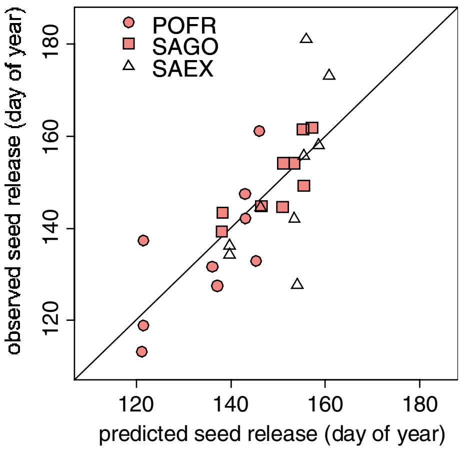

Figure 5. Predicted versus observed dates of seed release initiation for POFR, SAGO and SAEX at three Tuolumne River sites, 2002–2004. Seed release initiation was defined as the DY_{20obs}, the day of the year corresponding to the 20th quantile of the seasonal fecundity index distribution for each species (see text). Predicted dates (DY_{20pred}) were modeled using an empirical degree-day model. The 1:1 line represents a hypothetical perfect correspondence between predicted and observed values.

POFR, the site effect remained ($F_{2,4} = 8.13$, $P = 0.04$) even after translating release time as degree-days. For SAEX, neither site nor year was a significant factor predicting the DY_{20obs}; therefore the matching ANOVA of degree-day values was not relevant for evaluating the effectiveness of the heat sum model.

Table 3. Paired ANOVA Models for Seed Release Initiation (DY_{20obs}, units = days) and Corresponding Heat Sums (DD_{20obs}, units = degree-days)

	DF	SS	MS	F	*P*
POFR					
DY_{20obs}					
site	2	901.5	450.7	30.50	<0.01
year	2	748.6	374.3	25.33	<0.01
residuals	4	59.1	14.8		
DD_{20obs}					
site	2	12,678.2	6,339.1	8.13	0.04
year	2	689.5	344.8	0.44	0.67
residuals	4	3,118.4	779.6		
SAGO					
DY_{20obs}					
site	2	206.9	103.4	11.73	0.02
year	2	281.5	140.7	15.96	0.01
residuals	4	35.3	8.8		
DD_{20obs}					
site	2	6,199.9	3,100.0	3.04	0.16
year	2	271.1	135.5	0.13	0.88
residuals	4	4,082.8	1,020.7		
SAEX					
DY_{20obs}					
site	2	1,175.6	587.8	4.01	0.11
year	2	862.0	431.0	2.94	0.16
residuals	4	586.2	146.5		
DD_{20obs}					
site	2	39,527.3	19,763.6	2.04	0.25
year	2	3,218.8	1,609.4	0.17	0.85
residuals	4	38,827.9	9,707.0		

Data are the from the three Tuolumne River sites in 2002–2004 (n = 9 for each species).

Synchrony of Peak Runoff and Seed Release

We used the best base temperature from each species' degree-day models and the historical daily Modesto temperature data to project annual seed release periods for the last 75 years. For POFR, the projected peak seed release period (DY_{20pred} to DY_{80pred}) brackets the date of peak snowmelt in almost all years (Figure 6). In eight of nine observed examples on the Tuolumne River (three sites in 3 years), the POFR peak seed release period intersected the date of maximum spring runoff, which varied by almost 50 days. For SAGO and SAEX, peak snowmelt coincides with the beginning of the seed release period, resulting in the bulk of seed release occurring after floodwaters began to recede.

DISCUSSION

These results show that (1) patterns of propagule availability for Central Valley pioneer riparian trees

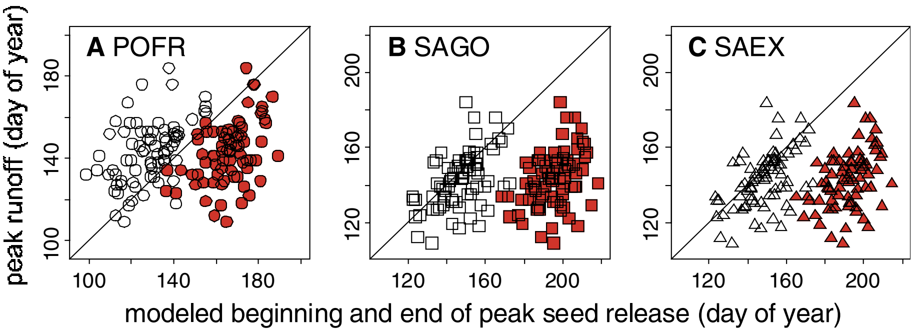

Figure 6. Tuolumne River observed peak runoff date plotted against projected peak seed release initiation (DY_{20}; *open symbols*) and end (DY_{80}; *closed symbols*) modeled using heat sums for all years from 1928–2003. Peak discharge intersects the modeled POFR seed release period in most years (that is, the 1:1 line divides the DY_{20} and DY_{80} dates). SAGO and SAEX projected seed release initiation coincide with peak discharge; most seed dispersal occurs during the descending hydrograph limb. Hydrologic data are actual Tuolumne River discharge at La Grange for the pre-dam period (1895–1970; USGS gauge # 11289650) combined with computed unimpaired discharge for the post-dam period 1971–2004 (Turlock Irrigation District). Temperature data are NCDC daily values for Modesto airport (Cooperating station #45738).

are species-specific with regard to seed longevity and seed release timing; (2) a degree-day model robustly predicts annual timing of seed release for the two tree species in the study; and (3) early-season temperature patterns likely serve as the common driver coordinating annual seed release with the spring snowmelt runoff pulse. Among the species in Salicaceae studied, the degree-day modeling approach works best for the two tree species, POFR and SAGO, and less well for SAEX, a clonally-propagating shrub species. Interannual differences in timing were better explained by temperature patterns than site-to-site differences, suggesting that seed development and release are also influenced by other local and/or genetic factors. Because the degree-day model reduces the uncertainty in predicting life history phenology for riparian trees, it may prove an effective component of process-based restoration approaches, for example providing annual targets for timing river flows to maximize seedling recruitment throughout a river basin (Rood and others 2005).

Patterns of Propagule Availability

Patterns of seed release timing, fecundity, and seed longevity differ for the three species in this study. As in similar semi-arid ecosystems, POFR seed release consistently precedes SAGO and SAEX (McBride and Strahan 1984a; Brock 1994; Johnson 1994). This pattern is consistent with their observed topographic distributions in riparian zones and dominant reproductive strategies. POFR trees, which release seeds during or shortly after peak snowmelt runoff (Figures 3, 6), typically inhabit higher floodplain surfaces. The willow species, which release seeds later during the snowmelt recession period, occur on lower bank surfaces that become dewatered at lesser flow levels (McBride and Strahan 1984b).

The high rates of initial seed viability we measured (Figure 2) match other laboratory trials for these species (Young and Clements 2003a, b). Seed longevity results also are consistent with previous work and indicate that the annual window of seed viability for Salicaceae species is limited to a few weeks. In this study and others, longevity was higher for *Populus* seeds, which are substantially larger than *Salix* seeds (van Splunder and others 1995; Karrenberg and others 2002). The estimate of POFR seed longevity in this study, 54 days, is shorter than another laboratory-tested estimate for this species (85 days), but longer than the 15-to 30-day results for batches stored under field conditions (Fenner and others 1984). Longevity estimates for SAGO (31 days) and SAEX seeds (44 days) are within the range of published values for these species and other riparian willows (Pelzman 1973; Niiyama 1990; Siegel and Brock 1990; van Splunder and others 1995).

These laboratory-derived estimates of initial seed viability and longevity are likely higher than experienced under field conditions (Pelzman 1973; Guilloy-Froget and others 2002). Adverse abiotic and biotic conditions (for example, exposure to increased humidity and high temperatures, insects and fungal pests) can reduce viability or inhibit dispersal (Smith and Berjak 1995), especially at the end of the growing season (Guilloy-Froget and others 2002). In addition, longer storage time caused a substantial delay in germination (Figure 2D), which some studies suggest results in seedlings of lower vigor and viability (Abdul-Baki and Anderson 1972; Bradbeer 1988; Smith and Berjak 1995).

Predicting Seed Release Timing

Understanding environmental forces that control propagule availability is important for predicting riparian community dynamics (Willson and Traveset 2000) and developing effective ecosystem restoration strategies such as flow releases to promote recruitment (Bovee and Scott 2002; Rood and others 2005). The results of this study confirm that early season temperature regime is an important factor controlling timing of seed development and release for the two dominant tree species in near-channel riparian communities along the Tuolumne River. The two-parameter heat sum model based on a simple, field-based index of fecundity reduces the temporal variation in the start of seed release by 40–67% over day-of-year averages (Table 2) and provides reasonable approximations of observed seed release timing (Figure 5). Cumulative heat loads account for a great deal of the variation in timing observed between years, and to some degree the variation observed between sites (Table 3).

These results reinforce the utility of degree-day models used in agricultural systems to predict temporal and geographic variation in developmental stages such as flowering and fruit ripening (Arnold 1959; Snyder and others 1999; Trudgill and others 2005). For long-lived woody species in natural settings, temperature is a major determinant of growth (Kalischuk and others 2001) and reproductive phenology (Bowers and Dimmitt 1994). For some species, temperature acts in conjunction with other factors such as day length (Kaszkurewicz and Fogg 1967; Howe and others 1995) and precipitation timing (Bowers and Dimmitt 1994; Kramer and others 2000) to cue physiological processes. These factors were not included in the Tuolumne River models because all sites had similar photoperiods and precipitation regimes.

The base temperatures that resulted in the best fitting models ranged from 14–16°C, which are higher than for other temperate plants (typical range 1–4°C), but are reasonable for C3 species from warm regions (Angus and others 1981; Trudgill and others 2005). Base temperatures range 10–15°C for woody desert plants (Bowers and Dimmitt 1994) and 7–16°C for most tropical crops (Angus and others 1981). Sensitivity analysis determined that the degree-day models in the present study are effective at a range of bases between 0 and 20°C (Figure 4). Other studies have shown a similar range of base temperatures resulting in minimal loss of model accuracy (Spano and others 1999).

Degree-day Model Applicability Across Species and Geographic Regions

The degree-day model was effective at predicting seed release timing for the two tree species in this study; however, predictions were much less precise for SAEX, the dominant riparian shrub. This species has a more diffuse dispersal period and lower individual fecundity than both POFR and SAGO (Table 1). For SAEX, the degree-day model improved seed release predictions very modestly and left substantial local variation in timing unexplained. This relative insensitivity to heat loads for triggering seed development and dispersal, combined with its shrub habit and strongly clonal reproduction strategy (Ottenbreit and Staniforth 1992; Douhovnikoff and others 2005) suggest that SAEX has fundamentally different responses to climate and flow patterns relative to the two tree species in our study. These differences may explain why SAEX is frequently observed to increase in abundance following dam closure (Pelzman 1973), whereas flow regulation generally has detrimental effects on long-term POFR and SAGO recruitment patterns (Fenner and others 1985; Scott and others 1997; Stella and others 2003).

Though seasonal temperature regime is undoubtedly a strong driver of reproductive timing for the trees, there appears to be strong local or ecotypic influences on timing as well. The degree-day model was much better at explaining interannual variation in timing compared to site-to-site differences (Table 3). Trees of all species at the downstream-most site, which also had the hottest early-season temperature regime, generally released seeds later compared to the two sites upstream. These results run contrary to degree-day model expectations, but make sense from a catchment perspective. On most rivers, downstream sites experience flood pulses later than upstream ones and have generally hotter temperature regimes due to elevation differences (Magilligan and Graber 1996). If it is advantageous to coordinate seed dispersal with spring flood peaks, then these species would be expected to develop an ecotypic gradient in degree-day thresholds that would be negatively correlated with elevation and longitudinal distance upstream.

Ecotypic or local influence on seed release timing likely occurs across river basins as well. We tested the generality of the Tuolumne model by collecting corresponding data for three riparian sites along the San Joaquin River in 2003. The same relative timing pattern occurred between species (POFR released earlier than the willows), but POFR trees on the San Joaquin released seeds approximately 2 weeks earlier than on the Tuolumne, and both willow species released seeds approximately 2 weeks later (Stella 2005). Annual growing season temperatures were consistently hotter at the San Joaquin sites compared to the Tuolumne sites. When we applied the Tuolumne River-based models to 2003 data from the three San Joaquin River sites, they did not accurately predict seed release timing for any species.

These results are not surprising, given that even in more controlled agricultural settings, model threshold and base parameter estimates vary depending on the year when the data were collected (Arnold 1959), the sites sampled (Bowers and Dimmitt 1994), and the parameter optimization method used (Snyder and others 1999). There is no consensus on why degree-day models are not effective beyond their calibration data. However, many studies have established that genetic factors are strong determinants of phenological differences within populations (Pauley and Perry 1954; McMillan and Pagel 1958; Fenner 1998). For example, results from common garden experiments indicate that the date of growth cessation in *P. deltoides* and *P. balsamifera* ssp. *trichocarpa* is negatively correlated with latitude of origin, suggesting that this phenological milestone has been selected for in response to local growing season duration (Pauley and Perry 1954).

To develop a more generally-applicable seed release model for a larger region (for example, the entire San Joaquin Basin), a broader range of sites would need to be sampled initially. Given this broader calibration data set, our research suggests that an effective empirical degree-day model can be developed with only one or two years of sampling, and that variation in seasonal timing in subsequent years can be accurately predicted. Some researchers suggest that degree-day model predictions may be refined by incorporating a photoperiod or physiological 'trigger date' variable (Bowers and Dimmitt 1994), and/or modeling biological development as a non-linear function of temperature (Arnold 1959; Shaykewich 1995). We did not develop these more complex models for the Tuolumne River basin model because experimental information on basic physiological requirements is lacking for the species in this study.

Implications for Restoring Riparian Communities

The synchrony of historical snowmelt timing with modeled peak seed release suggests that the degree-day model using a representative temperature record (for example, daily mean temperature at Modesto) is an effective and scale-appropriate integrator of environmental conditions within the entire Tuolumne River basin. The long-term correspondence of snowmelt runoff peak with hindcasted seed release periods (Figure 6) suggests that heat loads are a common driver controlling the annual timing of both factors (Cayan and others 2001). Though this general point may be self-evident, precisely modeling spring runoff volume and timing from temperature records is difficult given the complex interactions of precipitation patterns, topography, and thermodynamics that occur over whole watersheds (Ferguson 1999).

In light of the widespread and on-going river regulation on the Tuolumne River and other California rivers, the present study has important implications for community dynamics and riparian restoration strategies (Poff and others 1997; Rood and others 2005). In the semi-arid San Joaquin Basin, where the demand and cost for both water and ecosystem restoration are high, reducing the uncertainty around interannual release timing will allow for shorter and less costly spring flow pulses for restoration (Patten 1998; Naiman and others 2002; Poff and others 2003). It remains an open question whether such an approach would work under non-equilibrium ecological conditions generated by a substantially changed climatic regime (Hayhoe and others 2004; Lenihan and others 2003). Riparian trees, like many other species, adapt to interannual variation in heat loads, but there is a risk with directional climate change of decoupling physical ecosystem drivers such as precipitation and temperature regimes from their dependent biological processes that maintain these species in the ecosystem (Chiune and Beaubien 2001; Peneulas and Filella 2001).

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