Does smoke promote seed germination in 10 Interior West *Penstemon* species?

Paula J Fornwalt

ABSTRACT

Recent research has shown that exposing seeds to smoke stimulates germination for a multitude of plant species, including several species in the genus *Penstemon* (Scrophulariaceae). I evaluated whether smoke, either alone or followed by 10 wk of stratification (moist prechilling), influenced germination for 10 *Penstemon* species native to the Interior West of North America. Seeds were collected from 3 to 9 wild populations per species, with each population serving as a replicate for that species in the experimental design. I found that percent germination increased in response to smoke for 3 species, *Penstemon secundiflorus* Benth., *P. strictus* Benth., and *P. unilateralis* Rydb., with smoke-exposed seeds exhibiting 1.9-, 2.5-, and 1.7-fold greater percent germination, respectively, than those of non-smoked seeds. Increased germination in *P. unilateralis* was only observed for seeds that had also been stratified, while increased germination for *P. secundiflorus* and *P. strictus* was observed for both stratified and non-stratified seeds. I also found that percent germination was stimulated by stratification for 6 species, *P. auriberbis* Pennell, *P. eriantherus* Pursh, *P. glaber* Pursh, *P. rydbergii* A. Nelson, *P. secundiflorus*, and *P. strictus*. *Penstemon auriberbis*, *P. eriantherus*, and *P. secundiflorus* were the most responsive, with percent germination increasing 63.4-, 10.6-, and 9.7-fold, respectively, following stratification. These findings improve our understanding of the role of smoke, as well as the role of stratification, in *Penstemon* germination ecology and should be of use to those who wish to propagate *Penstemon* species for restoration, horticultural, research, and other purposes.

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beardtongues, fire, stratification, Scrophulariaceae

NOMENCLATURE
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Photos by Paula Fornwalt

Smoke has recently been shown to stimulate seed germination for hundreds of plant species, representing a multitude of families, genera, and ecosystems from around the world (Brown and van Staden 1997; van Staden and others 2000). Germination of smoke-stimulated species is cued by certain chemical compounds that are created during the combustion of plant material (Flematti and others 2004, 2011). In many cases, seeds of species previously found to be difficult to germinate using conventional techniques have germinated readily following exposure to smoke (Brown and others 1994; Dixon and others 1995; Keeley and Fotheringham 1998). Smoke-stimulated germination appears to be especially common for species from ecosystems where fire was a frequent historical disturbance (Brown and others 1994; Moreira and others 2010; but see Pierce and others 1995 for an exception).

In many grassland, shrubland, and forest ecosystems in western North America, penstemons (*Penstemon* spp. [Scrophulariaceae]; also commonly known as beardtongues) often become more abundant following burning (Vogl and Schorr 1972; Fulé and others 2001; Fornwalt and Kaufmann 2014). Thus, it seems plausible that seed germination for some *Penstemon* species may be enhanced by smoke. Indeed, seeds of several *Penstemon* species, particularly those occurring in historically frequent-fire ecosystems, have been shown to respond favorably to smoke exposure in laboratory settings. For example, Abella (2006, 2009), working with 8 species native to ponderosa pine–dominated (*Pinus ponderosa* Lawson & C. Lawson [Pinaceae]) forests of Arizona, found that watering seeds with an aqueous smoke solution enhanced seedling emergence for 5 of them: *Penstemon barbatus* (Cav.) Roth (beardlip penstemon), *P. pachyphyllus* A. Gray ex Rydb. (thickleaf beardtongue), *P. palmeri* A. Gray (Palmer's penstemon), *P. rostriflorus* Kellogg (Bridge penstemon), and *P. virgatus* A. Gray (upright blue beardtongue). Likewise, Keeley and Fotheringham (1998) found that both aqueous and gaseous smoke stimulated seed germination in the California chaparral species *Penstemon centranthifolius* (Benth.) Benth. (scarlet bugler). Schwilk and Zavala (2012) discovered that 8 min of exposure to gaseous smoke increased percent germination of *P. cobaea* Nutt. (cobaea beardtongue), a species native to the Texas plains.

Seed germination for other *Penstemon* species may also be enhanced by smoke, yet they remain untested. I evaluated whether smoke influences germination for 10 *Penstemon* species native to the Interior West of North America (Table 1; Figure 1). The species represent a wide range of habitats and historical fire regimes, from dry grasslands that historically experienced frequent fire (Guyette and others 2006; Stambaugh and others 2008) to moist subalpine forests where infrequent, high severity fire regimes operated historically (Romme 1982; Sibold and others 2006). Because germination for many species of *Penstemon* is improved by stratification treatments that expose seeds to prolonged periods of cold, moist conditions (Kitchen and Meyer 1991; Meyer and Kitchen 1994), and because smoke has the potential to act as a substitute for stratification (Schwilk and Zavala 2012), I further evaluated the interacting effects of smoke and stratification.

MATERIALS AND METHODS

Seed Collection

Mature seeds of 10 *Penstemon* species were collected from 3 to 9 wild populations in Colorado, Wyoming, New Mexico, and (or) Montana (Table 1; Figure 1). The majority of the seed collections (34 of 47) were conducted in Colorado and Wyoming by me and members of my laboratory in 2009 through 2011, with seeds gathered from a minimum of 20 individuals per population. The other 13 collections were conducted by

Figure 1. Penstemon glaber, P. secundiflorus, P. virens, and *P. whippleanus* (*left to right*) were 4 of the 10 species utilized in this experiment.

TABLE 1

Habitat, seed supplier, population location, elevation, and seed collection year for the 10 Penstemon *species evaluated in this article.*

Population	Seed supplier	County, State	Elevation (m)	Year
P. albidus Nutt. (white penstemon); Dry, open places of the western Great Plains				
Baca County	Alplains	Baca, CO	1555	2007
Pawnee Butte East	Fornwalt laboratory	Weld, CO	1650	2011
Pawnee Butte West	Fornwalt laboratory	Weld, CO	1650	2011
Rockport	Fornwalt laboratory	Weld, CO	1800	2011
P. auriberbis Pennell (Colorado beardtongue); Dry slopes and plains of Colorado's Arkansas River Valley				
Coaldale	Western Native Seed	Fremont, CO	2130	2009
Fremont County	Alplains	Fremont, CO	1890	2003
Huerfano County	Alplains	Huerfano, CO	1920	2003
P. eriantherus Pursh (fuzzytongue penstemon); Dry grasslands and shrublands of the Interior West				
Albany County	Alplains	Albany, WY	2200	2003
Park County	Alplains	Park, CO	2530	2007
Powell County	American Penstemon Society	Powell, MT	unavailable	2010
P. glaber Pursh (sawsepal penstemon); Dry, open montane and subalpine slopes of the central and southern Rockies				
Coaldale	Western Native Seed	Fremont, CO	1890	2009
Sunshine Canyon	Fornwalt laboratory	Boulder, CO	2570	2011
Gold Hill	Fornwalt laboratory	Boulder, CO	2620	2011
Park County	Alplains	Park, CO	2800	2003
Reynolds Ranch	Fornwalt laboratory	Boulder, CO	2640	2011
Estes Valley	Fornwalt laboratory	Larimer, CO	2750	2011
P. rydbergii A. Nelson (Rydberg's penstemon); Widespread throughout the Interior West, in moist montane and subalpine forests and meadows				
Fraser	Fornwalt laboratory	Grand, CO	2720	2011
Mountain Meadows	Fornwalt laboratory	Albany, WY	3110	2011
Saint Alban's Chapel	Fornwalt laboratory	Albany, WY	3170	2011
Taylor Park	Western Native Seed	Gunnison, CO	2900	2011
P. secundiflorus Benth. (sidebells penstemon); Eastern slope of the southern Rockies, in dry montane grasslands, shrublands, and forests				
Bald Mountain	Fornwalt laboratory	Boulder, CO	2150	2011
Calloway Hill	Fornwalt laboratory	Larimer, CO	2010	2011
Centennial	Fornwalt laboratory	Albany, WY	2530	2011
Douglas County	American Penstemon Society	Douglas, CO	unavailable	2008
Elbert County	Alplains	Elbert, CO	2030	2007
P. strictus Benth. (Rocky Mountain penstemon); Distributed throughout a wide range of southern Rocky Mountain and Southwestern forest and meadow habitats				
Angel Fire	American Penstemon Society	Colfax, NM	unavailable	2010
Centennial	Fornwalt laboratory	Albany, WY	2530	2011
Medicine Bow Trail	Fornwalt laboratory	Albany, WY	2550	2011
Sand Lake Road	Fornwalt laboratory	Albany, WY	2710	2011

continued

TABLE 1 *continued*

Habitat, seed supplier, population location, elevation, and seed collection year for the 10 Penstemon *species evaluated in this article.*

Population	Seed supplier	County, State	Elevation (m)	Year
P. unilateralis Rydb. (oneside penstemon); Montane/subalpine forests and meadows of the southern Rockies				
Beachon	Fornwalt laboratory	Teller, CO	2380	2011
Manitou	Fornwalt laboratory	Teller, CO	2380	2011
Sunshine Canyon	Fornwalt laboratory	Boulder, CO	2570	2011
P. virens Pennell ex Rydb. (Front Range beardtongue); Eastern slope of the southern Rockies, on open montane and subalpine slopes				
9J Road	Fornwalt laboratory	Douglas, CO	2500	2009
Bald Mountain	Fornwalt laboratory	Boulder, CO	2150	2011
Brown Ranchito	Fornwalt laboratory	Larimer, CO	2100	2011
Estes Valley	Fornwalt laboratory	Larimer, CO	2750	2011
Sunshine Canyon	Fornwalt laboratory	Boulder, CO	2570	2011
Heil Valley Ranch	Fornwalt laboratory	Boulder, CO	2000	2011
Mount Margaret	Fornwalt laboratory	Larimer, CO	2500	2011
Painted Rocks	Fornwalt laboratory	Teller, CO	2440	2009
Reynolds Ranch	Fornwalt laboratory	Boulder, CO	2640	2011
P. whippleanus A. Gray (Whipple's penstemon); Widespread throughout the Interior West, on open subalpine and alpine slopes				
Church Park	Fornwalt laboratory	Grand, CO	2930	2011
Gore Pass	Fornwalt laboratory	Grand, CO	2840	2011
Kelly Lake	Fornwalt laboratory	Jackson, CO	2900	2011
Mountain Meadows	Fornwalt laboratory	Albany, WY	3110	2011
Telephone Lakes	Fornwalt laboratory	Albany, WY	3200	2011
Willow Creek	Fornwalt laboratory	Jackson, CO	2830	2011

Notes: Habitat descriptions within the Interior West were taken from Nold (1999) and Lindgren and Wilde (2003).

Alplains (Kiowa, Colorado, USA), Western Native Seed (Coaldale, Colorado, USA), and the American Penstemon Society; these collections occurred from 2003 through 2011. Regardless of when and by whom the seeds were collected, immediately following collection, seeds were air-dried, sieved to remove excess chaff, and stored at room temperature (about 22 °C [72 °F]) in glass jars or paper envelopes.

Laboratory Procedures

For each species, I conducted a 2-factor experiment with 2 levels of smoke (smoked or not smoked) and 2 levels of stratification (stratified or not stratified), for a total of 4 treatment combinations. Each population served as a replicate for that species in the experimental design (Table 1). Experimentation was conducted from January through May 2012.

Two basic methods are commonly used to treat seeds with smoke—exposing seeds to gaseous smoke and soaking seeds in a smokewater solution (Landis 2000). I employed the latter method. First, approximately 100 seeds per population were placed into each of 4, 20-ml vials (0.7 oz) (1 vial per treatment combination). Next, Regen 2000 (Grayson Australia, Melbourne, Victoria), a commercially available smokewater concentrate, was diluted with water to make a 2% smokewater solution (sensu Adkins and Peters 2001), and seeds receiving the smoke treatment were soaked in 15 ml (0.5 oz) of this solution for 12 h. Seeds not receiving the smoke treatment were soaked in 15 ml of water for 12 h. Seeds were then drained, rinsed with water, and placed in Petri plates lined with 2 sheets of #2 Whatman filter paper moistened with water. A precise count of the total number of seeds in each plate was subsequently made.

Petri plates containing seeds not receiving the stratification treatment were immediately placed into an incubator programmed to 22 °C (72 °F) and a 12 h photoperiod. The plates were watered daily to keep the filter papers moist. Germinating seeds were counted daily for the first 7 d and every 2 or 3 d for 23 d thereafter (30 d total). Seeds were considered to have germinated when the radicle exceeded 2 mm in length. Germinants were removed from the Petri plates once counted. Moldy seeds that became soft or gelatinous were assumed to be dead and were also removed to avoid contamination.

In contrast, Petri plates containing seeds receiving the stratification treatment were immediately placed into unlit 5 °C (41 °F) incubators for 10 wk. During this period, the plates were checked every 2 or 3 d to ensure the filter papers were moist. Sometimes germinating seeds were found during the checks; these seeds were counted and removed from the plates. At the end of the stratification period, the plates were placed in incubators programmed to 22 °C (72 °F) and a 12 h photoperiod, and germination was monitored for 30 d as described above.

Statistical Analyses

The impacts of smoke, stratification, and smoke × stratification on percent germination were examined for each species individually using analysis of variance (ANOVA) in SAS 9.3 (SAS Institute, Cary, North Carolina). Percent germination per plate was calculated as the total number of germinating seeds divided by the total number of seeds. Percent germination per plate was not adjusted for the population's viable seed fraction, as this was not determined prior to initiating the experiment. The ANOVAs were conducted using PROC GLIMMIX and a binomial distribution. Replicates (populations) were treated as random effects. When the interaction term smoke × stratification was significant, I used least squares means with a Tukey-Kramer adjustment to examine pairwise differences. Significance was evaluated with a $P = 0.050$. Two species, *P. virens* and *P. whippleanus*, failed to achieve > 5% germination for any treatment combination and were not analyzed.

RESULTS

Percent germination for 4 of the 10 species I tested responded significantly to aqueous smoke treatments (Figure 2). *Penstemon secundiflorus*, *P. strictus*, and *P. unilateralis* germination was stimulated by smoke treatments. The influence of smoke treatments on *P. secundiflorus* and *P. strictus* germination did not vary with stratification, as indicated by the nonsignificant smoke × stratification interaction term. Averaged across both levels of stratification, germination for these species was 1.9-

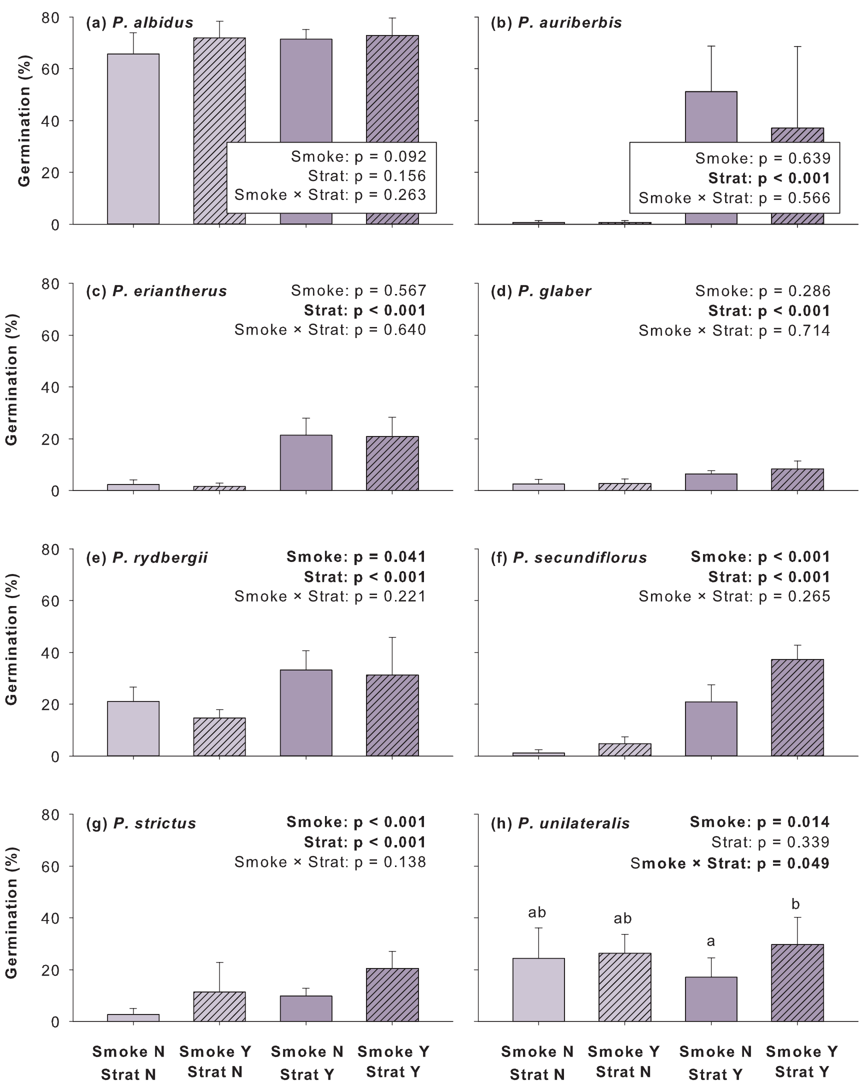

Figure 2. Mean percent germination of 8 *Penstemon* species following smoke and stratification treatments. ANOVA results (*P*-values) for each species are inset, with significant effects in bold. Error bars represent 1 standard error of the mean. "Smoke Y" and "Strat Y" indicate seeds were smoked/stratified; "Smoke N" and "Strat N" indicate that seeds were not smoked/stratified. Letters separate means for all 4 treatments when smoke ×stratification was significant.

and 2.5-fold greater, respectively, for smoked than for non-smoked seeds. In contrast, the response of *P. unilateralis* to smoke did vary with stratification. Smoke did not impact germination for *P. unilateralis* seeds that were not stratified (P = 0.578), but it stimulated germination 1.7-fold for stratified seeds (P = 0.006). *Penstemon rydbergii* germination was inhibited by smoke, with germination (averaged across both levels of stratification) of smoked seeds 0.8-fold lower than that of non-smoked seeds.

Percent germination was influenced by 10 wk of stratification for 6 species, *P. auriberbis*, *P. eriantherus*, *P. glaber*, *P. rydbergii*, *P. secundiflorus*, and *P. strictus*, with each of these species exhibiting higher germination rates for stratified than for non-stratified seeds (Figure 2). *Penstemon auriberbis, P. eriantherus*, and *P. secundiflorus* were the most responsive to stratification treatments; when averaged across both levels of smoke, these species exhibited 63.4-, 10.6-, and 9.7-fold increases, respectively, in percent germination following stratification. Average germination percentages of *P. glaber*, *P. rydbergii*, and *P. strictus* were approximately 2- to 3-fold greater following stratification.

DISCUSSION

This research contributes to a small but growing body of evidence that *Penstemon* seed germination is often benefited by exposure to smoke. Of the 18 *Penstemon* species that have now been tested for germination responses to smoke, 10 responded positively (Keeley and Fotheringham 1998; Abella 2009; Schwilk and Zavala 2012). While the smoke-stimulated increase in germination for some of these species was small and likely to be of only modest ecological significance (for example, *P. secundiflorus*, which increased 1.9-fold from 11 to 21% following smoke treatments; results herein), for others, the increase was marked (for example, *P. barbatus*, which increased 7.6-fold from 8 to 61% following smoke treatments [Abella 2009]). Evidence of widespread smoke-stimulated germination within genera has likewise been reported by others (Dixon and others 1995).

How may historical fire regimes influence smoke responsiveness in *Penstemon*? Many smoke-stimulated species are native to ecosystems where fire was a frequent historical disturbance (Brown and others 1994; Moreira and others 2010), leading to speculation that smoke may be cueing seeds of these species to germinate immediately following fire when resources such as light, water, and plant-available nitrogen are typically abundant (Wan and others 2001). And yet, smoke-stimulated germination has also been documented for species from areas where fires were not frequent historically (Pierce and others 1995). For *Penstemon*, it seems plausible that seeds from areas where historical fires occurred frequently may be more stimulated by smoke than those from ecosystems where historical fires occurred infrequently. For example, all of my sampled populations of *P. unilateralis*, a smoke-stimulated species, were growing in montane ponderosa pine–dominated forests of the Colorado Front Range. Historical fires in these forests likely occurred every few decades (Brown and others 1999). In contrast, all of my sampled populations of *P. rydbergii*, the germination of which was hindered by smoke treatments, were growing in subalpine sites of Colorado and Wyoming where historical fires likely occurred only every few centuries (Romme 1982; Sibold and others 2006). An explicit analysis utilizing *Penstemon* seeds from both frequent- and infrequent-fire ecosystems would go far to advance our understanding of fire adaptations in this genus.

While the focus of this experiment was to examine the role of smoke in stimulating germination, stratification more often produced a stimulatory effect for the species evaluated here. In fact, *P. auriberbis* appeared to require it—percent germination increased 63.4-fold from < 1 to > 35% following 10 wk of stratification. *Penstemon eriantherus* and *P. secundiflorus* germination also benefited greatly from stratification. Others have also shown that germinability for many *Penstemon* species can be enhanced by stratification (Kitchen and Meyer 1991; Meyer and Kitchen 1994; Lindgren and Schaaf 2004). When evaluating the impact of stratification on seed germination, it is also important to consider the length of the stratification period. While 10 wk is sufficient to optimize germinability for many *Penstemon* species, some species require longer stratification periods (Kitchen and Meyer 1991; Meyer and Kitchen 1994). It is possible that *P. virens* and *P. whippleanus*, which achieved only 1% and 3% germination, respectively, following 10 wk of stratification would have achieved greater germination with a longer stratification period. A more thorough experiment that evaluates percent germination following a range of stratification periods would provide additional insight on stratification requirements for these species.

Other factors may have influenced the results herein, for example, seed age. Seed germinability and responses to smoke and stratification treatments can change during storage time (Stevens and others 1981; Roche and others 1997; Lindgren and Schaaf 2004). While most of the seeds used here were less than 1 y old at the time the experiment began (70% of populations), some were up to 9 y old (9% of populations; see Table 1). Fortunately, *Penstemon* seeds tend to be long-lived (Stevens and others 1981; Lindgren and Schaaf 2004), and excluding 9 y old seeds from the analysis of *P. glaber* did not alter the response of this species to treatments. Unfortunately, similar analyses were not possible for the other species with 9 y old seeds because of inadequate sample sizes. Another factor that could have affected results is the concentration of the smoke-water solution. Very dilute smokewater solutions may not be potent enough to stimulate germination, while solutions that are very concentrated can inhibit germination (Jäger and others 1996; Adkins and Peters 2001). I attempted to minimize this factor by preparing my smokewater solution per the recommendations of the manufacturer of Regen 2000, which is the smokewater concentrate discussed in this article. Furthermore, the concentration of my solution was consistent with the optimal Regen 2000 concentration reported by Adkins and Peters (2001).

CONCLUSIONS

Smoke has been found to stimulate seed germination for hundreds of plant species (Brown and van Staden 1997; van Staden and others 2000). I found that percent germination for 3 of the 10 *Penstemon* species tested here was enhanced by aqueous smoke treatments, and one species was inhibited. Furthermore, percent germination for 6 species was enhanced by 10 wk of stratification. My findings improve our understanding of smoke's role in *Penstemon* germination ecology and should be of use to others who wish to propagate *Penstemon* species.

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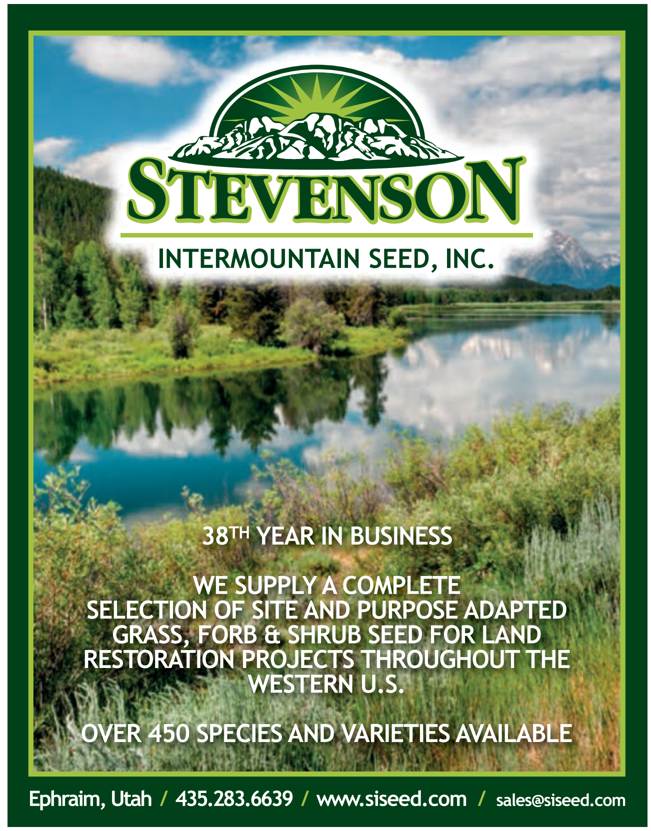

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