

Tarping and Inundation as Potential Control Mechanisms for Seed Banks of Red Sesbania (*Sesbania punicea*)

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The exotic shrub red sesbania is an increasingly problematic weed in riparian and wetland ecosystems of California. Current control methods focus on manual removal, followed by herbicide application. Although this method effectively removes mature stands, the control is temporary because the presence of a large seed bank results in rapid germination and growth of new seedlings. We measured the density of seed banks beneath stands of varying densities and evaluated the potential of tarping and inundation for control of red sesbania seed banks. As expected, the abundance of viable red sesbania seeds in the soil was significantly greater beneath high-density stands than it was beneath low-density stands. Results for inundation and tarping experiments were mixed. Sustained inundation significantly decreased survivorship of germinated seeds compared with the control, as well as causing a statistically significant reduction in germination. Seven months after tarping, during the fall/winter growing season, there was no significant effect on red sesbania seedling abundance, stump resprout abundance, or height. Germination in the laboratory was significantly reduced by extended exposure to temperatures of 60 C, although lower temperatures did not reduce germination. Red sesbania appears to be resilient to tarping as a control method, at least in the settings studied.

Nomenclature: Red sesbania, *Sesbania punicea* (Cav.) Benth. SEBPU.

Key words: Flooding, invasive species, riparian, wetland.

Control of invasive species is a critical issue in restoration ecology and land management, and better control methods are needed to ensure restoration success (D'Antonio and Meyerson 2002; Vitousek et al. 1997). Persistent soil seed banks of invasive plants, particularly leguminous shrubs, can be a major barrier to successful restoration (Alexander and D'Antonio 2003). These nonnative seed banks create a source of propagules that persist after aboveground biomass is removed (Holmes et al. 1987). Concomitantly, the presence of invasive plants can alter the abundance and diversity of seeds in the seed bank (Alexander and D'Antonio 2003).

Nonherbicide control of invasive plants is of increasing interest (Upadhyaya and Blackshaw 2007) because of

herbicide effects on nontarget plants (Crone et al. 2009) and public opposition to herbicide use in some areas. Inundation and tarping are two control methods that do not require herbicide application. Inundation (i.e., intentional flooding of a site) is an option for weed control in riparian areas along managed rivers, ponds, and wetlands, where structures may already be in place that allow for water-level control (Tu et al. 2001). Tarping—the practice of applying opaque plastic sheeting atop soil to exclude light and smother plants, as well as to increase solar heating—has been successful in controlling a variety of weed species, largely in agricultural contexts (Upadhyaya and Blackshaw 2007). Application of clear plastic films to maximize soil temperatures (solarization) is an alternative method to control weeds by decreasing the soil seed bank during periods when air temperatures are high (Elmore et al. 1997). Fall tarping has been shown to effectively decrease nonnative plant cover in grasslands (Niederer et al. 2014), winter tarping has been effective in controlling nonnative annual grasses for restoration of agricultural land (Marushia and Allen 2011), and woven black plastic tarping has proven successful in restoring a seasonal wetland in Australia (Grose 2012).

Red sesbania [*Sesbania punicea* (Cav.) Benth], a shrub in the Fabaceae family native to South America, has become a

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Management Implications

Inundation was the more-successful seed-bank control treatment studied because 2 mo of sustained inundation reduced *Sesbania punicea* seedling survivorship and caused a minor reduction in germination. However, this treatment did not eliminate the seed bank. It is possible that the surviving seeds and seedlings of *S. punicea* would be able to reestablish populations in inundated areas; thus, follow-up control methods may still be required. Whether the required duration of treatment is realistic in the field will depend upon the flood regime at potential sites and other management objectives, such as recreation and provision of wildlife habitat. Inundation would likely be most effective when *S. punicea* seedlings are small.

Tarping during the fall/winter growing season was not an effective control method for *S. punicea*. However, solarization (the practice of applying clear plastic film to maximize solar heating of the soil) could potentially be effective during hotter periods. Solarization during periods of average daily high temperatures warmer than 35 °C could potentially achieve the 60 °C soil temperatures we found were needed to reduce germination. Implementation of solarization is labor intensive, materials are expensive, and plastic sheeting must be monitored for holes, and patching performed if sheeting is damaged. Land managers will have to evaluate the labor costs of solarization compared with conventional biomass removal and herbicide treatments. Long-term control of *S. punicea* will be difficult because of its dense seed banks. Although complete eradication is unlikely, targeting small, isolated populations in the upstream portion of watersheds using conventional treatments may be the most-effective approach for minimizing downstream impacts.

problematic, invasive plant in wetland and riparian areas in California, the southeastern United States, and South Africa (Cuda et al. 1996; Hoffmann and Moran 1998; Hunter and Platenkamp 2003). In California, this species has spread to 13 counties, as far north as Shasta County and as far south as Fresno County, largely along major waterways (Calflora 2016). It has become particularly invasive along the San Joaquin River in California's Central Valley, where large-scale efforts to restore riparian ecosystems and endangered fish and wildlife populations are underway. One restoration action is the release of higher restoration flows from Friant Dam to support native salmonid populations. Unfortunately, increased flows have created nearly ideal conditions for *S. punicea* invasion by facilitating spread of the species downstream. *Sesbania punicea* was likely introduced to California through the horticultural trade (Hunter and Platenkamp 2003), not as an agricultural weed. On the San Joaquin River, its distribution is likely based on one or more upstream introductions and subsequent downstream dispersal throughout the riparian corridor.

Sesbania punicea can increase hydraulic roughness in river channels and disperses rapidly downstream because of its floating seed pods (Hoffmann and Moran 1988; Hunter

and Platenkamp 2003). This species also displaces native vegetation (Hunter and Platenkamp 2003), including species such as willows (*Salix* spp.) that are functionally and structurally important in riparian ecosystems. In addition, all parts of the plant are poisonous (Terblanche et al. 1966). This species is nitrogen fixing (Evans and Rotar 1987), which may potentially have beneficial effects on soil nutrients and nitrogen-limited plant species. However, in systems in which native plants are adapted to a low-nutrient environment, nitrogen-fixing species facilitate invasion by other nonnative species (Von Holle et al. 2006). *Sesbania punicea* could potentially provide habitat for nesting birds but does not appear to provide other significant habitat value.

Sesbania punicea seeds have an impermeable seed coat (a method of physical dormancy), which must be scarified for germination to occur (Graaff and van Staden 1984). The prolific seeding rate and the impermeable seed coat of *S. punicea* result in a large, persistent seed bank. Because germination occurs when water enters the seed after scarification and is not controlled by day length or other factors, *S. punicea* seeds can germinate year-round as long as temperatures are suitably warm (Graaff and van Staden 1984). Commonly, rapid seed germination and seedling growth after mechanical removal or herbicide treatment of mature *S. punicea* biomass have been observed (Graaff and van Staden 1984; Hunter and Platenkamp 2003).

Seed banks can be analyzed to directly inform control of invasive species and restoration efforts (Matzek and Hill 2012; Rayburn et al. 2016). These analyses can show whether seed banks of invasive species are reduced by restoration (Alexander and D'Antonio 2003) and which management strategies most effectively reduce these seed banks (Juran and Abella 2013). Few, if any, studies have examined *S. punicea* seed bank dynamics, and there are relatively few studies of riparian seed banks (Goodson et al. 2001). This lack of information is problematic given that *S. punicea* is still at a relatively early stage of invasion along California rivers. There is significant stakeholder interest in control before it becomes too widespread in these riparian systems, especially in the context of higher restoration flows.

Biomass removal in conjunction with herbicide application is most often used to control mature *S. punicea* plants; however, at present nonchemical control methods are desired by stakeholders (S. Weaver, personal communication). This is true for sensitive habitats, during portions of the year when herbicide use is prohibited, and in volunteer-based restoration projects in which participants do not wish to be exposed to herbicides. For alternatives to herbicide treatment of newly emerged seedlings, we investigated the effectiveness of inundation and tarping in reducing or eliminating *S. punicea* soil seed banks. Because our field experiments were limited to the fall/winter, we were not able to test solarization control of *S. punicea* in the field.

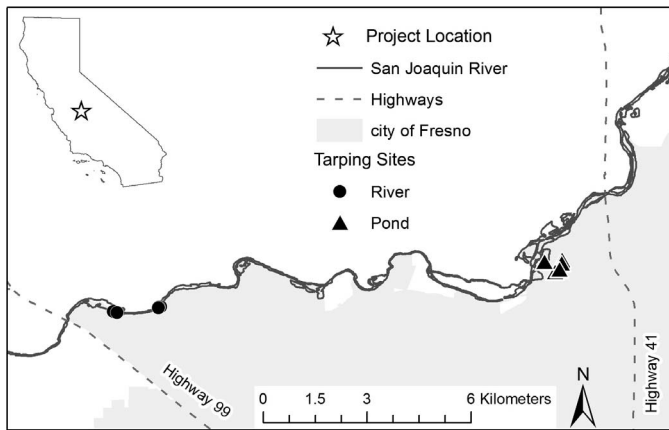


Figure 1. Study site location along the San Joaquin River corridor, north of the city of Fresno, CA. The tarping river plots are located on the banks of the San Joaquin River, and the pond plots are on the banks of a pond formed by gravel mining in the floodplain terrace of the San Joaquin River.

Alternatively, we investigated the potential of soil solarization as a seed bank control method by measuring germination responses to increasingly higher temperatures to understand the thermal tolerances of the seeds. In addition, we evaluated the extent of the seed bank by measuring seed abundance in the soil beneath low- and high-density stands to better understand the biology and invasion processes of *S. punicea*.

Our experiments tested the following hypotheses:

1. Initially, inundation increases germination because of the positive effects of soil moisture, but longer periods of inundation decrease germination because the seeds remain saturated. Survivorship of germinating seeds decreases as the duration of the inundation increases.
2. Higher temperatures and increased duration of exposure to higher temperatures both significantly decrease *S. punicea* germination.
3. Tarping decreases the abundance of germinating seeds, relative to control treatments. Longer duration of tarping treatments decreases *S. punicea* germination.

Materials and Methods

Study Site. All field work was performed in the riparian corridor of the San Joaquin River, in close proximity to the city of Fresno, CA (Figure 1). The study site was along the reach of the San Joaquin River bounded to the east by State Route 41 and to the west by State Route 99. This reach is heavily invaded by a variety of exotic plant species, including *S. punicea*. Study plots were located on three parcels; two parcels were owned by the State of California

(San Joaquin River Conservancy) and one was owned by the city of Fresno. Vegetation at the study site was characterized by grassland, willow scrub, low-density cottonwood and willow riparian woodlands, and disturbed areas (McBain and Trush, Inc. 2002; Moise and Hendrickson 2002). The study portion of the San Joaquin River was heavily mined for gravel in the past, altering its hydrogeomorphology and creating deep ponds that often capture the river during high flows (Kondolf et al. 2008; McBain and Trush, Inc. 2002). Tarping was tested both on the banks of the Fresno River and along the banks of adjacent gravel-mining ponds.

The study site was characterized by a Mediterranean climate, with hot summers and cool winters, and most of the precipitation occurring from October to April. During the tarping experiment (October through December), mean daily high temperature was 22.8 C (73.0 F), and mean daily low temperature was 7.8 C (California State University, Fresno, weather station data). We studied tarping during a portion of the year when herbicide use is restricted at the study site.

Laboratory Experiments. Soil Seed Bank Study. To quantify *S. punicea* seed banks, we measured soil seed abundance beneath low- (single plant) and high-density (mean \pm SE; here and below) (15.8 ± 1.8 stems m^{-2}) (1.5 ± 0.17 stems ft^{-2}) *S. punicea* stands. These stands were located in the riparian area adjacent to the river tarping sites (Figure 1); seed banks could not be sampled at pond sites because *S. punicea* stands were removed following tarping experiments by the land manager. We chose stands that were isolated from the seed rain of other *S. punicea* stands. We sampled four stands of each density using 50- by 50-cm (19.7- by 19.7-in) quadrats around the perimeter of each stand, with eight replicates. For low-density stands, the quadrats surrounded the single plant, with no separation between replicate quadrats. For high-density stands, the quadrats were evenly spaced around the perimeter of the stand. If the stand was generally linear in shape, then one quadrat was placed on each end, and three were placed along each side. Within each quadrat, we excavated the soil to a depth of 7 cm, based on Graaff and van Staden (1984), who found 100% emergence of viable *S. punicea* seeds from depths up to 7 cm. We sieved soil in the field and removed all *S. punicea* seeds. If a seed pod was on top of the soil in the quadrat, those seeds were also collected.

In the laboratory, we rinsed seeds to remove residual soil, counted the seeds, and placed the seeds on moist filter paper in petri dishes at room temperature. We separated normal and malformed or damaged seeds by appearance

and germinated them independently. We measured germination for 7 wk by counting germinated seeds every 3 d. In this case, physical dormancy in these seeds was broken through natural processes because we did not mechanically or chemically scarify the seeds. We counted and removed germinated seeds. Deionized water was added as needed to maintain moist conditions.

After 7 wk, we removed any rotten seeds, air-dried the remaining seeds, and submerged the remaining seeds in concentrated H₂SO₄ for 60 min to break the impermeable seed coat (Graaff and van Staden 1984). After acid scarification, we rinsed seeds in cool running water for 15 min to remove acid, placed them in petri dishes on moist filter paper at room temperature, and measured germination every 3 d for 7 additional wk. The combined germination before and after acid scarification determined the total number of viable *S. punicea* seeds in the seed bank.

Thermal Tolerance Experiment. To evaluate the vulnerability of *S. punicea* seeds to high temperatures (hypothesis 2), we measured germination responses to increased heat in the laboratory. We collected mature *S. punicea* seeds from the pond area of the study site (Figure 1) on July 11, 2014, for the thermal tolerance experiment. Because unscarified *S. punicea* seeds can remain in water for more than a year without imbibing or germinating (Bevilacqua et al. 1987), we chose to scarify the seeds. To imitate natural abrasive processes, which may occur during high flows, we shook seeds in a jar with pebbles for 5 min to abrade the impermeable seed coat, following the example of Hunter and Platenkamp (2003). We placed seed samples (four replicates of 25 seeds) in 55-ml (1.9-oz) glass vials with 25 g (0.88 oz) of moist sand (10% H₂O). We incubated vials at four temperatures: 40, 45, and 60 C, and at room temperature (for control samples) and three time durations: 48, 96, and 144 h. The 40 and 45 C treatments were based on maximum soil temperatures achieved at a depth of 7 cm during preliminary summer tarping tests, and the 60 C experiments were based on the upper limit of soil temperature under ideal solarization conditions in California (Stapleton et al. 2005).

Seed viability was determined by seed germination (emergence of the radicle) after the heat treatment. We placed seeds between moist filter paper in petri dishes in a 30 C incubator and counted seed germination every other day for 6 wk. Seeds that germinated were counted and removed from the dishes.

Inundation Tolerance Experiment. To study the effectiveness of inundation for controlling *S. punicea* seed banks

(hypothesis 1), we measured germination and survivorship under different inundation durations. We collected mature *S. punicea* seeds from the area adjacent to the river tarping plots on October 3, 2014, for the inundation experiment (Figure 1). To abrade the impermeable seed coat, we shook seeds in a jar with pebbles for 5 min. We added 50 ml of sieved soil from the study site to 250-ml glass jars, added 25 seeds, and mixed the seeds with the soil. To simulate the anaerobic conditions that exist during periods of inundation, we filled jars with 200 ml of water from the San Joaquin River, and capped jars were kept at room temperature. Control seeds were kept in a paper bag at room temperature. Treatments were 1, 2, 3, 4, and 5 mo of inundation, with each treatment replicated four times.

At 28-d intervals, we removed seeds from the jars by sieving and rinsing with cold running water. Seeds that had germinated during inundation were removed and counted. Ungerminated seeds that were still intact were tested for germination using the methods described for the soil seed-bank study above. We counted and discarded seeds that had disintegrated or begun to rot. After the first month, seeds that germinated during inundation were also monitored for further growth and survivorship. Seeds that germinated were counted every other day. Seeds that germinated in the petri dishes were discarded after monitoring for further growth and survivorship.

Tarping Experiment. To test hypothesis 3, we established plots in the summer of 2014 in two distinct areas: along the banks of the San Joaquin River (five sites), and along the periphery of a large pond formed by gravel mining (five sites) (Figure 1). Sites were chosen from areas of high *S. punicea* infestation in both areas. Mean stem density at pond plots was 22.1 ± 2.6 stems m⁻² ($n = 12$; three sites were unable to be measured) and stem density at river plots was 5.5 ± 0.9 stems m⁻² ($n = 15$). Each site was divided into three 2- by 2-m plots, with the lower edge of each plot 1 m from the water. We randomly assigned the three tarping treatments to each plot, including 4 wk of tarping, 6 wk of tarping, and no tarping (the control). *Sesbania punicea* and all other vegetation in the plot were manually removed (large shrubs cut using loppers and small shrubs pulled up) before the beginning of the study. On October 9 and 19, 2014, we installed black polyethylene plastic (4 mm [0.2 in]) over the experimental plots. Although heating of the soil was not the primary goal of tarping, this treatment can provide some heating benefit (Elmore et al. 1997). Before plastic installation, we wet the soil because heating benefits are most effective on wet soil (Elmore et al. 1997). We measured soil temperature to evaluate the

Table 1. One-way ANOVA results for red sesbania seed banks beneath low-density vs. high-density stands for normal seed and malformed seed numbers, and the percentage of scarified and unscarified germination.

Factor	Levels	Variable	DF ^a	DF error	F ratio	P value
Stand density	Low, high	Normal seed no.	1	84	20.6	< 0.001***
		Malformed seed No.	1	29	3.4	0.074
		% Unscarified germination	1	54	9.9	0.003**
		% Scarified germination	1	53	0.8	0.379

^a Abbreviation: DF, degrees of freedom.

P < 0.01, *P < 0.001.

potential of tarping to increase soil temperature. We buried an i-button thermochron (Maxim Integrated, San Jose, CA) 7 cm deep in the center of each plot, using a mesh plastic basket to ensure easy retrieval. We waterproofed the thermochrons with two coats of Plasti Dip (Plasti Dip International, Blaine, MN), which has minimal effects on temperature readings (Roznik and Alford 2012). The thermochrons measured temperature hourly for the duration of the experiment. The tarping plastic was kept as close to the soil as possible by burying the edges in trenches dug around the periphery of the plots. The plastic remained on the plots for 28 d (4-wk treatment) and 42 d (6-wk treatment). Upon removal of the plastic, we counted all *S. punicea* seedlings present. Subsequently, *S. punicea* seedling and stump resprout number and height were measured monthly between November 2014 and May 2015.

Data Analysis. For seed-bank abundance data, we used one-way ANOVAs to determine the effect of stand density on seed number, unscarified seed-germination percentage, and scarified seed-germination percentage. To meet normality assumptions, we log-transformed seed-bank abundance data and natural germination percentage, again adding a constant (1) to all values before transformation because of the high number of zero values. Acid-scarified germination percentage data were normally distributed, so those data were not transformed. For inundation tolerance data, we used two-way ANOVAs to determine the effects of inundation compared with control and length of inundation on seed germination and survivorship. We analyzed thermal tolerance data using a two-way ANOVA to determine the effects of temperature and exposure length on seed germination. We determined the effect of tarping and site (pond vs. river) on *S. punicea* seedling number, stump resprout number, seedling height, and stump resprout height with a two-way ANOVA for interactions in all 7 mo. Because trends were similar for all 7 mo, we only reported results from our final sampling in May 2015.

We initially included preremoval stem density in experimental plots as a covariate but removed those data from analysis because they were not significant. We log-transformed data from all parameters (seedling and stump resprout number and height) for the tarping experiment to meet normality assumptions, adding a constant (1) to all values before transformation because of the high number of zero values. When appropriate, we compared effects using Tukey's honestly significant difference (HSD) post hoc comparison test. We conducted all statistical analyses using SYSTAT 13 (Systat Software, San Jose, CA).

Results and Discussion

Laboratory Experiments. Seed Bank. The seed germination experiment revealed that the abundance of viable *Sesbania punicea* seeds in the soil seed bank was significantly greater beneath high-density stands than it was beneath low-density stands (Table 1). Mean abundance of normal seeds below high-density stands ($n = 32$) was 924.3 ± 140.0 seeds m^{-2} , whereas mean abundance of normal seeds below low-density stands ($n = 32$) was 23.4 ± 4.7 seeds m^{-2} . Germination percentages of normal and malformed seeds were not significantly different for untreated seeds ($F_{1, 83} = 0.2$; $P = 0.634$) or acid-scarified seeds ($F_{1, 78} = 0.0$; $P = 0.874$). Therefore, malformed and normal seed-germination percentages were combined for analyses. The natural germination percentage was significantly greater in high-density stands compared with low-density stands, but there were no significant differences in germination percentage between high- and low-density stands after acid scarification (Table 1).

The high abundance of *S. punicea* seeds beneath high-density stands, combined with their high viability and impermeable seed coats, indicates that soil seed banks of *S. punicea* will continue to be an issue in invaded areas. Mean percentage of germination was low for unscarified seeds ($n = 56$), at $5.6 \pm 1.2\%$, but much higher when the seed coat was broken through acid scarification ($n = 55$) at

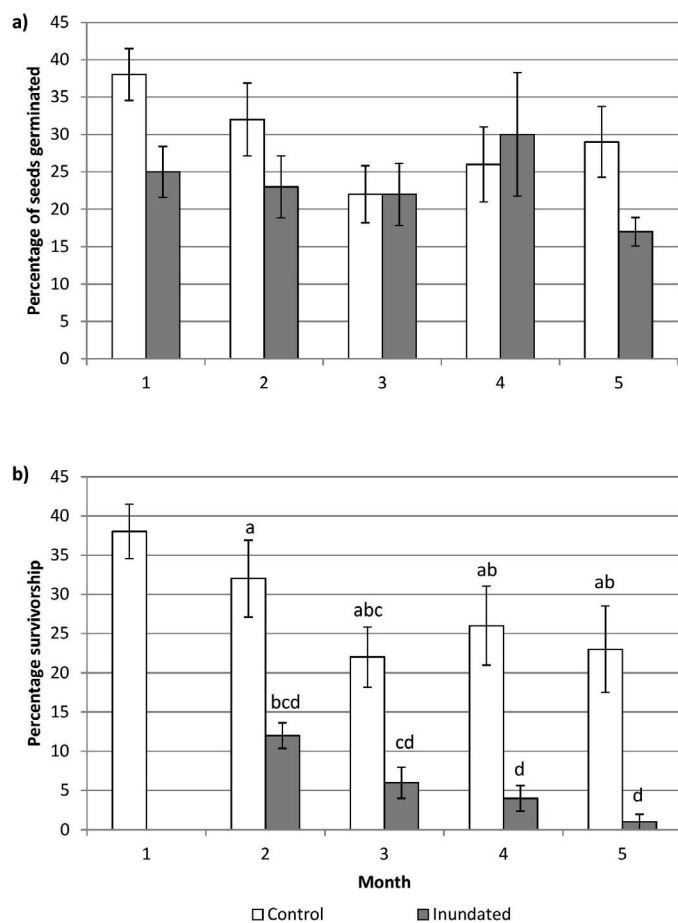


Figure 2. Percentage (\pm SE) of red sesbania seed germination (a) and survivorship (b) for two treatments (inundated and control) in the inundation-tolerance experiment. All seeds in the control treatments that germinated survived. Survivorship for inundated seeds was not measured in mo 1. Inundation treatments had significantly lower germination percentages compared with control treatments. For survivorship, columns without common letters differ significantly (Tukey's honestly significant difference test, $P < 0.05$).

40.9 \pm 3.9%. Graaff and van Staden (1984) found higher germination percentages (69.0 \pm 3.2%) for seeds collected directly from the plant and scarified in acid for 60 min. The high germination percentage after acid scarification indicates the high viability of *S. punicea* seeds in the soil seed bank, although germination was not quite as high as that of fresh seeds. Seeds in the soil seed bank will germinate once the impermeable seed coat is broken and water can enter the seed. The significantly higher germination percentage in higher-density stands may be explained by stand age and the subsequent age of *S. punicea* seeds in the soil. Valleriani and Tielbörger (2006) suggest that in density-regulated populations the probability of

seeds germinating—should increase with seed age. High-density stands are likely older than low-density (single individual) stands are, and seeds in the soil would likely be older as well. If Valleriani and Tielbörger (2006) are correct, then there would be a high probability for these older seeds to germinate.

Inundation Tolerance. Seeds from inundation treatments had significantly lower germination percentages compared with controls ($F_{1, 30} = 4.2$; $P = 0.050$) (Figure 2a). Germination did not differ between inundation durations. Seedling survivorship decreased significantly across inundation treatments, with 100% survivorship of germinated seeds in control treatments and 25% survivorship in inundation treatments (Figure 2b; $F_{1, 24} = 76.5$; $P < 0.001$).

Inundation has been shown to increase seed mortality in other species, likely because of anoxia. For example, increased seed mortality after burial and inundation was shown for green sorrel (*Rumex acetosa* L.) and for melaleuca [*Melaleuca quinquenervia* (Cav.) Blake] (Voeselek and Blom 1992; Thai et al. 2005). Flooding creates anaerobic conditions in the soil (Burgess 1967), and those low-oxygen conditions are the likely cause of *S. punicea* seedling death after germination. Ladrör et al. (1986) found delayed emergence and reduced growth in kidney bean (*Phaseolus vulgaris* L. [Fabaceae]) seeds exposed to 0 to 2% oxygen. Our results were similar to Abernethy and Willby (1999), who found that perennial floodplain species generally had significantly lower germination under inundated conditions. The effects of disturbance on invasive species is species dependent (Schoolor et al. 2010), so the effects of flooding on *S. punicea* seed banks should not be generalized to all invasive species.

Sesbania punicea seeds were able to germinate underwater, but sustained inundation reduced germination, survivorship, and establishment (Figure 2) and may, therefore, be a useful management strategy. Using inundation as a management technique would be most practical along managed rivers or wetlands where water levels can be controlled. An inundation period of 2 mo resulted in significant declines in *S. punicea* seedling survivorship, so that length of flooding would begin to deplete the seed bank. Because the San Joaquin River faces many demands on its water, releases solely for the control of *S. punicea* are not likely as a feasible management option. However, large quantities of water are occasionally released from Friant Dam and flow through the invaded portion of the river to meet water rights and restoration obligations. Assuming those flows actually inundate

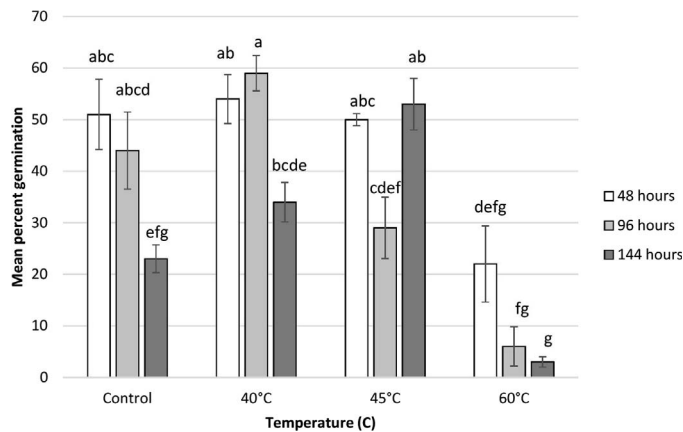


Figure 3. Mean percentage (\pm SE) of germination of red sesbania seeds under four temperature treatments and three durations in the thermal-tolerance experiment. Columns without common letters differ significantly (Tukey's honestly significant difference test, $P < 0.05$).

invaded areas for a substantial period of time, traditional control methods may be more effective because of seedling mortality and reductions in the seed bank. In addition, those releases would likely accelerate the recovery of native riparian vegetation. Releases into the San Joaquin River, which flooded the study site during the summer of 2014, averaged $36.8 \text{ m}^3 \text{ s}^{-1}$ for the period from July 15 to September 15, compared with average releases of $9.97 \text{ m}^3 \text{ s}^{-1}$ during same period in 2013 (California Department of Water Resources 2016). The 2014 releases resulted in $1.46 \times 10^8 \text{ m}^3$ more water being released from the reservoir. The costs of nonirrigation releases from Friant Dam in 2014 ranged from $\$0.013$ to $\$0.025 \text{ m}^{-3}$ (U.S. Bureau of Reclamation 2014), resulting in an estimate cost range of $\$1.88$ to $\$3.69$ million for flows that inundated the study site. These high costs highlight that flow releases solely for *S. punicea* control are unlikely. However, after extended periods of inundation, treatment with traditional control methods may be an effective method of *S. punicea* management because of the reduction in seedling survivorship. Additionally, inundation may be an option for smaller areas that can be flooded at a lower cost. Other drawbacks to inundation are the potential to transport the floating seed pods to other areas, spreading the invasion of *S. punicea*, and the potential for sustained flooding to negatively affect native plant and wildlife species.

To further quantify the effects of inundation, additional study is needed on the effects of duration and water depth on seedlings and small plants, not just on seeds, especially as field trials. Investigation of the effects of short durations of inundation on survivorship would be especially valuable

because shorter-duration inundation is likely to be more achievable for land managers. Stands of mature *S. punicea* along the San Joaquin River exposed to several months of inundation during the summer of 2014 showed development of aerenchyma and adventitious roots at the waterline, but there did not appear to be mass mortality (personal observation). These responses are typical for plants responding to hypoxia caused by flooding (Blom and Voeselek 1996). Early life-history stages of plants are generally more susceptible to stress, so targeting seedlings, instead of mature plants, may be more effective. The U.S. Army Corps of Engineers classifies *S. punicea* as a facultative wetland plant in the arid west and as facultative in the Atlantic and Gulf Coast plain (Lichvar et al. 2014), reaffirming its status as a plant adapted to transitional conditions. If inundation is used as a control method, targeting small, isolated populations of *S. punicea* and starting in the upstream portion of the watershed may have best results (Robison et al. 2013), although complete eradication of the species is unlikely (Swanton and Booth 2004).

Thermal Tolerance. The 60 C treatment showed the greatest reduction in germination across all durations, and 96 and 144 h exposures generally resulted in lower germination (Figure 3). Interestingly, the 144-h control treatment was significantly less than the 48- and 96-h treatment (Figure 3). It is possible that seeds were negatively affected by prolonged room temperature incubation in sand, although the mechanism is not clear. There were significant differences in germination among temperature treatments ($F_{3, 40} = 38.0$; $P < 0.001$), as well as among durations ($F_{2, 40} = 11.5$; $P < 0.001$). There was also a significant interaction between temperature and duration ($F_{6, 40} = 6.0$; $P < 0.001$).

In pairwise post hoc testing, the 60 C treatment significantly reduced germination, compared with the 40 C and 45 C temperatures and the control treatments ($P < 0.001$). There were no significant differences between the 40 C and 45 C temperatures and control treatments. Germination was significantly less with 96 h of exposure than it was with 48 h of exposure ($P = 0.020$). Germination was also significantly less for the 144-h exposure than it was for the 48-h exposure ($P < 0.001$). There was no significant difference between 96 and 144 h exposures ($P = 0.161$).

Cracked seeds were observed in these experiments, so high temperatures might increase the permeability of the seed coat for *S. punicea*, potentially exposing the seeds to greater thermal effects. Seed coats are important barriers to

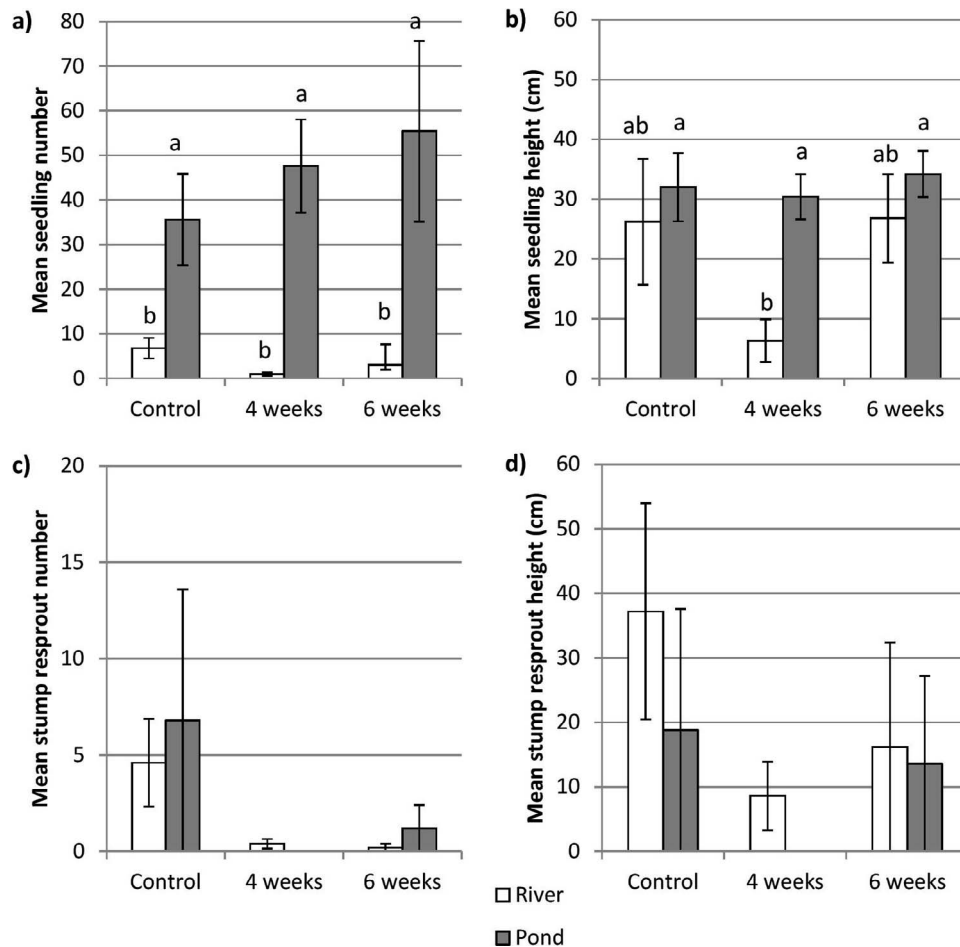


Figure 4. Results for (a) mean seedling number, (b) mean seedling height, (c) mean stump resprout number, and (d) mean stump resprout height measured 7 mo after the start of tarping, across three treatments: control (no tarping), 4 wk tarping, and 6 wk tarping. Columns without common letters differ significantly (Tukey's honestly significant difference test, $P < 0.05$). There were no significant differences in mean stump resprout number and the mean stump resprout height.

microbial activity, and the breaking of the seed coat could expose seeds to detrimental microbial activity (Baskin and Baskin 2014; Cohen et al. 2008). Because of the impermeable seed coat (a physical dormancy mechanism) of *S. punicea*, even if the soil surrounding the seed is moist, the seed may actually be exposed to dry heating because water does not enter the seed (Cohen et al. 2008). Dry heating is much less effective at increasing seed mortality than moist heating is (Egley 1990).

Tarping Experiment. Seedling number and seedling height were greater at pond sites than they were at river sites (Figure 4a), but tarping treatments did not have a significant effect on any response variables at either site (Table 2). Four weeks of tarping at the river sites resulted in the lowest seedling numbers per plot (1.0 ± 0.4) as well as the smallest seedling (6.3 ± 3.6 cm) and stump sprout

(8.6 ± 5.3 cm) heights (Figure 4). Stump resprout number was highest in control treatments and remained low in solarized sites, although there were no significant differences among treatments at either the river or pond sites (Figure 4c). There were no significant differences in stump resprout heights (Figure 4d).

Upon initial removal of the tarping plastic, we observed many *S. punicea* seedlings (10.0 ± 2.2 seedlings plot⁻¹) that had germinated under the plastic. Many of those seedlings were elongated and yellow. In fact, between removal of plastic and the initial monthly count, more than one-half of the seedlings died (5.9 ± 2.2 seedlings plot⁻¹).

Our experiment showed maximum soil temperatures of only 29.5 C to 38.5 C at a 7-cm depth in solarized plots, far below the temperature required for reduced germination that we measured in the laboratory (Figure 3). There were significant differences in mean temperatures between treatments ($F_{2, 27,527} = 251.8$; $P < 0.001$) and sites ($F_{1, 27,527} = 251.8$; $P < 0.001$).

Table 2. Two-way ANOVA results for tarping of red sesbania seed banks at the river and pond sites along the San Joaquin River, CA. Results 7 mo after the start of tarping treatments were analyzed.

Factors and interactions	Levels	DF		Seedling No.		Seedling height		Stump sprout No.		Stump sprout height	
		DF ^a	error	F ratio	P value	F ratio	P value	F ratio	P value	F ratio	P value
Site	River, pond	1	24	99.1	< 0.001***	9.943	0.004**	0.3	0.574	2.0	0.166
Treatment	4 wk tarping, 6 wk tarping, control	2	24	1.1	0.364	2.771	0.083	2.5	0.103	0.9	0.400
Site × treatment		2	24	3.2	0.060	2.237	0.129	0.5	0.618	0.5	0.618

^a Abbreviation: DF, degrees of freedom.

P < 0.01, *P < 0.001.

27,527 = 79.2; P < 0.001), and there was a significant interaction between treatment and sites ($F_{1, 27,527} = 468.8$; P < 0.001). For the hottest portion of the day, (1:00 P.M. TO 5:00 P.M.), mean temperatures followed trends similar to those described above (Table 3). In post hoc testing, 4- and 6-wk tarping soil temperatures in the plots were significantly greater than control temperatures (P < 0.001) but were not significantly different between temperatures at 4 and 6 wk of tarping (P = 0.339). There were significantly higher temperatures at river sites than there were at pond sites (P < 0.001). Although there was a statistically significant increase in temperature for tarping plots compared with control plots, the increase was, on average, less than 5 C.

Potentially larger seed banks at the ponds could explain the difference in seedling number between pond and river sites (Figure 4). There was a higher initial stem density at pond sites, although that was not statistically significant when analyzed as a covariate. Seed dispersal was also likely to affect seed-bank densities. In ponds, the seed pods that fell into the water were trapped within the pond and were deposited on the margins. Comparatively, seed pods that fell into the river were moved downstream to other locations, leading to less-dense seed banks beneath river stands.

Although tarping has been successful in controlling perennial weeds in wetland environments (Hutchinson and Viers 2011), we found that fall/winter tarping was not effective in controlling *S. punicea* seed banks. The burial depth of seeds in the soil seed bank may have an

influence on breaking of physical dormancy and vulnerability to tarping. Increased burial depth of physically dormant seeds generally decreased breaking of physical dormancy, possibly because of decreased maximum temperatures and reduced fluctuation in daily temperatures (Baskin and Baskin 2014). It is possible that increased temperatures deeper in the soil could result in lethal germination for deeply buried seeds if seedlings cannot reach the soil surface. As fall/winter tarping appears not to be an effective method for *S. punicea* control, the potential for biocontrol may be worth considering. Biocontrol using three weevil species from the native range of *S. punicea* has shown great success in South Africa (Hoffman and Moran 1991, 1998).

Although tarping during the fall/winter growing season did not decrease *S. punicea* germination, we found that the seeds were vulnerable to mortality at high temperatures (60 C) and long exposures (96 h) (Figure 3). This result shows that this species is a candidate for solarization. Cohen et al. (2008) found that solarization at high temperatures was effective at controlling orange wattle [*Acacia saligna* (Labill.) Wendl. f.], another perennial member of the Fabaceae family that produces large seeds with impermeable seed coats. Therefore, it is possible for these types of plants to be controlled with solarization. Soil temperatures may reach 60 C at shallow soil depths (5 cm) for a small portion of the day under optimal solarization conditions in California's Central Valley (Stapleton et al. 2005). Solarization treatments might control *S. punicea*, if temperatures and lengths of exposure were sufficient.

Table 3. Mean (\pm SE) and maximum soil temperature in tarping plots along the San Joaquin River, north of Fresno, CA. Temperatures measured from October to December 2014, between 1:00 P.M. and 5:00 P.M. at 7 cm below the soil surface.

	River			Pond		
	Control	4 wk	6 wk	Control	4 wk	6 wk
Mean \pm SE	20.2 \pm 0.14	22.1 \pm 0.15	24.4 \pm 0.18	20.9 \pm 0.20	22.3 \pm 0.14	20.4 \pm 0.12
Maximum	33.0	33.0	38.5	31.0	31.0	29.5

However, scarified *S. punicea* seeds are able to emerge from depths of up to 12 cm (Graff and van Staden 1984). Cohen et al. (2008) found maximum soil temperatures of only 45 C at 12 cm depths under normal tarping conditions, which is insufficient to decrease germination of *S. punicea* seeds (Figure 3), so even under optimal solarization conditions, the seed bank of *S. punicea* would not be completely eliminated. To maximize the effects of solarization, plots should be irrigated before application of plastic (Elmore et al. 1997). A downside to soil solarization is the potential negative effects on the seed bank of native plants. Gioria and Osborne (2009) found that native-plant soil seed banks in invaded riparian areas were less abundant and less diverse than those in noninvaded areas. The degraded native seed bank in invaded areas may be further deteriorated by solarization.

This study aimed to determine whether inundation or tarping could control *S. punicea* in invaded riparian areas in the Central Valley of California. Although *S. punicea* seeds were found to have lower germination at 60 C, tarping experiments conducted during the fall/winter growing season did not show success in controlling this species by diminishing the soil seed bank. Results from our laboratory study show that inundation is the most promising treatment for reducing the viability and establishment of *S. punicea* seeds from the soil seed bank. Future studies should test solarization in the hottest possible field conditions in the summer, as well as inundation experiments in the field.

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