How do riparian trees time the flood?
Synchrony of seed dispersal, hydrology and local climate in a semi-arid river basin.

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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) and *Salix gooddingii* (SAGO), the tree species that dominate near-channel riparian forest stands on regulated rivers in the San Joaquin Basin, CA. We fit a degree-day model to field data of seasonal propagule density and local temperature in 2002-2004 to predict the onset of the peak seed release 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) and May 30 for SAGO (range May 19-June 11). The heat sum model reduced the variance in predicted date of seed release onset by 68-70% over julian day means. The model was effective at predicting dispersal timing between years and between Tuolumne basin sites. The historical analysis suggests that POFR seed release coincided with peak runoff in almost all years, whereas SAGO dispersal occurred during the spring flood recession. Our modeling approach is a potentially valuable tool 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 events (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-lived availability of viable seedbed 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 trees are Fremont cottonwood (*Populus fremontii* S. Watson ssp. *fremontii*; hereafter referred to as POFR), and Goodding's black willow (*Salix gooddingii* C. Ball; hereafter referred to as SAGO) 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 the spring snowmelt pulse.

Declines in 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 Descamps 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 spring snowmelt flow pulse. Finally, we present an empirically-based approach to modeling the timing and relative density of pioneer riparian tree propagules throughout a river basin.

METHODS

Study area

The San Joaquin Basin covers 35,000 km^2 in California's southern Central Valley (Figure 1). It experiences a Mediterranean climate, with an average of 30 cm (range: 15-180 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 and Trush 2000). The tree 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 New Don Pedro Dam to the confluence of the San Joaquin River (Figure 1). Preliminary studies at these three sites confirmed our assumption that neither species maintains a seed bank from one year to the next (J. Stella, unpublished data). 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 in order to develop a predictive model. At each site, we selected 10 dominant female trees of 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-second 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 25x binocular magnification from a fixed point. We conducted repeat samples (approx. 5% of all surveys), as well as inter-observer trials to assess observer precision. In addition to seasonal seed density, we characterized the 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. At each site, air temperature was continuously recorded using HOBO Pro sensors (Onset Computer Corporation, Pocasset, MA) 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 trees of each species at the riparian phenology sites. For logistical reasons collections were limited to low branches <5 m high. 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 pappus 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 13-15 day intervals for a maximum of 5 trials per seed lot. Seeds were placed on 100mm 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, 2003b). 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 defined seed longevity as the storage time that reduces seed viability to 50 percent (Zasada and Densmore 1977; Karrenberg and others 2002). We calculated these values for each seed lot using a local linear interpolation of batch averages, then averaged all seed lots by species. We used analysis of variance (ANOVA) to test differences in seed longevity between species (main effects) and between sites (sites nested within species). Given our 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

We summarized tree vital data by species and site to evaluate the influence of site factors on tree size, growth and fecundity. Tree age estimates are minimum values since 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 three-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 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 our 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. Repeat catkin count observations indicate that our field methods are sufficiently precise at the site scale. The overall precision of these estimates had relative root mean square error (RMSE) +/- 10%.

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 julian dates corresponding to the 20th and 80th cumulative quantiles (referred hereafter to JD20 and JD80), which capture the middle 60 percent 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 (Zalom 1983; Fenner 1998). 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 (JD20) and peak duration (time interval from JD20 to JD80) 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

In order to improve the accuracy of predicting the beginning of the peak seed release window (the JD20), we developed a degree-day model using the seed release observations and continuous temperature records from our Tuolumne River sites. Our baseline for comparing model performance was the average observed julian date 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 (Zalom 1983; Bonhomme 2000). These models are well developed for annual agricultural crops and integrative pest management (*e.g.*, Arnold 1959), but applied less frequently to natural systems (*e.g.,* Cenci and Ceschia 2000) or to long-lived woody species (*e.g.*, Bowers and Dimmitt 1994). We developed a separate model for each species since they exhibit unique timing patterns, and optimized each degree-day model by empirically calculating the heat load that best predicts the observed onset of peak seed release ($JD20_{obs}$) for each site and year (Bowers and Dimmitt 1994; Cenci and Ceschia 2000).

In addition to seed release data, our 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). All model fits had r^2 values ≥ 0.93.

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 (Zalom 1983). We generated both parameters empirically, since experimental phenological data for riparian tree species are not available. The basic unit of the model is the degree-day (Snyder and others 1999), which we calculated using hourly-averaged temperature from our sites (Cesaraccio and others 2001):

$$D_d = \sum (T_h - \theta)/24 \qquad \text{(Eqn. 1)}$$

D_d represents daily degree-days, T_h is the mean hourly air temperature and θ is the model base temperature. When temperature was less than the base, the degree-day quantity is set to zero (Zalom 1983).

For all sites in all years, we calculated the cumulative degree-days corresponding to $JD20_{obs}$, 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 $DD20_{obs}$) on 1 January (Snyder and others 1999), which is approximately the long-term minimum temperature between growing seasons (NCDC 2005). We optimized the model base temperature, θ, for each species by calculating heat sums over all integer bases between 0-40 °C and selecting the model base that resulted in the lowest RMSE of predicted minus observed seed release, $JD20_{pred} - JD20_{obs}$ (Ring and others 1983; Snyder and others 1999).

We evaluated the degree-day model several ways. First, we compared the degree-day model mean square error (MSE) of predicted minus observed seed release initiation dates ($JD20_{pred} - JD20_{obs}$) to a null model MSE of observed dates ($JD20_{obs}$). Secondly, we evaluated whether the predicted dates of seed release initiation ($JD20_{pred}$) were reasonable estimators of observed dates ($JD20_{obs}$) using linear regression (Bowers and Dimmitt 1994). In a good model, a plot of predicted versus observed dates would closely fit a line with intercept and slope parameter values (0,1). 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 1000 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).

Lastly, we used paired ANOVA models testing main factor effects of site and year on two quantities, the julian day of peak seed release initiation ($JD20_{obs}$), and the heat sums that correspond to those dates ($DD20_{obs}$). We hypothesized that if site and year are significant factors in explaining variation in observed timing, that a universally predictive heat sum relationship would render all factors insignificant in a corresponding ANOVA model of observed degree-days. The ANOVA model of $JD20_{obs}$ values establishes the baseline factor influence on seed release timing, and the ANOVA model of $DD20_{obs}$ values tests the factor effects on residual variation in timing not explained by temperature. We analyzed POFR and SAGO separately, since the degree-day values were dependent on the base temperature used in each species' optimal degree-day model.

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 past 75 years using the best biological degree-day model and compared runoff timing for the same period. We selected as our snowmelt timing parameter the date of peak flow during the spring snowmelt period (Scott and others 1997), which 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). We identified snowmelt peak flow by constraining the temporal window after April 15 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 the annual seed release period for each species from 1928-2003 using mean daily temperature data from Modesto airport (National Climate Data Center cooperating station #45738), the longest local temperature record. Because long-term hourly temperature data were not available for this station, we re-parameterized our seed release model using mean daily temperature data from our sites (Zalom 1983) to calculate appropriate model parameters for the historical analysis. In addition to the $JD20_{pred}$ and $JD80_{pred}$, we computed the $JD50_{pred}$, or date corresponding to when 50% of catkins were open, in order to evaluate the projected time lag between peak flow and the midpoint of seed release. Time lag was calculated as the number of days between peak runoff and the $JD50_{pred}$, with positive values indicating later seed release.

RESULTS

Seed longevity, viability, and germination delay

Results of the seed germination trials indicate that both species have very high initial seed viability but differ in rates of seed longevity (Figure 2). Mean initial seed viability was 87% (SE ± 2%, *n* =104 trials) for POFR and 89% (SE ± 2%, *n*=60) for SAGO for batches collected during the early and middle part of each species' seed release periods. Late-season batches had close to zero viability for both 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 zero for SAGO (Figure 2). Seed longevity, or storage time corresponding to 50% germination, differed significantly by species ($F_{1,9} = 35.7$, $p<0.001$) and site nested within species ($F_{4,9} = 19.6$, $p<0.001$). Seed longevity was higher for POFR (54 mean ± 6 SE days) than for SAGO (31 ± 3 days). Between sites there was more variation in POFR seed batch longevity; site means ranged from 32 days (SE ± 4 days) to 71 days (SE ± 3days). SAGO seed longevity was more uniform across all sites. Note that these means do not include seeds from the late season batches that had near zero viability.

For both species, maximum germination generally occurred within two days of the beginning of the trial, but storage times longer than several weeks substantially delayed germination (Figure 3). 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 (Figure 3). Because seed longevity was lower for SAGO, most long-stored batches failed to attain 50% germination.

Stand characteristics and seed release patterns

The trees used in our phenology study are broadly representative of those in remnant riparian stands in the San Joaquin Basin (Table 1). These riparian forest neighborhoods had a typically open canopy structure with the occasional patch of dense tree regeneration along river and slough channels. Minimum age for all trees sampled was <70 years old; POFR trees were typically older and larger than SAGO. Most of the variation observed in tree ages and size was among sites, rather than between trees overall. POFR cohorts were typically 7-10 years older than the SAGO trees at each site. Among sites, the per-tree fecundity index ranged 13-28 catkins tree $^{-1}$survey $^{-1}$ for POFR and 19-37 catkins tree $^{-1}$survey $^{-1}$ for SAGO (Table 1).

Seed release for POFR preceded SAGO in all years at all sites along the Tuolumne River (Table 1; Figure 4). The mean start date for the peak seed release period (*i.e.,* the $JD20_{obs}$ metric using site-pooled data) was May 15 (range April 23-June 10) for POFR and May 30 (range May 19-June 11) for SAGO. Seed release was fairly 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, $F_{1,12} = 39.7$, $p<0.0001$), sites ($F_{2,12} = 17.1$, $p<0.001$) and years ($F_{2,12} = 17.1$, $p<0.001$). Bi-plots of the main effects indicated no strong factor interactions. The duration of peak seed release (the period from JD20 to JD80) varied by species ($F_{2,12} = 19.1$, $p<0.001$) and site ($F_{2,12} = 4.5$, $p=0.03$) but not by year ($F_{2,12} = 0.88$, $p=0.44$). Peak seed release lasted 24-43 days for POFR and 43-49 for SAGO (Table 1). When the data were pooled across all sites to evaluate basin-wide patterns, peak seed release coincided with the end of the historical Tuolumne River snowmelt runoff period, with POFR seed density reaching a maximum about a month earlier than SAGO density (Figure 5).

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 $JD20_{obs}$ better than the null model (julian day averages) for both species (Table 2). When converted to julian day predictions ($JD20_{pred}$) based on unique temperature records for each site and year, the model thresholds resulted in a lower MSE ($JD20_{pred}$ minus $JD20_{obs}$) than the comparable null model MSE for all species, which used julian day averages. The MSE associated with the degree-day model was 68% lower than that of the null model for POFR, and 70% lower for SAGO (Table 2).

A plot of seed release initiation dates generated by the model ($JD20_{pred}$) versus the observed values ($JD20_{obs}$) indicates that most points fall along the 1:1 line (Figure 6). Using the OLS bisector regression method (Isobe 1990), we generated linear parameter estimates that were within the 95% confidence intervals for the hypothesized parameters (intercept = 0 and slope = 1) for both species.

The paired ANOVA models testing site and year effects on the peak seed release initiation dates ($JD20_{obs}$) and the corresponding degree-day sums ($DD20_{obs}$) indicate that the degree-day model was effective at reducing the variation in both factors. In our baseline ANOVA models predicting the $JD20_{obs}$, site and year factors were significant at the $p<0.05$ level for both species (Table 3). Plot traces for site and year did not cross in either species model, indicating no strong factor interactions. In the matching ANOVA models testing $DD20_{obs}$, neither site nor year was significant for either species (Table 3). By expressing the seed release start date in cumulative degree-days, we were able to reduce both the site-to-site and annual variation in the onset of peak seed release.

Synchrony of peak runoff and seed release

We used the best overall base temperature from our three biological models using mean daily temperature 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 ($JD20_{pred}$ to $JD80_{pred}$)

brackets the date of peak snowmelt in almost all years (Figure 7). For SAGO, peak snowmelt coincides with the beginning of the seed release period, resulting in the bulk of seed release occurring after floodwaters began to recede. POFR peak release (the $JD50_{pred}$) lagged peak flow by less than a week on average (mean and SE = 6.5 +/- 1.6 days), whereas SAGO peak release lagged peak flow by almost a month (28.2 +/- 1.7 days).

DISCUSSION

Our results show that 1) patterns of propagule availability for Central Valley pioneer riparian trees are species-specific with regard to seed longevity and seed release timing; 2) a degree-day model robustly predicts annual timing of seed release; and 3) early-season temperature patterns likely serve as the common driver coordinating annual seed release with the spring snowmelt runoff pulse. These results suggest that we can use observed rates of seed release distribution and seed longevity to develop models of propagule availability for specific sites where we have climate records. This approach, which models seasonal propagule availability as a temporal density distribution promises to reduce the uncertainty in predicting life history phenology for riparian trees and to provide annual targets for timing river flows to maximize seedling recruitment throughout a river basin (Rood and others 2005).

Patterns of propagule availability

Though seed dispersal is short and intense for both POFR and SAGO, timing patterns, fecundity, and seed longevity differ between the species. Like similar semi-arid ecosystems, POFR seed release consistently precedes SAGO (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 concurrent with peak snowmelt runoff (Figures 5 and 7), typically inhabit higher floodplain surfaces whereas SAGO trees, which release seeds during the descending hydrograph limb, occur on lower bank surfaces that become dewatered later in the spring (McBride and Strahan 1984b).

The high rates of initial seed viability we found (Figure 2) match other laboratory trials for these species (Young and Clements 2003a, 2003b). However in some field experiments willow and cottonwood species have shown lower rates of initial seed viability and higher seasonal variation in viability (Pelzman 1973; Guilloy-Froget and others 2002). Our seed longevity results support earlier studies that demonstrated the higher longevity of the larger *Populus* seeds compared to the smaller *Salix* seeds (van Splunder and others 1995; Karrenberg and others 2002). Our estimate of POFR seed longevity, 54 days, is shorter than another laboratory-tested estimate for this species (85 days), but longer than the 15-30 day results for batches stored under field conditions (Fenner and others 1984). Longevity estimates for SAGO seeds are within the range of published values for these species and other riparian willows (Pelzman 1973; Siegel and Brock 1990; Niiyama 1990; van Splunder and others 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). Our results confirm that early season temperature regime is an important factor controlling timing of seed development and release in pioneer riparian trees. The two-parameter heat sum model presented here is a robust tool for predicting seed release timing for the

Tuolumne River based on a simple, field-based index of fecundity. The model MSE ($JD20_{obs}$ minus $JD20_{pred}$) was substantially lower for both species than the MSE of observed values (Table 2) and our modeled seed release initiation dates correspond well to observed dates (Figure 6). Cumulative heat loads predict both interannual and site-to-site variation in seed release very well; year and site terms drop out in ANOVA models when observed julian days, $JD20_{obs}$, are converted to degree-days, $DD20_{obs}$ (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). For long-lived woody species in natural settings, temperature is a major determinant of growth and reproductive phenology (Bowers and Dimmitt 1994), and for some species 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). We did not include these other factors in our model since all the Tuolumne sites had similar photoperiods and precipitation regimes.

The degree-day model is not applicable to all riparian woody species, however. During 2002-04 we collected comparable seed release data for narrow-leaved willow (*Salix exigua* Nutt.; SAEX), the dominant riparian shrub throughout the San Joaquin Basin. This species has a more diffuse dispersal period and lower individual fecundity than POFR and SAGO (J. Stella, unpublished data). When we modeled SAEX peak seed release initiation, the degree-day model improved predictions very modestly but 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 (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).

Another issue with degree-day models is their geographic applicability. We tested the generality of the Tuolumne model by collecting corresponding data for three riparian sites along the San Joaquin River sites in 2003. We observed the same relative timing pattern between species, but POFR trees on the San Joaquin released seeds approximately two weeks earlier than on the Tuolumne, and SAGO trees released seeds approximately two weeks later (J. Stella, unpublished data). Annual growing season temperatures were consistently hotter at the San Joaquin sites compared to the Tuolumne sites. When we applied our Tuolumne River-based model to 2003 data from the three San Joaquin River sites, it did not accurately predict seed release timing. These results are not surprising, given that parameter estimates for empirical degree-day models commonly vary depending on the temperature data range used to calibrate them (Arnold 1959; Bonhomme 2000). There is no consensus on why degree-day models are not effective beyond their calibration data. Several potential improvements to the simple linear model have been proposed including incorporating a photoperiod or physiological ‘trigger date’ variable (Bowers and Dimmitt 1994), and modeling biological development as a non-linear function of temperature (Arnold 1959). We did not develop these more complex models for our Tuolumne River basin model system because information on basic physiological requirements is lacking for these tree species. In order to develop a general seed release model for a larger region we would need to initially sample a broader range of sites and temperature regimes. Given this broader initial 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.

Modeling propagule availability

For riparian willow and cottonwood trees, pioneer species with short-lived seeds and no seed bank, timing of propagule availability has been considered strictly determined by the seed dispersal period (Mahoney and Rood 1998; Karrenberg and others 2002). However, our results show that there is some potential for short-term propagule storage within the ecosystem, at least for seeds that are not exposed to extreme adverse conditions in the period between catkin dehiscence and arrival at an appropriate seedbed. The primary methods of seed dispersal for these species are wind and water (Braatne and others 1996). Despite some recent field studies and experiments highlighting the potential importance of hydrochory in dispersal (Nilsson and others 1991; Merritt and Wohl 2002), key life history parameters such as dispersal distances and travel times are not well understood for these species. In light of this uncertainty, seed longevity should be taken into account when estimating the annual period of propagule availability (Pelzman 1973).

Using our empirical degree-day model of seed release timing and measured properties of seed longevity, we can construct a propagule availability distribution for each species at a particular site (Figure 8). This model takes into account the timing of both seed production and, implicitly, the processes of dispersal and short-term ecosystem storage that occur while seeds are still viable (Pelzman 1973). In theory, this modified distribution effectively lengthens the period of peak seed availability, especially for POFR, which has the most long-lived seeds (Figure 2a). This time extension may be important in evaluating the effects of late-season high flows on potential recruitment and community dynamics (Poff and others 1997; Rood and others 2005).

The model has two components, a temporal probability density of seed supply and a storage component that extends the end of the peak propagule availability window (Figure 8a). The propagule supply function (Figure 8a-c, bold line) is expressed as a relative density of seeds released over a growing season (Guilloy-Froget and others 2002). Its distribution is derived using optimized degree-day quantiles of seed release (*e.g*. $DD20_{pred}$, $DD50_{pred}$, $DD80_{pred}$) to drive a cumulative degree-day series calculated from local hourly temperature records. To this function we add the storage term (the shaded regions in Figure 8), which we derived empirically from lab germination trials (Figure 2).

It is important to note that the modeled distribution represents a potential propagule window under near-optimal conditions. There are several reasons why the idealized propagule storage component represented by the shaded polygons in Figure 8 is likely an over-prediction of reality. Adverse abiotic and biotic conditions (*e.g*., 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). Secondly, we observed that longer storage times caused a substantial delay in germination (Figure 3). Germination rate is positively correlated with rapid field emergence and seedling development (Abdul-Baki and Anderson 1972) and is used as a predictive measure for plant vigor (Bradbeer 1988; Smith and Berjak 1995), so increased storage time may have negative effects on seedling vigor, growth, and survival.

Poor site conditions, as a result of changes in river regulation or drought cycles may also influence propagule availability and distribution patterns along river corridors. Trees at one of our San Joaquin River sites had very low fecundity (0.6 +/- 0.2 catkins $tree^{-1} survey^{-1}$, mean and S.E.) which was correlated with small tree size (41.3+/- 8.9 cm dbh) and slow growth.(3.2 +/- 0.6

$mm^{1}year^{-1}$) (J. Stella, unpublished data). In environments where growth and survival of riparian trees is decreased due to natural drought or flow alteration (*e.g.*, Stromberg and Patten 1991; Scott and others 1999), the local seed supply may also be reduced. These conditions, if born out over large spatial scales, may result in large variation in propagule availability within river corridors (Johnson 1994; Cooper and others 1999), especially for basins such as the San Joaquin where riparian vegetation is extremely patchy (McBain and Trush 2002; Stella and others 2003).

Synchrony of peak runoff and propagule availability

The degree-day model provides a compelling mechanism for explaining the observed annual correspondence of seed release with unregulated peak flow. In eight of nine observed examples on the Tuolumne River (3 sites in 3 years), the POFR peak seed release period intersected the date of maximum spring runoff, which varied by almost 50 days (J. Stella, unpublished data). Furthermore, the long-term correspondence of snowmelt runoff peak with our hindcasted seed release periods (Figure 7) 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 quite difficult given the complex interactions of precipitation patterns, topography, and thermodynamics that occur over whole watersheds (Ferguson 1999). The synchrony of historical snowmelt timing with modeled peak seed release suggests that our heat load model using a single, coarse temperature record (daily mean temperature at Modesto) is an effective and scale-appropriate integrator of environmental conditions within the entire Tuolumne River basin. 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). Our research establishes that riparian trees 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).

Implications for restoring riparian communities

In light of the widespread and on-going river regulation on the Tuolumne River and within the San Joaquin River basin, our research has important implications for community dynamics and riparian restoration strategies. 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). Our Tuolumne River model is a reliable predictor of seasonal propagule availability for POFR and SAGO at the reach to river basin scale. As such, it is a valuable tool for timing flow releases to increase recruitment of native riparian trees throughout a river corridor (Poff and others 1997; Rood and others 2005). However, timing the flows correctly is only part of the story; there are other factors limiting pioneer riparian tree establishment, including seedling desiccation thresholds (*e.g.*, Segelquist and others 1993), channel and riparian zone morphology (*e.g.*, Johnson 1994; Auble and Scott 1998), and biotic interactions (*e.g.*, Peterson 2002) that together determine favorable conditions in any year (Mahoney and Rood 1998, Lytle and Merritt 2004). These factors need to be considered and integrated on a species-specific basis to design the most effective restoration strategies for riparian corridors in arid regions.

ACKNOWLEDGEMENTS

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REFERENCES

Abdul-Baki AA, and Anderson JD. 1972. Physiological and biochemical deterioration of seeds. TT Kozlowski, editor. Seed Biology. New York, NY:Academic Press. p 283-315.

Arnold CY. 1959. The determination and significance of the base temperature in a linear hear unit system. Proceedings of the American Society for Horticulture Science. 74:430-445.

Auble GT, and Scott ML. 1998. Fluvial disturbance patches and cottonwood recruitment along the upper Missouri River, Montana. Wetlands 18:546-556.

Bewley JD. 1997. Seed germination and dormancy. Plant Cell 9:1055-1066.

Bonhomme R. 2000. Bases and limits to using 'degree.day' units. European Journal of Agronomy 13:1-10.

Bovee KDaMLS. 2002. Implications of flood pulse restoration for Populus regeneration on the upper Missouri River. River Research and Applications 18:287-298.

Bowers JE, and Dimmitt MA. 1994. Flowering phenology of 6 woody-plants in the northern Sonoran Desert. Bulletin of the Torrey Botanical Club 121:215-229.

Braatne JH, Rood SB, and Heilman PE. 1996. Life history, ecology, and conservation of riparian cottonwoods in North America. RF Stettler, HD Bradshaw Jr., PE Heilman, TM Hinckley, editors. Biology of Populus and its implication for management and conservationNRC Research Press, National Research Council of Canada, Ottawa. p 57-86.

Bradbeer JW. 1988. Seed Dormancy and Germination. Blackie, Glasgow and London.

Bunn SE, and Arthington AH. 2002. Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. Environmental Management 30:492-507.

Cayan DR, Kammerdiener SA, Dettinger MD, Caprio JM, and Peterson DH. 2001. Changes in the onset of spring in the western United States. Bulletin of the American Meteorological Society 82:399-415.

Cenci CA, and Ceschia M. 2000. Forecasting of the flowering time for wild species observed at Guidonia, central Italy. International Journal of Biometeorology 44:88-96.

Cesaraccio C, Spano D, Duce P, and Snyder RL. 2001. An improved model for determining degree-day values from daily temperature data. International Journal of Biometeorology 45:161-169.

Chuine I, and Beaubien EG. 2001. Phenology is a major determinant of tree species range. Ecology Letters 4:500-510.

Cooper DJ, D. M. Merritt, D. C. Andersen, and R. A. Chimner. 1999. Factors controlling the establishment of Fremont cottonwood seedlings on the upper Green River, USA. Regulated Rivers: Research & Management 15:419-440.

Douhovnikoff V, McBride JR, and Dodd RS. 2005. Salix exigua clonal growth and population dynamics in relation to disturbance regime variation. Ecology 86:446-452.

Farmer RE, and Bonner FT. 1967. Germination and initial growth of Eastern Cottonwood as influenced by moisture stress, temperature, and storage. Botanical Gazette 128.

Feigelson ED, and Babu GJ. 1992. Linear-Regression in Astronomy .2. Astrophysical Journal 397:55-67.

Fenner M. 1998. The phenology of growth and reproduction in plants. Perspectives in Plant Ecology, Evolution and Systematics 1:78-91.

Fenner PR, Brady WW, and Patten DR. 1984. Observations on seeds and seedlings of Fremont cottonwood. Desert Plants 6:55-58.

Fenner PR, Brady WW, and Patten DR. 1985. Effects of regulated water flows on regeneration of Fremont cottonwood. Journal of Range Management 38:135-138.

Ferguson RI. 1999. Snowmelt runoff models. Progress in Physical Geography 23:205-227.

Gregory SV, Swanson FJ, McKee WA, and Cummins KW. 1991. An ecosystem perspective of riparian zones. Bioscience 41:540-551.

Guilloy-Froget H, Muller E, Barsoum N, and Hughes FMR. 2002. Dispersal, germination, and survival of Populus nigra L. (Salicaceae) in changing hydrologic conditions. Wetlands 22:478-488.

Hayhoe K, Cayan D, Field CB, Frumhoff PC, Maurer EP, Miller NL, Moser SC, Schneider SH, Cahill KN, Cleland EE, Dale L, Drapek R, Hanemann RM, Kalkstein LS, Lenihan J, Lunch CK, Neilson RP, Sheridan SC, and Verville JH. 2004. Emissions pathways, climate change, and impacts on California. Proceedings of the National Academy of Sciences of the United States of America 101:12422-12427.

Howe GT, Hackett WP, Furnier GR, and Klevorn RE. 1995. Photoperiodic Responses of a Northern and Southern Ecotype of Black Cottonwood. Physiologia Plantarum 93:695-708.

Isobe T, Feigelson ED, Akritas MG, and Babu GJ. 1990. Linear-Regression in Astronomy .1. Astrophysical Journal 364:104-113.

Johnson WC. 1994. Woodland expansion in the Platte River, Nebraska: patterns and causes. Ecological Monographs 64:45-84.

Karrenberg S, Edwards PJ, and Kollmann J. 2002. The life history of Salicaceae living in the active zone of floodplains. Freshwater Biology 47:733-748.

Kaszkurewicz A, and Fogg PJ. 1967. Growing Seasons of Cottonwood and Sycamore as Related to Geographic and Environmental Factors. Ecology 48:785-793.

Kramer K, Leinonen I, and Loustau D. 2000. The importance of phenology for the evaluation of impact of climate change on growth of boreal, temperate and Mediterranean forests ecosystems: an overview. International Journal of Biometeorology 44:67-75.

Lenihan JM, Drapek R, Bachelet D, and Neilson RP. 2003. Climate change effects on vegetation distribution, carbon, and fire in California. Ecological Applications 13:1667-1681.

Lytle DA, and Merritt DM. 2004. Hydrologic regimes and riparian forests: A structured population model for cottonwood. Ecology 85:2493-2503.

Lytle DA, and Poff NL. 2004. Adaptation to natural flow regimes. Trends in Ecology & Evolution 19:94-100.

Mahoney JM, and Rood SB. 1998. Streamflow requirements for cottonwood seedling recruitment--an integrative model. Wetlands 18:634-645.

McBain & Trush I. 2000. Habitat restoration plan for the Lower Tuolumne River corridor. Prepared for Tuolumne River Technical Advisory Committee, with assistance from U.S. Fish and Wildlife Service Anadromous Fish Restoration Program., Arcata, CA.

McBain & Trush I, editor. 2002. San Joaquin River Restoration Study Background Report. Prepared for Friant Water Users Authority, Lindsay, CA and Natural Resources Defense Council, San Francisco, CA.

McBride JR, and Strahan J. 1984a. Establishment and survival of woody riparian species on gravel bars of an intermittent stream. The American Midland Naturalist 112:235-245.

McBride JR, and Strahan J. 1984b. Fluvial processes and woodland succession along Dry Creek, Sonoma County, California. RE Warner and KM Hendrix, editors. California riparian systems: ecology, conservation, and management.University of California Press, Berkeley. p 110-119.

Merritt DM, and Wohl EE. 2002. Processes governing hydrochory along rivers: Hydraulics, hydrology, and dispersal phenology. Ecological Applications 12:1071-1087.

Naiman RJ, Bunn SE, Nilsson C, Petts GE, Pinay G, and Thompson LC. 2002. Legitimizing fluvial ecosystems as users of water: An overview. Environmental Management 30:455-467.

Naiman RJ, and Decamps H. 1997. The ecology of interfaces: riparian zones. Annual Review of Ecology and Systematics 28:621-658.

NCDC. 2005. 1971-2000 Daily station normals for Modesto City-County Airport (Coop ID # 045738). in. National Climatic Data Center/NESDIS/NOAA (http://www5.ncdc.noaa.gov/climatenormals/clim84/CA/CA045738.txt).

Neter J, Kutner MH, Nachtsheim CJ, and Wasserman W. 1996. Applied linear statistical models, 4th edition. R.D. Irwin, Homewood, IL.

Niiyama K. 1990. The role of seed dispersal and seedling traits in colonization and coexistence of Salix species in seasonally flooded habitat. Ecological Research 5:317-331.

Nilsson C, Gardfjell M, and Grelsson G. 1991. Importance of hydrochory in structuring plant communities along rivers. Canadian Journal of Botany 69:2631-2633.

Patten DT. 1998. Riparian ecosystems of semi-arid North America: Diversity and human impacts. Wetlands 18:498-512.

Pelzman RJ. 1973. Causes and possible prevention of riparian plant encroachment on anadromous fish habitat. Environmental Services Branch Administrative Report 73-1, California Department of Fish and Game, Region 1.

Penuelas J, and Filella I. 2001. Phenology - Responses to a warming world. Science 294:793-+.

Peterson D. 2002. The development of an alternative restoration strategy for Sacramento River riparian forests. Masters Thesis. California State University, Chico, Chico, CA.

Peterson DH, Smith RE, Dettinger MD, Cayan DR, and Riddle L. 2000. An organized signal in snowmelt runoff over the western United States. Journal of the American Water Resources Association 36:421-432.

Poff NL, Allan JD, Bain MB, Karr JR, Prestegaard KL, Richter BD, Sparks RE, and Stromberg JC. 1997. The natural flow regime: a paradigm for river conservation and restoration. Bioscience 47:769-784.

Poff NL, Allan JD, Palmer MA, Hart DD, Richter BD, Arthington AH, Rogers KH, Meyers JL, and Stanford JA. 2003. River flows and water wars: emerging science for environmental decision making. Frontiers in Ecology and the Environment 1:298-306.

Resh VH, Brown AV, Covich AP, Gurtz ME, Li HW, Minshall GW, Reice SR, Sheldon AL, Wallace JB, and Wissmar RC. 1988. The role of disturbance in stream ecology. Journal of the North American Benthological Society 7:433-455.

Ring DR, Harris MK, Jackman JA, and Henson JL. 1983. A Fortran computer program for determining start date and base temperature for degree-day models. Bulletin MP-1537, Texas Agricultural Experiment Station, Texas University System, College Station, TX.

Rood SB, Braatne JH, and Hughes FMR. 2003. Ecophysiology of riparian cottonwoods: stream flow dependency, water relations and restoration. Tree Physiology 23:1113-1124.

Rood SB, Samuelson GM, Braatne JH, Gourley CR, Hughes FMR, and Mahoney JM. 2005. Managing river flows to restore floodplain forests. Frontiers in Ecology and the Environment 3:193-201.

Schmid PE, Tokeshi M, and Schmid-Araya JM. 2000. Relation between population density and body size in stream communities. Science 289:1557-1560.

Scott ML, Auble GT, and Friedman JM. 1997. Flood dependency of cottonwood establishment along the Missouri River, Montana, USA. Ecological Applications 7:677-690.

Scott ML, Friedman JM, and Auble GT. 1996. Fluvial processes and the establishment of bottomland trees. Geomorphology 14:327-339.

Scott ML, Shafroth PB, and Auble GT. 1999. Responses of riparian cottonwoods to alluvial water table declines. Environmental Management 23:347-358.

Scott SJ, Jones RA, and Williams WA. 1984. Review of data analysis methods for seed germination. Crop Science 24:1192-1199.

Segelquist CA, Scott ML, and Auble GT. 1993. Establishment of Populus deltoides under simulated alluvial groundwater decline. The American Midland Naturalist 130:274-285.

Siegel RS, and Brock JH. 1990. Germination requirements of key southwestern woody riparian species. Desert Plants 10:3-8.

Smith MT, and Berjak P. 1995. Deteriorative changes associated with the loss of viability of stored desiccation-tolerant and desiccation-sensitive seeds. J Kigel and G Galili, editors. Seed Development and Germination. New York:Marcel Dekker, Inc. p 701-746.

Snyder RL, Spano D, Cesaraccio C, and Duce P. 1999. Determining degree-day thresholds from field observations. International Journal of Biometeorology 42:177-182.

Snyder RL, Spano D, Duce P, and Cesaraccio C. 2001. Temperature data for phenological models. International Journal of Biometeorology 45:178-183.

Sokal RR, and Rohlf FJ. 1995. Biometry, Third edition. W.H. Freeman and Company, New York, NY.

Stella JC, Vick JC, and Orr BK. 2003. Riparian vegetation dynamics on the Merced River. Pages 302-314 in PM Faber, editor. California Riparian Systems: Processes and Floodplains Management, Ecology, and Restoration (2001 Riparian Habitat and Floodplains Conference Proceedings), Sacramento, CA.

Stromberg JC, and Patten DT. 1991. Instream flow requirements for cottonwoods at Bishop Creek, Inyo County, California. 2:1-11.

Townsend CR, and Hildrew AG. 1994. Species traits in relation to a habitat templet for river systems. Freshwater Biology 31:265-275.

USACE. 2002. Sacramento and San Joaquin River Basins Comprehensive Study, Appendix B (Synthetic Hydrology Technical Documentation). US Army Corps of Engineers, Sacramento, CA.

Van Splunder I, Coops H, Voesenek LACJ, and Blom CWPM. 1995. Establishment of alluvial forest species in floodplains: the role of dispersal timing, germination characteristics and water level fluctuations. Acta Botanica Neerlandica (Royal Botanical Society of The Netherlands) 44:269-278.

Williams CA, and Cooper DJ. 2005. Mechanisms of riparian cottonwood decline along regulated rivers. Ecosystems 8:382-395.

Willson MF, and Traveset A. 2000. The ecology of seed dispersal. M Fenner, editor. Seeds: ecology of regeneration in plant communities. New York, NY: CABI Publishing. p 85-110.

Young JA, and Clements CD. 2003a. Germination of seeds of Fremont cottonwood. Journal of Range Management 56:660-664.

Young JA, and Clements CD. 2003b. Seed germination of willow species from a desert riparian ecosystem. Journal of Range Management 56:496-500.

Zalom FG, Goodell PB, Wilson WW, and Bentley WJ. 1983. Degree-days: the calculation and the use of heat units in pest management. Leaflet 21373, Division of Agriculture and Natural Resources, University of California, Davis, Davis, CA.

Zasada JC, and Densmore RA. 1977. Changes in seed viability during storage for selected Alaskan Salicaceae. Seed Science and Technology 5:509-518.

TABLE LEGENDS

Table 1. Tree data and seed release timing for Tuolumne River sites. Initiation of peak seed release for each year is the JD20, the julian day corresponding to the 20th quantile of the seasonal fecundity index distribution (see text). Peak period is the number of days between the JD20 and JD80, or 80th quantile. The JD20 varied substantially annually so all years are presented; interannual differences in peak period were small so all years are averaged. Age, size and growth data for POFR and SAGO are not necessarily representative of the whole stand, since only dominant female trees were selected for phenology observations.

Table 2. Optimized parameters for the seed release initiation degree-day models. Model base and threshold parameters are empirically-derived using hourly time steps (see text). Model MSE is calculated for predicted minus observed JD20 for each site and year (N=9). Null Model MSE is the MSE of the observed JD20 values. Values <1 for the MSE ratio indicate increased model performance over the null model, which is the julian day mean of the start of peak seed release.

Table 3. Paired ANOVA models for seed release initiation and corresponding heat sums. Expressing the seed release start date ($JD20_{obs}$) as a heat sum ($DD20_{obs}$) removes significant year and site effects from the paired ANOVA models. Data are the from the three Tuolumne River sites in 2002-04 (n = 9 for each species).

Table 1. Tree data and seed release timing for Tuolumne River sites.

	POFR			**SAGO**		
	TR1 (Ott)	**TR2 (Lakewood)**	**TR3 (Basso)**	**TR1 (Ott)**	**TR2 (Lakewood)**	**TR3 (Basso)**
n trees	11	11	10	10	10	11
Tree Vital Data						
Age[a] (years; median+range)	18 (12-29)	15 (10-19)	44 (20-55)	10 (7-15)	7 (4-16)	18 (9-67)
DBH[b] (cm; mean+SE)	69.7 (9.4)	75.4 (12.7)	86.7 (7.9)	34.8 (6.2)	15.7 (2.5)	44 (6.8)
Radial growth[c] (mm year^{-1}; mean+SE)	10.4 (1.3)	10.2 (1.8)	4.1 (0.9)	9.7 (1.2)	8.7 (1.8)	4.8 (1.2)
Fecundity index[d] (catkins survey^{-1} tree^{-1}; mean+SE)	27.5 (3.0)	14.3 (2.7)	13.2 (2.0)	36.6 (4.3)	26.8 (3.4)	18.7 (3.0)
Peak Seed Release Timing[e]						
2002 Initiation[f] (julian day[g])	148	132	127	161	145	154
2003 Initiation[e] (julian day[g])	161	133	142	162	149	154
2004 Initiation[e] (julian day[g])	137	113	119	145	139	143
Peak period duration[h] (days; mean+SE)	43 (5)	30 (2)	24 (1)	49 (2)	43 (5)	46 (3)

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[a] *Minimum age estimates, since some trees had rotten centers.*
[b] *Diameter at breast height, 1.37 m above the ground.*
[c] *Mean of last 3 years of radial growth increment.*
[d] *Calculated for each tree as the average catkin count per survey, 2002-04.*
[e] *All timing parameters calculated using the site-averaged seasonal fecundity index (see text).*
[f] *Peak seed release initiation is defined as the* $JD20_{obs}$ *, the julian day corresponding to the 20th quantile of cumulative catkin counts (see text).*
[g] *Julian day conversions: 91 = Apr 1; 121 = May 1; 152 = Jun 1; 182 = Jul 1; 213 = Aug 1.*
[h] *Defined as the period bracketed by the 20th and 80th quantiles of cumulative catkin counts (*$JD20_{obs}$ *to* $JD80_{obs}$*)*

Table 2. Optimized parameters for the seed release initiation degree-day models.

Degree-Day Model Summary	**POFR**	**SAGO**
n (sites*years)	9	9
Model Base (degrees C)	25	12
Model Threshold (degree-days)	27.1	492.3
Degree-Day Model MSE (days^2)	61.6	17.5
Null Model MSE (days^2)	189.9	58.2
MSE Ratio (Model/Null)	0.32	0.30

Table 3. Paired ANOVA models for seed release initiation and corresponding heat sums.

	DF	SS	MS	F	P
POFR					
Julian Day ($JD20_{obs}$)					
site	2	901.5	450.7	30.5	<0.01
year	2	748.6	374.3	25.3	<0.02
residuals	4	59.1	14.8		
Degree-Days ($DD20_{obs}$)					
site	2	959.9	480.0	2.5	0.20
year	2	58.1	29.0	0.2	0.86
residuals	4	760.7	190.2		
SAGO					
Julian Day ($JD20_{obs}$)					
site	2	206.9	103.4	11.7	0.02
year	2	281.5	140.7	16.0	0.01
residuals	4	35.3	8.8		
Degree-Days ($DD20_{obs}$)					
site	2	7784.6	3892.3	1.6	0.31
year	2	406.7	203.4	0.1	0.92
residuals	4	9887.4	2471.8		

FIGURE LEGENDS

Figure 1. The San Joaquin Basin. Solid dots indicate location of Tuolumne River phenology sampling sites, 2002-04. Open circles denote San Joaquin River sites where auxiliary data were collected in 2003.

Figure 2. Seed longevity 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 percent. Arrows indicate mean seed longevity for (a) POFR (54 days) and (b) SAGO (31 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.

Figure 3. Germination delay associated with seed storage time. Data points are number of days required to reach 50 percent germination for each seed batch; batches with <50% final germination are not plotted. The fitted line illustrates an exponential increase in germination delay with storage time after approximately three weeks. The fitted line uses the pooled data since both species had similar rates of germination delay.

Figure 4. Seasonal seed release density for POFR and SAGO trees at three Tuolumne River sites, 2002-04.

Figure 5. General patterns of seed release and historical unregulated flow along the Tuolumne River. Open symbols are average open catkin counts per tree for all surveys

from 2002-2004; data from all sites are pooled. Solid symbols and lines are a cubic B-spine fit to all values (smooth.spline function, S-plus, Insightful Corp.). The unregulated hydrograph is computed as the median daily values from 1971-2004 modeled discharge at La Grange, CA (Turlock Irrigation District).

Figure 6. Predicted versus observed dates of seed release initiation for POFR and SAGO trees at three Tuolumne River sites, 2002-2004. Seed release initiation was defined as the $JD20_{obs}$, the julian date corresponding to the 20th quantile of the seasonal fecundity index distribution for each species (see text). Predicted dates were modeled using an empirical heat sum model with hourly time steps. The 1:1 line represents a hypothetical perfect correspondence between predicted and observed values.

Figure 7. Tuolumne River observed peak runoff date plotted against projected peak seed release initiation (JD20; open symbols) and end (JD80; closed symbols) modeled using heat sums for all years from 1928-2003. Peak discharge intersects the modeled POFR seed release period in most years (*i.e.*, the 1:1 line divides the JD20 and JD80 dates). SAGO projected seed release initiation coincides 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).

Figure 8. Modeled propagule availability using seed release and seed longevity data for (a) a generalized case, and field-parameterized examples for (b) POFR and (c) SAGO. The seed release component is a probability function (bold line) using the optimized degree-day seed release model for each species and the degree-day record for a particular site and year (Basso Bridge site in 2004 for this example). The peak seed release period is defined by the JD20 (arrow 1) and JD80 (arrow 2), julian dates corresponding to 20th and 80th quantiles of seed release density. The shaded region represents the maximum potential propagule storage afforded by seed longevity (Figure 2). Storage potential varies with seasonal timing because seed batches collected late in the season had consistently low germination rates. Arrow 3 marks the modified JD80 using this approach and represents the maximum potential extension of the peak seed release period.

Figure 1.

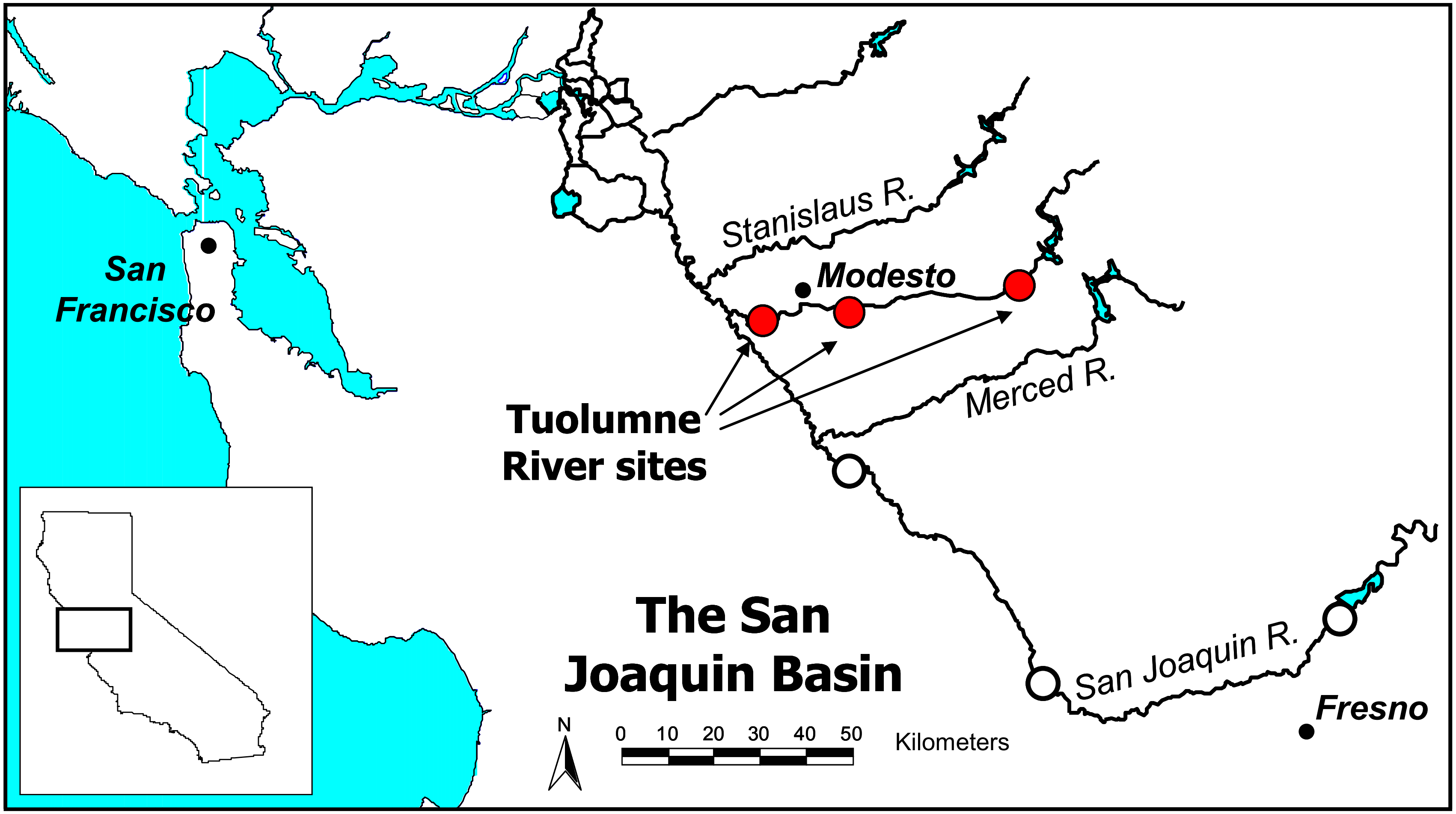
San Francisco
Stanislaus R.
Modesto
Tuolumne River sites
Merced R.
The San Joaquin Basin
San Joaquin R.
Fresno
N
0 10 20 30 40 50
Kilometers

Figure 2.

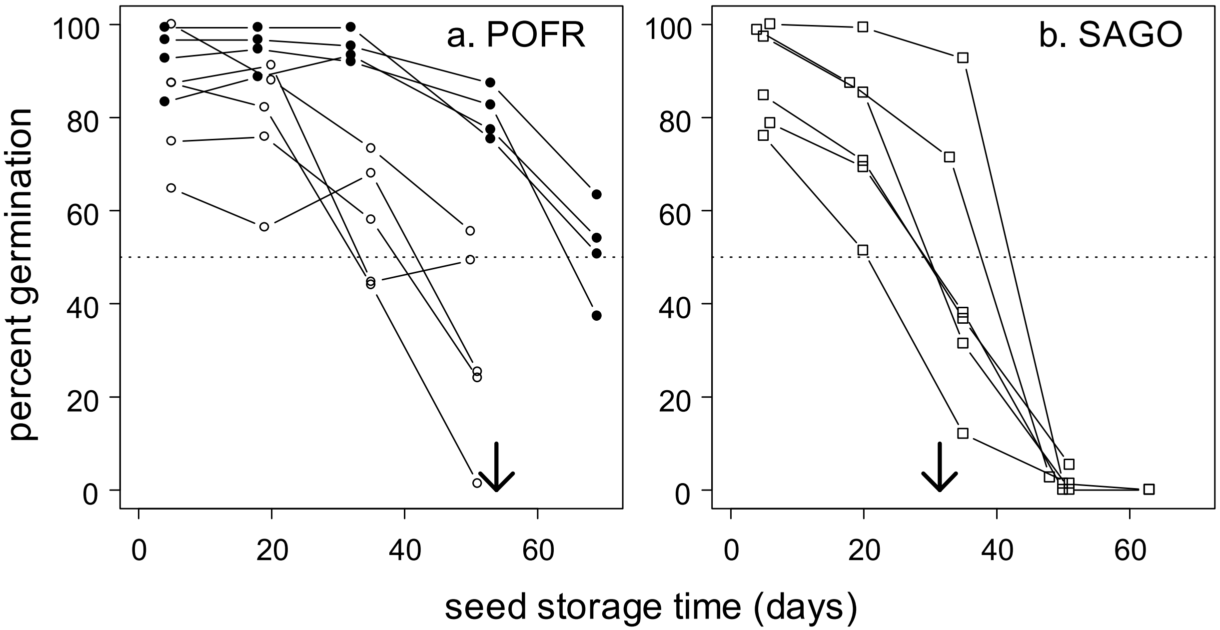
a. POFR
b. SAGO
percent germination
0
20
40
60
80
100
0
20
40
60
seed storage time (days)

Figure 3.

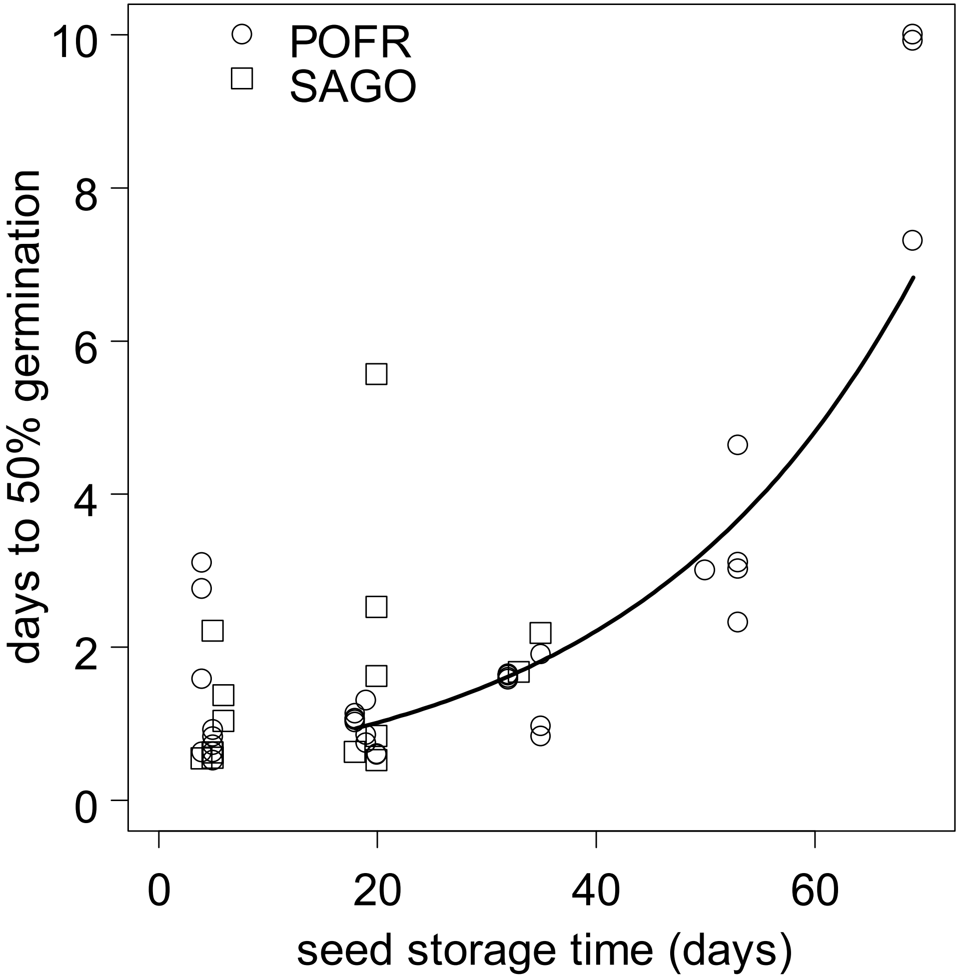
○ POFR
□ SAGO
days to 50% germination
0
2
4
6
8
10
seed storage time (days)
0
20
40
60

Figure 4.

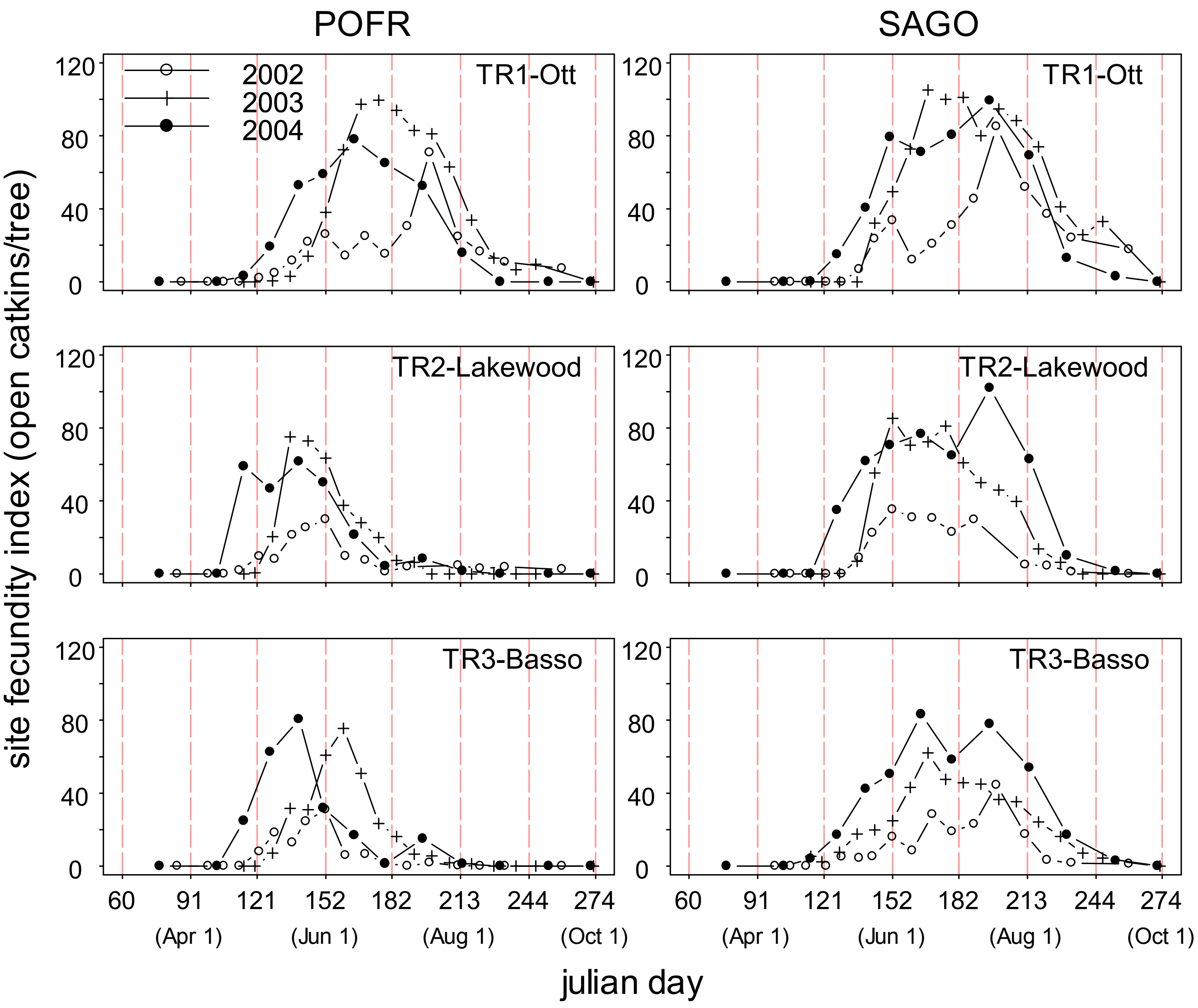
POFR
SAGO
2002
2003
2004
TR1-Ott
TR2-Lakewood
TR3-Basso
site fecundity index (open catkins/tree)
0
40
80
120
60
91
121
152
182
213
244
274
(Apr 1)
(Jun 1)
(Aug 1)
(Oct 1)
julian day

Figure 5.

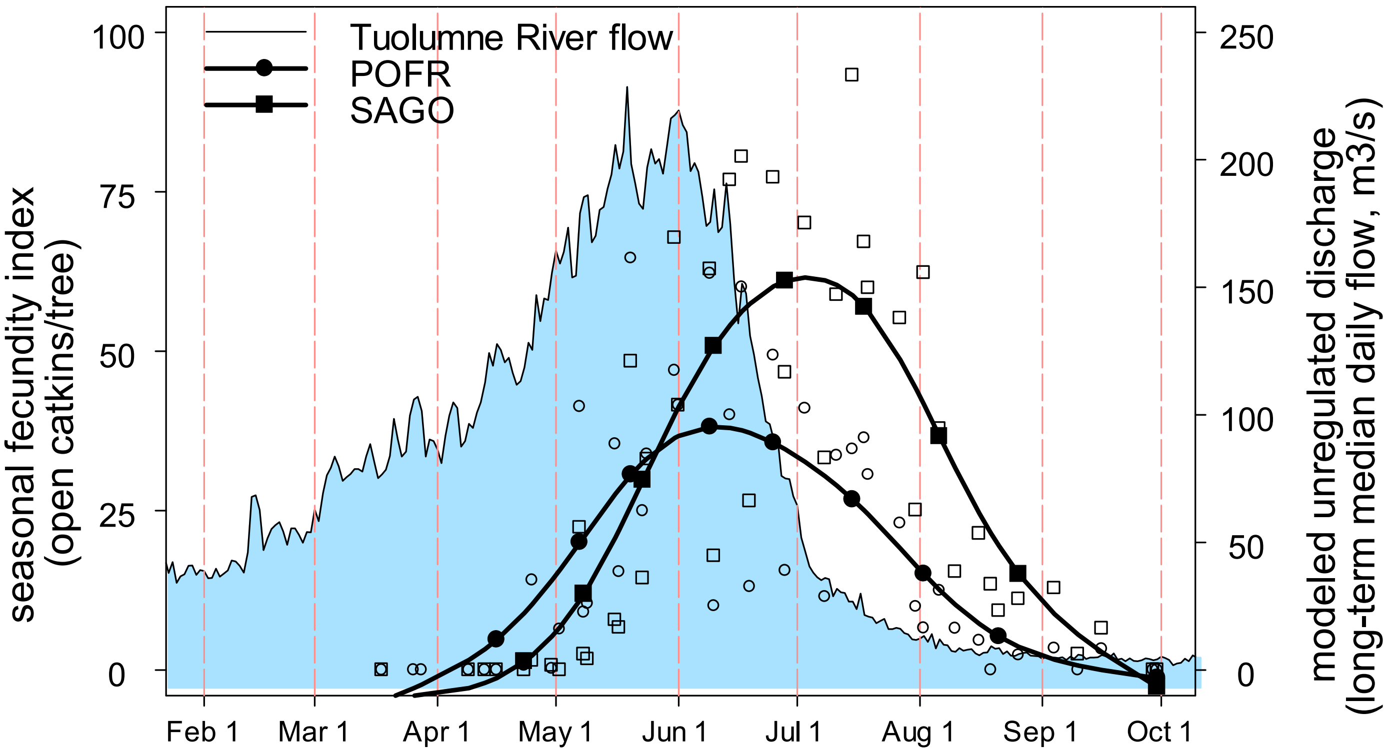
Tuolumne River flow
POFR
SAGO
seasonal fecundity index
(open catkins/tree)
100
75
50
25
0
modeled unregulated discharge
(long-term median daily flow, m3/s)
250
200
150
100
50
0
Feb 1
Mar 1
Apr 1
May 1
Jun 1
Jul 1
Aug 1
Sep 1
Oct 1

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Figure 6.

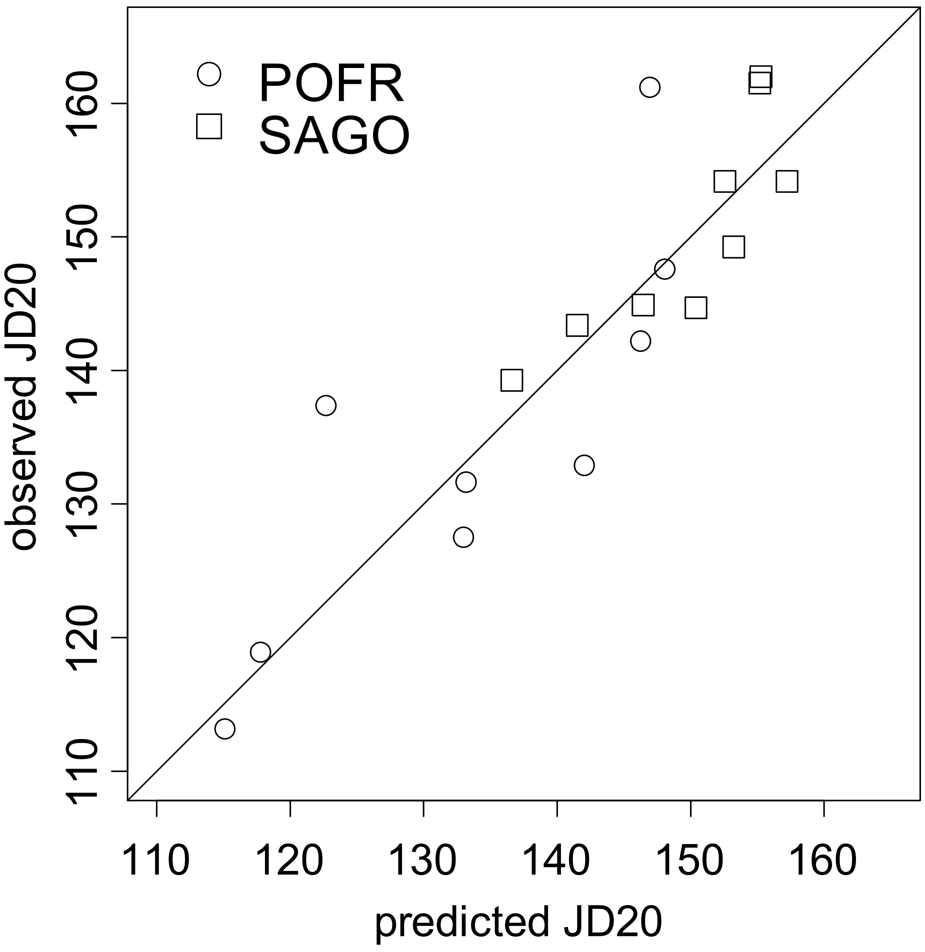

○ POFR
□ SAGO
observed JD20
110
120
130
140
150
160
predicted JD20
110
120
130
140
150
160

Figure 7.

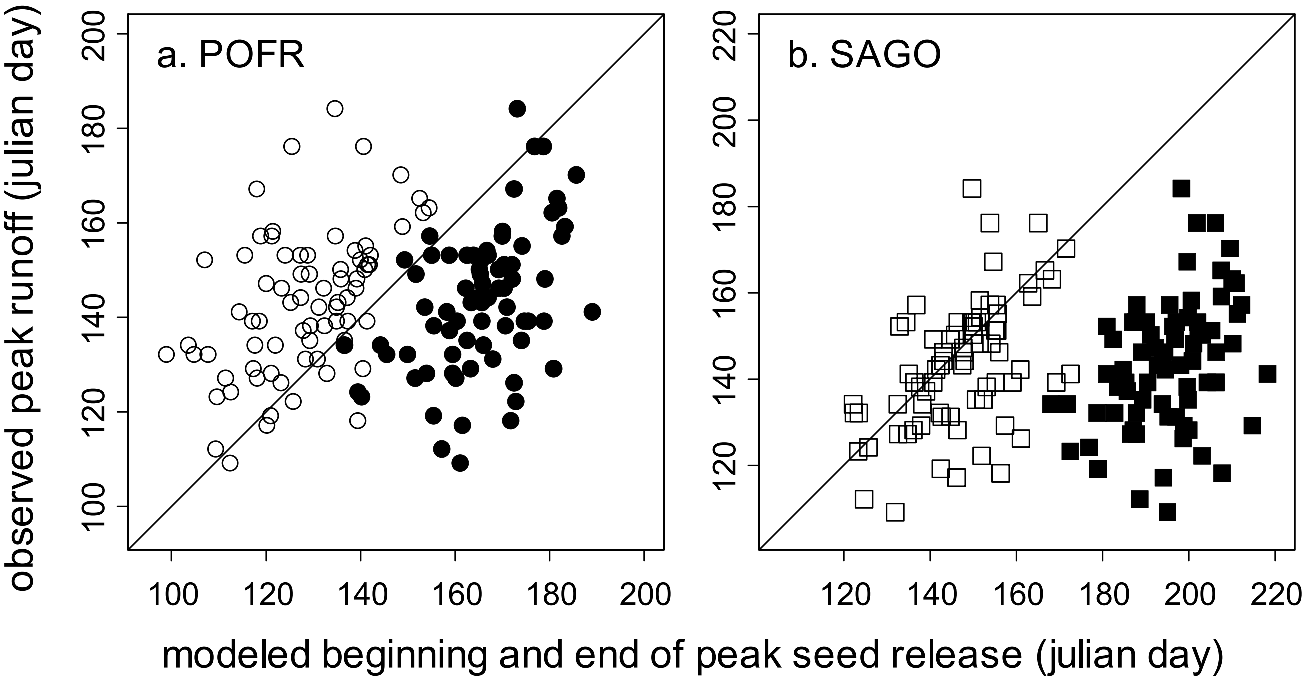
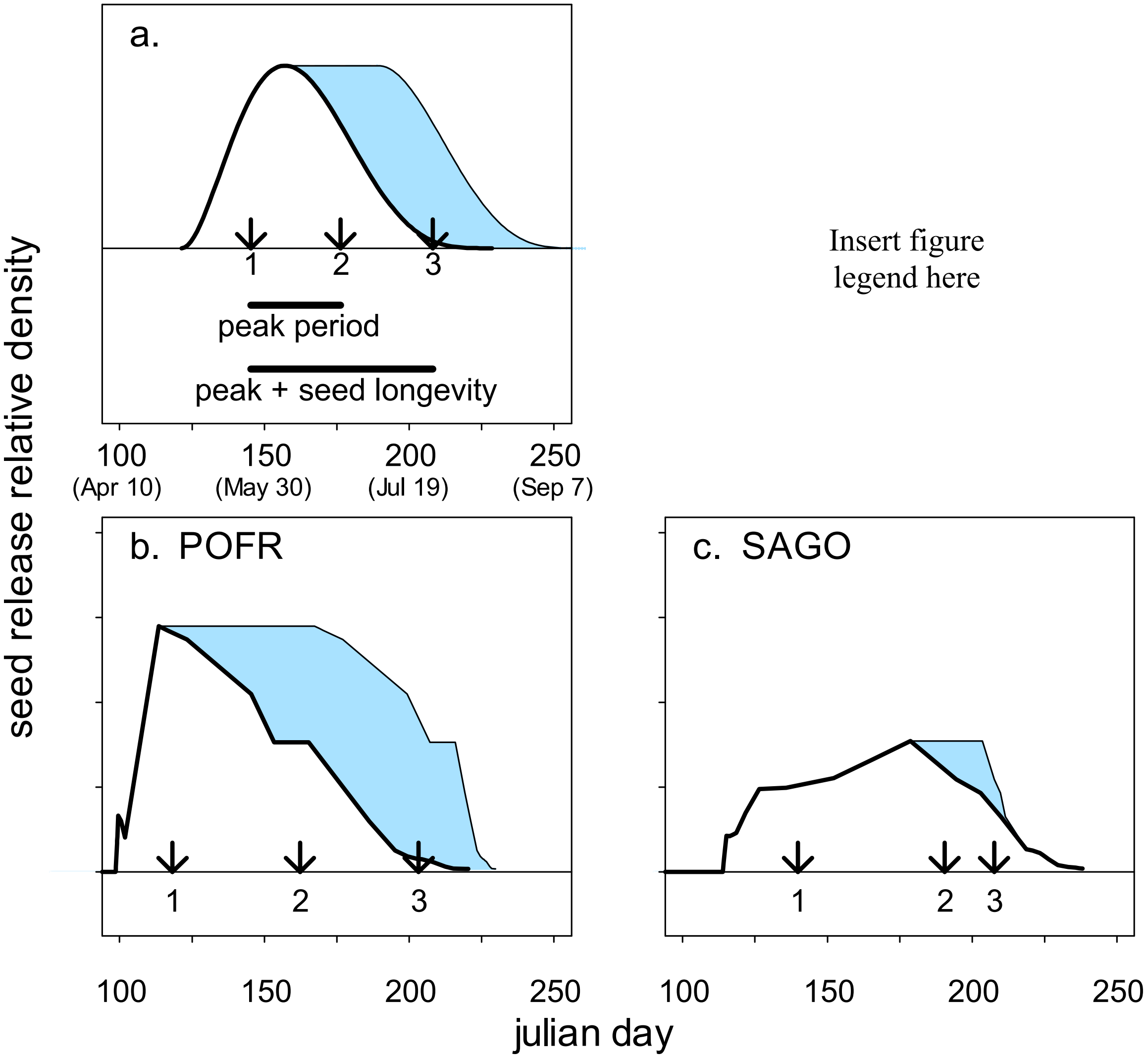

a. POFR
b. SAGO
observed peak runoff (julian day)
modeled beginning and end of peak seed release (julian day)
100
120
140
160
180
200
220

Figure 8.



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