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Strategies for Restoring Native Riparian Understory Plants Along the Sacramento River: Timing, Shade, Non-Native Control, and Planting Method

Prairie L. Moore[1], Karen D. Holl[2], and David M. Wood[1]

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ABSTRACT

Restorationists commonly plant overstory and understory species simultaneously at the outset of restoration, but a mature forest canopy may be necessary to facilitate survival of light-intolerant understory species. We conducted two experiments in riparian forest restoration sites along the Sacramento River to determine whether:

1. Introducing understory species is more successful at the beginning of restoration or after the canopy has developed;
2. Canopy cover directly (via reduced light) or indirectly (by reducing non-native competition) facilitates survival of native understory species; and
3. Seeding or planting seedlings of understory species is most effective.

Seven native understory species were introduced as both seeds and seedlings into an experiment that manipulated canopy cover (open or canopy) and non-native grass competition (control or grass-specific herbicide). We conducted another experiment using shade cloth to directly test the effect of different light levels on seedling survival and growth of three species. Both experiments showed that four species (*Aristolochia californica, Carex barbarae, Clematis ligusticifolia, and Vitis californica*) had higher survival under low-light conditions (canopy or shade cloth). In contrast, three species (*Artemisia douglasiana, Euthamia occidentalis* and *Rubus californica*) had similar survival across open and canopy conditions. Cover of unplanted understory vegetation (mostly non-native) was much lower under the canopy than in open plots treated with grass-specific herbicide. Establishment from seed was generally low and highly variable. Our results suggest that to restore understory species in riparian forests in north–central California: light-intolerant understory species should be planted after canopy closure; canopy cover is more effective than grass-specific herbicide at reducing non-native understory cover; and planting seedlings is more successful than direct seeding.

KEY WORDS

competition, direct seeding, facilitation, riparian understory, Sacramento River, seedling survival and growth

1 Department of Biological Sciences, California State University, Chico, CA 95929

2 Corresponding author: Environmental Studies Department, University of California, Santa Cruz, CA 95064; *kholl@ucsc.edu*

INTRODUCTION

The challenges and importance of restoring understory forest species have received increasing attention in recent years (reviewed by Flinn and Vellend 2005; Nilsson and Wardle 2005; Gilliam 2007). Traditionally, forest restoration efforts have focused on restoring trees and shrubs, while either overlooking the understory component or assuming it would self assemble over time (Young and Evans 2000; Hilderbrand and others 2005; Pensa and others 2008). Many studies, however, show that understory species often fail to colonize restored forests due to dispersal and recruitment limitations (e.g., McLachlan and Bazely 2003; Whigham 2004; Flinn and Vellend 2005; Shono and others 2006). A growing number of studies, primarily in the tropics, suggest that a closed canopy is necessary to facilitate survival of late successional forest species (Parrotta and Knowles 2001; Cabin and others 2002; Raman and others 2009). This result is problematic for restoration practitioners, as restoration budgets are commonly allocated for one to a few years; therefore, it is likely to be challenging to find funding to introduce later successional species after appropriate site conditions have developed.

Canopy cover may facilitate understory species directly, by ameliorating abiotic stress (e.g. decreased air and soil temperatures and increased humidity, soil moisture, and litter cover) (Zou and others 2005; Pages and Michalte 2006; Barbier and others 2008), or indirectly, by reducing competition with light-demanding non-native species that are common in disturbed landscapes (Levine 1999; Pages and Michalet 2003; Pensa and others 2008). Evidence exists for both direct and indirect canopy effects. Studies of shade-tolerant plants report that decreasing light can facilitate survival (e.g., Sack and Grubb 2002; Hastwell and Facelli 2003; Sanchez–Gomez and others 2006). Likewise, reducing competition through removal of non-native species by herbicides or physical means can increase native species establishment (D'Antonio and others 1998; Cabin and others 2002; Denslow and others 2006).

The method of species introduction, whether by sowing seed or planting seedlings, may influence the magnitude of canopy effects and the overall effectiveness of restoration efforts. The success of sowing seeds is limited by seed predation, seed germination, and early seedling survival (Nilson and Hjalten 2003; Doust and others 2006; Jinks and others 2006). Planting seedlings eliminates these losses but requires propagation facilities and is more costly and labor intensive. Evidence on the efficacy of seeding vs. planting seedlings is mixed; some studies have found greater survival and growth of planted seedlings as compared to those germinating from seed (Drayton and Primack 2000; Wallin and others 2009), whereas other studies have reported the opposite result (Halter and others 1993; Young and Evans 2000, 2005).

Large-scale riparian forest restoration along the Sacramento River in north-central California presents an ideal opportunity to investigate both the timing and method of understory restoration. Riparian forests along the middle Sacramento River have been altered by dams and levees, extensive industrial agriculture, logging, and urban development with <5% of the original forest remaining (Golet and others 2008). Since 1988, several nonprofit organizations and governmental agencies have carried out riparian forest-restoration projects on >2,500 hectares (ha) of land; these efforts have resulted in a valuable natural experiment. Before 2000, only native overstory trees and shrubs were planted. Since 2000, both overstory and native understory species were usually planted, the latter including a mix of herbs, vines, and low-growing shrubs. Surveys of many pre-2000 restoration sites have showed that few native understory species naturally colonize the restored forests (Holl and Crone 2004; McClain and others 2011). Instead, the understories are dominated by non-native forbs and grasses. Native understory cover, where it occurs, is higher in sites with lower non-native cover and greater canopy cover. This correlational evidence suggests that canopy cover may have a positive effect on understory species in this system, but an experimental test is required to separate out the effects of overstory cover and understory competition to help guide restoration efforts.

We conducted a factorial experiment in which we manipulated both canopy cover and competition with non-native grasses to determine whether: (1) it is better to introduce understory species into a site before or after the canopy has developed; (2) canopy cover directly (by reducing light and consequent abiotic stress) or indirectly (by reducing non-native competition) facilitates the survival of native understory species; and (3) seeding or planting understory species is more effective. We also conducted a "shade experiment" to test separately the effect of different light levels on seedling survival and growth. Finally, we compared survival rates of understory species in our experiments to those in actual restoration projects to determine the applicability of our results to larger-scale restoration efforts.

METHODS

Site Description

These studies were conducted at sites located between Hamilton City (39.7° N, 122° W) and Gerber (40° N, 122.2° W) in north-central California. Average annual rainfall is 531.6 m with high interannual variation and most rain falling between November and April. Average monthly temperatures range from 6 °C in December to 27 °C in July (California Department of Water Resources, Orland station). Sites are all located within the 2-year floodplain (i.e., land with an average 2-year flood recurrence frequency) and are separated by 0.5 to 65 km.

Species Description

We chose seven understory species with varied growth and dispersal forms that are common in the riparian forest understory and widely planted as part of restoration efforts (Table 1). These species (referred to by their genera) are common in remnant forests, but only *Artemisia* frequently establishes naturally in restored sites (Holl and Crone 2004).

Seeds for direct seeding and growing seedlings in both the canopy-herbicide and shade experiments were collected locally by The Nature Conservancy Sacramento River Office and The Floral Native Nursery (Chico, CA, USA). Six species were grown by Floral Native Nursery and were 6 to 12 months old and 2 to 10 cm tall at the time of planting. *Carex* seedlings were grown by Hedgerow Farms (Winters, CA, USA) and were 3 months old and 2 to 5 cm tall when planted. All species except *Carex* and *Rubus* were dormant (no leaves) at the time of planting.

Canopy–Herbicide Experiment

We conducted a factorial experiment in which we evaluated the effect of canopy cover (open or canopy) and non-native grass competition (control or grass-specific herbicide [GSH]) on native understory species; treatments are described in detail below.

Table 1 Study species including their growth and dispersal forms, seeding rates in the canopy-herbicide experiment, and shadehouse germination. Nomenclature follows Hickman (1993).

Latin name	Common name	Growth form	Disperal mechanism	Seeding rate (seeds m^{-2})		Shadehouse germination (%)	
				2005–2006	2006–2007	2005–2006	2006–2007
Aristolochia californica	Pipevine	vine	gravity	300	150	21.5	32.7
Artemisia douglasiana	Mugwort	herb	wind	500	750	5.2	23.2
Carex barbarae	Santa Barbara sedge	sedge	gravity	500	750	16.3	2.2
Clematis ligusticifolia	virgin's bower	vine	wind	500	500	32.8	23.2
Euthamia occidentalis	Goldenrod	herb	wind	500	500	64.0	37.0
Rubus ursinus	California blackberry	shrub	animal	300	500	35.8	60.7
Vitis californica	California grape	vine	animal	300	200	63.3	59.0

This experiment was replicated at three "old" sites, which were restored 7 to 10 years previously and had closed canopies. These old sites had been planted with overstory species, including *Acer negundo* (box elder), *Platanus racemosa* (sycamore), *Populus fremontii* (Fremont cottonwood), *Quercus lobata* (valley oak), and multiple *Salix* species (willow). Consistent with typical restoration practices in the region, these sites were managed for 3 years post-planting with irrigation, weed control, and replanting (if survival was less than the 80% required by restoration contracts); after 3 years all management ceased. The non-native grass competition treatment was also replicated at three 'new' restoration sites (one site restored in 2004 and two sites restored in 2007) where the canopy had yet to develop. All new and old sites were used for row crop or orchard agriculture for more than 30 years until 1 to 2 years before restoration.

In September 2005, we set up four blocks separated by >100 m at each site. Treatments were randomly assigned to 13 × 16 m plots, which were separated by 1 to 25 m. Blocks contained four plots at old sites (all open/canopy × control/GSH treatment combinations) and two plots at new sites where no canopy was present (open × control/GSH treatments). At one new site, a block was destroyed after a year so there were only three blocks.

For the non-native grass competition treatment, half the plots were sprayed with Round-up® in late October 2005, treated with Poast® (a GSH) a few days before planting in December 2005, and thereafter were sprayed with Poast approximately every other month (adjusted to the rate of grass growth) through March 2008. We had only to spray small patches in canopy plots, but grasses regrew quickly in open plots, and thus, required more herbicide. There was vigorous non-native forb growth in GSH plots, particularly at new sites. Because our goal was to reduce non-native competition, we mowed GSH plots at new sites in early spring and late fall 2007 and 2008; this is consistent with typical weed-control measures in this system. Mowing was not feasible in old sites because of the high stem density of woody plants.

Because the active ingredient in Poast (*sethoxydim*) inhibits the photosynthetic process in grasses only, we did not anticipate that Poast would have a negative effect on the non-grass species that we studied. To confirm that the specific formula of Poast we used did not negatively affect target species, we conducted a greenhouse study in which we compared growth and survival of sprayed and unsprayed plants of all species, and recorded no differences (data not shown).

At old sites, two plots in each block had a tree canopy and two 'open' plots did not. We located old site open plots in areas that had an existing canopy, which we cut and removed in September 2005. We did not choose naturally open areas in old sites because such open areas within a uniform plantation are largely due to shallow sand or gravel layers, which do not support trees (Alpert and others 1999). In other words, we wanted all plots to have a similar riparian forest soil texture. We augered a soil core in each plot, and relocated plots where the sand or gravel layer was <2 m from the surface.

In mid-December 2005, we planted ten seedlings of each of the seven species in 2 × 5 m quadrats within each plot; plants were separated by 1 m. There was extensive flooding in late December 2005 and early January 2006, so in late January 2006 we replaced the 4% of seedlings that had washed away.

In mid-December 2005, we manually scattered seeds of each species on the soil surface in a separate 2 ×2 m quadrat for each of the seven species. Because of very low seed germination in spring 2006, all seed quadrats were manually hoed, and seed was raked in (to improve soil–seed contact and minimize the risk of seeds washing away) during November and December of 2006. Seeding rates for both years are listed in Table 1. We determined seed viability rates by shadehouse germination trials initiated in January, following seeding in the field, and monitored at approximately 1-week intervals through May.

We recorded the number of seedlings in seeded quadrats in May 2006, 2007, and 2008. We measured planted seedling survival in May and September 2006 and 2007, and survival and cover (estimated to the nearest dm^2) in May 2008. At each sampling period we visually estimated cover of unplanted vegetation in each seeding and planting quadrat using a modified Braun Blanquet cover scale with cover classes: 0–1%, 1–5%, 5–25%, 25–50%, 50–75%, 75–95%, and 95–100%.

As described above, our experiment was specifically designed to test the effects of canopy cover and herbicide on seedling growth and survival. In addition, we collected data on soil organic matter and texture, light, and flood duration to characterize how these abiotic factors varied across treatments.

In fall 2006, we took 12, 10-cm deep × 2.5-cm diameter soil cores per plot. Cores were composited, dried at 35°C, passed through a 2-mm sieve, and analyzed for particle size using the hydrometer method and percent organic matter using modified Walkley–Black by the University of California, Davis Agriculture and Natural Resoures (ANR) Analytical Laboratory (ANRAL 2007).

We measured photosynthetically active radiation (PAR; 400 to 700 µmol m^{-2} s^{-1}) in canopy plots in August 2008 using a line quantum sensor (LI–191, LI–COR). At each plot, we took a reading in the open, ten readings evenly distributed throughout the canopy plots, and another in the open; all measurements were taken at 1-m height between 09:00 and 14:00. We divided the average of the canopy measurements by the average of the open measurements to calculate the percent PAR transmitted.

We recorded air temperature at the soil surface in each block every half hour during the winter with a HOBO temperature logger (Model UA-001-08, Onset Corporation, Bourne, MA, USA) to determine the duration of flooding, because loggers covered by water fluctuate less in temperature than those in air (Kreuzer and others 2003). We developed a flow chart (available from the senior author) using these temperature data, the air temperature and precipitation recorded by the nearest weather station, and the river level. Although our experiment was not aimed at testing how flooding affected seedling survival, we were concerned that the high variation in flood duration across blocks in the first year (2005–2006) could have confounded our results. We used regression to test the effect of the number of days underwater on plant survival at the end of the first growing season for each species × treatment combination. We calculated Pearson correlation coefficients between flood duration and soil texture parameters.

All analyses were conducting using either JMP 7.0 or SAS 9.13 software (SAS Institute Inc., Cary, NC, USA). Throughout, we report means ± 1 SE and consider $p < 0.05$ as significant. Values were tested for normality and homogeneity of variances, and log or arcsine square root (for percentages) transformed when necessary. In a few cases, values were ranked, when transforming did not serve to normalize the data, and then analyzed using the models described below. For all our analyses (described in detail below), our canopy treatment included three levels: new restoration open, old restoration open, and old restoration canopy.

To assess the effect of our treatments on reducing competition with non-native species, we compared cover of unplanted grasses and forbs (nearly all non-native) across treatments using a two-way ANOVA with canopy treatment, non-native grass competition (GSH or control), and their interaction as independent variables.

Planted seedling survival data for each species were analyzed using a multivariate repeated-measures ANOVA with canopy treatment, non-native grass competition, time, and interaction terms as independent variables, and Wilk's Lambda as the test statistic. These analyses showed that the GSH did not affect planted seedling survival, so we pooled the data from GSH/control treatments and report the results of a multivariate repeated-measures ANOVA with canopy treatment, time, and an interaction term. Similarly, we analyzed planted seedling cover in May 2008 (for quadrats with surviving individuals) across treatments using ANOVA both with and without the GSH/control treatment effect. We averaged the foliar cover of all surviving seedlings in each plot before analysis. In one old open quadrat, *Rubus* had five times more cover of any other quadrat; we removed this value because it unduly affected the analysis.

We calculated the number of seedlings observed in seeding quadrats in June 2007 and May 2008 as a percentage of the number of viable seed sown, and analyzed data using the same repeated-measures ANOVA models as for planted seedling survival. Because of the low number of seedlings in new and open seeded quadrats, we were unable to compare cover. For all analyses, we used Tukey's mean comparison tests to compare canopy treatments (new, old open, and old canopy).

Shade Experiment

We used different thicknesses of neutral shade cloth to test the direct effect of reduced light on native understory survival at two new restoration sites. In December 2006, 100 seedlings (2 to 10 cm tall and dormant) of each of three species (*Artemisia*, *Clematis*, and *Vitis*) were interplanted randomly in a 3 × 3 m grid at each site. We chose these species to represent a range of shade tolerances, based on the canopy-herbicide experiment. In April 2007, we randomly assigned the 468 surviving plants to one of four treatments (n = 35 to 43 seedlings/species/treatment): full sun; 30%, 60%, or 80% neutral shade according to the manufacturer (Greenhouse Megastore item SC-BL). Tomato cages (1 m tall × 0.33 m diameter at the top) were used to support the shade cloth. From 10:00 to 16:00, shade structures cast no shade onto adjacent plants. Cages were removed in November 2007 and replaced in March 2008, timed with the winter deciduous phenology of most riparian forest overstory species. In December 2007, we replanted places in the grid where plants had died, and new plants were randomly assigned to one of the four treatments (n = 17 to 29 new seedlings/species/treatment). To reduce the potentially confounding effect of herbaceous competition and test the direct effect of light level, we clipped all naturally establishing vegetation from March to June (peak growing season) in both years.

To quantify the microclimatic conditions in the shade treatments, we measured PAR using two Watch Dog sensors and data loggers (Models 200 and 36681, Spectrum Technologies, Plainfield, IL, USA). Sensors were placed 0.3 m above the ground, with one inside the shade structure and the other in full sun. PAR measurements were recorded at 15-min intervals for 24 hrs, and sensors were moved to a new cage daily for 24 d total in the summers of 2007 and 2008.

We recorded relative humidity and temperature at 30-min intervals at 0.5 = height in the four shade treatments simultaneously with four Watch Dog data loggers (Model 100, Spectrum Technologies). The full sun treatment logger was placed in a radiation shield. Loggers were moved weekly from May–September 2008.

We recorded plant survival in late May and early June of 2007 and 2008, and tested the effect of shading on seedling survival using chi-square tests. We did not compare plant cover because cages constrained the growth of some plants.

Understory Plant Survival in Restoration Sites

In order to compare survival in our experiments with survival of understory species in actual restoration projects after irrigation and weed management had ceased, we surveyed two, 4-year-old restoration sites (26.7 and 81.9 ha) planted by The Nature Conservancy (TNC). At the time of our survey in fall 2008, the sites had received no irrigation or weed management for one year.

We used the same methods that restoration practitioners use to estimate survival while sites are under active management (R. Luster, TNC, Chico, CA, pers. comm., 2009). At 22 randomly-selected locations at the large site and six locations at the small site, we counted living understory individuals in ten rows of ten planting points (separated by 3.4 m, 2800 points total) at which both an overstory and understory species had been planted. We calculated percent survival by using the planting frequency of each species as our expected value.

RESULTS

Canopy–Herbicide Experiment

Abiotic Conditions and Unplanted Understory Vegetation

Rainfall in the first year of the canopy–herbicide factorial experiment (2005–2006) was 117% of average (624.8 mm), which resulted in extensive flooding. In contrast, rainfall in the following 2 years was well below average with no flooding (2006–2007: 238 mm, 45%; 2007–2008: 373 mm, 70%). Experimental plots were covered by water for 2 to 45 days (mean 17 days) in 2005–2006. First-year survival of five of the seven species was not related to flood duration. However, *Aristolochia* first-year survival in the canopy treatment was lower in sites with longer flooding duration ($r^2 = 0.47$, $p < 0.0001$; survival was too low to analyze in other treatments), whereas *Artemisia* had higher survival in the longer-flooded sites in two treatments (new open: $r^2 = 0.14$, $p = 0.1091$; old open: $r^2 = 0.27$, $p = 0.0051$; old canopy: $r^2 = 0.34$, $p = 0.0026$). These results remained consistent through the end of the study (data not shown).

All plots had sandy loam soils, and soil organic matter was slightly higher under the canopy at old sites than at new sites ($F_{2,67} = 6.5$, $p = 0.0027$, Table 2). Soil particle size did not differ among the three treatments ($F_{2,67} = <1.6$, $p > 0.2$ in all cases, Table 2), but percent silt was higher ($r^2 = 0.22$, $p < 0.0001$) and percent sand was lower ($r^2 = 0.15$, $p < 0.0001$) in sites that flooded longer in the first year of the study. Percent PAR under in old canopy plots ranged from 1.8 to 19.1% (8.5 ± 1.0%).

The GSH reduced grass cover (GSH: $F_{1,64} = 63.9$, $p < 0.0001$; canopy [C]: $F_{2,64} = 25.2$, $p < 0.0001$; interaction [GSH × C]: $F_{2,64} = 6.4$, $p = 0.0030$, Figure 1), but unplanted forb cover was higher in GSH plots without a canopy (GSH: $F_{1,64} = 20.3$, $p < 0.0001$; C: $F_{2,64} = 35.0$, $p < 0.0001$; GSH × C: $F_{2,64} = 4.7$, $p = 0.0129$). Total unplanted understory cover was lower in GSH plots, but canopy cover reduced understory cover substantially more (GSH: $F_{1,64} = 27.0$, $p < 0.0001$; C: $F_{2,64} = 176.9$, $p < 0.0001$; GSH × C: $F_{2,64} = 1.4$, $p = 0.2470$, Figure 1).

Seedling Survival and Cover

The GSH treatment did not significantly affect seedling survival or cover of any species ($p > 0.05$ for both GSH and GSH × C effects in all cases). For all species (except *Artemisia*), there was a significant

Table 2 Soil organic matter and texture in new open, old open, and old canopy plots. Values are mean ± SE. Means with the same letter are not significantly different across treatments using Tukey's mean comparison procedure.

	New open	Old open	Old canopy
Organic matter	1.9 ± 0.1A	2.1 ± 0.1AB	2.3 ± 0.1B
% sand	38.6 ± 2.3	35.3 ± 2.2	35.3 ± 2.2
% silt	45.2 ± 1.9	49.5 ± 1.9	45.9 ± 1.9
% clay	16.1 ± 0.7	15.0 ± 0.7	15.1 ± 0.7

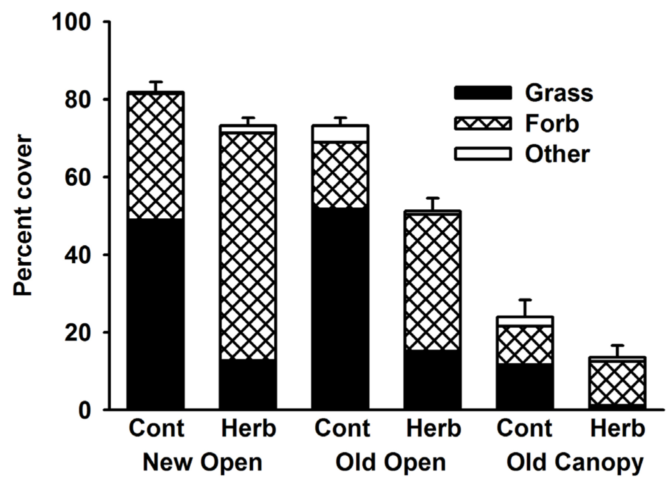

Figure 1 Percent cover of unplanted understory vegetation in new open, old open, and old canopy plots with (herbicide) and without (control) GSH. Error bars are 1 SE of total unplanted understory cover. Other includes sedges, rushes, and shrubs. The vast majority (>98% in all treatments) of unplanted grass and forb cover was non-native.

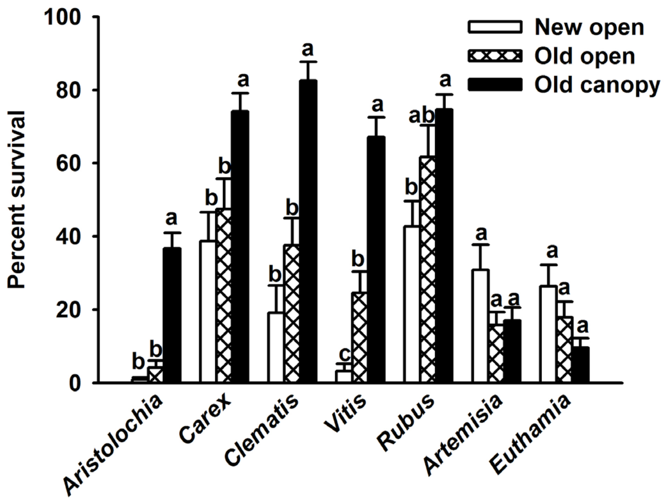

Figure 2 Percent survival of seedlings planted in the new open, old open, and old canopy treatments 2.5 years after planting (May 2008). Error bars are 1 SE. Means of the same species with the same letter are not significantly different across treatment using Tukey's mean comparison procedure. N = 22 to 24 plots per treatment. Full species names are listed in Table 1.

time-by-treatment interaction effect on planted seedling survival, with the treatment effect becoming stronger over time ($F_{8,128} > 4.4$, $p < 0.0001$ for six species; *Artemisia*: $F_{8,128} = 0.5$, $p = 0.8487$). By May 2008, four species (*Aristolochia*, *Carex*, *Clematis*, and *Vitis*) had higher survival under canopy at old sites than in the open at both old and new sites (Figure 2), and *Rubus* showed a similar trend, although the canopy and open treatments in old sites did not differ significantly. *Clematis* and *Vitis* had similar cover across treatments, and *Aristolochia* only survived under canopy. *Carex* and *Rubus* had higher cover in the open than under the canopy (Figure 3), in contrast to survival results. For two species (*Euthamia* and *Artemisia*), survival was similar across treatments (Figure 2), and cover was lower in canopy plots (Figure 3). *Artemisia* cover was higher in new plots than open old plots, but this trend was largely driven by data from one site.

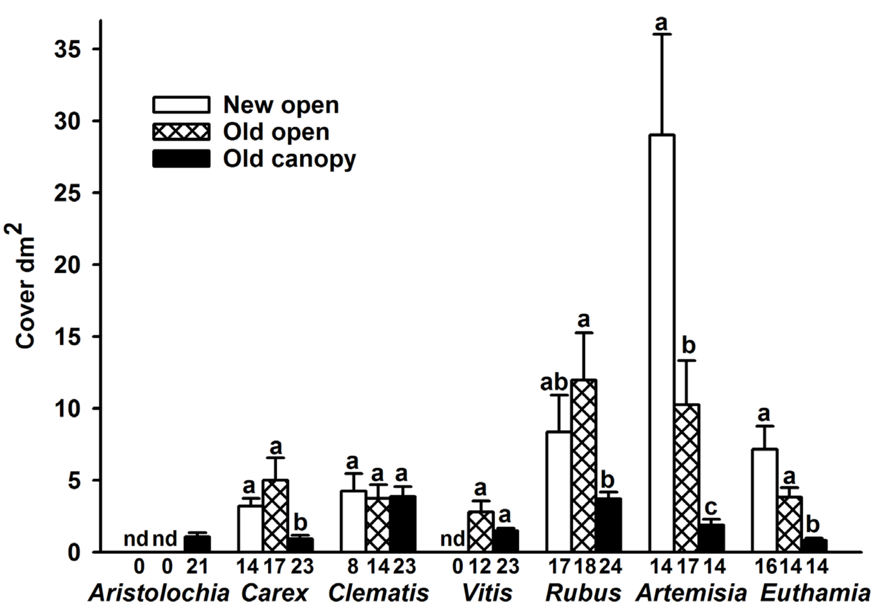

Figure 3 Total foliar cover of individual seedlings planted in the new open, old open, and old canopy treatments 2.5 years after planting (May 2008). Error bars are 1 SE. Means of the same species with the same letter are not significantly different across treatment using Tukey's mean comparison procedure. Numbers on x-axis are number of plots (out of 22 for new open and 24 for other treatments) with seedlings surviving to compare cover value; nd = no data for cover because there were no surviving seedlings. Full species names are listed in Table 1.

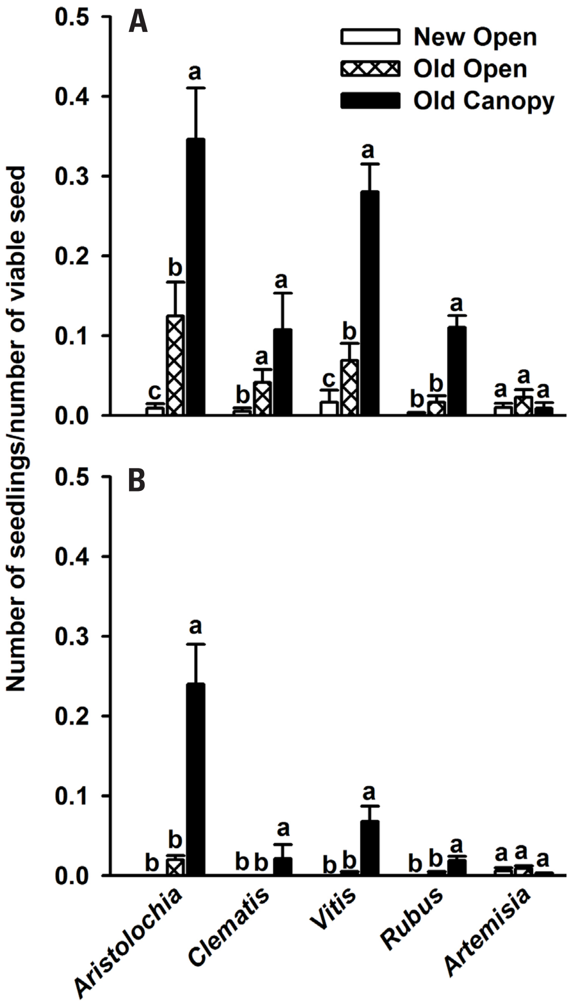

Figure 4 Number of seedlings/number of viable seeds in seeding plots in June 2007 (A) and May 2008 (B) in the new, old open, and canopy treatments. Error bars are 1 SE. Means of the same species with the same letter are not significantly different across treatment using Tukey's mean comparison procedure. Full species names are listed in Table 1. *Euthamia* and *Carex* data are not shown because of insufficient germination.

Seeding

For the first seeding, on average, less than 1% of the seeds resulted in seedlings the following spring, with the exception of *Rubus* (3%; data not shown). In the second seeding, the percentage of seedlings resulting from viable seed ranged from 0% to 16% across all treatments. Of the five species with sufficient seedlings to compare (Figure 4A), four had the lowest number of seedlings in new sites, intermediate numbers in old open plots, and the highest numbers in canopy plots. *Artemisia* and *Euthamia* germination in the field was low in all treatments, and <2% of *Carex* seed germinated in the field or shadehouse. Shadehouse germination in 2006–2007 for other species ranged from 23% for *Artemisia* to 61% for *Rubus* (Table 1). We recorded approximately one third the number of seedlings in May 2008 compared to the previous year, and nearly all surviving seedlings of all species were in canopy plots (Figure 4B).

Shade Experiment

PAR sensors showed that the actual amount of shade provided by the cloth differed from the manufacturer's specifications (30% shade cloth = 46 ± 4% full PAR, 60% shade cloth = 80 ± 2%, 80% shade cloth = 86 ± 2%), as compared to 91.5 ± 1% shade in the canopy plots (described above). Relative humidity and temperature did not differ significantly among the four shade treatments.

Consistent with results from the canopy–herbicide experiment, in both years *Clematis* had lowest survival in the open treatment (Table 3), and the few surviving *Vitis* seedlings were all in shade treatments. Survival of *Artemisia* seedling planted in 2007 did not differ significantly across treatments, although survival of seedlings planted in 2006 was lower in full sun as compared to shade treatments.

Understory Seedling Survival in Restoration Sites

Three species had high survival (*Artemisia* = 80%, *Rubus* = 91%, *Vitis* = 77%) in large-scale restoration plantings one year after irrigation was

Table 3 Percentage of seedlings planted in 2006 and 2007 surviving in four shade treatments by May 2008. X^2 (4 levels) compares all four PAR reduction levels. X^2 (open vs. shade) compares 0% PAR reduction with all other levels combined.

Species	Year planted	PAR reduction (%)				X^2 (p) 4 levels	X^2 (p) open vs. shade
		0	46	80	86		
Artemisia douglasiana	2006	17	43	43	40	7.1 (0.0690)	12.0 (0.0005)
Artemisia douglasiana	2007	76	84	78	82	0.7 (0.8674)	0.7 (0.3946)
Clematis ligusticifolia	2006	0	16	12	16	7.8 (0.0514)	7.1 (0.0076)
Clematis ligusticifolia	2007	7	28	55	52	19.8 (0.0002)	9.7 (0.0018)
Vitis californica	2006	0	0	5	0	—	—
Vitis californica	2007	0	7	17	18	—	—

[a] *Vitis* survival was too low to compare statistically.

removed and weed management ceased. Three species (*Aristolochia* = 58%, *Carex* = 50%, *Clematis* = 65%) had survival rates that were substantially below the minimum 80% typically required by restoration contracts, and *Euthamia* had particularly poor survival (17%).

DISCUSSION

Timing of Introduction of Forest Understory Species

Our results show that some species of understory riparian plants in north–central California have higher survival when planted under the forest canopy (Figures 2 and 4), and therefore should be introduced after the canopy has matured; these results are consistent with those from other forest systems (e.g., Yates and others 2000; Ashton and others 2001; Parrotta and Knowles 2001; Mottl and others 2006; Pages and Michalet 2006). Our canopy–herbicide experiment, shade experiment, and data from restoration sites agree that four species (*Aristolochia californica*, *Carex barbarae*, *Clematis ligusticifolia*, and *Vitis californica*) are better adapted to shaded conditions, as they had poor survival in the open, and similar growth (except *Carex*) in open and canopy conditions (Figures 2 and 3). In contrast, *Artemisia douglasiana* and *Euthamia occidentalis* had similar survival under both open and canopy conditions, and grew much more in open conditions, so they are well suited to introduce at the outset of restoration (this study; McClain and others 2011). In our experiments, *Rubus ursinus* had higher survival in the shade, but it also survived well in restoration sites when irrigated, and grew more in open conditions. Overall, our results show that in order to create a diverse understory community, species need to be considered individually, or perhaps as guilds of similarly adapted species, with some species planted at the outset of restoration efforts and others planted later, based on their specific ecological requirements.

Introducing species at different stages of the restoration process requires a longer-term budget and commitment than is typical of many restoration projects, so it may not be feasible to reintroduce species in stages. We, however, successfully introduced several species that rarely colonize naturally (Holl and Crone 2004; McClain and others 2011) into closed canopy restoration sites, without the necessity of irrigation or weed control. These results suggest that species could be introduced later with relatively minimal inputs. To rigorously compare the costs and benefits of planting shade-adapted species at the outset, versus later in restoration, it is important to monitor plant survival in restoration sites after irrigation is removed; our data from actual restoration projects indicate that monitoring only until management ceases overestimates the survival of some native species and, therefore, restoration success. Therefore, long-term monitoring, more than the 3 years currently typical in this system, is necessary to evaluate the success of native understory recovery.

Factors Affecting Growth and Survival

It is difficult to separate out direct vs. indirect effects of shading based on the canopy–herbicide experiment, given that the canopy treatment was more effective in reducing unplanted understory cover than our GSH treatment (Figure 1); so light level and non-native competition were confounded. The shade experiment, however, suggests that canopy cover directly facilitates survival of some species by reducing light. This facilitation phenomenon is commonly observed in stressful environments (reviewed in Brooker and others 2008). In the shade experiment, *Clematis* had higher survival in lower light conditions, where competition was controlled and temperature and humidity were similar across treatments. Moreover, *Clematis* and *Vitis* cover were similar in the canopy and open plots. These results, combined with physiological measurements on *Clematis* (Johnston 2009) and *Vitis* (Gamon and Percy 1990), suggest these species are adapted to intermediate light, particularly under drought conditions, whereas *Artemisia* is more tolerant of high light (Johnston 2009).

Other uncontrolled abiotic factors (e.g. flooding during the rainy season, and high temperatures and water limitation during the dry season) likely interacted to affect seedling cover and survival. Since we did not manipulate these factors experimentally, however, we can only speculate on their effects. Lower survival of *Clematis* and *Vitis* under shade cloth than in canopy plots may reflect the fact that shade cloth only reduces light levels and does not alter high temperatures, which affect survival and growth of *Vitis* (Gamon and Pearcy 1990). Slightly higher organic matter in canopy plots may have increased soil moisture and soil nutrient availability, which could enhance seedling growth (Chapin and others 1994; Lichter 1998). Flood duration (in the first year) significantly affected the survival of only two of seven species studied, which is not surprising given that most species were dormant, and these riparian species are adapted to flooding. Further research designed specifically to test flood tolerance and the effect of soil texture (which was correlated with flood duration) is needed before general conclusions can be made about how these factors influence restoration success and how restoration strategies should be tailored.

Reducing Non-Native Understory Competition

Our results clearly demonstrate that to reduce cover of non-native herbaceous and grass species simultaneously, it is more effective to establish a closed canopy than to apply GSH. Consistent with other canopy removal studies (Denslow and others 2006; Pages and Michalet 2006) cover of non-native understory species was higher in open plots. Although weed control by herbicide, mowing, or other methods may be necessary during the initial phase of restoration to establish canopy trees (Davies 1988; Lof and others 2006), our results, and others (Holl and Crone 2004; Rosas and others 2006; Cox and Allen 2008; McClain and others 2011) show that the effects of weed-control efforts (either guild-specific or broad-spectrum) are short-lived. In contrast, once the canopy has closed, controlling early-successional, light-demanding non-natives is no longer necessary.

Seeds vs. Seedlings

Several factors affect the choice of whether to introduce understory species by direct seeding or by planting seedlings. For all seven species studied, planted seedlings had greater survival than seedlings from sown seed, which agrees with some previous studies (Drayton and Primack 2000; Cabin and others 2002). Higher germination in the shadehouse than in the field suggests that field-sown seeds were consumed, washed away by floods, failed to germinate under field conditions, or germinated and died between surveys (Wenny 2000; Baeten and others 2009). Moreover, seedling mortality the first year after seeding was high. Planting older seedlings bypasses these phases, eliminating the uncertainty of whether seeds will germinate and survive for the first few months. Moreover, seedlings resulting from seed were an order of magnitude smaller than outplanted seedlings after 1.5 years, which makes them more susceptible to desiccation and herbivory, and will likely delay them reaching reproductive age (Drayton and Primack 2000).

In contrast, other studies have successfully established herb populations in secondary forests by sowing seed (Petersen and Philipp 2001; Graae and others 2004; Heinken 2004), with some studies finding higher survival and growth rates for plants established by direct seeding than transplanting (Welch 1997; Young and Evans 2000). Moreover, taproot deformities of container raised seedlings transplanted into the field have been found even years after transplanting (Halter and others 1993; Welch 1997; Young and Evans 2005). These contrasting results likely reflect the difference in the size of transplants and localized site conditions.

Restoration practitioners also must consider the cost and reliability of sowing seed vs. planting seedlings. Our seedlings cost $1.88 to purchase, whereas seeding averaged $1.00 per 75 to 100 viable seeds. Considering the low seed germination and survival rates in the field, we averaged one to two seedlings surviving (after 1.5 years) per $1.00 of seed in our second year of seeding, whereas almost no seedlings established the first year (likely because of both lack of site preparation and losses from flooding). We and others (Doust and others 2006) found it was essential to break up the ground and bury seeds, which is labor intensive when machinery cannot be used because of existing vegetation; therefore, our labor costs for seeding (on a per seedling basis) were approximately twice those of planting. In summary, our results show that whereas seeding is somewhat cheaper overall in this system, it is less reliable and results in smaller plants.

Management Recommendations

Our results demonstrate that it is feasible to introduce native understory species into older riparian forest restoration sites in north–central California without irrigation or weed control, and suggest some recommendations to increase the success of efforts to restore the native riparian understory across the range of site conditions we studied. First, we recommend transplanting seedlings over sowing seed for this system, due to the higher survival and greater size of planted seedlings, as well as the unpredictability of seeding (seed predation, failure to germinate, loss during flooding, early seedling survival). Second, some species can be introduced successfully during initial restoration plantings (e.g., *Artemisia, Euthamia*), whereas other shade-tolerant species (e.g. *Aristolochia, Clematis*) are likely to have higher survival if introduced after a canopy is established; the added cost of introducing plants in two stages may, however, make this approach impractical in some cases. Third, establishing a closed canopy is more effective than GSH for reducing cover of light-demanding, non-native understory species, which can outcompete native species. Finally, given the high mortality rate for some understory species once irrigation ceases, we recommend longer-term monitoring to provide a more accurate assessment of the success of vegetation restoration efforts in this system.

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