RESEARCH ARTICLE

Role of Temperature and Moisture in the Survival and Seedling Physiology of a Great Basin Perennial

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ABSTRACT

Munro's globemallow (*Sphaeralcea munroana*) is an important constituent of Great Basin communities and is commonly used in restoration; however, little is known about the influence of environmental conditions on early plant establishment. The objective of this study was to evaluate the response of Munro's globemallow to a suite of temperature and moisture conditions directly following germination. In addition, this work provides a rare insight into the physiology and development of this arid land species following germination. Our results indicate that temperature influences plant growth immediately after germination more than available moisture. In a growth chamber study, germinants subject to colder temperatures (17/3°C) had 53% fewer leaves, 78% lower leaf area, and less aboveground and belowground biomass (71 and 72 %, respectively) than their cohorts grown at 23/9°C. Decreasing irrigation frequency favored biomass allocation to the roots and a subsequent increase in root-to-shoot ratios. Neither temperature nor moisture had an influence on gas exchange. This evidence suggests that although this perennial forb shows considerable potential for restoration on arid sites, it may not be the best candidate for early competition with cool season grasses during its establishment phase. Because growth is hindered by cool temperatures, a later sowing date may improve establishment in nurseries, seed production areas, and restoration sites.

Keywords: gas exchange, germination, Munro's globemallow, perennial forb, restoration

The Great Basin ecosystem of North America has undergone significant disturbance and fragmentation due to overgrazing, shrub removal, and non-native species introduction over the past century (Mack 1981). Fire suppression and the aggressive spread of cheatgrass (*Bromus tectorum*) have been linked to a rapid increase in fire frequency, promoting extensive ecosystem conversion from sagebrush-dominated systems to annual grass communities. This has caused a change in available soil moisture, nutrient capital, and resource competition, further suppressing native plant establishment (D'Antonio and Vitousek 1992, Evans et al. 2001, Obrist et al. 2003). The current rate of habitat loss greatly surpasses system recovery, jeopardizing the populations of sagebrush-steppe animal obligates such as pygmy rabbit (*Brachylagus idahoensis*), Greater Sage-grouse (*Centrocercus urophasianus*), Brewer's Sparrow (*Spizella breweri*), as well as numerous pollinators (Gathmann and Tscharntke 2002, Walker 2004, Shipley et al. 2006, Gregg et al. 2008).

The use of endemic plant species in restoration is critical in promoting ecological recovery in this region. Seedling establishment is the most vulnerable stage in plant community development, especially in regions with restrictive growing conditions (Call and Roundy 1991). Wide diurnal temperature fluctuations, episodic precipitation pulses, and extensive droughts present major limitations to post-germination survival. Seedlings are more susceptible to environmental fluxes than mature plants because the maximum temperature and soil moisture changes occur in close proximity to the soil surface (Raynal and Bazzaz 1973, Regehr and Bazzaz 1976).

In the Great Basin, diurnal temperatures can fluctuate by 20°C (Smith and Nowak 1990), in part due to topographically-induced formation of nocturnal cold air drainage throughout the year (Osmond et al. 1990). The Great Basin-Mojave region has been characterized as the most arid habitat in North America, with precipitation averaging 50 to 300 mm annually. The potential evapotranspiration in this region is high, ranging between 1100 mm in the northern and 2000 mm in the southern portion of the basin (Flaschka et al. 1987). On an inter-annual basis, summer precipitation is highly variable, typically representing only 20 to 30% of total annual precipitation (Bell 1979). A substantial portion of available moisture is lost

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by the time air and soil temperatures are suitable for plants to become fully physiologically active, thus creating a strong disparity between maximum water availability and the ability of plants to use it (Caldwell 1985). For example, despite its abundance, winter precipitation may not be used during a considerable portion of the year as a result of cold temperatures, which create a reduction in the physiological plant activity. Moreover, in early spring, substantial moisture loss can occur via sublimation and evaporation. Therefore, the beginning of the growing season is directly correlated with the amount of winter-spring precipitation and the increase in air and soil temperatures (Turner and Randall 1987). The seasonal reduction in rainfall further enhances the importance of the cool spring growing season. As a result, most species initiate growth in March and April, when maximum daily temperatures range from 5°C to 18°C and night temperatures remain near freezing (Comstock and Ehleringer 1992, Parkinson 2008). At the soil surface, especially on sites where recent disturbance has considerably reduced the presence of plant cover, diurnal temperature differences are more pronounced. Clearly, the interaction between precipitation and temperature patterns bear considerable implications on the physiological ecology of the native flora.

One important constituent of Great Basin plant communities is Munro's globemallow (*Sphaeralcea munroana*). This endemic, perennial forb provides soil stabilization and is a source of nutrition for myriad animals (Beale and Smith 1970, Pendery and Rumbaugh 1986, Rumbaugh et al. 1993, Cane 2008). For these reasons, as well as its ability to tolerate disturbed sites, drought, and extreme temperatures, it is an important candidate for broad-scale restoration across its range. While native plants are fundamental in maintaining ecosystem function, the use of forbs in restoration is relatively recent and warrants exploration (Parkinson 2008). Little is known about the range of tolerance to environmental conditions that allows for successful establishment and growth of Munro's globemallow. Thus, our study objective was to evaluate the seedling morphological and physiological response to a suite of temperature and moisture conditions during germination and establishment in order to better inform restoration of this species.

Table 1. Location coordinates, elevation, and dates of Munro's globemallow (*Sphaeralcea munroana*) seed collections made throughout Oregon and Idaho, USA.

Location	Elevation (m)	Collection Date	State
N 43° 45.799′ W 117° 07.850′	779	04 June 2010	OR
N 43° 46.156′ W 117° 19.090′	749	06 June 2010	OR
N 43° 13.010′ W 119° 00.267′	1302	20 June 2010	OR
N 43° 47.356′ W 117° 37.859′	899	22 June 2010	OR
N 43° 52.827′ W 116° 47,030′	811	08 July 2010	ID

Methods

We collected seeds of Munro's globemallow from five locations throughout Oregon and Idaho, which were then bulked into a single seedlot (Table 1). To break physical seed dormancy, necessary for germination, seeds were scarified with a scalpel (Kildisheva et al. 2011), and were sown into 66 ml containers (Model RLC4, Stuewe and Sons, Inc., Tangent, OR). We augmented containers with mesh liners to prevent media loss, filled them with autoclaved sand, and placed them into four environmental growth chambers (Model E-30B, Percival Scientific, Inc., Perry, IA). Chambers were set to a 24/17°C diurnal cycle (8-hour day/16-hour night (Sabo et al. 1979). Seedlings were thinned to one plant per container 10 days after sowing (DAS) and randomly assigned to a temperature and moisture treatment. At this point, a one-time application of 18-24-16 (N-P-K) solution of fertilizer (Water Soluble Rose Plant Food, Scotts Co., Marysville, OH) was administered to all containers at a rate of 3.8 mg N per plant.

Prior to the start of the experiment, we obtained climate records from 1950 through 2010 for April, the usual germination time for Munro's globemallow (Parkinson 2008), using PRISM Data Explorer (prism-map.nacse.org/nn/) for each seed collection site coordinate and attained a mean diurnal temperature across sites. The resultant regime was 17/3°C (day/night), which was selected as one of the treatments. Using the same method, we calculated the average diurnal temperature increase between early and late spring temperatures for the seed collection sites, a time-frame during which most forb seeds germinate or are sown in the field, to obtain the second temperature treatment of 23/9°C (day/night). The diurnal transition followed a 13-hour day and an 11-hour night. Irradiance was set to 950 µmol $m^{-2}s^{-1}$. Relative humidity was ambient and ranged between 50 and 60%. Within each chamber, we subjected plants to one of the four moisture availability treatments (3-, 6-, 9- and 12-day intervals between recharging each container to saturation). Each temperature × moisture combination was randomly assigned 20 seedlings. Containers were subirrigated by placing them into deionized water for one hour. To mitigate the effects of environmental heterogeneity within chambers (Lee and Rawlings 1982), plants were randomized every three days. We attained between-chamber replication by repeating the study over two distinct time periods.

We conducted an assessment of mortality, physiological, and morphological parameters at the end of the 25-day period (35 DAS). For the purpose of uniformity, five seedlings from each temperature × moisture regime were randomly selected for physiological and morphological measurements.

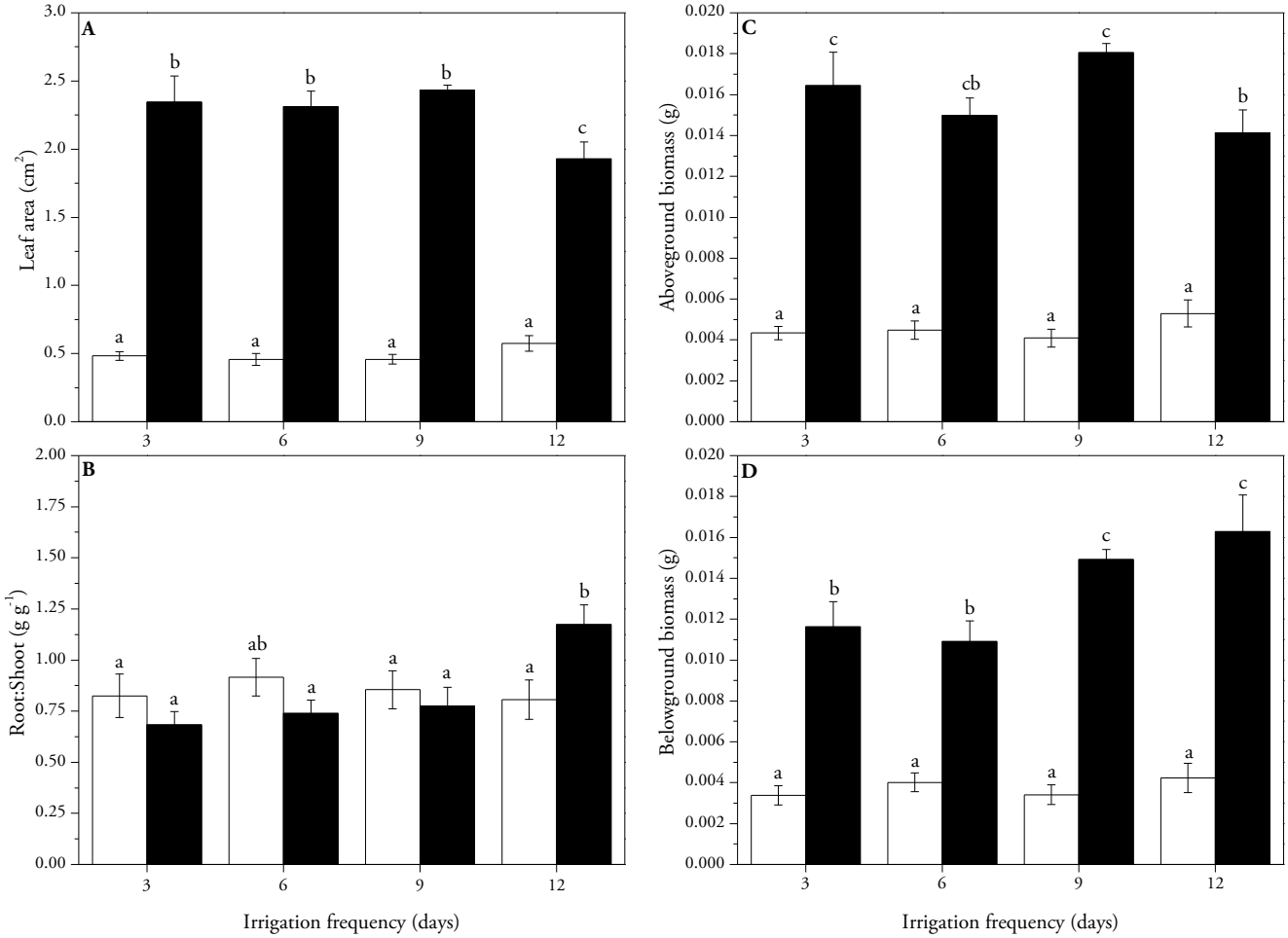

Figure 1. Interaction effects of temperature × moisture on (A) total leaf area, (B) root-to-shoot ratio, (C) aboveground, and (D) belowground biomass produced by Munro's globemallow (*Sphaeralcea munroana*) seedlings 35 days after sowing in response to two temperature × four moisture regimes. White bars represent the response of seedlings grown under the 17/3 °C, black bars denote seedling response to the 23/9 °C diurnal temperature regime. Each bar represents the mean response (±SE) of five replicates. Different letters indicate significant ($p < 0.05$) differences among treatments.

Gas exchange rates (i.e. photosynthesis, stomatal conductance, and transpiration) were evaluated within four hours of light period initiation using an LI-6400 Portable Photosynthesis System (Li-Cor, Inc., Lincoln, NE). Plants were gently removed from containers and separated by tissue type (i.e. root, shoot) from which we obtained the number of true leaves and leaf area using a flatbed scanner and the public domain image analysis program (ImageJ v. 1.17y rsb.info.nih.gov/ij/). Plant tissues were dried at 80°C for 24 hours, following which the above- and belowground biomass as well as the root-to-shoot ratios (R:S) were calculated. The cumulative plant mortality for each treatment was recorded upon the termination of the experiment.

We used a split-plot design with two temperature regimes (whole-plot) and four moisture levels (sub-plot), where individual growth chambers were treated as blocks and moisture treatments were completely randomized within chambers. We used a mixed effects model (PROC MIXED) to test the main effects of temperature and moisture by nesting the block (chamber) within temperature. The testing period was not a significant variable, and was thus eliminated from the analysis. Pair-wise comparisons (a = 0.05) of the least square mean estimates (LSMEANS) were made for all temperature, moisture, and temperature × moisture interactions. Statistical analysis was conducted with SAS (SAS v. 9.2, SAS Institute Inc., Cary, NC).

Results

Leaf area, R:S, above- and belowground biomass were significantly influenced by the temperature × moisture interaction (Table 2; Figure 1A–D). This interaction was largely driven by temperature, with less plant development and biomass production under cooler conditions (Table 3). At 17/3°C these parameters remained statistically similar, irrelevant of moisture availability. However, we saw significant treatment differences in these factors under the warmer growing conditions (23/9°C). Leaf area decreased significantly relative to more frequent (≤ 9 days) irrigation (Figure 1A). This relationship was not as strong for the aboveground biomass, as plants grown

Table 2. Results of the mixed model analysis for the effects of temperature, moisture, and their interaction on the morphological and physiological responses of Munro's globemallow seedlings 35 days after sowing.

Source of Variation	Temperature	Moisture	Temperature × Moisture
Mortality	$F_{1,6}$=0.23; *P*=0.6515	$F_{3,18}$=1.62; *P*=0.2202	$F_{3,18}$=1.33; *P*=0.2948
True leaf number	$F_{1,6}$=18.38; ***P*=0.0052**	$F_{3,18}$=2.28; *P*=0.0817	$F_{3,18}$=2.19; *P*=0.0915
Leaf area	$F_{1,6}$=47.72; ***P*=0.0005**	$F_{3,18}$=1.87; *P*=0.1370	$F_{3,18}$=4.98; ***P*=0.0027**
Aboveground biomass	$F_{1,6}$=31.90; ***P*=0.0013**	$F_{3,18}$=1.27; *P*=0.2878	$F_{3,18}$=3.66; ***P*=0.0140**
Belowground biomass	$F_{1,6}$= 16.98; ***P*=0.0062**	$F_{3,18}$=3.78; ***P*=0.0127**	$F_{3,18}$=3.15; ***P*=0.0268**
Root:Shoot	$F_{1,6}$=0.01; *P*=0.9416	$F_{3,18}$=3.02; ***P*=0.0317**	$F_{3,18}$=4.77; ***P*=0.0034**
Photosynthesis	$F_{1,6}$=5.09; *P*=0.0649	$F_{3,18}$=0.67; *P*=0.5699	$F_{3,18}$=0.30; *P*=0.8260
Transpiration	$F_{1,6}$= 2.80; *P*=0.1450	$F_{3,18}$=2.09; *P*=0.1041	$F_{3,18}$=0.01; *P*=0.9977
Conductance	$F_{1,6}$= 1.36; *P*=0.2872	$F_{3,18}$=2.40; *P*=0.0706	$F_{3,18}$=0.21; *P*=0.8899

under a 6-day irrigation interval exhibited a similar response as their cohorts subjected to the driest regime (0.015 and 0.014 g, respectively) (Figure 1C). Seedlings grown under the two most moisture-limited conditions (9- and 12-day irrigation intervals) produced the most (p = 0.0268) belowground biomass (Figure 1D). Finally, seedlings grown at the 12-day irrigation interval at (23/9°C) produced the highest R:S (1.17) compared to all treatment combinations excluding the 17/3°C (6-day irrigation interval) treatment, which also produced a high mean R:S (0.92), but was not statistically different (p > 0.05) from any of the moisture × temperature treatment combinations (Figure 1B). Within the significant temperature × moisture interaction (Table 2), temperature was the primary driver of change for leaf area and aboveground biomass (p = 0.0005 and p = 0.0013, respectively) while moisture availability was responsible for changes in R:S (p = 0.0317). Both temperature and moisture contributed (p = 0.0062 and p = 0.0127, respectively) to the belowground biomass production of seedlings in response to the different temperature × moisture treatments. Seedlings grown at 17/3°C produced fewer true leaves (1.4 ± 0.3) than those grown at 23/9°C, (2.9 ± 0.3).

Plant mortality, photosynthesis, conductance, and transpiration did not differ significantly between the temperature × moisture treatment combinations (Table 2). Mortality ranged between 3.5 and 7.5 seedlings per treatment at the end of the experimental period. Because the gas exchange values for Munro's globemallow have not been previously presented, they are included as Table 4.

Discussion

Our study suggests that following germination of scarified seeds, Munro's globemallow seedlings are relatively resilient to temperature increases and moisture fluctuations. In general, the imposed average April temperatures and moisture availability regimes applied in this study did not induce extensive seedling mortality. However, short-term resilience is not necessarily indicative of long-term persistence. Because plant development was influenced by temperature differences, it is possible that survivorship may differ during the course of an entire growing season (Everett et al. 1980, Parkinson et al. 2013). Due to the brevity of the period suitable for growth in the Great Basin, plants must establish adequate root systems early in the season as available water shifts downwards in the

Table 3. Morphological responses of Munro's globemallow seedlings to growth under two temperature × four moisture regimes 35 days after sowing. Different letters indicate significant (p < 0.05) differences among treatments.

	Temperature	Irrigation frequency (days)			
	(°C)	3	6	9	12
Mortality	**17/3**	7.50±3.8^{a}	6.50±3.3^{a}	6.75±3.3^{a}	7.0±4.6^{a}
	23/9	6.50±1.0^{a}	6.25±1.3^{a}	4.25±1.1^{a}	3.5±1.2^{a}
True leaf number	**17/3**	1.50±0.1^{a}	1.40±0.1^{a}	1.40±0.1^{a}	1.3±0.1^{a}
	23/9	2.80±0.2^{b}	3.10±0.2^{b}	3.20±0.2^{b}	2.8±0.2^{b}
Leaf area (cm^2)	**17/3**	0.48±0.0^{a}	0.46±0.0^{a}	0.46±0.0^{a}	0.57±0.2^{a}
	23/9	2.30±0.2^{b}	2.30±0.1^{b}	2.40±0.0^{b}	1.9±0.1^{c}
Aboveground biomass (g)	**17/3**	0.004±0.0^{a}	0.004±0.0^{a}	0.004±0.0^{a}	0.005±0.0^{a}
	23/9	0.02±0.0^{c}	0.015±0.0^{cb}	0.02±0.0^{c}	0.01±0.0^{b}
Belowground biomass (g)	**17/3**	0.003±0.0^{a}	0.004±0.0^{a}	0.003±0.0^{a}	0.004±0.0^{a}
	23/9	0.01±0.0^{b}	0.01±0.0^{b}	0.02±0.0^{c}	0.02±0.0^{c}
Root:Shoot (g g^{-1})	**17/3**	0.83±0.1^{a}	0.92±0.1^{ab}	0.85±0.1^{a}	0.81±0.1^{a}
	23/9	0.68±0.1^{b}	0.74±0.1^{b}	0.77±0.1^{b}	1.17±0.1^{c}

Table 4. Gas exchange responses of Munro's globemallow seedling growth under two temperature and four moisture regimes. Variation in photosynthesis rate (mol CO_2 $m^{-2}s^{-1}$), stomatal conductance (mol $m^{-2}s^{-1}$), and transpiration (mmol $m^{-2}s^{-1}$) were measured 35 days after sowing. None of the values are significantly different between or within columns ($p < 0.05$).

Irrigation Frequency (days)	Photosynthesis (mol CO_2 $m^{-2}s^{-1}$)		Conductance (mol $m^{-2}s^{-1}$)		Transpiration (mmol $m^{-2}s^{-1}$)	
	17/3 °C	23/9 °C	17/3 °C	23/9 °C	17/3 °C	23/9 °C
3	13.12±1.27	8.90±0.65	0.21±0.02	0.18±0.03	0.004±0.0006	0.003±0.0003
6	13.18±1.75	8.23±0.68	0.19±0.03	0.15±0.02	0.004±0.0007	0.003±0.0003
9	12.27±1.44	9.07±0.86	0.19±0.03	0.16±0.02	0.004±0.0006	0.003±0.0003
12	10.95±1.86	7.97±0.85	0.16±0.03	0.10±0.02	0.003±0.0006	0.002±0.0003

soil profile, in order to ensure survival prior to entering mid-summer dormancy (Fernadez and Caldwell 1975, Smith et al. 1997). Evidence suggests that in cold deserts, herbaceous perennial phenology can be compressed or expanded on an interannual basis in correlation with temperature and precipitation patterns (Everett et al. 1980, Ogle and Reynolds 2004). Thus, further research focused on the relation of Munro's globemallow seedling growth rates early in the season to subsequent phenology and survival in the Great Basin is necessary.

Our results suggest that the combined influence of warmer temperature and limited moisture reduced aboveground biomass production. Lei (1999) presented analogous findings exhibited by herbaceous perennials (including *Sphaeralcea* sp.) in the Mojave Desert, which reduced their aboveground biomass in response to the inter-annual reduction in winter and spring precipitation. Similarly, the absence of a significant gas exchange response in our experiment suggests that seedlings were able to curtail moisture demands by reducing their transpirational surface area, as opposed to decreasing stomatal conductance. In addition, the decline in moisture availability encouraged root production in the two most water-limited treatments (9- and 12-day irrigation interval). Higher temperatures amplified the effects of moisture deficit, inducing the highest belowground biomass production under the warmer, drier conditions. The R:S values ranged from 0.68 to 1.17, which correspond to those reported for a number of mature Great Basin perennials (Caldwell et al. 1977), and may further increase later in the growing season as plants strive to acquire water from increasingly lower portions of the soil profile (Smith et al. 1997).

While seedling gas exchange was not influenced by the imposed treatments, the net photosynthetic assimilation values were similar to those observed in several Great Basin woody perennials (Caldwell et al. 1977). It is possible that over the course of the growing season continued moisture and temperature stresses would result in differences in seedling gas exchange (Link et al. 1994, Huxman et al. 2004). Under the tested conditions, temperature was the single largest driver of plant behavior. Although moisture limitations are likely to become more pronounced later in the growing season, moisture alone did not elicit a strong physiological and morphological response during initial seedling establishment. Low temperatures impeded plant growth, presumably through the reduction in belowground biomass (McMichael and Burke 1998). Root growth was driven by both moisture availability and temperature, but under cool edaphic conditions the temperature influence tended to supersede the role of moisture. The warmest, driest conditions curtailed aboveground biomass production and increased growth belowground, without affecting gas exchange rates. This implies that seedlings of Munro's globemallow are reasonably drought tolerant even during early development. Because cool night temperatures pose a stricter growth limitation than moisture, sowing at a time when diurnal temperatures corresponds more closely with the 23/9°C regime may optimize the establishment of Munro's globemallow, when seed dormancy is alleviated.

In the Great Basin, the use of endemic forbs in seeding mixes aims to improve community composition and reduce the spread of cheatgrass. This cool-season annual grass is able to initiate growth at low temperatures in late winter or early spring and to maintain a higher root and shoot relative growth rate compared to native flora, making it an aggressive colonizer (Aguirre and Johnson 1991, Arredondo et al. 1998). As a result, effective completion in stands with existing cheatgrass can only be achieved by species with a high cold temperature threshold for growth and development (Parkinson 2013). From this work, it is evident that the growth rate and development of Munro's globemallow is significantly reduced by cooler temperatures, making it a sub-optimal early spring competitor with cheatgrass. Once established, however, it seems that the species is able to persist in the presence of cheatgrass with only partial reduction in biomass (Parkinson et al 2013). Furthermore, its drought tolerance during early development makes Munro's globemallow suitable for arid land restoration and a valuable component in seed mixes.

Conclusions

The difficulty and expense associated with restoring degraded lands in the Great Basin warrants a more

physiologically and phenologically minded approach to native plant selection in order to effectively reduce the spread of invasive species and strengthen floral community resilience. To date, Great Basin shrubs and grasses have been the focus of plant research; however, considering the ecological importance of forbs, their successful use in restoration requires a thorough understanding of their establishment behavior. Munro's globemallow shows considerable potential for restoration use on arid sites, but is negatively affected by low temperatures, which could make it a poor competitor with cool season grasses during the establishment phase. To ameliorate this, a later sowing date may improve establishment in nurseries, seed production areas, and on restoration sites.

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