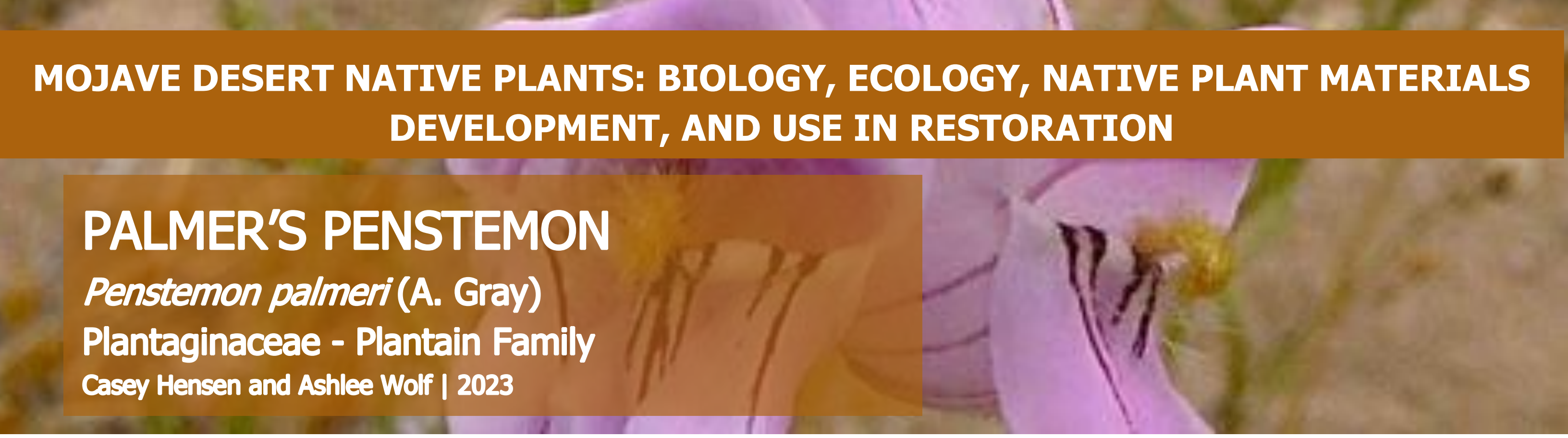

MOJAVE DESERT NATIVE PLANTS: BIOLOGY, ECOLOGY, NATIVE PLANT MATERIALS DEVELOPMENT, AND USE IN RESTORATION

PALMER'S PENSTEMON

Penstemon palmeri (A. Gray)

Plantaginaceae - Plantain Family

Casey Hensen and Ashlee Wolf | 2023

ORGANIZATION

NOMENCLATURE

Palmer's penstemon (*Penstemon palmeri* A. Gray) is in the plantain family, or Plantaginaceae (ITIS 2023). The genus *Penstemon* was formerly placed in Scrophulariaceae (the figwort family) and is still classified in this family by the U.S. Department of Agriculture (USDA NRCS 2023). However, genetic research has reclassified the genus into Plantaginaceae (Olmstead et al. 2001, Oxelman et al. 2005).

NRCS Plant Code.

PEPA8 (USDA NRCS 2023).

Synonyms.

Penstemon palmeri var. *bicolor, Penstemon palmeri* subsp. *eglandulosus*, *Penstemon palmeri* var. *eglandulosus*, *Penstemon palmeri* var. *grinellii*, *Penstemon palmeri* var. *macranthus*, and *Penstemon palmeri* var. *palmeri* (Tropicos 2023).

Common Names.

Palmer's penstemon, scented beardtongue, and Palmer's scented beardtongue (SEINet 2023a).

Subtaxa.

Currently, there are three varieties of Palmer's penstemon recognized by the Integrated Taxonomic Information System (ITIS):

- *Penstemon palmeri* var. *palmeri*
- *Penstemon palmeri* var. *eglandulosus*
- *Penstemon palmeri* var. *macranthusi*

Chromosome Number.

The chromosome number for Palmer's penstemon is 2n=16, 32 (Wetherwax and Holmgren 2012)

Since Palmer's penstemon possesses intraspecific ploidy variation (differences in chromosome numbers between individuals or populations), it may be necessary to assess the cytotypes of populations prior to mixing seed sources or starting propagation. Combining incompatible cytotypes can result in loss of fitness and fertility in plantings (Kramer et al. 2018).

Hybridization.

Palmer's penstemon is capable of hybridization, like many others in the genus *Penstemon* (Straw 1955, Ellstrand et al. 1996, Lindgren and Schaaf 2007). *Penstemon* x *bryantiae* is a fertile hybrid resulting from crosses with Palmer's penstemon and showy penstemon (*P. spectabils*) at the California Botanic Gardens in southern California. The hybrid's growth habit more closely resembles *P. spectabilis* (Everett 1950). Additional literature suggests Palmer's penstemon can cross with scarlet bugler (*P. centranthifolius*) (crosses are approximately 35% fertile) and Grinnell's beardtongue (*P. grinnellii*) (fertility unknown) in wild populations (Straw 1955). In Arizona, there are reports of a putative hybrid, *Penstemon* x *mirus*, between Palmer's penstemon and firecracker penstemon (*P. eatonii*) (FNA 2023). Palmer's penstemon can freely hybridize with the rare species, Pinto beardtongue (*P. bicolor*), where the two species co-occur (Glenne 2003). The geographic range of Palmer's penstemon has expanded due to its frequent use in revegetation projects, causing it to more frequently overlap with Pinto beardtongue. Hybridization poses a risk to the genetic integrity and viability of Pinto beardtongue populations (Glenne 2003).

DESCRIPTION

Palmer's penstemon is a perennial forb that grows between 50-140 cm tall, depending on elevation (higher elevation populations are typically shorter in stature) (SEINet 2023a). It has few to several erect stems and forms a taproot that acts as an anchor. Palmer's penstemon has both basal and cauline leaves. The basal and lower cauline leaves are ovate in shape with tapered bases and coarsely dentate margins (Freeman 2020). The upper cauline leaves are opposite (occurring in 5 to 8 pairs), clasping or perfoliate at the base, ovate to triangular in shape with acute apices, and coarsely dentate along the margins (distals sometimes entire). The inflorescence consists of 5-10 whorls of cymes (2-5 flowered) that are brightly colored with blue, lavender, violet and pink (sometimes pale pink to white). The calyx is 5-7 mm long, margins membranous, entire, and sometimes wavy or irregularly toothed. The petals are 17-20 mm long, bilabiate, with the lobes of the lips showing a lot of variation in size and form (equal, spreading, projecting, and the lower lip occasionally bearded). Throats are inflated and constricted at the orifice. Nectar guides are reddish purple. The male stamen is slightly exerted with the tips hooked and densely bearded. The fruits of Palmer's penstemon are capsules that are 11-16 mm long and glandular-puberulent near the tips (Freeman 2020). The large stature of Palmer's penstemon along with its highly fragrant flowers helps distinguish it from different species (SEINet 2023a).

Figure 1: A Palmer's penstemon individual. Photo: Jean Pawek

Figure 2: The inflorescence of Palmer's penstemon. Photo: Jean Pawek

Varieties or Subspecies.

The variety *palmeri* has corolla tubes that are 4-6 mm in length and can be distinguished from var. *eglandulosus* by its glandular-pubescent peduncles, calyces, and pedicles.

The variety *eglandulosus* has corolla tubes that are 4-6 mm in length and can be distinguished from var. *palmeri* by its glabrous peduncles, calyces, and pedicles.

The variety *macranthus* can be distinguished from the other two varieties by its longer corolla tubes, 7-8 mm long. This variety only occurs in Nevada and outside of the Mojave Desert ecoregion.

DISTRIBUTION AND HABITAT

Palmer's penstemon is native to the Mojave Basin and Range and several surrounding ecoregions in the Southwestern United States (SEINet 2023a; Figure 3). In central and northern Arizona, it is primarily found in the Arizona-New Mexico Mountains, Arizona- New Mexico-Plateau, and Colorado Plateau ecoregions. Records extend further north into Nevada and Utah, west into Colorado and New Mexico, and more sparsely, into Montana, Idaho, and Washington. (SEINet 2023a). Occurrences within and on the margins of the species range may be due to anthropogenic introductions in revegetation projects and subsequent establishment and spread of populations.

Habitat and Plant Associations.

Palmer's penstemon is generally found in washes and canyons, roadsides, and bajadas, growing in full sun. Throughout its range, it can be found in blackbrush, sagebrush, Joshua tree, pinyon-juniper woodlands, and ponderosa pine communities (Peterson and Ogle 2003, SEINet 2023a).

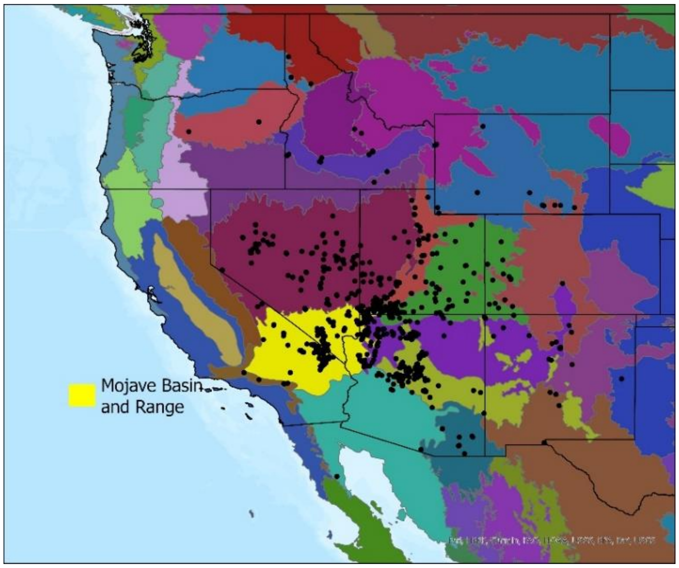

Figure 3: Distribution of Palmer's penstemon based on georeferenced herbarium specimens and verified observations (black circles, SEINet 2022) with EPA Level III Ecoregions (US EPA 2015). The Mojave Basin and Range ecoregion is shown in yellow.

In the Mojave Desert, Palmer's penstemon occurs along gentle slopes, roadsides, valley floors and washes (BLM SOS 2022). Associated species are blackbrush (*Coleogyne rasmosissima*), Mojave yucca (*Yucca schidigera*), banana yucca (*Yucca baccata*), desert willow (*Chilopsis linearis*), single-leaf pinyon (*Pinus monophylla*), buckhorn cholla (*Cylindropuntia acanthocarpa*), rubber rabbitbrush (*Ericameria nauseosa*), sandhill sage (*Artemisia filifolia*), desert almond (*Prunus fasciculata*), Virgin River brittlebush (*Encelia virginensis*), turpentine broom (*Thamnosma montana*), cliffroses (*Purshia* spp.), snakeweeds (*Gutierrezia* spp.), and needlegrass (*Achnatherum* spp.) (Ogle et al. 2013, BLM SOS 2022, SEINet 2023b).

Figure 4: Palmer's penstemon growing along a roadside. Photo: Jean Pawek

Figure 5: Palmer's penstemon habitat near the margins of a public path: Jean Pawek

Climate.

The Mojave Desert is characterized by low annual precipitation (5-25 cm or 2-10 inches in valley areas), with most rainfall occurring in the winter and a smaller amount during summer thunderstorms (Randall et al. 2010). Heterogenous climate patterns across the region are influenced by large-scale patterns and regional topography and are important drivers of local adaptation and intraspecific variation (Shryock et al. 2018, Baughman et al. 2019) and phenological events (Beatley 1974). Specifically, the reproductive phenology of many desert plant species is highly responsive to pulses in rainfall over short time scales (Bowers and Dimmitt 1994, Zachmann et al. 2021).

Climate information is derived from the climate-based provisional seed transfer zones (PSZs) where Palmer's penstemon occurs (Shryock et al. 2018; Table 1). According to herbarium specimen locations (SEINET 2022), Palmer's penstemon has been documented in all PSZs in the Mojave Desert ecoregion except Zones 27 and 28, which have the lowest annual average precipitation. It has been most frequently documented in Zone 20 and 26 and least documented in Zone 24 (Table 1). The average annual precipitation in the PSZs where Palmer's penstemon occurs in the Mojave Desert ecoregion is 20 cm (7.9 inches), with an average of 6.4 cm (2.5 inches) falling in the summer and an average of 13.6 cm (5.4 inches) falling in the winter. Note, herbarium specimen locations may not represent the full distribution and abundance of Palmer's penstemon due to sampling biases.

Elevation.

Palmer's penstemon grows at elevations between 1,000 ft (204 m) and 7,000 ft (2134 m) (SEINet 2023a)

Soils.

Palmer's penstemon prefers well-draining, dry soils (Peterson and Ogle 2003, Calscape 2023). It will typically do well on infertile and disturbed soils that are texturally sandy or decomposed granite. Palmer's penstemon grows best in soils that are weakly saline and weakly acidic (pH 6-8) (Calscape 2023).

There is no evidence of interaction between biological soil crusts and Palmer's penstemon in the literature.

Table 1: Climate of the provisional seed zones (PSZ) where Palmer's penstemon occurs within the Mojave Desert ecoregion (Shryock et al. 2018).# = the number of herbarium or verified observations of Palmer's penstemon within the PSZ (SEINet 2022); MAP=mean annual precipitation; SP=summer precipitation, or the mean precipitation that falls in the summer (May-October); WP= winter precipitation, or the mean precipitation that falls in the winter (November-April); MAT=monthly average temperature; Range= Average of the monthly temperature ranges (monthly maximum minus monthly minimum).

PSZ	#	MAP (cm)	SP (cm)	WP (cm)	MAT (C)	Range (C)
20	138	25.5	10.5	14.9	15.3	34.5
21	63	15.6	6.2	9.4	18.8	38.4
23	54	15.8	5.4	10.4	16.1	35.9
22	36	36.1	13.3	22.8	10	32.4
25	32	16.5	6.2	10.3	18.9	34.6
26	10	14.5	2.7	11.8	16.8	34.9
24	3	10.7	2.8	7.9	18.8	38.6
29	3	25.5	4.2	21.4	13.8	31.7

ECOLOGY AND BIOLOGY

Palmer's penstemon is a short-lived (4-5 years) perennial herb (Monsen and Shaw 1983, Cronquist et al. 1984). It grows in open areas with full sunlight, and occasionally in partial shade (Peterson and Ogle 2003, Calscape 2023).

Reproduction.

Breeding System.

Palmer's penstemon depends entirely on outcrossing and it does not have the ability to vegetatively reproduce or self-fertilize (Walker-Larsen and Harder 2001). This self-incompatibility may be due to the offset maturation of male and female floral parts, thus preventing self-fertilization, as observed in other species of Penstemon (Salas-Arcos et al. 2017).

Reproductive Phenology.

Observations show that flowering may begin as early as April, peak in May through July, and taper off by August (iNaturalist 2023, SEINet 2023b). Mature capsules and seeds occur more commonly at the end of the flowering season, but it is not unusual for multiple reproductive stages (budding, flowering, and seeding) to occur simultaneously on a single plant stalk (Peterson and Ogle 2003, iNaturalist 2023).

Pollination.

Palmer's penstemon pollinators generally include bees, butterflies, and moths (Ley et al. 2020), with occasional bee and wasp nectar robbers (Walker-Larsen and Harder 2001). Its intoxicatingly sweet nectar and smell attracts several species such as: digger bees (*Anthophora urbana*), bumblebees (*Bombus* spp.), carpenter bees (*Xylocopa* spp.), Ashmeadilla bees (*Ashmeadiella australis* Cockerell), and sweat bees (*Lasioglossum hyalinum*, *L. incopletum*, and *L. nevdadense*) (Allred 1969, Thomson et al. 2000, Wilson 2004, Carril et al. 2018).

Seed and Seedling Ecology.

Palmer's penstemon seed is dispersed when wind shakes the stalks, effectively launching the seeds away from the maternal plant (Meyer 2008a, Ogle et al. 2013). Palmer's penstemon exhibits a wide range of variation in dormancy and germination patterns within populations, and even within seeds produced from a single individual, exposed to different light and temperature conditions (Kitchen and Meyer 1992). Germination is seasonally bimodal, with seeds germinating in both fall and spring in response to varying temperature and light cues (Kitchen and Meyer 1992, Meyer and Kitchen 1992). Cyclic dormancy patterns permit year-to-year persistence in the seed bank and seeds can bank for at least two springs prior to germination (Meyer and Kitchen 1992). In the fall, light exposure increases germination rates, a potential adaptation to habitats with surface disturbance or instability that expose seeds on the surface. Seeds require a relatively long period of favorable moisture to germinate. Seedlings emerge in early spring or late fall and develop quickly. (Meyer and Kitchen 1992, Peterson and Ogle 2003). There is no evidence of ecotypic differentiation in germination patterns in this species which may partially explain its ability to establish from seed outside of its native range (Meyer and Kitchen 1992).

Palmer's penstemon seedlings are considered vigorous and compete well (Monson and Shaw 2001). Once established, Palmer's penstemon is self-perpetuating due to ample seed production and dormancy patterns that allow seeds to germinate and establish when conditions are favorable (Monson and Shaw 2001).

Species Interactions.

Belowground Interactions.

No specific belowground interactions have been identified for Palmer's penstemon, though it is claimed to be mycorrhizal dependent (Granite Seed 2023).

Palmer's penstemon is susceptible to root rot by fungal pathogens in soil including the genera *Rhizoctonia* and *Fusarium*. Infections are most severe when plants are growing in poorly draining loamy and clay textured soils (Meyer 2008b, Ogle et al. 2013).

Wildlife and Livestock Use.

Palmer's penstemon has good forage value as it stays green throughout the growing season (Peterson and Ogle 2003). Specifically, the seeds and foliage are desirable forage for deer, antelope, and birds. Ungulates (hooved animals) browse Palmer's penstemon during the winter and spring (Smith and Beale 1980, Plummer et al. 1995). Additionally, Palmer's penstemon can provide cover for small bird species (Peterson and Ogle 2003).

There is currently no evidence of use by the threatened Mojave Desert tortoise (*Gopherus agassizii*) for either cover or forage (Esque et al. 2021).

Other Notable Species Interactions.

Shrubs such as big sagebrush (*Artemisia tridentata*) can have facilitative effects on Palmer's penstemon, evidenced by increased survival of transplanted Palmer's penstemon seedlings under shrubs compared to open spaces in the Great Basin (Poulos et al. 2014). While shrubs may initially inhibit Palmer's penstemon seedling emergence, they can increase seedling survival (Poulos 2013). It was also found that transplanted shrub soils may help penstemon populations persist during dryer years.

Palmer's penstemon is the larval host plant of the Arachne checkerspot (*Poladryas arachne*) and the variable checkerspot (*Euphydryas chalcedona*) butterflies (The Xerces Society 2016). It is also host to the common buckeye (*Junonia coenia*), Edith's checkerspot (*Euphydryas editha*), California tiger moth (*Leptarctia californiae*), Mesquite looper moth (*Rindgea cyda*), geometrid moth (*Archirhoe neomexicana*), and the beardtongue plume moth (*Paraplatyptilia fragilis*) (Calscape 2023).

Disturbance Ecology.

Palmer's penstemon can colonize burned areas and roadsides and can successfully establish when seeded into disturbed areas (Walker and Powell 1999a, Brooks and Matchett 2003).

Palmer's penstemon is not fire-tolerant but can be somewhat fire-resistant. This may be due to leaves staying green and retaining high moisture content throughout the growing season (Ogle et al. 2013).

In a greenhouse experiment with seed sourced from the Colorado Plateau, Palmer's penstemon did not compete well with cheatgrass (Bromus tectorum) compared to other native plant species (Barak et al. 2015).

Ethnobotany.

Palmer's penstemon is used by the Kayenta Navajo tribe as a snakebite remedy. A poultice of the plant is applied to snakebite sores (Wyman and Stuart 1991).

Horticulture.

Palmer's penstemon is a common addition to ornamental and pollinator gardens due to its pleasant fragrance, low water requirements, colorful flowers, and green appearance during the dry season.

DEVELOPING A SEED SUPPLY

A robust and stable supply of genetically appropriate seed is needed to meet restoration demands in response to expanding environmental stressors from land degradation, invasive species, and climate change. Restoration success is, in part, predicated on applying the right seed in the right place, at the right time (PCA 2015). Developing a restoration seed supply involves coordination across many partners in all steps of the process: from conducting wildland collections to propagating materials in nurseries and agricultural fields to eventual seeding or outplanting at restoration sites. Appropriate protocols for preserving genetic diversity and adaptive capacity should be in place (Erickson and Halford 2020) and seed origin should be documented for certification purposes and other seed planning considerations.

Seed Sourcing.

Seed sourcing can influence restoration outcomes due to local adaptation (Custer et al. 2022), landscape genetic patterns (Massatti et al. 2020, Shryock et al. 2021) and differing ability to adapt to current and future climate conditions (Bucharova et al. 2019). However, there has been relatively little research evaluating seed sourcing strategies in actual restoration settings where many additional factors influence performance (Pizza et al. 2023).

While non-local sources can perform well in meeting initial restoration goals such as establishment and productivity (Pizza et al. 2023), evidence of local adaptation and its influence on restoration outcomes can take decades to emerge for long-lived species (Germino et al. 2019) Further, plants have coevolved with interacting organisms, such as pollinators and herbivores, that can exhibit preferential behavior for local materials (Bucharova et al. 2016, 2022).

Empirical seed transfer zones have not been developed for Palmer’s penstemon. The Desert Southwest Provisional Seed Zones (PSZs) may be used to plan seed sourcing in the absence of species-specific information. The Desert Southwest PSZs use twelve climatic variables that drive local adaptation to define areas within which plant materials may be transferred with higher probability of successful establishment and reduced risk of introducing maladapted ecotypes (Shryock et al. 2018). Overlaying PSZs with Level III ecoregions can serve to further narrow seed transfer by identifying areas of both climate similarity inherent in the PSZs and ecological similarity captured by the ecoregion, namely vegetation and soils. Within the PSZs and ecoregion areas, further site-specific considerations such as soil, land use, species habitat and microclimate affinities, and plant community may be relevant to seed sourcing decisions.

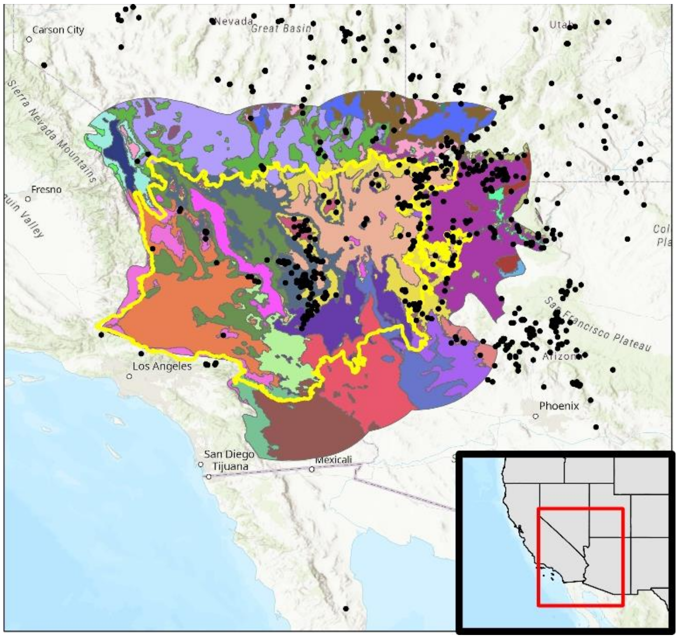

Figure 6: The distribution of Palmer's penstemon across the Desert Southwest Provisional Seed Zones (Shryock et al. 2018). Occurrences (black dots) are based on georeferenced herbarium specimens and verified observations (SEINet 2023). The Mojave Basin and Range Level III ecoregion (yellow outline) is buffered up to 100 km in all directions. PSZs do not always extend a full 100 km beyond the Mojave ecoregion.

The USGS Climate Distance Mapper Tool incorporates the Southwest Deserts Seed Transfer Zones with climate models and can serve to guide seed sourcing according to current and projected climate conditions.

Commercial Seed Availability and Germplasm Releases.

Palmer's penstemon is sometimes available for purchase from large-scale commercial seed vendors. However, availability may be inconsistent, and sources may be limited to a narrow range of appropriate seed zones. Commercially available seed may not be source identified, and source seed zone information may not be available.

The cultivar 'Cedar' was developed by the U.S. Forest Service in 1985 from variety palmeri seeds collected near Cedar City, Utah in a mixed pinyon-juniper, big sagebrush plant community. Cedar is best adapted to areas above 3,500 ft in elevation that receive 10 to 16 inches of rainfall (Ogle et al. 2013).

Wildland Seed Collection.

Wildland seed collection involves visiting naturally occurring populations of target species to provide source seed for propagation, restoration, and research. Ethical practices are intended to prevent overharvesting by limiting harvests to no more than 20% of available seed (BLM 2021). However, in arid regions and in drought conditions, it may be best to adapt this guidance to collect no more than 10% of available seed due to limited regeneration and low-density populations (Asbell 2022, personal communication). Several practices are in place to ensure proper genetic diversity is captured from the source population. These include collecting from the entire population uniformly, sampling a diversity of phenotypes and microclimates, and collecting in various time windows to capture phenological and temporal diversity (BLM 2021).

Seed Collection Timing.

Palmer's penstemon is typically collected between June and September with the majority of collections occurring in July (BLM SOS 2022).

Collection Methods.

Palmer's penstemon can be harvested by hand stripping or clipping whole stems (Peterson and Ogle 2003, Meyer 2008b). Capsules retain the seed for extended durations. Collect once the capsules have dried and the seeds are hard and dark in color. Since the flowering of Palmer's penstemon is indeterminate, there may be immature and mature pods on the same individual. This trait may require multiple collection visits to capture a wider range of phenology (Peterson and Ogle 2003).

Post-Collection Management.

Immediately following collection, seeds should be properly managed to avoid damage or declines in viability during transport and temporary storage. Seed should be dried and ventilated to prevent molding (Pedrini and Dixon 2020). Ventilation can be achieved by collecting and storing seed in breathable containers, such as paper or cloth bags.

To dry material before storage or processing, spread it in a single layer on trays or newspaper indoors in a well-ventilated room, or outdoors in a shaded area (BLM 2021). Collected material should be visually inspected for seed-predating insects (Pedrini and Dixon 2020). If seed predation is observed, consider fumigation with No-Pest Strips. After collection, prevent exposure to excessively hot or cold temperatures during transportation and temporary storage by keeping seed in a dry, insulated container (e.g., a cooler) in a shaded area while in the field (BLM 2021).

Figure 7: Collected mature capsule and seed of Palmer's penstemon; scale shown in mm. Photo: BLM NV060

Figure 8: Bare seed of Palmer's penstemon. Photo: Jean Pawek

Seed Cleaning.

Cleaning Palmer's penstemon involves removing seed from the capsule and separating out non-seed material. Seed can be loosened from the capsule with a hammer mill, brush machine, barley de-bearder, or hand sieves (Peterson and Ogle 2003, Barner 2009, Wall and MacDonald 2009). One method to separate the chaffy material involves setting a blower at 1.25 speed and then sieving with a #12 screen for any additional large chaff (Wall and MacDonald 2009).

One record of seed cleaning methods from the Bend Seed Extractory describes using a Westrup Model LA-H laboratory brush machine, with a #10 mantel, at medium speed to break down the capsules and loosen seed. Then seed was air screened using a Clipper with a 1/17 top screen and a 40 x 40 wire bottom screen and the machine set to medium speed with medium to low air (Barner 2009).

Seed from small collections can be extracted by breaking capsules and shaking seed loose through a screen (Meyer 2008b).

Seed Storage.

Palmer's penstemon seed is orthodox (SER SID 2023). The seeds of Palmer's penstemon tend to remain viable for several years under cool, dry conditions (Peterson and Ogle 2003). When stored in warehouse conditions, Palmer's penstemon maintained 80% germinability for five years. Viability decreased to 50% after 15 years in storage (Stevens et al. 1981).

In general, seeds should be stored in cool and dry conditions, out of direct sunlight, to maintain viability. Optimal conditions for medium-term storage of orthodox seeds (up to 5 years) are 15% relative humidity and 15° C (59° F). For long-term storage (>5 years), completely dried seeds should be stored at -18° C (0° F) (De Vitis et al. 2020, Pedrini and Dixon 2020).

Seed Testing.

After collection, a representative sample of each seed lot must be tested in an appropriate seed lab to ensure purity and germination meet minimum standards defined by the Association of Official Seed Analysts (AOSA 2016) and species standards from state-level certification programs as available. A set of "principles and standards for native seeds in ecological restoration" (Pedrini and Dixon 2020) outlines further guidelines specific to native plants, including procedures for obtaining representative samples of seed lots and incorporation of dormancy measures into seed testing and labels.

The AOSA includes Palmer's penstemon in their testing protocols to determine germination rates. These protocols include placing the seeds in a covered petri dish with a layer of either blotter paper, filter paper, or moist substrate. Temperature is set to a constant 15°C under a cool white fluorescent or LED (Light-Emitting Diode) light for at least 8 hours at 750-1250 lux. The first germination count can begin after 14 days and end up to 28 days (AOSA 2016).

The germination and viability rates of penstemon seed can also be tested using a combination of gibberellic acid (GA)-enhanced germination testing followed by tetrazolium (TZ) staining (Meyer 2008b). To do so, seeds are placed on blotting paper with 500 ppm of GA and chilled at 2-5°C for up to 60 days, followed by incubation at 15°C for 14 days. Count germinants (defined by radicle emergence) as they appear. For any ungerminated seed, viability can be assessed with TZ staining (Kitchen and Meyer 1991, Meyer 2008b).

The methods for TZ staining include imbibing seeds for 24 hours, using a needle to puncture the seed coat, then placing them in 1% TZ for 12 hours at room temperature. To evaluate, cut the seed longitudinally. If non-viable, embryos may present with a yellow color (not stained) while a pink color indicates viability. If seeds were recently harvested, a cut test to locate the live white endosperm may be a sufficient test (Kitchen and Meyer 1991).

Wildland Seed Yield and Quality.

Wild-collected Palmer's penstemon seed is generally high quality, with an average of 91% fill, 97% purity and 94% viability indicated by tetrazolium tests across 4 Seeds of Success collections (BLM SOS 2022, Table 2). Wild collections contain an average of over 463,000 pure live seeds (PLS) per pound (BLM SOS 2022, Table 2).

Table 2: Seed yield and quality of Palmer's penstemon seeds collected in the Mojave Basin and Range Ecoregion, cleaned by the Bend Seed Extractory and tested by the Oregon State Seed Laboratory or the USFS National Seed Laboratory (BLM SOS 2022). Fill (%) was measured using a 100 seed X-ray test. Viability (%) was measured using a tetrazolium chloride test.

	Mean	Range	Samples
Bulk weight (lbs)	1.3	0.18-3.45	4
Clean weight (lbs)	0.27	0.07-0.62	4
Purity (%)	97	95-97	4
Fill (%)	91	77-96	4
Viability (%)	94	92-96	4
Pure live seeds/lb	463,261	393,508-548,173	4

Wildland Seed Certification.

The Association of Official Seed Certifying Agencies (AOSCA) sets the standards for seed certification and provides guidance on production, identification, distribution, and promotion of all certified seed, including pre-varietal germplasm. Pre-varietal germplasm (PVG) refers to seed or other propagation materials that have not been released as varieties (AOSCA 2022). Pre-varietal germplasm certification programs for source-identified materials exist in several states encompassing the Mojave Desert ecoregion including California (CCIA 2022), Utah (UTCIA 2015), and Nevada (NDA 2021). Arizona does not have a PVG certification process at this time. Source-Identified (SI) germplasm refers to seed collected directly from naturally occurring stands (G0), or seed grown from wildland-collected seed in agricultural seed increase fields (G1-Gx) that have not undergone any selective breeding or trait testing. These programs facilitate certification and documentation required for wildland-collected seed to be legally eligible for direct sale or seed increase in an agricultural setting. Certified SI seed will receive a yellow tag, also referred to as an SI-label, noting key information about the lot including the species, the generation of seed (G0-Gx), source location, elevation, seed zone, etc. (UTCIA 2015, NDA 2021, CCIA 2022).

Wildland seed collectors should be aware of documentation required for seed certification. The Seeds of Success data form and protocol (BLM 2021) include all appropriate information and procedures for site documentation and species identification verification to meet certification requirements for wildland sourced seed. Seed certifying agencies may also conduct site inspections of collection locations prior to certification—specific requirements for inspections vary by state and are at the discretion of the certifying agency.

AGRICULTURAL SEED PRODUCTION

In general, Palmer's penstemon will do best planted in full sun in moderately-to-medium coarse soil with a neutral to slightly basic pH (Granite Seed 2023). No information specific to Mojave seed sources was found in the literature or through personal communication. Most information available on producing Palmer's penstemon seed in agricultural settings is from the U.S. Department of Agriculture and pertains to the Cedar cultivar.

Agricultural Seed Field Certification.

As with wildland source seed (see Wildland Seed Certification section), seed grown in an agricultural seed increase field must also be certified by an official seed certifying agency, where programs exist. Field grown seed is also certified and labeled as Source-Identified (SI), as long as it has not undergone selective breeding or testing. Seed field certification includes field inspection, seed testing for purity and germination (see Seed Testing section), and proof of certification for all source or parent seed used to start the field (AOSCA 2022). The SI-label or "yellow tag" for seed from a seed increase field denotes information about source seed, field location, and generation level (G1-Gx) indicating if there is a species-specific limitation of generations allowed to be grown from the original source (e.g., in a species with a three-generation limit, G1/G3, G2/G3, G3/3) (AOSCA 2022).

There are no species-specific standards for Palmer's penstemon certification in the states where it occurs.

Isolation Distances.

Sufficient isolation distances are required to prevent cross-pollination across seed production crops of Palmer's penstemon from different sources or other *Penstemon* species. Table 3 summarizes the isolation distances required for PVG certification in Utah for outcrossing perennial species (UCIA 2023). California, Nevada and Arizona do not specify these standards for Source Identified PVG seed of Palmer's penstemon.

Table 3: Crop years and isolation distance requirements for pre-varietal germplasm crops of Palmer's penstemon CY= crop years, or the time that must elapse between removal of a species and replanting a different germplasm entity of the same species on the same land. I= isolation distance, or the required distance (in feet) between any potential contaminating sources of pollen.

	G1		**G2**		**G3+**	
State	CY	I	CY	I	CY	I
Utah	3	900-600	2	450-300	1	330-165

Site Preparation.

Fields should be as weed-free as possible prior to planting. Site preparation to reduce undesirable vegetation should be planned and implemented well in advance of field establishment (USDA NRCS 2004). If fields are uncultivated or fallow and have perennial or annual weeds, one or more years of intensive cultivation (i.e. cover cropping) and herbicide treatment may be necessary (USDA NRCS 2004). After managing undesirable species, final seedbed preparation can include shallow tilling followed by packing to promote a finely granulated, yet firm seedbed that allows soil to seed contact, as well as facilitation of capillary movement of soil moisture to support seedling development (USDA NRCS 2004).

Mulching and weed control can strongly benefit stand establishment of Palmer's penstemon (Ogle et al. 2013). Weed barrier fabric allows for closer spacing, reduces weeds, and can conserve soil moisture (Ogle et al. 2013).

Seed Pre-treatments.

Palmer's penstemon seeds can have an after-ripening period of 3 to 4 months (Peterson and Ogle 2003). Prechilling seed can enhance germination of Palmer's penstemon (Peterson and Ogle 2003). Some growers in the Mojave Desert report using cold stratification for Palmer's penstemon seeds (Sturwold et al. 2022, personal communication), and others find that Mojave sources do not require cold stratification (Plath 2023, personal communication; Pettersson and Asbell 2024, personal communication). A standard stratification practice for Palmer's penstemon involves prechilling the seed for 8 to 12 weeks in cold, moist conditions. Then seeds can be sown into containers by pressing seed into the soil surface and storing them in cool (36 °F), dark conditions for an additional 8 to 12 weeks. Then plants can be moved into a greenhouse and propagated for 8 to 12 weeks prior to transplanting (Peterson and Ogle 2003). The use of gibberellic acid can help break seed dormancy when applied at 250 mg/L (Kitchen and Meyer 1992). See additional information under Seed and Seedling Ecology and Seed Testing.

Seeding Techniques.

Palmer's penstemon can be directly sown or transplanted from containerized stock to start a seed increase field.

Direct seeding in the fall allows for natural cold stratification of the overwintering seed, which will germinate in the following year. Seed can be drilled to a depth of ¼ inch or less at a rate of 1.5 to 3 pounds pure live seed per acre (lbs PLS/acre)— a shallow planting depth is beneficial for light-induced germination. Rows should be spaced 30-36 inches apart, with 18 inches of space between plants within rows (Peterson and Ogle 2003).

Establishment and Growth.

Generally, Palmer's penstemon seedlings are vigorous (Peterson and Ogle 2003). Flowering of new plants shouldn't be expected until the second growing season at minimum.

Weed Control.

Generally, weeds can be manually removed or carefully spot-sprayed with non-selective herbicide as they emerge. In smaller fields, hand rogueing weeds can be sufficient (Hagman 2023, personal communication).

There are a limited number of herbicides registered and labeled for use on native plant crops. See the Native Seed Production guide from the Tucson Plant Materials Center (USDA NRCS 2004) for further details on weed management in native seed production fields.

If used, the type of herbicide should be carefully considered as Palmer's penstemon is broad-leafed and therefore broadleaf herbicides (e.g., 2,4-D) are not recommended. Stands typically only need weed control during establishment (Peterson and Ogle 2003).

Pest Management.

Palmer's penstemon can experience pests and disease in cultivation.

Aphids and grasshoppers have been identified to damage new stands of Palmer's penstemon. Aphids can be treated by spraying with soap and water (Johnson 2023, personal communication). Pesticide may be needed to treat grasshoppers, though this may cause harm to pollinators and other beneficial insects (Peterson and Ogle

2003). If insecticides are determined to be necessary to control an infestation, precautions for avoiding or minimizing harm to beneficial insects include: avoiding systemic neonicotinoid insecticides in favor of "contact" insecticides; selecting products with low toxicity or short residual toxicity such as insecticidal soaps; applying insecticide when plants are not flowering; and spot treating infestations as opposed to blanket application over the entire field (Borders and Lee-Mader 2014).

In Colorado, a penstemon weevil (*Hesperobarus* spp.) was identified in a Palmer's penstemon production field (Ogle et al. 2013). It is difficult to control once the damage has been observed, especially when weevils feed on the taproot.

Palmer's penstemon is susceptible to fusarium wilt disease from fungal pathogens in irrigated fields (Meyer 2008b). Additionally, irrigated fields may be subject to similar diseases associated with alfalfa and potatoes (disease not specified) (Stevens and Monsen 1988). Since Palmer's penstemon is sensitive to overwatering, reduced irrigation can mitigate pathogen impacts.

Damage from wildlife and rodents may occur in Palmer's penstemon fields. Physical barriers (such as chicken wire) can help keep out larger animal pests (Peterson and Ogle 2003).

Pollination Management.

Growing native plants in or near their native range increases the likelihood that compatible pollinators will be able to find and pollinate the crop (Cane 2008). In general, growers can consider implementing pollinator management and stewardship practices to augment and attract existing pollinator communities. Specific practices will depend on the plant species' pollination needs, and the biology of the pollinators. For example, if a plant relies on native solitary bees, growers can create nesting opportunities adjacent to or within the field perimeter with downed woody material or crafted bee boxes (Cane 2008, MacIvor 2017). In some cases, there may be a need to supplement with managed pollinators through honeybee or bumblebee rental services to ensure pollination of wildflower crops for seed increase (Cane 2008).

Currently, there are no recommended pollination management practices for Palmer's penstemon. Generally, growers may stagger production by rotating fields and avoid growing multiple kinds of penstemon to prevent hybridization (Hagman 2023, personal communication).

Irrigation.

Generally, Palmer's penstemon has low water needs (Calscape 2023) and may only need supplemental water during the establishment period (Meyer 2008b). Palmer's penstemon crops can be highly sensitive to over-watering (Kratsch 2013).

Many growers apply uniform watering techniques regardless of species due to their set infrastructure and labor resources. For example, at the Tucson Plant Materials Center, all fields are watered with flood irrigation (Dial 2023, personal communication). After seeding, fields are irrigated to maintain a moist soil surface and avoid soil crusting that would interfere with germination. Once plants are established, fields are flooded approximately every four weeks during the growing season. Irrigation frequency will depend on heat and precipitation levels and may be as frequent as every two weeks during the hottest part of the year to minimize plant stress which can decrease seed yield (Dial 2023, personal communication).

Other growers utilize drip irrigation and find flood irrigation does not adequately penetrate the soil in arid growing conditions (Hagman 2023, personal communication).

Seed Harvesting.

Seeds generally ripen from mid-August to mid-September, or 6 to 8 weeks after peak flowering (Peterson and Ogle 2003). Generally, the window for harvest is wide due to indeterminate ripening over a long period of time (Peterson and Ogle 2003). Small-scale seed increase fields may be harvested by hand following similar methods as in wildland collections (see Collection Methods). Stalks can also be clipped before the capsules open (as they will open after harvest), but the seeds must already be darkening. A combine can also be used, but this will not allow for multiple harvest events since the entire stalk is harvested with both ripe and unripe material (Peterson and Ogle 2003).

Seed Yields and Stand Life.

The cultivar, Cedar, yields an average of 100 pounds of seed per acre (not specified if this is bulk weight or pure live seed). Since Palmer's penstemon is short-lived, vigor and yield decline after 4-5 years (Peterson and Ogle 2003).

NURSERY PRACTICE

See Seed Pre-treatments for methods on germinating Palmer's penstemon applicable to nursery settings. Generally, growers find that penstemon are propagated easily from seed and do well in containerized production (Plath 2023, personal communication; Johnson 2023, personal communication). Penstemon generally do best when sown into elongated containers such as tree pots and in soils that are medium-coarse (such as vermiculite or chopped sphagnum moss) (Everett 1950, Meyer 2008b). However, they do fine with transplanting from smaller containers into one-gallons (Wallace 2023, personal communication). Seedlings are ready for hardening off and outplanting after 3 to 4 months but can remain in pots for longer (Meyer 2008b). The survival of transplants is typically high, especially when given extra water at time of transplant to rid the soil of air pockets (Meyer 2008b). At the Living Desert Zoo and Gardens, growers found that plants could be killed if watered in the summer and suggest keeping plants dry (Sturwold et al. 2022, personal communication).

At the Mojave Desert Land Trust, growers sow seeds in late fall and early winter into flats with a mix of perlite, vermiculate, and fertilizer (Pettersson and Asbell 2024, personal communication). The flats are kept constantly moist during the germination stage which usually lasts about two to three weeks with temperatures ranging from 45 to 75 °F. After germination, watering is reduced to discourage the seedlings from dampening off. Recent germination rates using this practice have been up to 57%. After two to three months, the seedlings are transplanted into one-gallon containers. The plants are generally ready for outplanting after about nine to ten months from germination. To harden the plants off prior to outplanting, they are brought out from the greenhouse into an outdoor area after the chance of frost has passed (usually mid-April) (Pettersson and Asbell 2024, personal communication).

An experiment at the Agricultural Experiment station in Greenville, Utah found that Palmer's penstemon grew best in a pot-in-pot design (PIP) compared to the conventional above ground method (Cardoso et al. 2006). A PIP system is when plants are grown in tree containers filled with a substrate and positioned inside another larger "socket" container that may be permanently installed in the ground. Placing the pots in an in-ground containerized setting reduces damage to root systems, moderates winter soil temperatures within the pot, and can reduce moisture loss from the pot. In this experiment, seeds were started in 164 cm3 cells and were later transplanted into a 1-gallon pot. The soil medium consisted of a 5:4:1 mix of composted bark, screen pumice, and peat moss. A slow release granular and micronutrient fertilizer was used, and plants were irrigated with overhead pop-up spray systems every morning for 10 minutes (Cardoso et al. 2006).

REVEGETATION AND RESTORATION

Since it is an early successional forb that can readily establish from seed, Palmer's penstemon is useful for soil stabilization on depleted, disturbed, and erosive areas such as mines and roadsides (Richards et al. 1988, Peterson and Ogle 2003). It can enhance habitat for pollinators and wildlife (Uncompahgre Plateau Project 2008, NRCS 2011, Ogle et al. 2011). Additionally, Palmer's penstemon can be used for reseeding in post-fire sites throughout the Colorado Plateau (Uncompahgre Plateau Project 2008, Fuhrmann 2008).

Anthropogenic activities, especially mining and agriculture, have increased the prevalence of soil nutrients such as zinc and salt. Zinc, at high levels, can be lethal to plant communities. Palmer's penstemon has been found to have a high tolerance to zinc when experimentally exposed to high concentrations of the mineral. As such, it is a recommended reclamation species for zinc-contaminated sites (Paschke et al. 2006). However, Palmer's penstemon has shown some sensitivity when re-introduced into disturbed sites with saline soils (Zollinger et al. 2007).

Due to its easy germinability and general establishment success, Palmer's penstemon is more likely to be used for wildland seeding practices rather than whole-plant salvage or outplants.

Wildland Seeding and Planting.

Wildland Seedings.

Palmer's penstemon is best applied in a multi-species seed mix to avoid creating a monoculture.

One study on BLM land near St. George, Utah included Palmer's penstemon in a multi-species seed mix on a highly disturbed Mojave Desert site (Ott et al. 2011). The plot had variable topography with a sand pit and rock quarry. The land was originally damaged by mining, grazing, and off-road vehicles. To prepare the site, it was cleared of refuse and sculpted with a bladed tractor. The sites were disked before seeding. The site was drill seeded with the mix at a rate of 19.5 lbs PLS per acre (including 1.0 lbs/acre of Palmer's penstemon). There was no mention of seed source or supplemental watering. After several years, Palmer's penstemon established well in portions of the site that were rocky and sandy, increasing in number each subsequent year (Ott et al. 2011).

Palmer's penstemon was included in a multi-species seed mix to revegetate roads in the Mojave Desert in Southern Nevada (Walker and Powell 1999b). The mix included twelve native species hand sown in January at a rate of 40 pounds per acre (including 3 lbs/acre of Palmer's penstemon). Seed sourcing was not specified. The site was assessed in April and the researchers found 267 Palmer's penstemon plants per 40 square meters in the seeded area and it was one of the most dominant seeded species in the restored area. No further monitoring results were reported to assess establishment and persistence.

Another study used Palmer's penstemon in a native seed mix in Piceance Basin, Colorado (Johnston 2019). Damage from oil and gas practices were common in the area, thus the experimental site sought to simulate similar conditions by running a bulldozer through each site. Invasives were spot treated with herbicide. Seeds for this study were obtained commercially. The seed mix was blended with rice hulls for even distribution for application. The seeds were drilled 1 cm deep on the flatter plots and were hand broadcast and raked in on rough plots. The Palmer's penstemon cultivar, Cedar, was used at 1.7 PLS/acre. Results showed an increase in overall cover that increased with time. General forb cover increased from 9% in 2011 to 18.1% in 2014 with Palmer's penstemon accounting for 6.6% of total cover (Johnston 2019).

Less success was seen in an aerial application on post-burn sites in pinyon juniper woodlands on the Colorado Plateau (Grant-Hoffman et al. 2018). Palmer's penstemon was included in a seed mix (obtained from the BLM) that was aerially seeded on the damaged sites over 2 consecutive years at 13 lbs/acre. When the sites were sampled four years later, none of the Palmer's penstemon seeds had established (Grant-Hoffman et al. 2018).

Wildland Plantings.

A study of shrub interactions with Palmer's penstemon was conducted in Millville, Utah (Poulos et al. 2014). The study site was within a big sagebrush community with native grasses and forbs and few invasive grasses. Some past grazing damage was present. Palmer's penstemon seed was collected from roadsides and washes within the Harris Springs area in Nevada. The seeds were germinated, and 383 seedlings were acquired and grown in a 3:1 sand to peat moss mix. Plants were watered daily and fertilized monthly. To prepare the field site, some of the understory was experimentally removed. Once Palmer's penstemon seedlings were planted, they were given supplemental water to help establishment. There was no mortality recorded in the first month, but by day 60 (mid-summer), some seedlings began to die. Results showed that the probability of survival for Palmer's penstemon was highest for those transplanted under shrubs that had no other understory plants (up to 86% reduced risk of mortality). There was also a greater chance of survival (91%) when plants were placed in cleared open plots with shrubs (Poulos et al. 2014).

ACKNOWLEDGEMENTS

Funding for *Mojave Desert Native Plants* was provided by the Bureau of Land Management, Mojave Native Plant Program. The conceptual framework and design of the Mojave Native Plant Guide was developed by Corey Gucker and Nancy Shaw in [Western Forbs: Biology, Ecology, and Use in Restoration]. Cierra Dawson and Brooke Morrow developed maps and summarized data for climate, seed collection, and seed certification sections. Scott Harris (IAE) and Lenna Pettersson (Mojave Desert Land Trust) provided content review. Thank you to Madena Asbell and Lenna Pettersson (Mojave Desert Land Trust); Kelly Wallace (Song Dog Nursery, Lake Mead National Recreation Area); Tren Hagman (Granite Seed); Amy Johnson (Las Vegas State Tree Nursery); Steve Plath (Desert Seeds Resource Center); Paul Sturwold, Mack Nash, Mark Reeder, and Jose Marfori (The Living Desert Zoo and Gardens); and Heather Dial (USDA Natural Resources Conservation Service) for providing information on their experience working with Palmer's penstemon or other Mojave Desert native plants. Thank you to Judy Perkins (BLM) for coordination, content review, and initiating this project.

LITERATURE CITED

Allred, D. M. 1969. Bees of the Nevada Test Site. The Great Basin Naturalist 29:20–24.

AOSA. 2016. AOSA Rules for Testing Seeds, Volume 1. Principles and Procedures. Association of Official Seed Analysts, Wichita, KS.

AOSCA. 2022. How AOSCA tracks wildland sourced seed and other plant propagating materials. Association of Official Seed Certifying Agencies, Moline, IL.

Asbell, M. 2022, November 17. Director of Plant Conservation Programs, Mojave Desert Land Trust. Phone call about *Encelia actoni* and *Encelia farinosa*.

Barak, R. S., J. B. Fant, A. T. Kramer, and K. A. Skogen. 2015. Assessing the Value of Potential "Native Winners" for Restoration of Cheatgrass-Invaded Habitat. Western North American Naturalist 75:58–69.

Barner, J. 2009. Propagation protocol for production of Propagules (seeds, cuttings, poles, etc.) Penstemon palmeri A. Gray seeds USDA FS - R6 Bend Seed Extractory Bend, Oregon. https://npn.rngr.net/renderNPNProtocolDetails?selectedProtocolIds=scrophulariaceae-penstemon-3734.

Baughman, O. W., A. C. Agneray, M. L. Forister, F. F. Kilkenny, E. K. Espeland, R. Fiegener, M. E. Horning, R. C. Johnson, T. N. Kaye, J. Ott, J. B. St. Clair, and E. A. Leger. 2019. Strong patterns of intraspecific variation and local adaptation in Great Basin plants revealed through a review of 75 years of experiments. Ecology and Evolution 9:6259–6275.

Beatley, J. C. 1974. Phenological Events and Their Environmental Triggers in Mojave Desert Ecosystems. Ecology 55:856–863.

BLM. 2021. Bureau of Land Management technical protocol for the collection, study, and conservation of seeds from native plant species for Seeds of Success. U.S. Department of the Interior, Bureau of Land Management.

BLM SOS. 2022. USDI Bureau of Land Management, Seeds of Success. Seeds of Success collection data.

Borders, B. D., and E. Lee-Mader. 2014. Milkweeds: A Conservation Practitioner's Guide. The Xerces Society for Invertebrate Conservation, Portland, OR.

Bowers, J. E., and M. A. Dimmitt. 1994. Flowering phenology of six woody plants in the northern Sonoran Desert. Bulletin of the Torrey Botanical Club 121:215–229.

Brooks, M. L., and J. R. Matchett. 2003. Plant Community Patterns in Unburned and Burned Blackbrush (coleogyne Ramosissima Torr.) Shrublands in the Mojave Desert. Western North American Naturalist 63:283–298.

Bucharova, A., O. Bossdorf, N. Hölzel, J. Kollmann, R. Prasse, and W. Durka. 2019. Mix and match: regional admixture provenancing strikes a balance among different seed-sourcing strategies for ecological restoration. Conservation Genetics 20:7–17.

Bucharova, A., M. Frenzel, K. Mody, M. Parepa, W. Durka, and O. Bossdorf. 2016. Plant ecotype affects interacting organisms across multiple trophic levels. Basic and Applied Ecology 17:688–695.

Bucharova, A., C. Lampei, M. Conrady, E. May, J. Matheja, M. Meyer, and D. Ott. 2022. Plant provenance affects pollinator network: Implications for ecological restoration. Journal of Applied Ecology 59:373–383.

Calscape. 2023. Palmer's Penstemon, Penstemon palmeri. https://www.calscape.org/Penstemon-palmeri-(Palmer's-Penstemon)?srchcr=sc6564bea04ce8a.

Cane, J. H. 2008. 4. Pollinating Bees Crucial to Farming Wildflower Seed for U.S. Habitat Restoration. Pages 48–65 Bee Pollination in Agricultural Eco-systems. First edition. Oxford University Press, Oxford, England.

Cardoso, G., R. Kjelgren, T. Cerny-Koenig, and R. Koenig. 2006. Pot-in-Pot Production of Six Intermountain West Native Herbaceous Perennial Species Grown in Containers. Journal of Environmental Horticulture 24:77–83.

Carril, O. M., T. Griswold, J. Haefner, and J. S. Wilson. 2018. Wild bees of Grand Staircase-Escalante National Monument: richness, abundance, and spatio-temporal beta-diversity. PeerJ 6:e5867.

CCIA. 2022. Pre-Variety Germplasm Program. California Crop Improvement Association. University of California, Davis, CA. https://ccia.ucdavis.edu/quality-assurance-programs/pre-variety-germplasm.

Cronquist, A., A. H. Holmgren, N. H. Holmgren, J. L. Reveal, and P. K. Holmgren. 1984. Intermountain flora: Vascular plants of the intermountain west, U.S.A. New York Botanical Garden, N. Y.

Custer, N. A., S. Schwinning, L. A. DeFalco, and T. C. Esque. 2022. Local climate adaptations in two ubiquitous Mojave Desert shrub species, Ambrosia dumosa and Larrea tridentata. Journal of Ecology 110:1072–1089.

De Vitis, M., F. R. Hay, J. B. Dickie, C. Trivedi, J. Choi, and R. Fiegener. 2020. Seed storage: maintaining seed viability and vigor for restoration use. Restoration Ecology 28:S249–S255.

Dial, H. 2023, May 10. Phone call with Heather Dial (USDA NRCS) about bush muhly growing practices.

Ellstrand, N. C., R. Whitkus, and L. H. Rieseberg. 1996. Distribution of spontaneous plant hybrids. Proceedings of the National Academy of Sciences 93:5090–5093.

Erickson, V. J., and A. Halford. 2020. Seed planning, sourcing, and procurement. Restoration Ecology 28:S219–S227.

Esque, T. C., L. A. DeFalco, G. L. Tyree, K. K. Drake, K. E. Nussear, and J. S. Wilson. 2021. Priority Species Lists to Restore Desert Tortoise and Pollinator Habitats in Mojave Desert Shrublands. Natural Areas Journal 41.

Everett, P. 1950. The Californian Penstemons. Aliso 2:155–198.

FNA. 2023. Penstemon palmeri - FNA. http://dev.floranorthamerica.org/Penstemon_palmeri.

Freeman, C. C. 2020. Penstemon palmeri - FNA. http://floranorthamerica.org/Penstemon_palmeri.

Fuhrmann, K. 2008. Restoring Burned Area Fire Regimes at Zion National Park:24.

Germino, M. J., A. M. Moser, and A. R. Sands. 2019. Adaptive variation, including local adaptation, requires decades to become evident in common gardens. Ecological Applications 29:e01842.

Glenne, G. 2003. Reproductive biology, hybridization isolating mechanisms, and conservation implications of two rare subspecies of Penstemon bicolor (Brandeg.) Clokey and Keck: Ssp. bicolor and ssp. roseus Clokey and Keck (Scrophulariaceae s.l.) in Clark County, Nevada. Utah State University.

Granite Seed. 2023. Palmer Penstemon | Penstemon Palmeri | Granite Seed. https://graniteseed.com/seed/wildflowers-forbs/penstemon-palmeri/.

Grant-Hoffman, M., A. Lincoln, and J. Dollerschell. 2018. Post-Fire Native Seed Use in Western Colorado: A Look at Burned and Unburned Vegetation Communities 38:286–297.

Hagman, T. 2023, March 6. Granite Seeds: Conversation about seed production practices (video call).

iNaturalist. 2023. Penstemon palmeri. Denver Botanic Gardens - Gardens Navigator.

ITIS. 2023. ITIS - Report: Penstemon palmeri. https://www.itis.gov/servlet/SingleRpt/SingleRpt?search_topic=TSN&search_value=33738#null.

Johnson, A. 2023, March 8. Las Vegas State Tree Nursery. Conversation about nursery growing, seed collection and restoration practices (video call).

Johnston, D. B. 2019. Rough Soil Surface Lessens Annual Grass Invasion in Disturbed Rangeland. Rangeland Ecology & Management 72:292–300.

Kitchen, S. G., and S. E. Meyer. 1991. Seed germination of intermountain penstemons as influenced by stratification and GA treatments 9:51–56.

Kitchen, S. G., and S. E. Meyer. 1992. Temperature-mediated changes in seed dormancy and light requirement for Penstemon palmeri (Scrophulariaceae). Great Basin Naturalist 52.

Kramer, A. T., T. E. Wood, S. Frischie, and K. Havens. 2018. Considering ploidy when producing and using mixed-source native plant materials for restoration. Restoration Ecology 26:13–19.

Kratsch, H. 2013. Report of the Intermountain Native Plants Cooperative. Volume 5. NPC.

Ley, E. L., L. Stritch, and G. Soltz. 2020. Selecting plants for pollinators: a regional guide for farmers, land managers, and gardeners in the Colorado Plateau semidesert province. NAPPC and Pollinator Partnership.
Lindgren, D. T., and D. M. Schaaf. 2007. Penstemon: A Summary of Interspecific Crosses. HortScience 42:494–498.
MacIvor, J. S. 2017. Cavity-nest boxes for solitary bees: a century of design and research. Apidologie 48:311–327.
Massatti, R., R. K. Shriver, D. E. Winkler, B. A. Richardson, and J. B. Bradford. 2020. Assessment of population genetics and climatic variability can refine climate-informed seed transfer guidelines. Restoration Ecology 28:485–493.
Meyer, S. E. 2008a. The Woody Plant Seed Manual. U.S. Department of Agriculture, Forest Service.
Meyer, S. E. 2008b. Scrophulariaceae-Figwort family penstemon, beardtounge. Woody Plant Seed Manual - USDA FS Rocky Mountain Research Station.
Meyer, S. E., and S. G. Kitchen. 1992. Cyclic Seed Dormancy in the Short-Lived Perennial Penstemon Palmeri. Journal of Ecology 80:115–122.
Monsen, S. B., and N. Shaw. 1983. Managing Intermountain Rangelands: Improvement of Range and Wildlife Habitats : Proceedings of Symposia,. U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station.
Monson, S. B., and N. L. Shaw. 2001. Development and use of plant resources for western wildlands. Pages 47–61 Shrubland ecosystem genetics and biodiversity: proceedings;
NDA. 2021. Certified Seed Program. Nevada Department of Agriculture. Sparks, NV. https://agri.nv.gov/Plant/Seed_Certification/Certified_Seeds/.
NRCS. 2011. Conservation Plant Releases-Los Lunas Plant Materials Center. http://plant-materials.nrcs.usda.gov/nmpmc/releases.html.
Ogle, D. G., S. Peterson, and L. St. John. 2013. Plant Guide for Palmer's penstemon (Penstemon palmeri). USDA-Natural Resources Conservation Service, Plant Materials Center. Aberdeen, Idaho 83210.
Ogle, D., D. Tilley, J. Cane, L. St. John, K. Fullen, M. Stannard, and P. Pavek. 2011. Plants for pollinators in the intermountain west.
Olmstead, R. G., C. W. de Pamphilis, A. D. Wolfe, N. D. Young, W. J. Elisons, and P. A. Reeves. 2001. Disintegration of the Scrophulariaceae. American Journal of Botany 88:348–361.
Omernik, J. M. 1987. Ecoregions of the Conterminous United States. Annals of the Association of American Geographers 77:118–125.
Ott, J. E., E. D. McArthur, and S. C. Sanderson. 2011. Vegetation dynamics at a Mojave Desert restoration site, 1992 to 2007. Natural Resources and Environmental Issues 16.
Oxelman, B., P. Kornhall, R. G. Olmstead, and B. Bremer. 2005. Further disintegration of Scrophulariaceae. TAXON 54:411–425.
Paschke, M. W., L. G. Perry, and E. F. Redente. 2006. Zinc toxicity thresholds for reclamation forb species 170:317–330.
PCA. 2015. National seed strategy for rehabilitation and restoration, 2015-2020. Plant Conservation Alliance. U.S. Department of the Interior, Bureau of Land Management, Washington, D.C.
Pedrini, S., and K. W. Dixon. 2020. International principles and standards for native seeds in ecological restoration. Restoration Ecology 28:S286–S303.
Peterson, J. S., and D. G. Ogle. 2003. PALMER'S PENSTEMON - USDA NRCS. U.S. Department of Agriculture.
Pettersson, L., and M. Asbell. 2024, January 24. Growing experience with Penstemon Palmeri at the Mojave Desert Land Trust Native Plant Nursery.
Pizza, R. B., J. Foster, and L. A. Brudvig. 2023. Where should they come from? Where should they go? Several measures of seed source locality fail to predict plant establishment in early prairie restorations. Ecological Solutions and Evidence 4:e12223.
Plath, S. 2023, March 1. Desert Seeds Resource Center: Conversation about nursery propagation and restoration practices for Mojave native plants (video call).

Plummer, A. P., A. C. Hull, G. Stewart, and J. H. Robertson. 1995. Seeding rangelands in Utah, Nevada, southern Idaho, and western Wyoming. Washington, DC: U.S. Department of Agriculture, Forest Service:73.

Poulos, J. M. 2013. Interspecific interactions between Penstemon palmeri and shrubs in the arid shrublands of the Spring Mountains, Nevada. Utah State University.

Poulos, J. M., A. P. Rayburn, and E. W. Schupp. 2014. Simultaneous, independent, and additive effects of shrub facilitation and understory competition on the survival of a native forb (Penstemon palmeri). Plant Ecology 215:417–426.

Randall, J. M., S. S. Parker, J. Moore, B. Cohen, L. Crane, B. Christian, D. Cameron, J. B. Mackenzie, K. Klausmeyer, and S. Morrison. 2010. Mojave Desert Ecoregional Assessment. The Nature Conservancy of California:210.

Richards, R. T., J. C. Chambers, and C. Ross. 1988. Use of Native Plants on Federal Lands: Policy and Practice. Journal of Range Management 51:625–632.

Salas-Arcos, L., C. Lara, and J. F. Ornelas. 2017. Reproductive biology and nectar secretion dynamics of Penstemon gentianoides (Plantaginaceae): a perennial herb with a mixed pollination system? PeerJ 5:e3636.

SEINet. 2023a. SEINet Portal Network - Penstemon palmeri. https://swbiodiversity.org/seinet/taxa/index.php?taxon=Penstemon+palmeri&formsubmit=Search+Terms#.

SEINet. 2023b. SEINet Portal Network. http//:swbiodiversity.org/seinet/index.php.

SER SID. 2023. Seed Information Database. https://ser-sid.org/.

Shryock, D. F., L. A. DeFalco, and T. C. Esque. 2018. Spatial decision-support tools to guide restoration and seed-sourcing in the Desert Southwest. Ecosphere 9:e02453.

Shryock, D. F., L. K. Washburn, L. A. DeFalco, and T. C. Esque. 2021. Harnessing landscape genomics to identify future climate resilient genotypes in a desert annual. Molecular Ecology 30:698–717.

Smith, A. D., and D. M. Beale. 1980. Pronghorn antelope in Utah: Some research and observations. Salt Lake City, UT: Utah Division of Wildlife Resources:88.

Stevens, R. J., K. R. Jorgensen, and J. N. Davis. 1981. Viability of seed from thirty-two shrub and forb species through fifteen years of warehouse storage 41:274–277.

Stevens, R., and S. Monsen. 1988. "Cedar" Palmer Penstemon: A Selected Penstemon for Semiarid Ranges 10:163–164.

Straw, R. M. 1955. Hybridization, Homogamy, and Sympatric Speciation. Evolution 9:441–444.

Sturwold, P., M. Nash, M. Reeder, and J. Marfori. 2022, December 15. The Living Desert Zoo and Botanic Gardens. Converstation with garden team about nursery growing, seed collection and restoration practices. (video call).

The Xerces Society. 2016. Gardening for Butterflies: How You Can Attract and Protect Beautiful, Beneficial Insects. Timber Press.

Thomson, J. D., P. Wilson, M. Valenzuela, and M. Malzone. 2000. Pollen presentation and pollination syndromes, with special reference to *Penstemon*. Plant Species Biology 15:11–29.

Tropicos. 2023. Missouri Botanical Garden. http://www.tropicos.org.

Uncompahgre Plateau Project. 2008. The Progress Report for the Uncompahgre Plateau Native Plant Program FY 2007.

US EPA, O. 2015, November 25. Ecoregions of North America. Data and Tools. https://www.epa.gov/eco-research/ecoregions-north-america.

USDA NRCS. 2004, September. Native Seed Production, Tucson Plant Materials Center. Tucson Plant Materials Center.

USDA NRCS. 2023. The PLANTS Database. Natural Resources Conservation Service, National Plant Data Team, Greensboro, NC USA. https://plants.usda.gov/home.

UTCIA. 2015. Certified wildland. Utah Crop Improvement Association, Logan, UT. https://www.utahcrop.org/certified-wildland/.

Walker, L. R., and E. A. Powell. 1999a. Effects of Seeding on Road Revegetation in the Mojave Desert, Southern Nevada. Ecological Restoration, North America 17:150–155.

Walker, L. R., and E. A. Powell. 1999b. Effects of Seeding on Road Revegetation in the Mojave Desert, Southern Nevada. Ecological Restoration, North America 17:150–155.
Walker-Larsen, J., and L. D. Harder. 2001. Vestigial Organs as Opportunities for Functional Innovation: The Example of the Penstemon Staminode. Evolution 55:477–487.
Wall, M., and J. MacDonald. 2009. Processing seeds of California native plants for conservation, storage, and restoration. Rancho Santa Ana Botanic Garden, Claremont, Calif.
Wallace, K. 2023, January 24. Lake Mead National Recreation Area, Song Dog Nursery: Conversation about Growing Mojave Desert Native Plants (video call).
Wetherwax, M., and N. H. Holmgren. 2012. *Penstemon palmeri* var. *palmeri*. https://ucjeps.berkeley.edu/eflora/eflora_display.php?tid=63305.
Wilson, M. V. 2004. An Ecological Re-Assessment of Dorena Prairie after Seven Years of Management: Conditions in 2003 and changes since 1996. Page 26 pp. USDI Bureau of Land Management, Eugene District, Eugene, Oregon.
Wyman, L. C., and H. K. Stuart. 1991. The Ethnobotany of the Kayenta Navaho, Albuquerque. The University of New Mexico Press, page 43. http://naeb.brit.org/uses/25931/.
Zachmann, L. J., J. F. Wiens, K. Franklin, S. D. Crausbay, V. A. Landau, and S. M. Munson. 2021. Dominant Sonoran Desert plant species have divergent phenological responses to climate change. Madroño 68.
Zollinger, N., R. Koenig, T. Cerny-Koenig, and R. Kjelgren. 2007. Relative Salinity Tolerance of Intermountain Western United States Native Herbaceous Perennials. HortScience 42:529–534.

RESOURCES

AOSCA NATIVE PLANT CONNECTION

https://www.aosca.org/wp-content/uploads/Documents/AOSCANativePlantConnectionBrochure_AddressUpdated_27Mar2017.pdf

BLM SEED COLLECTION MANUAL

https://www.blm.gov/sites/default/files/docs/2021-12/SOS%20Technical%20Protocol.pdf

OMERNIK LEVEL III ECOREGIONS

https://www.epa.gov/eco-research/level-iii-and-iv-ecoregions-continental-united-states

CLIMATE SMART RESTORATION TOOL

https://climaterestorationtool.org/csrt/

MOJAVE SEED TRANSFER ZONES

https://www.sciencebase.gov/catalog/item/5ea88c8482cefae35a1faf16

MOJAVE SEED MENUS

https://rconnect.usgs.gov/MojaveSeedMenu/

AUTHORS

Casey Hensen, Conservation Technician, Tucson AZ | caseyhensen@appliedeco.org

Ashlee Wolf, Ecologist, Institute for Applied Ecology, Tucson, AZ | ashleewolf@appliedeco.org

Hensen, Casey and Ashlee Wolf. 2023. Palmer's penstemon (*Penstemon palmeri*). In: Mojave Desert Native Plants: Biology, Ecology, Native Plant Materials Development, And Use in Restoration. Corvallis, OR: Institute for Applied Ecology. Online: https://www.blm.gov/programs/natural-resources/native-plant-communities/native-plant-and-seed-material-development/ecoregional-programs

COLLABORATORS