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RESEARCH ARTICLE

Informing native plant sourcing for ecological restoration: cold-hardiness dynamics, flowering phenology, and survival of *Eriogonum umbellatum*

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Despite advances in restoration of degraded lands around the world, native plants are still underutilized. Selection of appropriate plant materials is a critical factor in determining plant establishment and persistence. To better inform decision-making, we examined cold-hardiness dynamics, flowering phenology, and survival among five geographically distinct sulfur-flower buckwheat (Polygonaceae: *Eriogonum umbellatum* Torr.) populations in a common garden. LT_{50} (a measure of freezing injury) was determined every 6 weeks across a complete year; one population was also evaluated at the source. Cold-hardiness dynamics were similar across populations, with annual fluctuations in mean LT_{50} exceeding 40°C. Rate of deacclimation (i.e. loss of cold tolerance) in spring varied across populations and was not related to the elevation from which a population came. Plants were less cold hardy in October 2014 compared to October 2013, likely reflecting a response to colder local conditions in 2013. Although the range of LT_{50} was similar for a single comparison of common garden versus wild-grown plants, wild-grown plants acclimated and deacclimated earlier than common garden-grown plants. Plants derived from a low-elevation population showed delayed flowering phenology, while high-elevation populations showed earlier flowering phenology, with one high-elevation population having the lowest survival rate in the common garden. These results suggest that while considerable plasticity in seasonal cold-hardiness dynamics occur, population variability in deacclimation and flowering phenology have implications for selection and movement of sulfur-flower buckwheat for ecological restoration.

Key words: cold hardiness, common garden, LT_{50}, native plant sourcing, population variability, sulfur-flower buckwheat

Implications for Practice

- Though climatic differences exist among source locations, neither timing of cold acclimation in the fall nor depth of cold hardiness in the winter differed among populations of sulfur-flower buckwheat.
- Populations differed in spring deacclimation rate and flowering phenology, with consequences for survival in a common garden. Higher-elevation populations that were moved to lower elevations developed earlier than local sources, making them vulnerable to early-season freeze events and increased potential for mortality.
- Given that provenance strategies are often based on precipitation and temperature profiles, these results have notable importance for the selection and movement of plant material.
- Results are particularly significant for ecosystems that rely on snowpack for insulation and seasonal moisture given the predicted prolonged periods of drought associated with future climate conditions.

Introduction

There is growing interest in using a diverse mix of native species to restore the natural structure and ecological function of degraded habitats (e.g. Richards et al. 1998; Tischew et al. 2011; Shaw et al. 2012) but much work remains to determine best provenance management strategies and propagation techniques for many native species (e.g. Ladouceur et al. 2017; Breed et al. 2018). Plant material sourcing for restoration projects has traditionally relied on local provenances, but given consequences of habitat fragmentation and climate change, local sources may not be available in sufficient quantities (Broadhurst et al. 2008) or may not be superior (Hancock et al. 2013; Gellie et al. 2016). As such, alternative sourcing strategies are being explored to increase the adaptive potential of restored populations now and in anticipated future climates (Vander Mijnsbrugge et al. 2010;

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Breed et al. 2013; Prober et al. 2015). Mechanisms are being put in place for investigating and resolving such issues associated with the increased demand for native species. For example, the Great Basin Native Plant Selection and Increase Project was a cooperative endeavor initiated in 2002 between the USDI Bureau of Land Management, Great Basin Restoration Initiative and the US Forest Service, Rocky Mountain Research Station to increase the availability of native plant material and improve success in restoring native plant communities across the sagebrush steppe ecosystem (Shaw 2003).

The sagebrush steppe ecosystem of the Intermountain West of North America is a contemporary example of how overexploitation, invasive species, and an altered fire regime are driving rapid changes in dryland ecosystem structure and function across enormous spatial scales (Pellant et al. 2004; Coates et al. 2015; Svejcar et al. 2017). Non-native species, whether introduced intentionally [e.g. crested wheatgrass (*Agropyron cristatum* [L.] Gaertn.)] or accidentally [e.g. cheatgrass (*Bromus tectorum* L.) and medusahead (*Taeniatherum caput-medusae* [L.] Nevski)], have altered fire regimes and reduced species diversity by impeding post-disturbance recruitment of native species (e.g. Knapp 1996; Lesica & DeLuca 1996; Henderson & Naeth 2005; Davies & Svejcar 2008). Because of this, restoring rangelands dominated by non-native species has been challenging (Pellant et al. 2004; Davies et al. 2013; Parkinson et al. 2013). Attempts at restoration with native species have typically relied on aerial- and/or drill-seeding of grass and shrub species, and have seen limited success (Knutson et al. 2014).

Sulfur-flower buckwheat (*Eriogonum umbellatum* Torr.) is one of many native species selected for evaluation and increase for use in sagebrush steppe ecosystem restoration. It is a low-growing, evergreen, woody perennial in the buckwheat family (Polygonaceae) (Young-Mathews 2012) that is native to western North America at elevations ranging from 200 to 3,700 m (Dyer et al. 2011; USDA NRCS 2015). Sulfur-flower buckwheat is highly variable with numerous subspecies distributed across its range from California to western Canada and east into Colorado and New Mexico (Dyer et al. 2011). The species is particularly valuable to pollinators (James et al. 2014) and provides forage for many species of birds, mammals, and insects (Young-Mathews 2012). It is beneficial for use in reestablishing native plant communities where the existing local seed bank has been lost (Parris et al. 2010). Protocols have been developed for container stock production (e.g. Luna & Corey 2008), seed production (Archibald 2006; Shock et al. 2017), and to improve germination (Kramer & Foxx 2016).

Winter dormancy is an adaptive mechanism where plants suspend growth in response to changes in photoperiod and temperature to survive conditions of freezing temperatures and drought. Cold acclimation (or hardening) and deacclimation (or dehardening) are important processes associated with dormancy and are linked to numerous structural, metabolic, and physiological changes within the plant (Gusta & Wisniewski 2013). Plasticity in a plant's capacity to acclimate and deacclimate has important implications for the selection and movement of plant material, as has been shown for other plant species (St. Clair 2006). Much of the work on plant cold hardiness has focused on economically valuable tree species (e.g. Thomas & Lester 1992; St. Clair 2006; Porter et al. 2013) and crops (e.g. Li & Sakai 1978) with comparatively little work on native shrubs, forbs, and grasses (e.g. Hou & Romo 1997, 1998; Loik & Redar 2003; Herriman & Davis 2012; Venn et al. 2013).

Elevation ranges within the sagebrush steppe ecosystem, where sulfur-flower buckwheat naturally occurs, exceed 3,700 m and diurnal, seasonal, and annual temperature fluctuations can be extreme (Svejcar et al. 2017). Because low-temperature exposure is one factor known to limit plant persistence and long-term restoration success, the objective of this research was to assess seasonal cold-hardiness dynamics, flowering phenology, and survival among geographically unique populations of sulfur-flower buckwheat grown in a common garden. Specifically, this research sought to answer the following questions: Do geographically distinct populations differ regarding cold-hardiness depth, fall cold tolerance acclimation rate, or cold tolerance loss in the spring? Does flowering phenology differ among these populations? If so, are there consequences associated with these phenologic differences relating to survival? The results of this research can be used to develop hypotheses related to factors that drive the phenology of this species and the consequent implications these relationships may have for the selection and movement of plant material for restoration.

Methods

In June 2006, the US Forest Service, Rocky Mountain Research Station established a sulfur-flower buckwheat common garden in Boise, ID (elevation 845 m). The garden was installed using a random five-block design, with each block containing 20 plants from 16 geographically distinct populations across the sagebrush steppe ecosystem. For this study, five populations (collection numbers 01, 13, 25, 36, and 37) with a minimum of five plants were selected for cold-hardiness evaluation based on broad ecological variation, representing an elevation range of 855 to 1,856 m and five provisional seed zones (Fig. 1; Table 1; Bower et al. 2014). In addition, five plants of one population (01) were sampled at their site of origin. More source origin research was of interest, but logistically not feasible. Winter access and the need to process samples within 48 hours of collection to assess cold hardiness necessitated the use of the closest population (01) to the common garden location.

For cold-hardiness evaluation, plant material was collected and processed every 6 weeks for 1 year: 25 October, 2013; 4 December, 2013; 21 January, 2014; 7 March, 2014; 17 April, 2014; 30 May, 2014; 12 July, 2014; 25 August, 2014; and 16 October, 2014. The tissues collected at each interval were subjected to a series of cold temperatures and assessed for cell damage, enabling us to create a sigmoidal response function with a derived variable (LT_{50}), which was used to analyze differences across time and populations (Fig. S1, Supporting Information).

One plant from each of the five populations was sampled from each block. When possible, tissue samples for each source

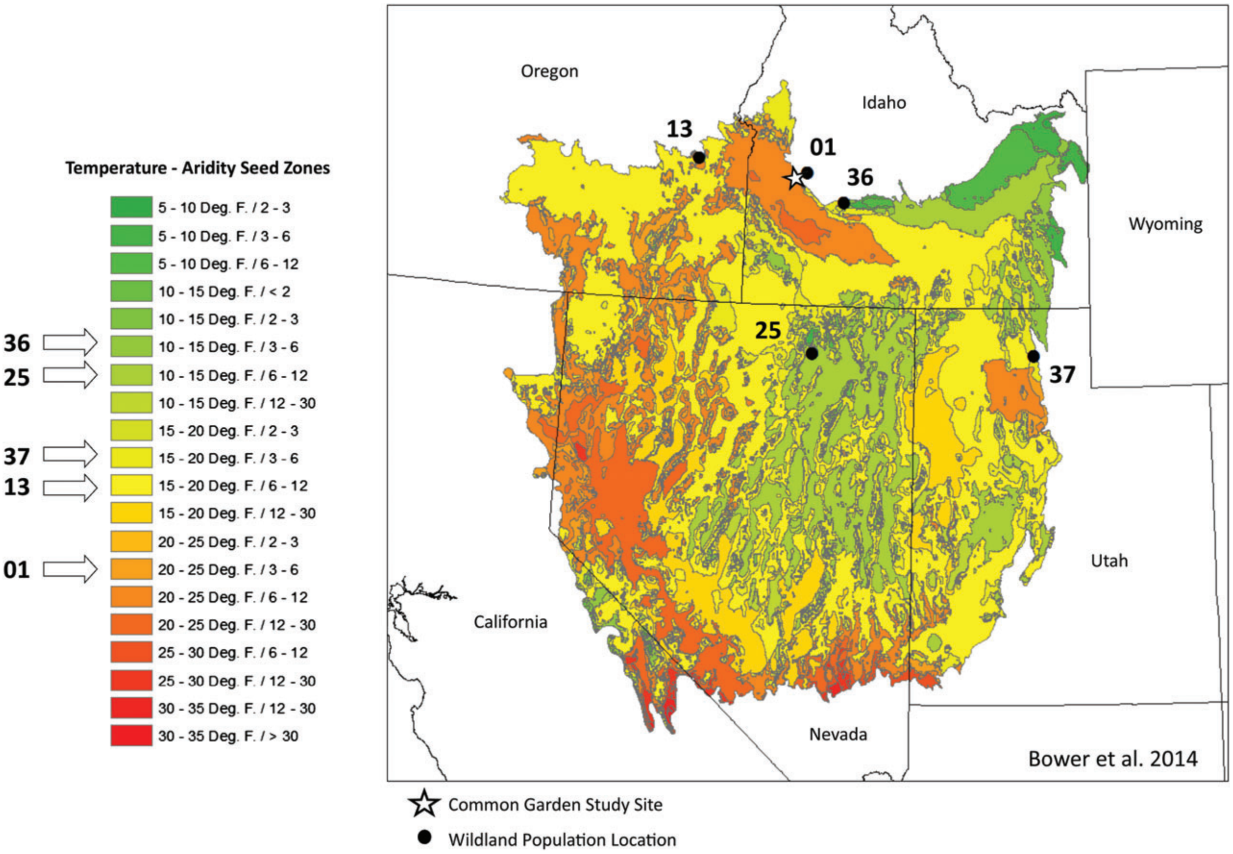

Figure 1. Five wildland seed collection sites (represented as 01, 13, 25, 36, 37) and common garden location of sulfur-flower buckwheat populations investigated for cold hardiness, flowering phenology, and survival expressed on the sagebrush steppe ecosystem provisional seed zone map (Bower et al. 2014).

Table 1. Collection site and climatic data for five sulfur-flower buckwheat populations grown in a Boise, ID common garden and evaluated for cold hardiness, flowering phenology, and survival. [a]Population 01 was evaluated both in the common garden and at the source location. [b]Based on 30-year (1981–2010) precipitation and temperature normals (PRISM 2018).

					Precipitation (cm)[b]		*Temperature (°C)*[b]		
Population	*County, State*	*Latitude*	*Longitude*	*Elevation (m)*	*Annual*	*Growing Season (March–October)*	*Annual*	*Winter (December–March) Minimum*	*Spring (March–June) Minimum*
01[a]	Boise, ID	43.665	−115.979	964	47.8	22.3	9.3	−6.6	−1.8
13	Malheur, OR	43.799	−117.890	855	27.0	16.0	9.9	−6.9	−1.3
25	Elko, NV	41.392	−115.794	1,856	28.8	16.4	6.0	−11.6	−5.8
36	Elmore, ID	43.296	−115.327	1,607	56.4	24.4	6.4	−9.6	−5.1
37	Box Elder, UT	41.388	−112.025	1,385	68.8	40.4	9.2	−8.4	−1.8
Common garden	Ada, ID	43.598	−116.162	847	33.5	18.1	10.3	−5.4	−0.4

were harvested from the same plants for the duration of the study. When insufficient tissue was available for processing, the next closest plant within the same population block was used. For the wildland source location of population 01, five plants separated by a minimum of 15 m were selected. Minimum and maximum daily actual and long-term average temperatures for the common garden location over the sampling period are shown in Figure S2 (National Climatic Data Center 2015). Long-term average precipitation and temperature profiles of the source locations and the common garden are shown in Figure S3 (PRISM 2018).

Representative healthy leaves were used for cold-hardiness evaluation. Leaves were harvested with greater than 5 cm of stem material attached, wrapped in distilled water-soaked paper towels, placed in a plastic zipper storage bag, transported in a cooler with buffered ice, and refrigerated at 2°C to help preserve the integrity of the tissues before processing. Samples were processed at the University of Idaho Center for

Forest Nursery and Seedling Research laboratory in Moscow, ID (46°43′31.9686″N, 116°57′20.4408″W) within 48 hours of collection.

Tissue collections were removed from the refrigerator in blocks (five plants at a time from the common garden, one plant from the source location), allowed to reach ambient temperature, double rinsed in distilled water to remove any external ions and debris, blotted dry with paper towels, and allowed to air dry. Once dry, 6.5 mm diameter leaf tissue discs were punched, avoiding leaf edges and main veins. When possible, one disc was sampled per leaf; however, depending on leaf size and available vegetative material, up to three discs per leaf were used. Each round of evaluation produced 30 replicates from 210 samples (7 test temperatures × 5 plants × 6 sources), with each sample consisting of five leaf discs. Leaf discs were placed in 20 mL wide-mouth scintillation copolymer plastic vials containing 2.5 mL distilled water and a grain of sand to promote ice nucleation and decrease surface tension. Airtight screw caps were placed on all vials and the vials were placed in the freezer at ambient temperature.

The experimental design examined tissue damage at a 5°C/hour rate of decrease (ramp) and 1-hour specific temperature hold. The freeze cycle duration was 14 hours 24 minutes, starting from ambient temperature and ramping down to the first test temperature in 1 hour 24 minutes, maintaining leaf integrity. Seven temperatures were tested: 2, −7, −14, −21, −28, −35, and −40°C. The 2°C temperature was considered a nonfreeze-induced damage control treatment. Freezing rate and temperature were controlled via a ScienTemp Lo-Cold programmable freezer (ScienTemp Corp., Adran, MI). As samples were removed from the freezer, they were allowed a gradual thaw in the 2°C refrigerator, then warmed to ambient temperature. Once warmed, 7.5 mL of distilled water was added to each of the vials, bringing the liquid volume to 10 mL. Samples were then shaken at a rate of 100 RPM for 1 hour. Solutions were measured for initial electrolyte (ion) leakage via electrical conductivity (EC) with a SevenEasy conductivity meter (Mettler Toledo, Columbus, OH). Samples were then autoclaved (Market Forge Sterilmatic, Vernon Hills, IL) at 121°C for 20 minutes, achieving 100% cell damage. Once cooled, vials were shaken at 100 RPM for 1 hour before final EC readings were taken.

Initial EC values were divided by post-autoclave EC values to calculate cell damage expressed through electrolyte leakage (%EL). Using the calculated %EL of the control treatments (2°C), the index of injury (IOI) was calculated to account for non-cold-induced tissue damage suffered during sample processing:

$$\begin{aligned}\mathrm{IOI} = \ & [(\%\mathrm{EL} - \mathrm{AVE\ Control}\%\mathrm{EL}) / \\ & (100 - \mathrm{AVE\ Control}\%\mathrm{EL})] * \ 100\end{aligned}$$

Using the calculated IOIs, nonlinear regressions were performed using R x64 3.1.2 (R Core Team 2015) statistical software, fitting three-parameter logistic sigmoidal functions for each plant at each time period, to derive a measure of cold hardiness expressed as LT_{50} for a given population at a given time. LT_{50} is the temperature at which 50% of total EL occurs (Jacobs et al. 2008).

In 2009 and 2010 (3 and 4 years after planting), flowering phenology (i.e. stalk elongation [>5 cm], floral bud formation, anther exertion, flowering [>50%], fruit development, and fruit maturation) was monitored for each population in the common garden. In 2010, monitoring began after plants had already begun to elongate, form floral buds, and exert anthers in some cases, so these three variables were excluded from the analysis.

Survival was assessed in 2007, 2008, and 2017 (i.e. 1, 2, and 11 years after planting). Due to high plant mortality as a result of errant plot maintenance, data from a single block of population 01 was excluded from the analysis ($n = 4$).

Three SAS software models were used to analyze the data (version 9.4; SAS Institute, Cary, NC) via PROC GLIMMIX). The LT_{50} models included the fixed effects of population and sampling date, as well as their interaction, with replicate included as a random effect. To compare LT_{50} of plants from population 01 growing in the common garden versus the source location at each sampling date, least square means were analyzed using *t* tests. Survivorship and flowering phenology models included the fixed effect of population. Treatment comparisons were evaluated at $\alpha = 0.05$ and adjusted for multiple comparisons as appropriate.

Results

Although seasonal cold-hardiness dynamics were comparable across populations, with annual fluctuations in mean LT_{50} exceeding 40°C (Fig. 2), values differed significantly among populations ($p = 0.0009$) and across sampling dates ($p < 0.0001$), with a significant interaction between the two main effects ($p = 0.0011$) (Table S1). For all populations, plants were in their most cold-hardy state in December 2013, with LT_{50} reaching −56 to −58°C and in their least cold-hardy state between April and May 2014, with LT_{50} ranging from −10 to −16°C (Table 2). Comparing populations within each sample date revealed a significant difference in LT_{50} among populations in March 2014 (Table 2; Fig. 3). During this spring sampling date, plants from all populations were deacclimating, but populations 36 and 37 remained significantly more cold hardy (to −45°C) than populations 13 and 25, which were hardy to temperatures of −34°C and −28°C, respectively. LT_{50} did not differ significantly among populations at any of the other sampling dates (Table 2; Fig. 3).

Further, across all populations, plants were significantly less cold hardy in October 2014 compared to October 2013 (Fig. 2). October 2013 was notably colder than October 2014, with mean daily maximum temperatures of 16.9 and 21.1°C and mean daily minimum temperatures of 3.3 and 8.0°C (Table S2). Correspondingly, LT_{50} ranged from −36 to −45°C across populations in October 2013 compared to −21 to −28°C in October 2014.

Analysis of LT_{50} values of common garden and wild-grown plants from population 01 revealed a significant interaction between the main effects of population (i.e. common-garden

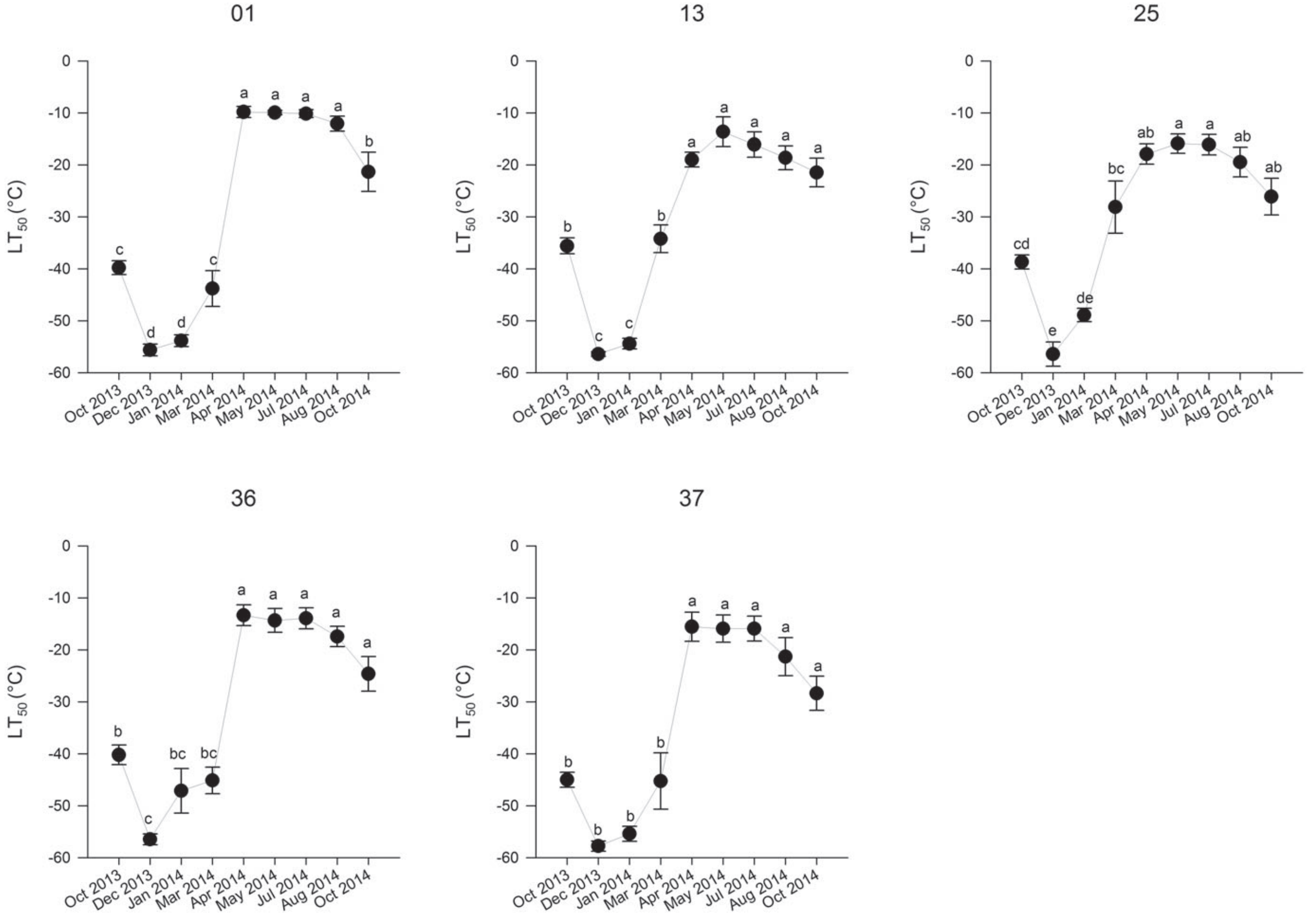

Figure 2. Mean (±SE) temperature (°C) at which 50% of electrolyte leakage occurred during cold-hardiness testing (i.e. LT$_{50}$) for sulfur-flower buckwheat populations across the 12-month sampling period. Within each population, mean values not sharing a letter differ significantly across sampling dates.

Table 2. Mean (±SE) temperature (°C) at which 50% of electrolyte leakage occurred during cold-hardiness testing (i.e., LT$_{50}$) for five sulfur-flower buckwheat populations grown in a common garden across nine sampling dates. Populations with significantly different LT$_{50}$ within a sampling date do not share a letter (March 2014 only).

Date	*Population 01*	*Population 13*	*Population 25*	*Population 36*	*Population 37*
October 2013	−39.79 (1.33)*A*	−35.61 (1.53)*A*	−38.71 (1.35)*A*	−40.22 (1.90)*A*	−45.00 (1.45)*A*
December 2013	−55.65 (1.12)*A*	−56.42 (0.43)*A*	−56.44 (2.36)*A*	−56.48 (1.05)*A*	−57.78 (0.98)*A*
January 2014	−53.85 (1.16)*A*	−54.43 (1.03)*A*	−48.91 (1.29)*A*	−47.13 (4.31)*A*	−55.40 (1.44)*A*
March 2014	−43.79 (3.44)*AB*	−34.25 (2.67)*BC*	−28.13 (5.02)*C*	−45.13 (2.57)*A*	−45.26 (5.42)*A*
April 2014	−9.83 (1.06)*A*	−19.01 (1.41)*A*	−17.93 (1.94)*A*	−13.35 (2.00)*A*	−15.57 (2.78)*A*
May 2014	−9.96 (0.42)*A*	−13.63 (2.87)*A*	−15.91 (1.86)*A*	−14.35 (2.29)*A*	−15.93 (2.61)*A*
July 2014	−10.14 (0.76)*A*	−16.09 (2.44)*A*	−16.12 (1.98)*A*	−13.93 (2.04)*A*	−15.93 (2.42)*A*
August 2014	−12.07 (1.43)*A*	−18.65 (2.29)*A*	−19.48 (2.84)*A*	−17.45 (1.96)*A*	−21.32 (3.66)*A*
October 2014	−21.34 (3.78)*A*	−21.49 (2.74)*A*	−26.12 (3.52)*A*	−24.64 (3.34)*A*	−28.38 (3.29)*A*

vs wild-grown) and sampling date ($p < 0.0001$) (Table S3). Although the range of LT$_{50}$ was similar for common garden- and wild-grown plants, wild-grown plants acclimated and deacclimated earlier than common garden-grown plants (Table S4; Fig. 4).

Flowering phenology also differed across populations ($p < 0.0001$ for all variables examined in 2009 and 2010; Fig. 5). High-elevation populations (i.e. 25 and 36) presented significantly earlier flowering phenology compared to other populations, while across variables, low-elevation population 13 developed significantly later in the season compared to other populations.

Survival differed significantly across sulfur-flower buckwheat populations each year ($p < 0.0001$ for 2007 and 2008 and $p = 0.0006$ for 2017; Fig. 6). Across years, survival was lowest for population 25 (with 75, 74, and 54% survival 1, 2,

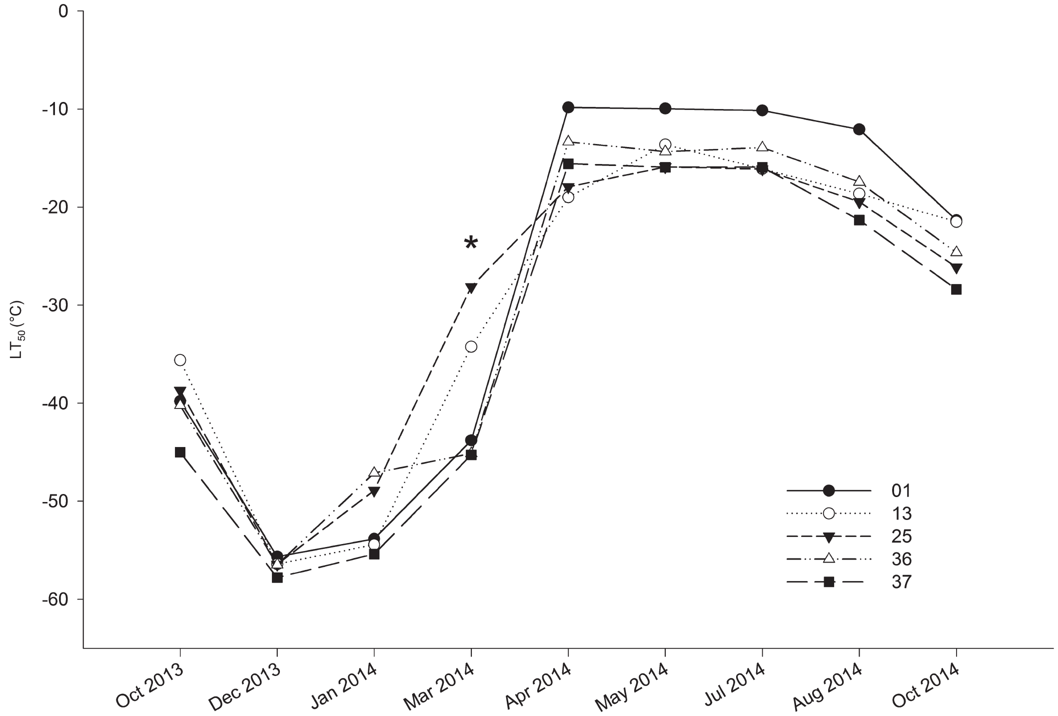

Figure 3. Mean temperature (°C) at which 50% of electrolyte leakage occurred during cold-hardiness testing (i.e. LT$_{50}$) for sulfur-flower buckwheat populations across nine sampling dates. Significant differences among populations at a given date are indicated with an asterisk.

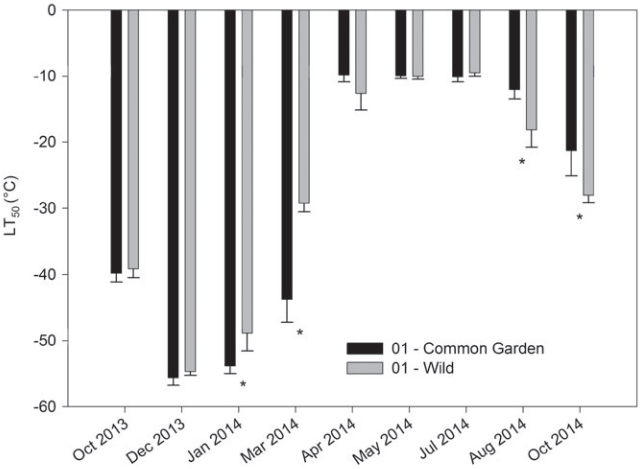

Figure 4. Mean (−SE) temperature (°C) at which 50% of electrolyte leakage occurred during cold-hardiness testing (i.e. LT$_{50}$) for common garden- and wild-grown sulfur-flower buckwheat plants from population 01 across nine sampling dates. Significant differences are indicated with an asterisk.

and 11 years in the common garden) and was greatest for population 13 (with 98, 96, and 87% survival 1, 2, and 11 years in the common garden). For all populations, survival was significantly lower in 2017 compared to 2007 and 2008 ($p = 0.0238$ for 01; $p = 0.0070$ for 13; $p = 0.0002$ for 25; $p = 0.0022$ for 36; and $p = 0.0019$ for 37).

Discussion

Tracking five geographically distinct populations of sulfur-flower buckwheat in a common garden revealed patterns of seasonal cold-hardiness dynamics and flowering phenology that have implications for plant material selection and movement. Results showed that sulfur-flower buckwheat populations have considerable capacity to respond to local (i.e. common garden) conditions regarding cold-hardiness dynamics; however, timing of deacclimation and flowering phenology varied across populations grown in a common garden, which had implications for plant survival.

The risk of cold injury is highest when plants are actively growing and hard frosts are likely. Earlier leafing out and development have been linked to more frequent and more serious frost damage (Price & Waser 1998; Inouye et al. 2002), resulting in decreased survival. Therefore, most damage results from late spring frosts when plants are resuming growth, or less commonly from early fall frosts around the time of growth cessation (Cannell et al. 1985; Timmis et al. 1994). By adjusting cold hardiness and flowering phenology along elevation gradients, plants avoid damage from freezing temperatures (Lenz et al. 2013), irrespective of their elevation of origin (Vitasse et al. 2013).

Generally, common garden experiments have shown that populations from high elevations develop earlier than those from low elevations (Worrall 1983; Von Wuehlisch et al. 1995; Acevedo-Rodriguez et al. 2006). Populations from high elevations may require fewer forcing hours and thus may be at a

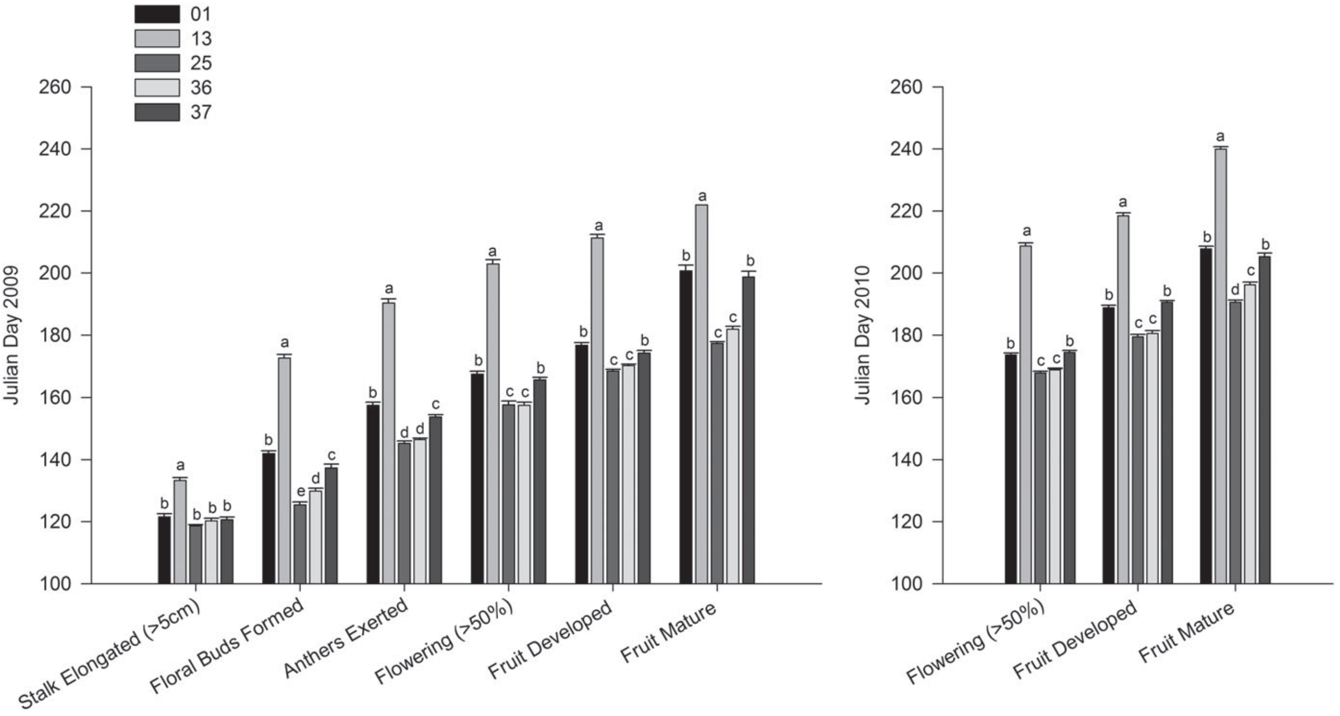

Figure 5. Flowering phenology (mean + SE; $n = 50$) of five sulfur-flower buckwheat populations grown in a common garden. Populations with significantly different phenology for a given variable do not share a letter.

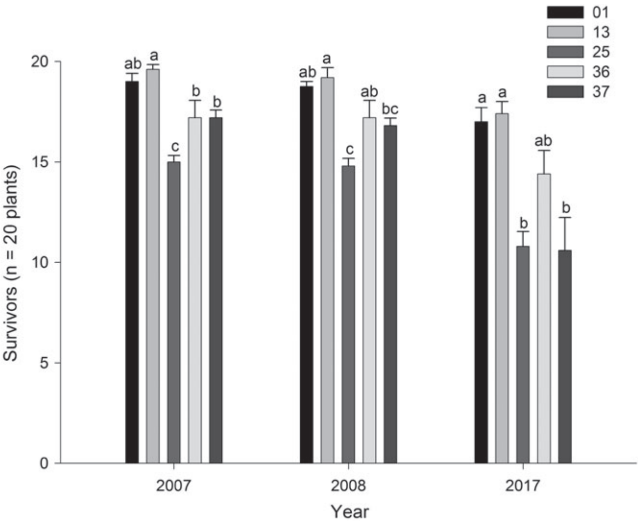

Figure 6. Survivorship (mean + SE; $n = 5$) across five sulfur-flower buckwheat populations grown in a common garden. Populations with significantly different survivorship for a given year do not share a letter.

selective disadvantage because they are more susceptible to late spring frosts, as was the case for our study in which populations 25 and 36 from higher elevations exhibited earlier flowering phenology compared to population 13 sourced from a much lower elevation. Despite a higher risk of spring cold injury, earlier regrowth in the spring may be a mechanism to allow populations at high elevations to fully use the relatively short growing season (Sagnard et al. 2002). Spring frost damage due to early deacclimation considerably affects a plant's fitness and reduces its yearly growth (Leinonen & Hanninen 2002). It is possible that early deacclimation and flowering phenology of population 25 in the spring left plants vulnerable to cold damage, causing greater cold injury and ultimately higher mortality. This hypothesis is supported by the survival data in that population 25 had significantly lower survival rates than other populations. If and how quickly plants can reacclimate in response to unfavorable temperatures is an important parameter that remains to be explored (Kalberer et al. 2007; Pagter & Williams 2011). Genecological approaches are needed to examine genetic variation in these adaptive traits and explore how they correlate with source climates, particularly temperature, aridity, and photoperiod (Harrington et al. 2010; Gould et al. 2011; St. Clair et al. 2013).

Population differences in deacclimation timing in March 2014, as indicated by greater LT_{50} for populations 25 (−28°C) and 13 (−34°C) compared to populations 36 (−45°C) and 37 (−45°C) suggest that lengthening the growing season could be a more important driving force in adaptation than avoidance of spring cold injury. Not only do these results highlight the importance of matching phenology to the climate of the particular restoration site, but they also have implications for how populations may respond to climate change. Sagebrush steppe ecosystems rely on winter snowfall and spring runoff for moisture, and in much of the region overall warming is predicted to increase the proportion of cool-season rainfall at the expense of snowpack (Chambers 2008; Mote et al. 2013). Previous research found that the timing of snowmelt had a greater impact on sulfur-flower buckwheat phenology than did temperature (Sherwood et al. 2017). Further research to understand how additional life history traits of this species correlate with seasonal cold-hardiness dynamics will help to more accurately predict its future distribution and will better inform the appropriate selection and movement of plant material for ecological restoration and assisted migration.

Nonetheless, our results provide evidence that populations have considerable capacity to respond to local (i.e. common garden) conditions with regard to cold-hardiness dynamics. Phenotypic plasticity in cold hardiness was not observed in red alder (*Alnus rubra* Bong.; Porter et al. 2013) or western white pine (*Pinus monticola* Douglas ex D. Don; Thomas & Lester 1992). In our study, evidence of plasticity was found when comparing LT_{50} of population 01 grown in the common garden to that of the source location. Although the range of LT_{50} was similar for common garden- and wild-grown plants, wild-grown plants acclimated and deacclimated earlier than common garden-grown plants, evidence that plants adjusted their cold hardiness to specific site conditions. Further, plants across all populations were significantly less cold hardy in October 2014 compared to October 2013, which was notably colder than October 2014.

High-elevation environments impose particularly severe constraints on plant establishment and influence phenology, owing to the short growing season, low temperatures, and persistence of snow cover (Körner 2007; Premoli et al. 2007). Although largely driven by temperature and precipitation, snow persistence on these dry, open, rocky sites that sulfur-flower buckwheat occupies is highly influenced by wind, slope, aspect, and microtopography. Populations 13 and 25 are separated by 1,000 m in elevation; thus, it is likely that the type of precipitation may affect the phenological differences between these populations. Since we do not have sufficient climate data at the population source it is difficult to interpret these differences. In addition to temperature and precipitation, there is a need to determine whether other variables, including snow depth and duration as well as pollinator life-history, affect establishment success and phenology of sulfur-flower buckwheat populations.

Plant tissues such as buds, stems, leaves, and roots differ in cold hardiness and further investigation of these differences may prove crucial. For instance, deciduous broad-leaved trees generally exhibit freezing resistance ranging from −15 to −25°C in roots, from −25 to −35°C in shoot buds, and from −30 to −50°C in twigs and stems (Flint 1972; Larcher 2005; Körner 2012). With additional cold-hardiness investigations, assessment of overall cold hardiness across all tissue types may be beneficial (Aitken & Adams 1996). Roots may be most susceptible to frost damage, particularly with reductions in the insulating snow cover in response to climate change (Groffman et al. 2001; Schaberg et al. 2008). Additionally, greater measurement resolution, particularly in the spring and fall may capture fine scale differences in cold-hardiness dynamics among populations that may have been undetected in this study.

Our study provides evidence of adaptive differences among a small sample of sulfur-flower buckwheat populations. Although sample size precludes a meaningful correlation analysis of cold hardiness, flowering phenology, and survival with different climate variables, trends in our data suggest that climatic differences among source locations influence phenology. Populations observed to deacclimate earliest (13 and 25) were sourced from locations that were both warmest (13) and coldest (25) of the locations assessed; thus, while natural selection for cold hardiness may be hypothesized to be a function of cold temperatures in the fall, winter, or early spring, there is no evidence of this in our study. Interestingly, both early-deacclimating populations were sourced from locations receiving the least amount of precipitation (both overall and during the growing season), suggesting that natural selection for early deacclimation may be a function of drought avoidance. Both populations with the earliest flowering phenology (25 and 36) were sourced from the coldest locations, providing evidence that they may require fewer forcing hours and flower quickly once conditions become favorable. There is no evidence that flowering phenology is driven by drought in that these populations were sourced from locations receiving among the most (36) and least (25) precipitation of the study. Future research with the requisite data and sample size to facilitate hypothesis testing will improve our understanding of the relative roles of temperature (chilling and forcing), photoperiod, and drought on phenology of this species.

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Supporting Information

The following information may be found in the online version of this article:

Table S1. Type III tests of fixed effects from analysis of variance of LT_{50} among five sulfur-flower buckwheat populations grown in a common garden across nine sampling dates (df = degrees of freedom).

Table S2. Boise, ID sulfur-flower buckwheat common garden average, low, and high daily temperature maximum and minimum in October 2013 and October 2014.

Table S3. Type III tests of fixed effects from analysis of variance of LT_{50} between common garden- and wild-grown sulfur-flower buckwheat plants from population 01 across nine sampling dates (df = degrees of freedom).

Table S4. Mean (±SE) temperature (°C) at which 50% of electrolyte leakage occurred during cold-hardiness testing (i.e. LT_{50}) for population 01 sulfur-flower buckwheat plants grown in the common garden and in the wild.

Figure S1. Flow diagram detailing the steps involved from sample collection through estimation of the temperature (°C) at which 50% of electrolyte leakage occurred during cold-hardiness testing (i.e. LT_{50}) for five sulfur-flower buckwheat populations grown in a common garden across nine sampling dates.

Figure S2. Boise, ID sulfur-flower buckwheat common garden daily temperature maximum and minimum expressed over 30-year daily averages (1981–2010; PRISM 2018).

Figure S3. Temperature and precipitation of source locations for five sulfur-flower buckwheat populations and the common garden location based upon 30-year averages (1981–2010; National Climatic Data Center 2015).

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