Blowout penstemon (*Penstemon haydenii* S. Watson [Scrophulariaceae]) in bloom.

Breaking primary seed dormancy in Gibbens' beardtongue (*Penstemon gibbensii*) and blowout penstemon (*Penstemon haydenii*)

Kassie L Tilini, Susan E Meyer, and Phil S Allen

ABSTRACT

This study established that chilling removes primary seed dormancy in 2 rare penstemons of the western US, Gibbens' beardtongue (*Penstemon gibbensii* Dorn [Scrophulariaceae]) and blowout penstemon (*Penstemon haydenii* S. Watson). Wild-harvested seeds were subjected either to moist chilling at 2 to 4 °C (36–39 °F) for 0, 4, 8, 12, and 16 wk or to approximately 2 y of dry storage. Seeds of both species were dormant at harvest and responded positively to chilling. *Penstemon gibbensii* germination increased linearly with length of chilling, and collections from sites with longer winters required a longer chilling period to break dormancy. With longer chilling durations, most seeds germinated during the chilling treatment. *Penstemon haydenii* germination increased to nearly 100% after 4 or more wk of chilling followed by incubation under a cool, diurnally alternating temperature regime (10–20 °C [50-68 °F]) but did not germinate during chilling treatments regardless of duration. Under constant (15, 20, 25 °C [59, 68, 77 °F]) or warmer (15–25 °C, 20–30 °C [59–77 °F, 68–86 °F]) alternating post-chilling temperature regimes, germination was consistently < 15%. Without chilling, dry storage increased germination (from 0–15%) in *P. haydenii*. By contrast, *P. gibbensii* seeds showed no increase in germination following dry storage, where germination in both recently harvested and 2-y-stored seeds averaged 16% without chilling. These insights will assist propagation and reintroduction strategies for restoring populations of these rare species.

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KEY WORDS

alternating temperature, cold stratification, dry after-ripening, habitat-correlated, pre-chilling, seed germination, Scrophulariaceae

CONVERSIONS

°F = (°C × 1.8) + 32

1 mm = 0.04 in

NOMENCLATURE

USDA NRCS (2016)

Photos by Bonnie Heidel

The regulation of seed dormancy has 2 main functions: 1) to optimize germination timing for maximum seedling establishment success, and 2) to promote carryover of seeds by preventing complete germination within the year following production (Meyer 1992). The first function enables a species to avoid precocious germination under unfavorable environmental conditions. Seed dormancy has evolved in response to contrasting selection pressure, particularly climate regimes, in distinct habitats (Meyer and Monsen 1991) and is known as "predictive" dormancy (Venable and Lawlor 1980). Predictive seed dormancy can often be broken by specific environmental cues that precede optimal conditions for field establishment. For example, several spring-emerging species within the genus *Penstemon* germinate only when incubated at cool temperatures (Allen and Meyer 1990), whereas several other penstemons require a period of moist chilling for dormancy to be broken (Kitchen and Meyer 1991; Meyer 1992; Meyer and Kitchen 1994). In laboratory experiments, seeds from different populations of the same *Penstemon* species showed varying degrees of dormancy that were correlated with the duration of winter snow cover (Meyer and others 1995). Seeds from populations with more severe winters and longer periods of snow cover required longer chilling to break dormancy than did seeds from populations characterized by shorter, milder winters. Results from common-garden experiments confirmed this habitat-correlated variation, suggesting a genetic basis for germination differences both among populations and between individual penstemon plants (Meyer and others 1995).

The second function of seed germination regulation enables a species to establish a persistent seedbank. This regulation is referred to as cue-nonresponsive dormancy and is not overcome by cues associated with optimum conditions for seedling establishment within the first year (Venable and Lawlor 1980; Meyer and others 2005; Bewley and others 2013). High cue-nonresponsive dormancy provides species with a strategy to avoid complete germination under environmental conditions potentially unfavorable for seedling survival, a strategy frequently termed "bet hedging" (Venable and Lawlor 1980). In laboratory experiments with seeds of 16 *Penstemon* species, 3 species produced seeds that exhibited high cue-nonresponsive dormancy as indicated by germination < 15% even after chilling for 16 wk (Kitchen and Meyer 1991).

A nondormant seed will germinate readily when suitable environmental conditions are present (Baskin and Baskin 2004). The need for conditions conducive to germination

Figure 1. Gibbens' beardtongue (*Penstemon gibbensii*) plant (A) and close-up view (B).

also applies after release from primary dormancy. Similar to other species that break seed dormancy in response to moist chilling, many penstemon species are early spring-emerging species that require cool incubation temperatures for germination. In a study of 3 penstemon species, seed germination decreased markedly when incubation temperature increased above 20 °C. A cool incubation temperature of 15 °C consistently produced maximum germination (Allen and Meyer 1990).

Penstemon gibbensii Dorn (Scrophulariaceae) and *Penstemon haydenii* S. Watson are rare penstemons that occupy specific edaphic environments. *Penstemon gibbensii* inhabits shale and sandy-clay slopes of the Brown's Park geological formation in Colorado, Utah, and Wyoming (Heidel 2009) (Figure 1). Very little is known concerning the germination ecology of this species. *Penstemon haydenii* is endemic to only 2 known population centers, the sand hills of west-central Nebraska and the Ferris Dunes of Carbon County, Wyoming (Heidel 2012) (Figure 2). It was listed as Endangered by the US Fish and Wildlife Service in 1987 (USFWS 1987). Considerable research has been performed on Nebraska populations. Flessner and Stubbendieck (1989) examined the effects of moist chilling at 3 °C on *P. haydenii* seeds and reported that while stratification for 6, 12, and 18 wk increased germination from 8 to 21%, chilling did not consistently enhance germination. The post-chilling incubation temperatures used in their study, however, were much higher than the optimum temperature for *Penstemon* germination reported by Allen and Meyer (1990) and by Meyer and others (1995) and thus may have inhibited germination even with an appropriate chilling treatment.

The study reported herein was conducted to better understand requirements for breaking primary seed dormancy in *P. gibbensii* and *P. haydenii*. Primary objectives of this study were 1) to determine the role of moist chilling in breaking seed dormancy in wild-collected seeds, and 2) to determine if seeds exhibit dry after-ripening. Secondary objectives were 1) to examine differences in chilling requirement for *P. gibbensii* seeds collected from across its geographic and elevational range (using elevation, mean winter precipitation, and mean winter temperature as indicators of habitat), and 2) to determine optimum post-chilling temperatures to stimulate germination in *P. haydenii*. Characterizing the mechanisms regulating germination in these 2 rare *Penstemon* species and developing treatments to overcome seed dormancy will assist conservation efforts by helping to optimize propagation techniques for reintroduction and recovery efforts.

Figure 2. Blowout penstemon (*Penstemon haydenii*) plant on sand dune slope (A) and close-up view (B).

MATERIALS AND METHODS

Seeds of *P. gibbensii* and *P. haydenii* were collected from sites in Utah and Wyoming (Table 1). For each collection, ripe seeds were hand-harvested on a single date. While we did not quantify the number of seeds harvested from a particular plant, conscious effort was made to collect a roughly similar number of seeds from at least 50 *P. gibbensii* and 100 *P. haydenii* plants that were distributed across the collection site, ensuring adequate genetic representation at the population level. Seedlots were bulked, then cleaned by screening through a series of graded seed sieves (Seedburo, Plaines, Illinois). Seed-sized chaff was separated using a handmade seed blower. Seeds were then stored in manila envelopes under ambient laboratory conditions (20–22 °C, 20–30% relative humidity) until experiments were conducted. Viability of the seedlots at the start of each experiment was determined using either a cut test (AOSA 1988) or tetrazolium staining (Grabe 1970). All experiments included 4 replications of 25 seeds per treatment for each seedlot in a completely randomized design, a level of replication shown to be adequate for detecting biologically meaningful differences in germination response (Meyer and others 1995). Seeds were placed on water-saturated germination blotters (Anchor Paper, St Paul, Minnesota) in 15 × 100 mm plastic Petri plates to maintain adequate moisture and were watered as needed during incubation. Chilling treatments were performed with imbibed seeds in a dark chamber held at 2 to 4 °C. Incubation chambers (for post-chilling or no-chilling incubation treatments) were set to alternate daily between 2 temperatures for 12 h at each temperature, with a 12-h photoperiod (cool-white fluorescent light) corresponding to the warmer temperature. During chilling and post-chilling incubation, plates were examined periodically and germinated seedlings (radicle > 1 mm) were counted and removed. At the conclusion of each experiment, viability of ungerminated seeds was determined using either a cut test or tetrazolium staining. Any viable, ungerminated seeds were classified as dormant.

Gibbens' Penstemon Germination Experiments

Chilling experiments for *P. gibbensii* were conducted in winter 2010–2011 and included both 2009 and 2010 seed collections (Table 1). Seeds from each collection were either placed directly into incubation at 10 to 20 °C without chilling or subjected to chilling at 2 to 4 °C for 4, 8, 12, or 16 wk. Following chilling, plates were transferred to incubation at 10 to 20 °C and scored for germination twice weekly for 4 wk.

Penstemon gibbensii germination response to after-ripening was also determined. Seeds from the same collections tested in winter 2010–2011 were stored for approximately 2 y under laboratory conditions. Subsamples of the stored seeds were then placed directly into 10 to 20 °C incubation and scored for germination as before. Germination percentages without chilling were then compared for recently harvested and stored seeds.

Blowout Penstemon Germination Experiments

Penstemon haydenii primary dormancy and its response to moist chilling were studied using a similar experimental design as described for *P. gibbensii*, with chilling durations of 0 to 16 wk followed by 28-d incubation at 10 to 20 °C. Seeds were collected from a single site (Bear Mountain in the Ferris Dunes, Carbon County, Wyoming; Table 1). One seedlot was collected in the late summer of 2010; its germinability at 10 to 20 °C without chilling was determined within 2 mo of collection. These seeds were then stored under ambient laboratory conditions for 2 y. The second seedlot was collected in summer 2012 just prior to the initiation of the chilling experiment. Both lots were included in the experiment to determine chilling response.

In an additional experiment to determine the optimum post-chilling incubation temperature for *P. haydenii* germination, we subjected seeds from the Bear Mountain 2012 seedlot (Table 1) to moist chilling as previously described for 4 wk. Following chilling, seeds were subjected to one of 6 incubation treatments: constant 15 °C, alternating 10 to 20 °C, constant 20 °C, alternating 15 to 25 °C, constant 25 °C, or alternating 20 to 30 °C, all with a 12-h photoperiod. Seeds were scored for germination every 2 d for 4 wk, and remaining ungerminated seeds were tested for viability.

The after-ripening response for *P. haydenii* was evaluated for the 2010 seedlot by comparing the germination response at 10 to 20 °C without chilling for recently harvested seeds and for seeds stored for 2 y and then incubated at 10 to 20 °C.

Statistical Analysis

For each experiment, germination data expressed as proportion of viable seeds for each replicate were arcsine-square-root-transformed to increase homogeneity of variance and analyzed using SAS v. 8.1 PROC GLM (SAS Institute, Cary, North Carolina); germination is reported as percentage data in the results. Chilling, after-ripening, and incubation temperature experiments with *P. haydenii* were analyzed using analysis of variance (ANOVA) with treatment (chilling duration, seed age, or mean temperature and temperature alternation regime, respectively) as fixed main effects. For *P. gibbensii*, analysis of variance was used to evaluate after-ripening as described above. Differences among means were evaluated in these analyses using LSMEANS separations from ANOVA. We used ANCOVA (analysis of covariance) with chilling duration as the continuous variable and population as the class variable to analyze the *P. gibbensii* chilling experiment because germination percentage showed a linear response to chilling dura-

TABLE 1

Location, habitat, and collection year and seed viability information for seedlots of Penstemon gibbensii *and* Penstemon haydenii *used in germination experiments.*

Species and Site	Location	Elevation (m)	Nov–Mar precipitation (mean, mm)	Nov–Mar temperature (mean, °C)	Collection year	Initial viability (%)
Penstemon gibbensii						
Brown's Park, UT	40.84730 N 109.05286 W	1700	59	–1.1	2009 2010	82 92
Sand Point, WY	41.03800 N 107.79553 W	1900	116	–3.3	2010	96
Flat Top, WY	41.16385 N 107.82316 W	2320	189	–2.6	2010	80
Penstemon haydenii						
Bear Mountain, WY	42.24348 N 107.07086 W	2100		–2.1	2010 2012	93 97

Notes: Climate data based on latitude and longitude are interpolated 30 y means (1980–2010) obtained from http://www.prism.oregonstate.edu/explorer/. Collection sites for *P. gibbensii* are representative of the full geographic and elevational range of the species, whereas the collection site for *P. haydenii* was representative of the geographically and elevationally restricted range of this species in Wyoming.

tion. Both germination during chilling and total germination (that is, germination during chilling plus germination during post-chilling incubation at 10 to 20 °C) were included as response variables.

RESULTS

Penstemon gibbensii

Penstemon gibbensii seeds showed a strong positive response to chilling for 8 or more wk (Figure 3). Both percentage of seeds that germinated during chilling and total germination increased as an approximately linear function of chilling duration (Figure 3). The population main effect was significant for total germination but not for germination in chilling. A significant chilling by population interaction occurred for both response variables, however, with the slope of the chilling response significantly lower for the high-elevation Flat Top collection than for the other 3 collections, whose slopes did not differ. Total germination following 16 wk of chilling ranged from 28% for Flat Top to 98% for the Brown's Park 2010 collection, while germination during chilling for 16 wk ranged from 26 to 86%. The percentage of viable seeds that germinated during chilling treatments for the longer chilling periods was relatively uniform across populations and averaged 60% for the 12-wk and 90% for the 16-wk chilling treatment.

A 2-y period of dry storage had no significant effect on the germination of *P. gibbensii* seeds (mean germination for recently harvested seeds = 16.3%, for 2-y-stored seeds = 15.3%; seed age main effect: $F_{1,18} = 0$; $P = 0.9647$). The percentage of seeds germinating increased slightly following prolonged dry storage for the Brown's Park 2010 collection (26–30%), remained unchanged for Flat Top (0–1%), and decreased slightly (22–15%) for Sand Point, but these differences were not statistically significant (population by seed age interaction: $F_{2, 18} = 1.51$, $P = 0.2481$).

Penstemon haydenii

Recently harvested *P. haydenii* seeds from both Bear Mountain collections (2010 and 2012) were completely dormant without chilling. Chilling of any duration from 4 to 16 wk followed by incubation at 10 to 20 °C resulted in near-complete germination of both lots when tested in 2012 (Figure 4). A 4-wk chilling treatment was sufficient to break dormancy completely. In contrast with *P. gibbensii*, *P. haydenii* seeds did not germinate in chilling even after extended periods but germinated readily in post-chilling incubation after chilling of any duration from 4 to 16 wks. We observed a slight but significant trend for germination to decrease after prolonged chilling (mean germination 96% after 16-wk chill).

The post-chilling incubation temperature had a profound effect on germination for *P. haydenii* (Figure 5). Fluctuating post-chilling incubation temperatures stimulated significantly higher germination than did constant incubation temperatures. The 3 alternating temperature treatments resulted in significantly greater germination percentages than did any constant temperature treatment. In addition, the coolest alternating incubation treatment (10–20 °C) stimulated significantly higher germination than did higher alternating temperatures. In this treatment, *P. haydenii* seeds showed almost complete germination (96%), whereas at constant temperatures germination never exceeded 2%, and at higher alternating temperatures never exceeded 15%.

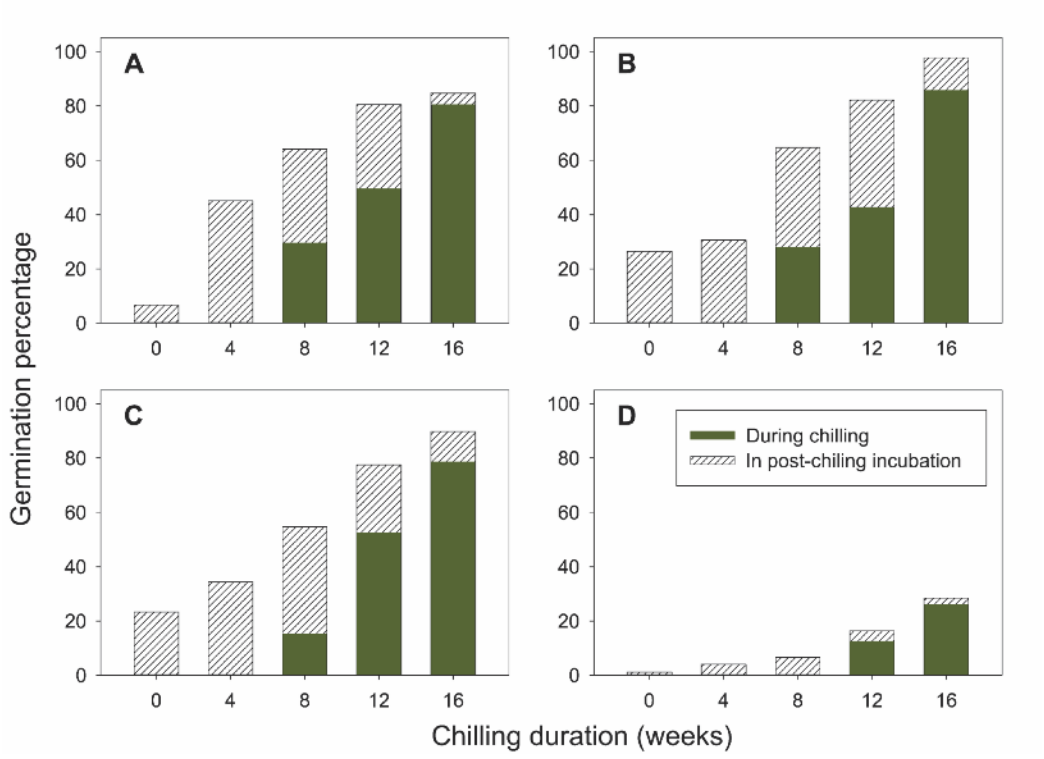

Figure 3. Percentage of *P. gibbensii* seeds germinating during (green) and following (hatched) chilling for 0–16 wk at 2–4 °C with post-chilling incubation at 10–20 °C for 28 d: Brown's Park, UT 2009 (A); Brown's Park, UT 2010 (B); Sand Point, WY 2010 (C); Flat Top, WY 2010 (D). Total germination: chilling duration main effect $F_{1,68} = 247.62$, $P < 0.0001$; population main effect $F_{3,68} = 13.23$, $P < 0.0001$; chilling duration by population interaction: $F_{3,68} = 4.62$, $P = 0.0053$; germination during chilling: chilling duration main effect $F_{1,72} = 483.04$, $P < 0.0001$; population main effect not significant; chilling duration by population interaction: $F_{3,72} = 13.75$, $P < 0.0001$. Means separations and error bars across chilling treatments are not shown because the response variable chilling duration was analyzed as a continuous variable using ANCOVA.

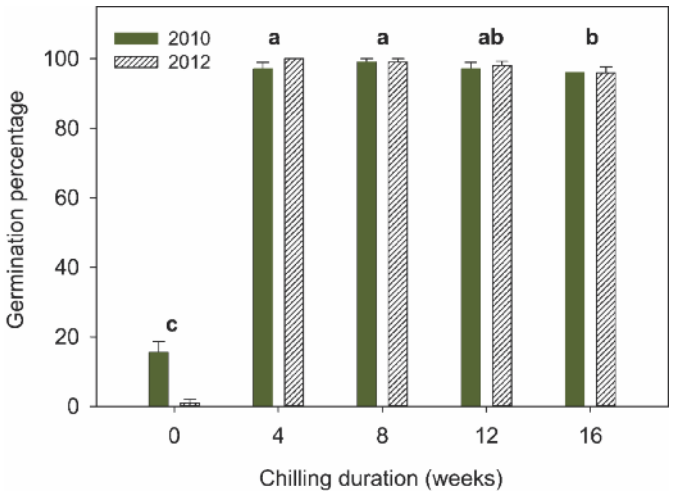

Figure 4. Percentage of *P. haydenii* seeds germinating following chilling for periods of 0–16 wk at 2–4 °C with post-chill incubation at 10–20 °C for 28 d (error bar = standard error). Chilling duration main effect: $F_{4, 30} = 224.87$, $P < 0.0001$; collection year main effect not significant; chilling duration by collection year interaction: $F_{4, 30} = 5.86$, $P = 0.0013$. The means separation shown is for the chilling duration main effect. Pairs of bars headed by different letters were significantly different at $P < 0.05$.

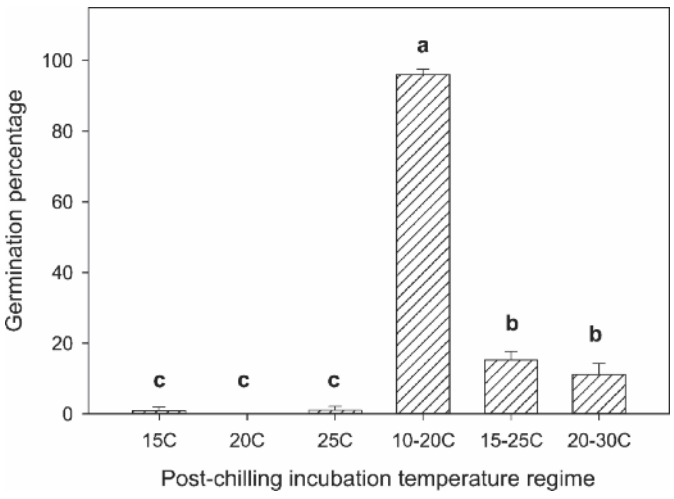

Figure 5. Percentage of *P. haydenii* seeds germinating after 28 d under 6 constant and alternating incubation temperature regimes following 4 wk of moist chilling at 2–4 °C (error bar = standard error). Temperature main effect: $F_{2, 18} = 85.74$, $P < 0.0001$, alternating temperature regime; main effect: $F_{1, 18} = 313.77$, $P < 0.0001$; mean temperature by temperature alternation regime interaction: $F_{2, 18} = 78.91$, $P < 0.0001$. Bars headed by different letters were significantly different at $P < 0.05$.

Penstemon haydenii seed germination was significantly increased by after-ripening ($F_{1,6} = 70.43$, $P = 0.0002$). Recently harvested *P. haydenii* seeds collected in 2010 failed to germinate in incubation without chilling (< 1%). Following approximately 2 y of dry storage, germination increased to 15%. Recently harvested seeds from the 2012 collection were also highly dormant, but responded to chilling in the same manner as the older lot (see Figure 4). The significant interaction between seed age (year of collection) and chilling was attributable solely to the difference in response for the treatment without chilling.

DISCUSSION

Our results indicate that seeds of both *P. gibbensii* and *P. haydenii* exhibit strong primary dormancy. Dry after-ripening for 2 y slightly improved germination for *P. haydenii* but not for any collection of *P. gibbensii*. By contrast, moist chilling resulted in significantly improved germination that occurred either during moist chilling (*P. gibbensii*) or following the chilling treatment (both species). Without this dormancy-breaking treatment, neither species achieved high germination. For spring-emerging species such as these, primary dormancy acts to prevent precocious germination during late summer, autumn, and early winter. Seedling establishment success is maximized by timing germination to follow shortly after snowmelt, as has been shown for other *Penstemon* species (Meyer and Kitchen 1994; Meyer and others 1995).

The depth of primary dormancy in *P. gibbensii* appeared to vary inversely with elevation, which along with winter precipitation served as a proxy for habitat in our study. Flat Top, the highest-elevation *P. gibbensii* population, had lower germination percentages than did populations at lower elevation sites, a difference that increased with chilling duration. Higher elevation at the site of origin has often been associated with increased dormancy in the seeds of other taxa (Meyer and Monsen 1991; Cavieres and Arroyo 2001) including other penstemon species (for example, Meyer 1992). Mean winter precipitation at the Flat Top site was 189 mm, compared to 59 to 116 mm at the lower elevation sites, suggesting that snow is likely to persist for longer at this site (Table 1). A longer moist chilling requirement could prevent seeds from germinating before snowmelt and the onset of spring temperatures favorable for seedling establishment. Also, seeds at lower elevation sites may spend much of the winter at below freezing temperatures with little snow cover, conditions not conducive to dormancy release, whereas at Flat Top the seeds are more likely to spend time at effective chilling temperatures beneath the snow.

Seeds of the Flat Top collection showed a positive germination response to increased chilling duration, but even after 16 wk, germination was only 26%. This trend suggests that a longer chilling treatment could have resulted in even greater germination, but it is also possible that the chilling temperature used in our experiment was too high for optimal dormancy release for seeds of this species. The temperature beneath deep snow cover is maintained near a constant 0 °C, and our chilling treatment was slightly higher than this. Another possibility is that a large fraction of the seeds in this lot exhibited cue-nonresponsive dormancy. This collection was made in late summer, which could have biased the collection for seeds with higher dormancy relative to the other collections, which were made earlier in the season. Habitat-correlated variation in chilling response coupled with a combination of chilling-responsive predictive dormancy and cue-nonresponsive dormancy within the same seed population is common in other Intermountain penstemon species (Meyer and others 1995).

Unlike seeds of *P. gibbensii*, *P. haydenii* seeds germinated almost completely following just 4 wk of moist chilling, and no *P. haydenii* seeds germinated during chilling regardless of duration. As a sand dune endemic, *P. haydenii* has seeds that inhabit environments that are very dry during much of the year with a relatively small window for timing successful seedling establishment. Strong selection pressure for appropriate timing of germination likely renders these seeds capable of accurately sensing changes in weather from winter to spring and responding quickly to take advantage of the limited time when water is available in the spring before the sand dries out. The Bear Mountain population of *P. haydenii* is in an extreme environment—a dry, sandy, high-elevation site with long, cold winters (Table 1). Germination during winter could result in seedling death from frost, leading to the prediction that this population of *P. haydenii* would have tightly regulated primary dormancy so as not to germinate either too early or too late. In the field, *P. haydenii* apparently does not form a persistent near-surface seedbank (Tilini 2013). Relying on recently produced seeds for seedling establishment is associated with the need to closely regulate seed germination through cue-responsive primary dormancy. This plant may also rely on perennial belowground stems to recover from repeated burial due to shifting sand in order to survive during years when either seed production or seedling establishment is unsuccessful.

Penstemon haydenii seeds germinated best at cool, diurnally fluctuating incubation temperatures following moist chilling. When combined with at least 4 wk of moist chilling, incubation at cooler, fluctuating temperatures stimulated much higher germination than was reported for this species in Nebraska by Flessner and Stubbendieck (1989). These researchers, however, included only treatments in which moist chilling was followed by higher incubation temperatures that were likely prohibitive of germination. In our experiment, 4 wk of moist chilling followed by the same warmer incubation temperatures resulted in levels of germination similar to those in the Nebraska studies. The conclusion by Flessner and Stubbendieck that moist chilling was ineffective as a dormancy-breaking treatment was

contradicted in our study when chilling was combined with a cool, alternating incubation temperature regime. In this case, chilling was a highly effective method for breaking primary dormancy and stimulating seed germination in *P. haydenii*. We acknowledge the possibility that the drier high-elevation habitat of Wyoming *P. haydenii* may have led to ecotypic differentiation that caused it to respond differently from Nebraska populations from more mesic low-elevation sites. As discussed earlier, penstemon germination responses to moist chilling have been shown to exhibit ecotypic variation associated with elevation and climate regimes (Meyer 1992; Meyer and Kitchen 1994; Meyer and others 1995). These early studies were all conducted using 10 to 20 °C as a post-chilling incubation temperature, based on work showing that penstemon seeds germinate to high percentages only at relatively low temperatures (Allen and Meyer 1990).

Penstemon haydenii also exhibited a strong positive response to alternating relative to constant incubation temperatures. All alternating temperature regimes yielded significantly higher germination than did any of the constant temperature regimes. This positive response of *P. haydenii* to fluctuating temperatures is consistent with the hypothesis that temperature fluctuation provides a mechanism for sensing seed burial depth (Thompson 1974; Bewley and others 2013). Diurnal temperature fluctuations are greatest near the soil surface, which would stimulate germination of shallowly buried seeds. Deeply buried seeds would be less likely to germinate because soil acts as a buffer against temperature variation, and fluctuations in temperature are dampened as soil depth increases (Ghersa and others 1992). Burial by sand and subsequent re-excavation is a frequent occurrence for *P. haydenii* seeds. The ability to restrict germination to optimum burial depths would be beneficial to seedling success.

After-ripening, the processes of breaking primary dormancy through dry storage (Hilhorst and Karssen 1992; Bewley and others 2013), did not increase germination of *P. gibbensii* seeds, which rely more heavily on environmental cues received in the imbibed state for germination than when seeds are dry, a result also reported for *P. eatonii* as well as other *Penstemon* species (Meyer 1992; Meyer and others 1995). *Penstemon haydenii*, however, showed a small but positive germination response to prolonged dry storage (that is, dry after-ripening; Beckstead and others 1996). The ecological relevance of this response is not known, as seeds in the field would never experience prolonged conditions at moderate temperature as they did in laboratory storage.

CONCLUSION

Similar to many other penstemon species we have investigated, seed dormancy in *P. gibbensii* and *P. haydenii* can be broken by moist chilling followed by incubation at cool temperatures. Seeds of *P. gibbensii* will likely require a longer chilling period if they are collected from sites where seeds experience a longer period of winter snow cover. In addition, germination of *P. haydenii* seeds is promoted by exposure to incubation under alternating temperature cycles following chilling and may show slightly improved germination following prolonged dry storage. The experiments reported here address release only from primary dormancy. We have evidence that secondary dormancy induced by deep burial might also play a role in optimizing germination timing for *P. haydenii* (Tilini 2013).

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