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MIMICKING FIRE FOR SUCCESSFUL CHAPARRAL RESTORATION

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ABSTRACT

Following disturbance, seed pre-treatment is essential for re-establishing many species with low germination rates. However, some seeds, such as those from chaparral plants, do not respond to common horticultural treatments. Instead, methods that mimic chaparral's natural succession cues (e.g., fire) should be used to improve seed germination and restoration success. Fire effects, such as heat, charate, leachate, smoke, and/or liquid smoke, are effective in breaking long-term seed dormancy in many chaparral plants. The challenge is to break seed dormancy in a cost- and time-efficient manner that can be used in large-scale restoration projects. Results of our study show that short-term exposure (10 minutes to one hour) to liquid smoke and/or heat enhances seed germination of *Adenostoma fasciculatum* Hook. & Arn. (chamise), *Ceanothus cuneatus* (Hook.) Nutt. (buckbrush), and *Salvia mellifera* Greene (black sage). Chamise seeds treated with liquid smoke have the greatest percent increase of seed germination odds: 394%, from the control ($P < 0.000$). Buckbrush seeds treated with liquid smoke and heat have the greatest percent increase of seed germination odds: 953%, from the control ($P < 0.000$). Black sage seeds treated with heat have the greatest percent increase of seed germination odds: 354%, from the control ($P < 0.000$). Implementing these procedures in restoration may reduce the seed costs of certain species by nearly 90%.

Key Words: *Adenostoma fasiculatum*, *Ceanothus cuneatus*, chaparral restoration, fire effects, liquid smoke, *Salvia mellifera*, seed dormancy.

Chaparral is a major vegetation type that covers seven percent of California (Keeley and Davis 2007). Chaparral communities are impacted by recurrent fires, as well as mining, brush clearing, and other human activities. Restoration of resprouting shrub-dominated chaparral (as opposed to mere establishment of a vegetative cover) has proven challenging, especially in areas disturbed by mining. The introduced, invasive grass *Festuca perennis* (L.) Columbus & J. P. Sm. (Italian ryegrass) has often been used for revegetation and slope stabilization following disturbance, but it has been observed that this grass retards the natural establishment and succession of native chaparral shrubs (Barro and Conrad 1987, 1991; Janicki unpublished). Some investigators have found that the addition of organic material, compost, and/or mycorrhizal fungi significantly improves revegetation efforts on road-cuts, mines, or other disturbed areas where only decomposed granite remains (Claassen and Marler 1998; Claassen and Zasoski 1998; Curtis and Claassen 2007). Despite the availability of these tools, many chaparral restoration projects are unsuccessful for at least 20 years; characteristic dominate shrubs are infrequent at restoration sites (Cione et al. 2002; Meira-Neto et al. 2011).

Many chaparral shrubs have very low germination rates unless exposed to fire or fire effects (Stone and Juhren 1951, 1953; Went et al. 1952; Sweeny 1956; Keeley 1987; Keeley and Fotheringham 1998). Common horticultural methods for breaking seed dormancy are not effective for dominant chaparral shrubs (Quick 1935; Stidham et al. 1980; Emery 1988). A promising restoration strategy has been demonstrated in South African fynbos, a homolog to California's chaparral. There, restoration researchers utilized seeds' natural responses to fire to enhance seed germination. (Baxter and Van Staden 1994; Dixon and Roche 1995; Dixon et al. 1995; Read et al. 2000; Matesanz and Valladares 2007). Chaparral restoration could also benefit from scientifically supported fire effects to pre-treat seeds. To improve restoration we should adapt known fire-effect treatments (liquid smoke or heat and/or charate) that increase seed germination for *Adenostoma fasciculatum* Hook. & Arn. (chamise), *Ceanothus cuneatus* (Hook.) Nutt. (buckbrush), and *Salvia mellifera* Greene (black sage) (Jager et al. 1996; Keeley 1987; Keeley et al. 2005).

We seek to improve chaparral restoration in the central Coast Range of California by

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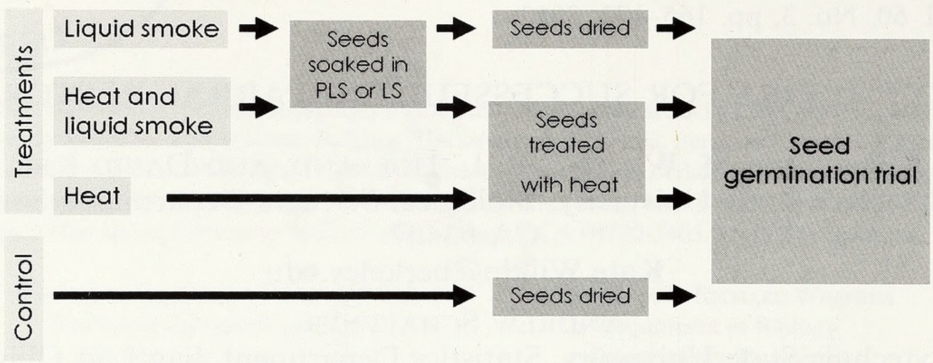

FIG. 1. Experimental design schematic. LS = liquid smoke diluted with water. PLS = pure liquid smoke.

evaluating the potential of inexpensive and commercially available fire-effect treatments to increase seed germination. Our treatments differ from those used in other studies because we include exposure to heat and/or Wright's Hickory Seasoning (a commercial liquid smoke produced by B&G Foods, Inc.) and our sample sizes are more than 10 times as great (Keeley 1987; Keeley et al. 2005). We test the hypothesis that seed germination rates differ significantly between treatments and the control, and between treatment methods. We then quantify the changes treatments produce in germination rates and evaluate if the seed pre-treatments' percent increase of seed germination odds and their associated costs are beneficial to restoration.

METHODS

Seed Collection and Storage

S&S Seeds of Carpinteria, California hand collected chamise, buckbrush, and black sage seeds during fall 2006 and 2007 in southern California. Seed pods and stems were macerated with a de-bearding machine and separated by size and density with an air-screen machine. Trials 1–3 tested fall 2006 seeds for germination during winter 2006–2007 and fall 2007. Trial 4 tested fall 2007 seeds for germination during winter 2007–2008. Before germination tests, seeds were stored at room temperature in plastic mesh bags under ambient light conditions.

Seed Treatments

Thirty seeds at a time were placed onto unbleached coffee filters, tied with natural twine, and then submerged in Wright's Hickory Seasoning diluted with water in varied proportions (referred to as liquid smoke [LS] dilution hereafter) for 10 min (Jager et al. 1996; Keeley et al. 2005) (Fig. 1). We applied the temperature and heating periods that yield the highest germination in Keeley (1987): chamise, 70°C for one hr; buckbrush, 100°C for five min; black sage, 70°C for five min. To simulate the drying process that occurs after hydroseeding, we dried samples in a forced-air convection oven at 30°C for one hr, unless the sample was designated for heat treatment. Only one treatment type was dried at a time in the oven to eliminate air contamination with LS. If a heat treatment was tested, heat was applied directly after soaking. Table 1 displays the treatment dilutions and/or heat levels and number of seeds for each treatment.

Seed Germination Trials

Following the methods of Keeley (1987), each set of 30 treated seeds was sown in 60 × 15 mm sterilized plastic Petri dishes lined with two layers of Whatman #1 filter paper. Two days after the treatments, seed germination was initiated by adding one and one-half to two ml of water to each Petri dish. Each dish was then placed inside a plastic bag to reduce evaporation and gas transfer between treatments, placed in a growth chamber, and cold stratified at ~4°C for one mo under ambient light conditions. The bag was then placed under a diurnal light schedule with temperatures ranging from 12°–18°C for eight wk. Every week, samples were randomly rearranged within the growth chamber to reduce environmental effects. After cold stratification, seeds were examined weekly for six wk for epicotyl emergence, which marks germination. Germinated seeds were recorded and then removed (Baskin and Baskin 1998).

Analysis

Data were analyzed with Minitab 15 Statistical Software (2007). For each species, a logistic regression model blocked by trial was used to assess the effects of treatments on germination rates. Model fit was assessed by Pearson, Deviance, and Hosmer-Lemeshow "goodness of fit" tests. Due to the large number of treatments compared, statistical significance was assessed using both Fisher and Bonferroni adjusted α-values based on the number of comparisons with α = 0.05. Bonferroni-adjusted α-values for

TABLE 1. NUMBER OF SEEDS TESTED PER SPECIES, TRIAL, AND TREATMENT. Several replicates (30 seeds each) were included in each trial though the numbers of replicates per treatment and per trial were not necessarily similar. The control was present in every trial. The treatment names indicate the concentration of Wright's Hickory Seasoning liquid smoke diluted with water (if applied), the duration of soaking in liquid smoke if it exceeds 10 minutes (if applied), and heat (if applied) refers to heat treatments following Keeley (1987): chamise 70°C for one hour, buckbrush 100°C for five minutes, black sage 70°C for five minutes. LS = liquid smoke; PLS = pure liquid smoke.

	Chamise					Buckbrush				Black sage				
Treatment/trial	1	2	3	4	Total	1	2	4	Total	1	2	3	4	Total
control	90	150	150	150	540	90	150	150	390	90	60	120	150	420
heat	—	—	—	90	90	—	—	180	180	—	—	—	150	150
PLS	—	—	180	180	360	—	—	—	—	—	—	—	150	150
PLS heat	—	—	—	270	270	—	—	300	300	—	—	—	300	300
1:10 LS	—	—	—	150	150	—	—	—	—	—	—	—	150	150
1:10 LS heat	—	—	—	150	150	—	—	180	180	—	—	—	120	120
1:100 LS	90	90	120	120	420	90	210	—	300	90	90	150	150	480
1:100 LS heat	—	—	—	180	180	—	—	150	150	—	—	—	150	150
1:1000 LS	90	120	180	—	390	90	150	—	240	90	150	150	—	390
1:2000 LS	90	120	150	—	360	90	180	—	270	90	90	150	—	330
1 hr PLS	—	—	180	—	180	—	—	—	—	—	—	—	—	—
4 hrs PLS	—	—	180	—	180	—	—	—	—	—	—	—	—	—
18 hrs PLS	—	—	210	—	210	—	—	—	—	—	—	—	—	—
27 hrs PLS	—	—	180	—	180	—	—	—	—	—	—	—	—	—
30 hrs PLS	—	—	180	—	180	—	—	—	—	—	—	—	—	—
Total	360	480	1710	1290	3840	360	690	960	2010	360	390	570	1320	2490

TABLE 2. RESULTS FOR CHAMISE. The tabulated values from left to right include the percent seed germination, change compared to the control (percent change in seed germination odds and 95% confidence interval for percent change in seed germination odds with all treatments compared to the control, and P-value), and significant similarities (Bonferroni-adjusted value for multiple comparisons and Fisher test). Bonferroni-adjusted value for multiple comparisons is $\alpha = 0.00048$ with a group value of $\alpha = 0.05$ and the comparisons are indicated with numbers. Fisher comparisons are based on $\alpha = 0.05$ and indicated with letters. Groups sharing a common letter and/or number are not significantly different. The treatment names indicate the concentration of Wright's Hickory Seasoning liquid smoke (LS) diluted with water (if applied), the duration of soaking in LS if it exceeds 10 minutes (if applied), and heat (if applied) refers to heat treatments following Keeley (1987): chamise 70°C for one hour. LS = liquid smoke; PLS = pure liquid smoke; an asterisk (*) designates the recommended treatment; and double asterisks (**) designate the recommended treatment if hydroseeding.

		Change compared to control			Significant similarities	
Treatment	Germination (%)	Change (%)	95% confidence interval (%)	P	Bonferroni-adjusted for multiple comparisons	Fisher test
control	4	—	—	—	3	a
1:2000 LS	0	−83	(−98, 34)	0.094	23	a
1:1000 LS	2	45	(−39, 246)	0.397	123	a
1:100 LS	8	125	(24, 309)	0.008	123	bcd
1:10 LS	17	109	(9, 300)	0.027	123	bcd
PLS	16	243	(96, 501)	0.000	1	bdef
heat	12	45	(−35, 223)	0.360	123	c
1:100 LS heat	17	109	(11, 291)	0.022	123	bcd
1:10 LS heat**	30	347	(145, 717)	0.000	12	f
PLS heat	20	161	(47, 363)	0.001	123	bde
1 hr PLS*	9	394	(122, 999)	0.000	12	ef
4 hrs PLS	7	294	(71, 807)	0.001	123	b
18 hrs PLS	0	−76	(−97, 90)	0.177	123	a
27 hrs PLS	1	−72	(−96, 122)	0.229	123	a
30 hrs PLS	0	—	—	—	123	a

multiple comparisons for chamise, buckbrush, and black sage were respectively $\alpha = 0.00048$, $\alpha = 0.0018$, and $\alpha = 0.0011$.

RESULTS

Chamise

Nine treatments significantly increased percent odds of seed germination relative to the control ($P < 0.027$), whereas five treatments did not differ significantly from the control ($P > 0.05$) (Table 2). One hour pure liquid smoke (PLS) increased percent odds of seed germination the most (394%; 95% CI: 122% to 999%, $P < 0.000$). Other promising treatments included 1:10 LS dilution with heat, four-hour PLS, and PLS that respectively increased percent odds of seed germination by 347%, 294%, 243% ($P < 0.000$, 0.000, 0.001). Other treatment estimates ranged from a 161% increase (PLS with heat, $P < 0.001$) to a 83% decrease (1:2000 LS dilution) ($P < 0.094$) of seed germination odds. Three treatments (1:2000 LS dilution, 8-hour PLS, and 27-hour PLS) negatively affected germination though reductions were not significant ($P < 0.094$, 0.177, 0.229). The treatments with more than a 200% seed germination odds increase listed above (including one hour PLS, 1:10 LS dilution with heat, four-hour PLS, and PLS) are not significantly different from one another ($P > 0.273$).

Buckbrush

Three treatments significantly increased percent odds of seed germination relative to the control ($P < 0.045$), whereas three did not differ significantly from the control ($P > 0.05$) (Table 3). PLS with heat increased percent odds of seed germination the most (953%; 95% CI: 228% to 3281%, $P < 0.000$). Both heat and 1:10 LS dilution with heat increased percent odds of seed germination 267% ($P < 0.045$, 0.045). All other treatment estimates ranged from a 77% increase (1:1000 LS dilution) to a 31% decrease (1:100 LS dilution, $P < 0.609$) of seed germination odds. PLS with heat significantly increased percent odds of seed germination relative to both heat and 1:10 LS dilution with heat ($P < 0.000$, 0.002).

Black Sage

All treatments significantly increased percent odds of seed germination relative to the control ($P < 0.044$) (Table 4). Heat increased percent odds of seed germination the most (354%; 95% CI: 172% to 657%, $P < 0.000$). Other promising treatments include PLS with heat, 1:100 LS dilution with heat, 1:2000 LS dilution, 1:10 LS dilution and heat, and 1:100 LS dilution, which increased seed germination odds by 228%, 195%, 185%, 168%, and 138% respectively ($P < 0.000$,

TABLE 3. RESULTS FOR BUCKBRUSH. The tabulated values from left to right include the percent seed germination, change compared to the control and pure liquid smoke with heat (percent change in seed germination odds and 95% confidence interval for percent change in seed germination odds with all treatments compared to the control and compared to pure liquid smoke with heat, P-value), and significant similarities (Bonferroni-adjusted value for multiple comparisons and Fisher test). No seeds germinated with 1:2000 liquid smoke therefore these results could not be compared to Change compared to the control or Change compared to pure liquid smoke with heat. Bonferroni-adjusted value for multiple comparisons is $\alpha = 0.0018$ with a group value of $\alpha = 0.05$ and the comparisons are indicated with numbers. Fisher comparisons are based on $\alpha = 0.05$ and are indicated with letters. Groups sharing a common letter and/or number are not significantly different. The treatment names indicate the concentration of Wright's Hickory Seasoning liquid smoke diluted with water (if applied) and heat (if applied) refers to heat treatments following Keeley (1987): 100°C for five minutes. LS = liquid smoke; PLS = pure liquid smoke; an asterisk (*) designates the recommended treatment.

Treatment	Germination (%)	Change compared to control			Change compared toPLS and heat			Significant similarities	
		Change (%)	95% confidence interval (%)	P	Change (%)	95% confidence interval (%)	P	Bonferroni-adjusted for multiple comparisons	Fisher test
control	1.03	—	—	—	−91	(−97, −69)	0.000	1	a
1:2000 LS	0.00	—	—	—	—	—	—	12	—
1:1000 LS	0.83	77	(−80, 1455)	0.609	−83	(−98, 79)	0.140	1	abc
1:100 LS	1.67	24	(−47, 2094)	0.195	−68	(−96, 157)	0.287	12	abc
heat	6.67	267	(3, 1208)	0.045	−65	(−82, −33)	0.002	1	b
1:100 LS heat	1.33	−31	(−88, 318)	0.690	−93	(−98, −73)	0.000	13	a
1:10 LS heat	6.67	267	(3, 1208)	0.045	−65	(−82, −33)	0.002	13	b
PLS heat*	17.00	953	(228, 3281)	0.000	—	—	—	23	c

0.000, 0.000, 0.000, 0.000). The remaining three treatments only had relatively small percent increase of seed germination odds, which were less than 138% ($P < 0.044$). While heat significantly increased percent odds of seed germination over five treatments, it is not significantly different from all treatments ($0.0011 < P < 0.050$).

DISCUSSION

Short periods of exposure (10 minutes to four hours) to LS and/or heat significantly enhance seed germination of chamise, buckbrush, and black sage. The stimulatory effect of these treatments was retained when seeds were re-dried and stored for two days. Recommended seed treatments have the highest percent increase of seed germination odds and may be statistically significant. In the case of statistically similar treatments, cost, empirical seed germination, and practicality were taken into consideration. In addition, LS-only treatments are also recommended because large industrial ovens may not be readily available for heat treatments.

Chamise

The recommended treatment for chamise (among three similar treatments) is PLS for one hour because it has the highest estimate of percent increase of seed germination odds. For chamise, the power (probability of the procedure to find a significant difference among treatments with differences as subtle as those seen with our sample size) is only 52%. With our minimum number of seeds per treatment (150), we can only detect germination rate differences as large as 18–20% with 90–95% probability, respectively. To determine if the 1:10 LS dilution with heat treatment is statistically different from all other treatments, then 14 and 17 replications (420 and 510 seeds) would need to be completed for 90 and 95% power, respectively. While PLS for one hour is recommended, this treatment may not be best for hydroseeding because we observed a percent reduction in seed germination odds as soaking time increases. If hydroseeding, the recommended treatment is 1:10 LS dilution for 10 minutes with heat, which is only significantly different from the control and PLS for one hour (Table 2).

Buckbrush

The recommended treatment for buckbrush is PLS with heat. No LS-only treatments significantly increased seed germination odds; therefore, no other treatments are recommended ($P \geq 0.195$). These statistical findings differ from Keeley's (1987), whose data did not show charate addition to be statistically different from the control. However, Keeley's (1987) data for charate addition and 100°C for five minutes is

TABLE 4. RESULTS FOR BLACK SAGE. The tabulated values from left to right include the percent seed germination, change compared to the control and heat (percent change in seed germination odds and 95% confidence interval for percent change in seed germination odds with all treatments compared to the control and compared to heat, P-value), and significant similarities (Bonferroni-adjusted value for multiple comparisons and Fisher test). Bonferroni-adjusted value for multiple comparisons is α = 0.0011 with a group value of α = 0.05 treatments and the comparisons are indicated with numbers. Fisher comparisons are based on α = 0.05 and are indicated with letters. Groups sharing a common letter and/or number are not significantly different. The treatment names indicate the concentration of Wright's Hickory Seasoning liquid smoke diluted with water (if applied) and heat (if applied) refers to heat treatments following Keeley (1987): 70°C for five minutes. LS = liquid smoke; PLS = pure liquid smoke; an asterisk (*) designates the recommended treatment; and double asterisks (**) designate the recommended treatment if no oven is available.

		Change compared to control			Change compared to heat			Significant similarities	
Treatment	Germination (%)	Change (%)	95% confidence interval (%)	P	Change (%)	95% confidence interval (%)	P	Bonferroni-adjusted for multiple comparisons	Fisher test
control	8	—	—	—	−78	(−87, −63)		1	a
1:2000 LS**	12	185	(63, 397)	0.000	−37	(−67, −18)	0.150	23	bcd
1:1000 LS	7	87	(4, 234)	0.036	−59	(−79, −21)	0.008	123	cd
1:100 LS	15	138	(53, 271)	0.000	−47	(−67, −17)	0.006	23	cd
1:10 LS	22	77	(2, 207)	0.044	−61	(−76, −36)	0.000	12	c
PLS	26	120	(28, 277)	0.004	−51	(−70, −21)	0.004	123	cd
heat*	42	354	(172, 657)	0.000	—	—	—	3	b
1:100 LS heat	32	195	(75, 398)	0.000	−35	(−59, 4)	0.074	23	bcd
1:10 LS heat	30	168	(54, 368)	0.001	−41	(−64, −2)	0.043	23	cd
PLS heat	34	228	(106, 420)	0.000	−28	(−52, 8)	0.113	3	bd

five times greater than the control. Statistical differences in our experiments can be attributed to larger sample sizes.

Black Sage

The recommended treatment for black sage is heat. For black sage, heat produced the greatest percent increase of seed germination odds. The probability of detecting differences between treatments was only 30%. As a result, we cannot conclude that the heat-only treatment increased seed germination odds relative to the other treatments, even though it had the largest observed percent increase of seed germination odds. The minimum number of seeds per treatment (150) can detect germination-rate differences only as large as 18–20% with 90–95% probability, respectively. To determine if heat is statistically different from all other treatments, 26 and 32 replications (780 and 960 seeds) would be required to detect an effect size of 8% with 90 and 95% certainty, respectively. If an oven is not available, then the alternative recommended treatment is 1:2000 LS dilution. 1:2000 LS dilution had the next highest percent change in seed germination odds when a treatment did not include heat, but this treatment was also not significantly different from others (Table 4).

Cost of Treatments

Seed pre-treatment is most economically beneficial when seeds have very low germination rates without treatment and large germination rates after treatment, and when the seed costs are high and the cost of treatment is low. Therefore, it is necessary to compare the cost of pre-treatments, both in terms of material and human resources, to the money saved from increased seed germination odds. The pre-treatments would be economically viable only if the resulting increase in seed germination odds decreased seed cost and if the pre-treatments cost less than the seed cost avoided. The pre-treatments would be most cost effective on plants such as chamise and buckbrush, whose seed germination odds increase dramatically from 4–18% and 10–57%, respectively. For these examples, one pound of treated seed would be equivalent to more than four or five pounds of untreated seeds. Savings are calculated based on the cost of one pound of native seeds from S&S Seeds in 2009 ($37), labor for one hour ($14), cost of supplies (LS varies based on concentration: $2.00 per treatment for PLS to $0.14 for 1:2000 LS dilution). Pre-treating chamise, buckbrush, and black sage may save an estimated $112, $337, and $115, respectively, by making one pound of seed equivalent to four or five pounds (95% CI: $38–$249, $68–$1198,

\$48–\$227) ($P < 0.000, 0.000, 0.000$). These seed pre-treatments are economically beneficial and should be used in restoration projects.

Conclusion

Establishing dominant shrubs, such as the ones studied here, is integral for both short-term and long-term restoration success. In the short-term, there is literally a "race between rates of shrub recovery" and non-native annual grass colonization (Keeley 2004) since shrubs are excluded by these grasses if they don't colonize the site early on (Shultz et al. 1955). In the long term, shrub establishment will build post-fire resilience and decrease the risk of catastrophic failure due to lack of seed bank and resprouting shrubs following an inevitable future fire (Meira-Neto et al. 2011). Unfortunately, many restoration sites in both chaparral and chaparral-like shrublands throughout other Mediterranean regions fail to establish shrubs (Cione et al. 2002; Meira-Neto et al. 2011). Our proposed seed treatments are one step to improve shrub colonization in California's chaparral. These treatments in coordination with other techniques to increase shrub establishment and survivorship will set a trajectory for long-term restoration success.

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