Restoration Potentials and Challenges for *Sphaeralcea munroana*

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Abstract: Munro's globemallow (*Sphaeralcea munroana* [Douglas] Spach) is an herbaceous perennial and an important candidate for use in restoration due to its ecological significance and environmental resilience. The species' popularity among growers and land managers has recently increased but there is still a lack of information regarding seed dormancy and early seedling physiology, making the effective use of the species difficult. This paper provides a review of existing literature on S. *munroana's* habitat, restoration potential, seed dormancy, and seedling physiology.

Keywords: Physical dormancy, physiological dormancy, Munro's globemallow, Great Basin, seedling physiology, Malvaceae

Introduction

The arid-steppe of North America's Great Basin (Figure 1) is delineated by the Colorado and Columbia Plateaus, the Sierra Nevada Mountains, and the Mojave Desert. The region's unique geomorphology has a considerable effect on the climate, which is dominated by temperature extremes and low, primarily winter, precipitation (Knapp 1996). The vegetative communities of this area are characterized by the presence of shrubs, perennial bunchgrasses, and forbs (Holmgren 1972).

As an ecological unit, the Great Basin has suffered from substantial disturbance and fragmentation as a result of overgrazing, shrub removal, and non-native plant introduction (Mack 1981). Natural fire suppression over several decades and the rampant spread of cheatgrass (Bromus tectorum L.) have been linked to a 4 to 10 fold increase in fire incidence in the course of the last century (D'Antonio and Vitousek 1992). Frequent fires have promoted a widespread system conversion from sagebrush- to annual grass-dominated communities, which has reduced the available soil moisture, contributed to nutrient depletion, and increased resource competition (Billings 1990;Whisenant 1990; D'Antonio and Vitousek 1992; Obrist and others 2003). By recent estimates, the rate of habitat loss significantly exceeds the rate of ecosystem recovery, further threatening the populations of sagebrush-steppe obligates (i.e. pygmy rabbit, greater sage-grouse, and Brewer's sparrow) (Wisdom and others 2005; Parkinson 2008). In addition, the predicted rise in CO2 has been projected to enhance biomass production of C3 annual grasses, which could further exacerbate ecosystem conversion (Smith and others 1987; Smith and others 2000; Grunzweig and Korner 2001). As a result, the use of endemic plant species in restoration of disturbed cites in the Great Basin is critical in promoting ecological recovery.

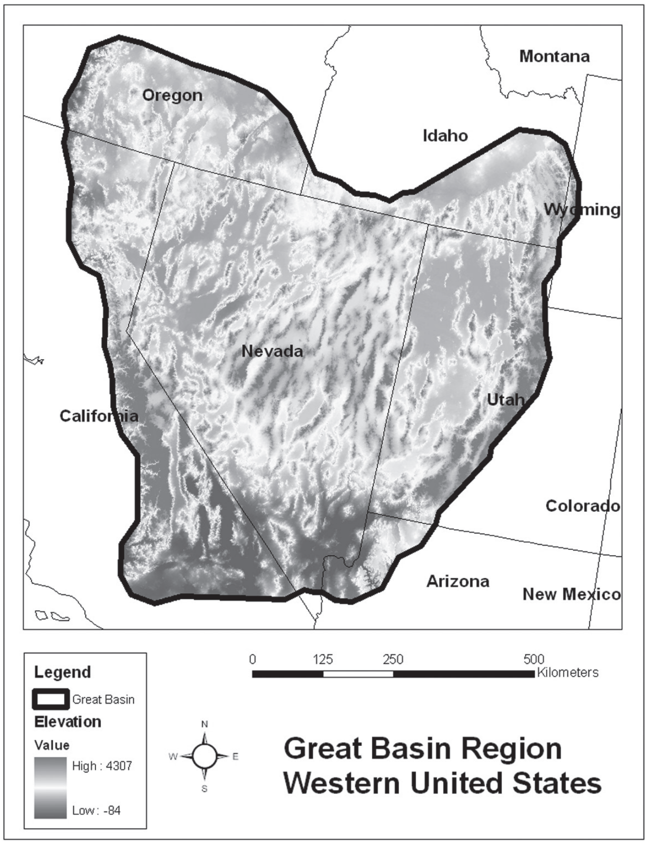

Figure 1. General outline of the Great Basin region of the Western United States.

Herbaceous perennials comprise a substantial portion of the Great Basin floristic communities and are an integral component of these systems. The use of native species in restoration is optimal because they are evolutionarily adapted to withstand severe climate conditions, provide long-term soil stabilization, and foster habitat biodiversity. Despite the importance of their role, the use of forbs in habitat restoration is relatively novel and largely unexplored (Parkinson 2008). One such species, Munro's globemallow (Sphaeralcea munroana (Douglas) Spach) (Malvaceae), is a desirable candidate for revegetation; however, its use is constrained by the lack of information regarding its requirements for successful germination and establishment.

Species Overview

Sphaeralcea munroana is a cool-season herbaceous perennial endemic to the Great Basin. Plants initiate growth from a caudex in the form of multiple, unbranched stems and typically reach 20 to 80 cm (8 to 30 in) in height. Showy, orange inflorescences are produced from May to August. Subsequent seeds are arranged in a schizocarp, composed of 10 to 12 mericarps that form a ring, each containing 1 to 2 pubescent seeds 1.5 mm (0.06 in) in length (Rydberg 1917; Lyons 1995). *S. munroana* is able to establish on disturbed sites and survive drought and temperature extremes. In addition to its resilience, this plant is an essential forage source for numerous rodents, lagamorphs, and ungulates (Beale and Smith 1970; Pendery and Rumbaugh 1986; Rumbaugh and others 1993; Pavek and others 2011). Furthermore, it provides nutrition for 20 generalist and 3 specialized (*Diadasia diminuta, D. lutzi*, and *Colletes sphaeralcea*) bee species (Cane 2008). These attributes have made S. munroana an important candidate for broad-scale restoration across its native range.

To date, seed dormancy of *S. munroana* has presented a major limitation to both in situ and ex situ germination. Several studies have explored the dormancy mechanisms and methods for dormancy break in the *Sphaeralcea* genus, but much still remains ambiguous (Page and others 1966; Roth and others 1987; Kildisheva and others 2011; 2012). Moreover, little is known about seedling tolerance to temperature and moisture stress. Ehleringer and Cooper (1998) suggest that desert globemallow (*S. ambigua* A. Gray), native to the Mojave Desert, is "a short-lived, opportunistic species that establishes during wet years but demonstrates higher mortality during dry years due to relatively low water use efficiency". Whether this life strategy is shared by *S. munroana* is unclear. Plant establishment is the most critical phase in determining future survival and persistence (Harper 1977); thus, seedling post-germination responses to temperature and moisture stress are especially important.

Seed Dormancy

Vleeshouwers and others (1995) suggest that dormancy is "a seed characteristic, the degree of which defines what conditions should be met to make the seed germinate". This is an evolutionary response to temporal variation in environmental conditions, which allows for different species to be favored over time (Rees 1996). Several types of dormancy exist and are defined based on the mechanisms that prevent germination.

Physical dormancy is common among desert species (including several in the *Sphaeralcea* genus) and is thought to have developed to prolong seed longevity (Page and others 1966; Sabo and others 1979; Roth and others 1987; Baskin and Baskin 1998; Smith and Kratsch 2009). Physically dormant seeds often possess a palisade layer of lignified cells that prevent water entry into the seed (Corner 1951; Vazquez-Yanes and Perez-Garcia 1976). Water imbibition is critical because it drives seed expansion (necessary for germination) and is dependent on the interaction between the growth potential of the embryo and the constraints imposed by the seed coat (Kucera and others 2005). Imbibition in many seeds with physical dormancy is regulated by a specialized anatomical structure, defined as the "water gap", which is located within the seed coat. The water gap becomes permeable when exposed to temperature flux, drying, or scarification, thus allowing imbibition into an otherwise impermeable seed (Baskin and Baskin 1998; Baskin and others 2000). The location, anatomy, and morphology of the water gap demonstrate intra- and extra-family variability (Baskin and others 2000). The chalazal region has been documented as a critical site for water entry in a number of *Malvacea* species, including Abelmoschus esculentus (L.) Moench, *Gossypium hirsutum* L., *Sida spinosa* L. (Christiansen and Moore 1959; Egley and Paul 1981; 1982; Serrato-Valenti and others 1992) and more recently in *Sphaeralcea munroana* (Kildisheva and others 2011). In these species, the water gap is obstructed by 2 tissue types. Maternal tissue forms a cap that projects downward into the chalazal slit and mesophyll tissue projects upward. At the initiation of dormancy break, a section of these tissues that radially surround the chalazal slit become partially permeable and allow imbibition, which leads to a separation of the palisade and sub-palisade layer of cells causing the formation of a blister (Serrato-Valenti and others 1992). At the point when water surrounds the entire palisade layer of the seed coat, the mesophyll cracks, allowing the upper portion of the palisade cells to continue swelling. This process eventually causes a detachment of the blister roof, allowing for full imbibition (Serrato-Valenti and others 1992).

Natural phenomena, such as abrasion by sand and stones (in rapidly moving washes during periods of flooding), temperature fluctuations, fires, and animal digestion are thought to alleviate physical dormancy (Went 1955; Gutterman 1993; Baskin and Baskin 1998).

A number of ex situ techniques (Table 1), primarily chemical and mechanical scarification, have been used to promote germination of physically dormant species (Page and others 1966; Roth and others 1987; Hoffman and others 1989; Baskin and Baskin 1998). Page and others (1966) observed an average of 35% germination improvement of two accessions of *S. grossulariifolia* (Hook. & Arn.) Rydb. following submergence in sulfuric acid compared to the control (0%). Correspondingly, a 10 min submergence of *Sphaeralcea* seeds in 18 M sulfuric acid increased germination of S. *coccinea* (Nutt.) Rydb. (77%) and 2 accessions of *S. grossulariifolia* (69 and 62%) compared with the control (5, 14, and 32%, respectively), but did not improve germination of *S. munroana* (8%) relative to the control (2%) (Roth and others 1987). Additionally, organic solvents have been successful at alleviating dormancy in species with impermeable seed coats. A 4-hr submergence in diethyl dioxide improved germination of *S. grossulariifolia* to 67% compared with 0% reported for untreated seeds (Page and others 1966). Roth and others (1987) also note that a 3-hr soak in diethyl dioxide significantly enhanced germination of *S. coccinea* (36%), *S. munroana* (53%), and 2 accessions of *S. grossulariifolia* (89 and 68%) compared with the control (5, 2, 14, and 32%, respectively). Despite its efficacy, chemical scarification can be hazardous, cause embryo damage, and present serious health risks to humans (Mallinckrodt Baker 2008 a, b). As a result, alternative methods of seed treatment may be desirable.

Another technique for improving imbibition of impermeable seeds is through wet heat scarification. Emergence in boiling water improved seed permeability of several *Malvaceae* species, presumably by unblocking the water gap (Christiansen and Moore 1959; Baskin and Baskin 1997, Kildisheva and others 2011). For example, seeds of *Iliamna corei* Sherff (*Malvaceae*) germinated to 93% (as compared to 0% germination of the control), following a 5-sec submergence in boiling water (Baskin and Baskin 1997).

Higher germination has also been achieved by mechanical scarification. The International Seed Testing Association (ISTA) suggests the use of scarification to break physical seed dormancy of *Althaea* hybrids (*Malvaceae*) (ISTA 2011). Similarly, seeds of *I. corei* germinated to 100% following manual scarification with a single edge razor blade (Baskin and Baskin 1997). Scarification with a blade followed by submergence in water for 24 hours resulted in 93% germination of *S. munroana* seeds (Kildisheva and others 2011). Although effective, these techniques are time consuming and unrealistic for use as operational seed treatments.

A number of mechanical scarification methods designed for treating large seed quantities exist; however, few have proven to be successful in alleviating dormancy in *Sphaeralcea* species. Primarily a result of scarification severity, embryo damage often overshadows the dormancy-breaking effects of the treatment. Page and others (1966) report decreases in germination of *S. grossulariifolia* with the duration of scarification time in a sandpaper-lined rotating drum, while Roth and others (1987) suggest that seeds of *S. grossulariifolia, S. coccinea,* and *S. munroana* perished following mechanical scarification, regardless of treatment duration. More recently, rotating rock tumblers filled with abrasive media have been used to promote germination of some physically dormant species, providing a potential alternative to traditionally used scarification techniques (Dreesen 2004). However, Kildisheva and others (2012) found 72 hour tumbling with dry aluminum oxide grit ineffective in creating significant germination improvements in germination behavior of *Sphaeralcea munroana*. While, Smith and Kratsch (2009) observed only a minor increase (21%) in germination following a 24-hr tumbling of *S. abmigua, S. coccinea*, and *S. munroana* seeds.

Other less traditional techniques, such as fire and heating treatments, may be employed to effectively induce permeability in physically dormant seeds. For example, *I. corei* demonstrated increased germination

Table 1. Summary of seed treatments for breaking dormancy in *Sphaeralcea* species

Species	Seed Treatment	Germination (versus the control)	Source
Sphaeralcea ambigua	Source	45% v. 18%	*Dunn 2011*
	Mechanical scarification	36% v. 18%	*Dunn 2011*
Sphaeralcea coccinea	Diethyl dioxide (3 hours)	38% v. 5%	*Roth and others 1987*
	Mechanical scarification + 30-day stratification	85% v. 5%	*Dunn 2011*
	Mechanical scarification	52% v. 5%	*Dunn 2011*
	Sulfuric acid + diethyl dioxide (3 hours)	67% v. 5%	*Roth and others 1987*
	Sulfuric acid (10 minutes)	77% v. 5%	*Roth and others 1987*
Sphaeralcea grossulariifolia	Diethyl dioxide (3 hours)	80% v. 23%	*Roth and others 1987*
	Diethyl dioxide (4 hours)	67% v. 0%	*Page and others 1966*
	Mechanical scarification	47% v. 0%	*Page and others 1966*
	Sulfuric acid (up to 30 minutes)	35% v. 0%	*Page and others 1966*
	Sulfuric acid (10 minutes)	66% v. 23%	*Roth and others 1987*
Sphaeralcea munroana	Boiling water	49% v. 11%	*Kildisheva and others 2012*
	Diethyl dioxie (3 hours)	38% v. 2%	*Roth and others 1987*
	Sulfuric acid + diethyl dioxide (6 hours)	29% v. 2%	*Roth and others 1987*
	Mechanical scarification + 24-hour soak in water	93% v. 17%	*Kildisheva and others 2011*
Combined lot: *Sphaeralcea ambigua, S. coccinea, S. munroana*	Mechanical scarification + 6 week stratification	84% v. 5%	*Smith and Kratsch 2009*
	Mechanical scarification	52% v. 5%	*Smith and Kratsch 2009*
	Rock Tumbling (24 hours)	26% v. 5%	*Smith and Kratsch 2009*

Only treatments resulting in significant ($p<0.05$) improvements in germination relative to the control are reported.

following simulated annual summer burning (1 to 2 min), with the highest germination achieved after 6 years (39 ± 6%) compared with the control (0%) (Baskin and Baskin 1997). In some cases, dry heat may be a substitute for fire, often achieving better results. For example, Baskin and Baskin (1997) found that several dry heat temperatures and exposure durations optimized the germination of *I. corei*.

Although the majority of physically dormant species do not exhibit additional dormancy, some do, including several members of *Malvaceae* (Baskin and Baskin 1998). Physiological dormancy, frequent in cold desert forbs, describes seeds that possess embryos with low growth potentials. This condition is caused by the presence of chemical inhibitors and can be relieved by stratification (Baskin and Baskin 1998). Gibberellic acid (GA3) has successfully served as a proxy for stratification for a number of physiologically dormant species (Timson 1966; Pinfield and others 1972). The exogenous application of GA3 is thought to enhance germination by increasing the growth potential of the embryo and by overcoming the mechanical constraints that prevent radical emergence (Karssen and others 1989; Hilhorst and Karssen 1992; Hilhorst 1995; Bewley 1997; Koornneef and others 2002; Leubner-Metzger 2003). In addition, exogenous application of GA3 alone, or in combination with scarification, significantly amplified the germination capacity of several species in the *Cactaceae,* including *Cereus spp., Echinocactus grusonii* Link and Otto, Hildman and Monats, *Leuchtenbergia principis* Hook., *Sclerocactus mariposensis* (Hester) Taylor, and *Harrisia fragrans* Small (Krulik 1981; Moreno and others 1991; De La Rosa-Ibarra and Garcia 1994; Dehgan and Perez 2005). However, recent evidence (Kildisheva and others 2011) suggest that the treatment of *S. munroana* seeds with GA3 alone or in combination with scarification does not provide any additional benefits to germination, suggesting a lack of influence of chemical inhibitors on germination.

Some authors suggest (Dunn 2011; Smith and Kratsch 2009) that in addition to being physically dormant, seeds of *Sphaeralcea* species also exhibit physiological dormancy. The mixture of physical and physiological dormancy is called combined dormancy and requires physical dormancy to be broken prior to breaking physiological dormancy in order to allow for seed imbibition (Nikolaeva 1969; Baskin and Baskin 1998). Dunn (2011) observed improvements in germination of *Sphaeralcea ambigua* (45%) and *S. coccinea* (85%) following the combination of scarification and a 30-d stratification relative to the control (18 and 5%, respectively). Smith and Kratsch (2009) suggest that a 6-wk stratification of scarified seeds of *S. grossulariifolia, S. parvifolia* A. Nelson, and S. munroana resulted in greater germination than from either treatment alone. However, Kildisheva and others (2011) failed to find similar results following the combination of scarification and 6-wk stratification of *S. munroana* seeds; suggesting that other factors (i.e. storage conditions, seed collection timing, or climatic features during seed set) likely play a significant role in dormancy development and should be further explored.

Temperature and Moisture as Limiting Factors to Seedling Development

In regions where growing conditions are limiting, plant establishment is the most vulnerable phase in vegetative community development (Call and Roundy 1991). In the arid-steppe ecosystem of the Great Basin, broad diurnal temperature fluctuations, periodic precipitation pulses, and significant droughts impose key restraints to post-germination survival. The maximum temperature and soil moisture variations take place in close proximity to the soil surface, making seedlings more susceptible to environmental fluctuations than mature plants (Bazzaz and Mezga 1973; Raynal and Bazzaz 1973; Regehr and Bazzaz 1976). Thus, opportunities for plant establishment in the Great Basin are strongly limited by its environmental conditions.

Diurnal temperature can vary by 20 °C (36°F), while seasonal differences can be on the order of 40 °C (72°F) (Smith and Nowak 1990). These oscillations can be made even greater throughout the year by the nocturnal cold aid drainage which are a feature of this region's topography (Osmond and others 1990). The Great Basin-Mojave system is described as the most xeric habitat in North America, with precipitation ranging between 50 and 300 mm (2 and 12 in) annually. Due to low humidity and abundant irradiance the rate of potential evapotraspiration is high, averaging between 1100 and 2000 mm (43 and 79 in) in the northern and southern sections of the basin, respectively (Flaschka and others 1987). Summer precipitation is highly variable, generally accounting for only 20 to 30% of total annual precipitation (Bell 1979). A substantial portion of the available moisture is significantly depleted by the time atmospheric and edaphic conditions become suitable for plants to be fully physiologically active; thus, there is a temporal difference between maximum water availability and the ability of plants to use it (Caldwell 1985). The combined effects of precipitation and temperature patterns result in substantial implications with regard to the physiology of the native plant communities. The start of the growing season in this region is directly associated with the rise in temperatures and the amount of available winter-spring precipitation, making the time of growth initiation in the spring critical (Turner and Randall 1987). Most species begin growth in March and April, a time when maximum daily temperatures range between 5 and 15 °C (41 and 59 °F) and night temperatures persist near 0 °C (32 ° F) (Thornthwaite 1948; Comstock and Ehleringer 1992).

Plant photosynthetic rates demonstrate substantial temperature dependence. At low temperatures, photosynthetic rates are reduced due to the decline in enzyme-catalyzed reaction rates. As temperatures rise, carbon assimilation rises until a maximum (defined as a "temperature optimum") is reached, and declines once the optimum has been exceeded (Comstock and Ehleringer 1992). The maximum photosynthetic rates exhibit considerable variability, and are primarily governed by environmental conditions. At the beginning of the growing season, when day-time temperatures do not exceed 20 °C (68 °F), the temperature optimum form many Great Basin shrubs is 15 °C (59 °F), increasing by 5 to 10 °C (9 to 18 °F) later in the season (Caldwell 1985). The maximum CO2 assimilation rates of shrubs native to this region, under natural or irrigated conditions, range from 14 to 19 µmol CO2 m^{-2} s^{-1} (Depuit and Caldwell 1973; Caldwell and others 1977). At this time, most research has focused on examining the photosynthetic behavior of perennial shrubs, with little attention given to herbaceous species. However, the phenological cycles of herbaceous and woody perennials are different, and may be expressed through variation in photosynthetic behavior.

The increasing prominence of native forbs in restoration programs requires a clear understanding of the physiological ecology of these species. Furthermore, knowledge regarding the photosynthetic behavior of members of the *Malvaceae* family is lacking. In a cultivation setting, *Sida spinosa*, *Gossypium herbaceum* auct. non L., and *Gossypium arboreum* L. , demonstrate relatively high CO_2 compensation points that are associated with large net CO_2 fixation and faster growth rates (Chen and others 1970). In the Great Basin, however, rapid growth rates can create severe internal moisture deficits, making the ability of plants to effectively regulate moisture loss imperative.

In general, low spring temperatures allow for higher water-use efficiency as cold soils reduce leaf conductance, but freezing night temperatures prevent full reduction in stomatal opening during the day, when moisture loss is high (Smith and Novak 1990). As soil moisture deficits increase with seasonal warming, plant water content declines, resulting in a lower turgor pressure. Under these conditions, turgor-dependent processes such as leaf expansion and root elongation are suppressed. Decreases in turgor have been linked to reductions in aboveground plant area and overall growth rates (Taiz and Zeiger 2006). Moisture restrictions cause a greater portion of photosynthates to be distributed to the root system, promoting belowground biomass production. Thus, root-to-shoot ratios (R:S) are a direct result of a dynamic equilibrium between water uptake and photosynthesis (Taiz and Zeiger 2006). R:S of desert perennials exhibits considerable variability among species, ranging from 0.15 to 6.77, with lower R:S values characteristic of plants in the northern Great Basin as compared to much higher ratios for plants found in the Mojave and Sonoran Deserts (Barbour 1973; Caldwell and others 1977). To date, most research has characterized mature perennial shrub and grass species, while much less is known about growth dynamics of forbs, especially shortly following establishment. A recent study examining the effects of 2 temperature (17/3 °C and 23/9 °C [63/37 °F and 73/48 °F]) and 4 moisture regimes (3-,6-,9-, and 12-d irrigation interval) on seedling responses of *S. munoroana* 35 days following establishment suggest that low diurnal temperatures impacted growth immediately after germination to a greater extent than did available moisture (Kildisheva and Davis 2012). Seedlings grown under the warmest, most arid conditions reduced their aboveground biomass while increasing belowground biomass production, with no changes in gas exchange rates; indicating high drought tolerance even during early development (Kildisheva and Davis 2012). Thus, *S. munroana* exhibits considerable potential for restoration use on arid sites, but may be a suboptimal competitor with cool season grasses in the spring, and may benefit from later sowing when night temperatures are above 3 °C (37 °F) (Kildisheva and Davis 2012). However, resilience early in the growing season doesn't necessarily indicate long-term survival; thus, further research which relates growth rates at the beginning of the season to consequent survival and phenology is essential.

Conclusions

Considering the rate of habitat degradation in the Great Basin, revegetation with native plants is integral to ecosystem function and resilience. *Sphaeralcea munroana* is a species with a high restoration potential; but the success of its use requires a better understanding of seed dormancy, storage conditions, and collection timing. Furthermore, the Great Basin climate is characterized by wide diurnal temperature fluctuations, episodic precipitation pulses, and extensive droughts which can severely limit seedling establishment and survival; thus, research linking early seedling performance with future growth and phenology is necessary.

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