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

CREOSOTE BUSH

Larrea tridentata (DC.) Coville

Zygophyllaceae - Caltrop Family

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ORGANIZATION

NOMENCLATURE

Creosote bush (*Larrea tridentata* (DC.) Coville) belongs to the Zygophyllaceae or caltrop family (USDA NRCS 2023).

NRCS Plant Code.

LATR2 (USDA NRCS 2023).

Synonyms.

The Flora of North America (FNA) lists the following synonyms: *Larrea divaricata var. arenaria* (L. D. Benson) Felger, *L. divaricata subsp. tridentata* (de Candolle) Felger & C. H. Lowe, *L. glutinosa* Engelmann, *L. tridentata var. arenaria* L. D. Benson, and *L. tridentata var. glutinosa* Jepson (Porter 2020).

Common Names.

Creosote bush, creosote bush or creosote. Common names in Spanish include gobernadora, guamis, and hediondilla (Porter 2020).

Subtaxa.

There has been speculation that creosote bush should be divided into three subtaxa corresponding to three chromosome races (see below). However, the chromosome races geographically overlap and cannot be morphologically distinguished. As such, no varieties or subspecies are currently recognized by FNA (Porter 2020).

Chromosome Number.

The chromosome numbers for creosote bush are 2n=26, 52, 78 (CCDB 2023). The species comprises three chromosome races that are generally differentiated across the Warm Desert regions of North America (Chihuahuan, diploid, 2n = 26; Sonoran, tetraploid, 2n = 52; Mojave, hexaploid, 2n = 78), however some geographic overlap does occur (Laport et al. 2016). In the contact zones where cytotypes broadly co-occur, they can differ in habitat affiliations and flowering times that may limit hybridization. However, genetic evidence suggests some degree of intercytotype gene flow where tetraploids and hexaploids overlap (Laport et al. 2016). The hexaploid appears to be the most common race for the Mojave Desert region (Porter 2020).

Since creosote bush possesses intraspecific ploidy variation (differences in chromosome numbers between 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.

Although intercytotype hybridization has been documented, there is no evidence of hybridization with other related species (Laport et al. 2016).

DESCRIPTION

Creosote bush is a perennial evergreen shrub of up to 3.5 meters tall. It produces multiple, many branched slender stems which are reddish when young, and become gray or black at maturity (Porter 2020). Creosote bush has opposite leaves which consist of a pair of leaflets that are united at the base. Leaflets are 4-18mm long by 1-8.5mm wide, dark green and shiny, and are very aromatic, especially after rainfall (Porter 2020, SEINet 2023). Deciduous awns of up to 2mm are present between each leaflet pair (Porter 2020). Creosote bush produces yellow showy flowers which sit solitary on pedicles of 3-13mm in length and are born from the leaf axils (Porter 2020, SEINet 2023). Its flowers are up 3cm in diameter with ovoid, appressed and pubescent sepals, and 5 yellow petals of 7-11mm in length (Porter 2020, SEINet 2023). Its flowers possess stamens of 5-9mm in length and filaments of 4-8mm in length (Porter 2020). Creosote bush produces globose capsule fruits which are 4.5mm in diameter (excluding the hairs) and covered in white, pilose-wooly hairs. Each fruit consists of 5 nutlets (Porter 2020, SEINet 2023).

Figure 1: A creosote bush individual. Photo: Sue Carnahan

Figure 2: The yellow, showy flowers of creosote bush. Photo: Patrick Alexander

DISTRIBUTION AND HABITAT

Creosote bush is widespread throughout the warm desert regions of the southwest United States and northern Mexico (Figure #). It is commonly found in the Mojave Basin and Range, Sonoran Desert, Madrean Archipelago, and south into the Chihuahuan Desert and the Baja Peninsula.

Habitat and Plant Associations.

Creosote bush is nearly ubiquitous in the regions where it occurs, and it often forms large, monospecific stands. NatureServe recognizes three habitat alliances (Creosote bush Chihuahuan Desert Scrub, Creosote bush - Burrobush Bajada & Valley Desert Scrub, and Creosote bush - Ocotillo Upper Bajada & Rock Outcrop Desert Scrub) and 57 habitat associations defined by the presence of creosote bush (NatureServe 2024). Creosote bush-dominated desert scrub associations constitute the vegetation matrix through the valleys, plains, and low hills of the Mojave Desert (NatureServe 2024). The creosote bush-burrobush (*Ambrosia dumosa*) vegetation community covers approximately 70% of the Mojave Desert (McAdoo et al. 1983)

Common associated species in the Mojave Desert include burrobush (*Ambrosia dumosa*), Joshua tree (*Yucca brevifolia*), brittlebush (*Encelia farinosa*), Ephedra (*Ephedra spp.*), desert Indianwheat (*Plantago ovata*), six-week fescue (*Vulpia octoflora*), cheesebush (*Ambrosia salsola*), water-jacket (*Lycium andersonii*), cottontop cactus (*Echinocactus polycephalus*), fourwing saltbush (*Atriplex canescens*), chamise (*Eriogonum fasciculatum*), Fremont's dalea (*Psorothamnus fremontii*), big galleta (*Hilaria rigida*), chollas (*Cylindropuntia* sp.), and others. Common invasive species found in association with creosote bush include red brome (*Bromus rubens*), redstem stork's bill (*Erodium cicutarium*), and Mediterranean grass (*Schismus* sp.) (BLM SOS 2022, NatureServe 2024).

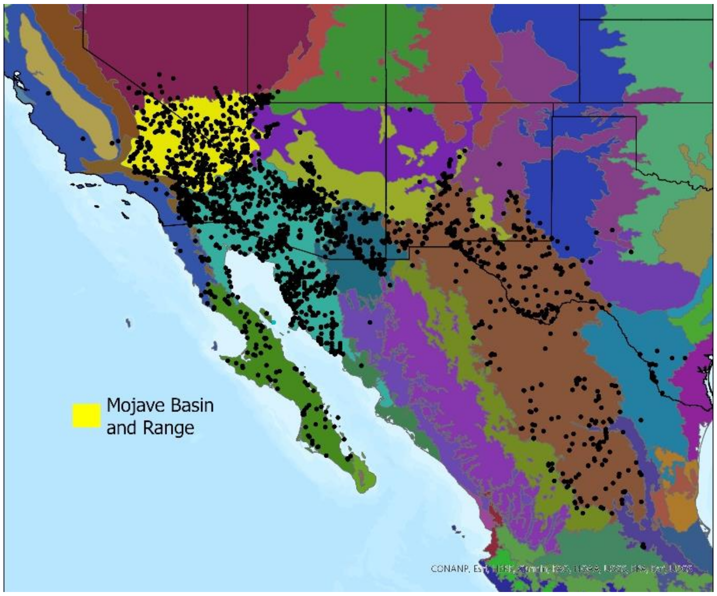

Figure 3: Distribution of creosote bush based on georeferenced herbarium specimens and verified observations (black circles, SEINet 2022) with EPA Level III Ecoregions (US EPA 2015). The Mojave Basin and Range ecoregion is shown in yellow.

Figure 4: Creosote bush as the dominant vegetation in an open desert habitat in New Mexico. Photo: Patrick Alexander

Figure 5: Creosote bush in the Mojave Desert in Utah Photo: BLM UT930

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 creosote bush has been documented (Shryock et al. 2018; Table 1). According to herbarium specimen locations (SEINET 2022), creosote bush is documented in all PSZs in the Mojave Desert ecoregion but is most frequently documented in Zones 21 and 26 and least documented in Zone 22 (Table 1). The average annual precipitation in the PSZs where creosote bush occurs in the Mojave Desert ecoregion is

17.8 cm (7.0 inches), with an average of 5.7 cm (2.2 inches) falling in the summer and an average of 12.1 cm (4.7 inches) falling in the winter. Note, herbarium specimen locations may not represent the full distribution and abundance of creosote bush due to sampling biases.

Table 1: Climate of the provisional seed zones (PSZ) where creosote bush occurs within the Mojave Desert ecoregion (Shryock et al. 2018).#Records = the number of herbarium or verified observations 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)
21	166	15.6	6.2	9.4	18.8	38.4
26	123	14.5	2.7	11.8	16.8	34.9
24	72	10.7	2.8	7.9	18.8	38.6
29	68	25.5	4.2	21.4	13.8	31.7
25	66	16.5	6.2	10.3	18.9	34.6
27	61	9.6	3.3	6.3	20	36.7
23	48	15.8	5.4	10.4	16.1	35.9
20	47	25.5	10.5	14.9	15.3	34.5
28	41	7.8	2.4	5.3	22.3	41.3
22	4	36.1	13.3	22.8	10	32.4

Elevation.

Creosote bush is generally found at elevations between sea level and 5,000 ft (1524 m) (Porter 2020, SEINet 2023).

Soils.

Creosote bush typically occurs in slightly acidic to slightly basic soils that are rocky, sandy, or gravelly (Calscape 2023) where it's often associated with alluvial and granite to volcanic deposits. It can tolerate saline and sodic soils (BLM SOS 2022). It can establish in fine soil layers over hard-pan caliche (Chew 1982).

Creosote bush has complex interactions with biological soil crusts. In a study of nitrogen and carbon movement between creosote bush and moss-dominated biocrusts in the Sonoran Desert, researchers found that the fungi mediate the movement of nitrogen (from biocrust to creosote bush) and carbon (from creosote bush to biocrust) and that this “fungal loop” of nutrient translocation can occur between individuals with up to 1 meter distance of spatial separation (Carvajal Janke and Coe 2021).

In northern Mexico, researchers found that biocrust (lichen and cyanobacteria morphotypes) had significantly higher cover under creosote bush compared to other shrubs and open areas, suggesting a species-specific facilitative association with creosote bush, potentially due to higher soil moisture beneath the creosote bush canopy (Gutierrez et al. 2018).

ECOLOGY AND BIOLOGY

Creosote bush is long-lived and highly drought adapted. Individual shrubs can live up to 100 years, and clonal individuals are estimated to live for over 11,000 years (Vasek 1980, Cody 2000). Creosote bush is highly drought tolerant due to several physiological adaptations including an ability to shift hydraulic behavior in response to moisture availability on relatively short time scales (Guo et al. 2020). Further, hydraulic behavior is driven by strong patterns of local adaptation to variation in winter and summer precipitation and temperature (Custer et al. 2022). In a multiple common garden experiment, creosote bush plants from populations with wetter-colder winters and less variable summer precipitation exhibited faster growth rates in more mesic gardens but lower survivorship in the most arid garden. Plants from populations with more warm-dry winters and variable summer precipitation generally exhibited more conservative traits like lower average leaf cover and shorter leaf duration before shedding (Custer et al. 2022).

Creosote bush is deeply rooted. However, roots can extend up to 13 ft (4 m) outwards from the shrub and approximately 70% of the fibrous root system is within 1 ft (0.30 m) of the soil surface (Briones et al. 1996, Gibbens and Lenz 2001), allowing them to rapidly intercept moisture from precipitation events.

Creosote bush is categorized as a “decreaser” in response to disturbance in the Mojave and Sonoran Deserts (Abella 2010).

Reproduction.

Breeding System.

Creosote bush reproduces both sexually and vegetatively. The age distribution of creosote bush populations indicates that sexual reproduction and subsequent successful germination events are rare (Barbour 1968).

As an individual shrub grows and ages, new stems are produced on the outer edges of the plant while the oldest branches at the center die out (Vasek 1980). This causes the shrub to gradually expand outwards and form a clonal ring with an empty center, sometimes up to many meters in diameter (Cody 2000).

Reproductive Phenology.

Creosote bush flowers most abundantly in spring but can flower anytime of the year after adequate rainfall, and it has one of the lowest rainfall thresholds (12mm) for blooming in the Mojave Desert (Bowers and Dimmitt 1994). Herbarium specimen data show the highest number of flowering individuals are collected in April and May in the Mojave Desert (SEINet 2023). Wildland seed collections of creosote bush typically occur in May through July, with the majority occurring in June (BLM SOS 2022).

Pollination.

Creosote bush has one of the most diverse pollinator guilds documented (Wcislo and Cane 1996). Creosote bush flowers are rich in pollen and nectar rewards that attract a wide array of pollinating insects, especially bees, including 22 specialist pollinators and over 80 generalists (Hurd and Linsley 1975, Minckley et al. 1999). The majority of the pollinators visit during the spring bloom, but a portion (39 species) also visit in the later summer-fall bloom and an even smaller portion (8 species) only visit winter blooms (Hurd and Linsley 1975)

Seed and Seedling Ecology.

Creosote bush seeds are dispersed by tumbling over the ground away from the parent plant, assisted by the wind. They are too heavy to be carried aloft by wind and their trichomes are not stiff enough to be caught in animal fur (Maddox and Carlquist 1985).

Creosote bush exhibits episodic recruitment, typically in response to winter rains (Ackerman 1979, McAuliffe 1988). However, it can germinate under a wide array of temperatures, including after rains during the hottest time of the year in the Mojave Desert (June-September) (Ackerman 1979). Research on germination in the field in Death Valley found that creosote bush germinates at temperatures above 17 ° C (62 °F) and below 30 °C (86 °F) (Went 1948).

Both ants and rodents remove creosote bush seeds (Suazo et al. 2013). Shucking and burial of seeds by rodents may help with germination and seedling survival (Chew and Chew 1970). However, both insects and rodents contribute to seedling mortality by digging and grazing young plants (Steenbergh and Lowe 1969).

Species Interactions.

Belowground Interactions.

Creosote bush exhibits root-mediated allelopathy: roots exude compounds that inhibit the root growth of adjacent plants, of both other species and other creosote bush individuals (Mahall and Callaway 1991).

See Soils for further information on creosote bush interactions with soil microorganisms.

Wildlife and Livestock Use.

Due to its ubiquity and vertical structure, creosotebush is an important habitat and occasional food plant for a variety of wildlife. Its canopy often offers the only shade available, creating a cooler microclimate where small mammals and reptiles find temporary refuge or establish burrows or dens. For example, desert kit foxes (*Vulpes macrotis arsipus*) and kangaroo rats, both banner-tailed (*Dipodomys s. spectabilis*) and Merriam's (*Dipodomys m. merriami*),preferentially construct their dens beneath shrub canopies, including creosote bush (Monson and Kessler 1940, Zoellick et al. 1989). The extensive burrow systems of kangaroo rats in association with creosote bush may increase mortality of creosote bush in the Mojave Desert, potentially due to direct damage to plant roots or loss in soil moisture caused by tunnelling (McAuliffe 1988).

Creosote bush is also an important habitat plant for the federally threatened Mojave desert tortoise (*Gopherus agassizii*), which frequently creates burrows below the shrub's canopy (Esque et al. 2021). Even after fire, dead creosote bush provides vertical structure and thermal refuge for desert tortoises (Drake et al. 2015).

In a study tracking the movement and habitat use of the federally endangered Sonoran pronghorn (*Antilocapra americana sonoriensis*), researchers found that the pronghorn use the creosote bush-burrobush habitat associations more than expected (DeVos Jr. and Miller 2005).

Although creosote bush produces secondary terpene metabolites as an anti-herbivory strategy (Palo and Robbins 1991), some animals consume parts of the shrub. Notably, jackrabbits (*Lepus* spp.) browse the twig ends of creosote bush (Gibbens et al. 1993). Woodrats (*Neotoma lepida*) feed on creosote bush leaves, though the compounds in the leaves may cause the woodrats to have increased water demands and reduced energy (Mangione et al. 2004).

Creosote bush is not browsed by domestic livestock such as cattle or sheep and can be toxic if consumed, though it is avoided due to its unpalatability (Mabry et al. 1977). Although it is not grazed, it can be trampled or damaged when livestock will dig wallow beds beneath the shrubs to take advantage of the shade they provide (Webb and Stielstra 1979).

Pathogens.

An endoyphytic fungi (*Phoma* sp.) can colonize the leaves of creosote bush and cause minor impacts such as small necrotic spots or black pustule-like fruiting structures (Strobel et al. 2011). This fungal pathogen produces hydocarbons and volatile organic compounds that may have applications as biofuels (Strobel et al. 2011).

Other Notable Species Interactions.

Creosote bush can function as a benefactor species for desert annuals that preferentially grow under the shrub's canopy compared to open spaces (Schafer et al. 2012, Badano et al. 2016, Braun and Lortie 2020, Ruttan et al. 2021). However, the proximity resulting from this facilitation can come at a cost for the benefactor or the protégé when both are in bloom—pollinators may spend less time visiting creosote bush if there are more desirable flowers beneath the shrub's canopy (Ruttan et al. 2021) and vice-versa, there can be reduced pollinator visitation to the protégé when pollinators are more attracted to the creosote bush flowers (Braun and Lortie 2020).

Burrobush serves as nurse plant for creosote bush seedlings, which are more often found under burrobush canopies than open spaces (McAuliffe 1988). The creosote bush seedlings establish and grow beneath the burrobush canopy and eventually, the burrobush will die, presumably from competition from the young creosote bush plant (McAuliffe 1988). Notably, creosote bush seedlings are not found under canopies of older creosote bush plants (McAuliffe 1988).

Creosote bush may inhibit germination of other species. For example, bush muhly (*Muhlenbergia porteri*) and black grama (*Bouteloua eriopoda*) seeds treated with extracts of creosote bush have reduced radicle and shoot growth, indicating creosote bush may inhibit seedling establishment due to water-soluble chemical compounds from creosote bush that can leach into the soil (Knipe and Herbel 1966). Despite potential germination inhibition, bush muhly is commonly found growing beneath creosote bush. Still, bush muhly and creosote bush compete for moisture, nutrients, and sunlight while sharing a common footprint (Welsh and Beck 1976, Castellanos-Perez 2000). In a study in the Chihuahuan Desert, researchers found that creosote bush growing without bush muhly had higher photosynthesis rates and stomatal conductance than those growing with bush muhly, suggesting that bush muhly can negatively impact the ecophysiology of creosote bush (Castellanos-Perez 2000). Similarly, they found that bush muhly growing alone had higher net assimilation rate (rate of increase of dry weight per unit of leaf area) than plants growing with creosote bush (Castellanos-Perez 2000). Bush muhly has also been shown to increase in cover when creosote bush live canopy was reduced after herbicide (dicamba) treatments, potentially due to release from competition and inhibition (Whitford et al. 1978).

Creosote bush is a host plant to multiple lepidopteran species including the creosote moth (*Digrammia colorata*), the greasewood moth

(*Agapema galbina*), and a species of giant silkworm moth (*Sphingicampa heiligbrodti*) (Robinson et al. 2010). The specialist moth, creosote bush bagworm (*Thyridopteryx meadii*), uses creosote bush leaves as egg casting material.

Creosote bush is a host to the creosote lac scale (*Tachardiella larrea*), an insect that secretes a resinous compound, known as lac, onto the plant's stems. Lac is similar to plastic in that it is liquid when warm but hardens when cool, forming strong bonds. Lac from the creosote lac scale was used by indigenous people to seal containers, and other species of lac scale insects have economic importance (Sutton 1990).

Disturbance Ecology.

Creosote bush generally decreases in response to disturbances such as root plowing (Roundy and Jordan 1988) and surface disturbing activities like roads and military camps (Prose et al. 1987). However, it has been shown to resprout from physical vehicle damage (being driven over) (Gibson et al. 2004).

Historically, creosote bush communities experienced relatively infrequent fires due to their sparse vegetative cover (Brooks and Minnich 2006). However, in years with sufficient winter precipitation, increased annual plant cover can serve as fine fuels to allow fire to spread between perennial plants. Moreover, the proliferation of invasive annual grasses creates more contiguous and persistent fine fuel loads, initiating a grass/fire cycle that can lead to a complete vegetation community conversion in which invasive grasses dominate (Brooks and Minnich 2006). Creosote bush is poorly fire adapted and has limited resprouting ability after burns (Humphrey 1974, Abella et al. 2021). Fires generally result in high mortality and slow recovery of creosote bush (McLaughlin and Bowers 1982, Brown and Minnich 1986, Abella et al. 2009). Creosote bush resprout frequency depends on fire timing and intensity, as well as the age of burned plants (White 1968). However, creosote bush stems that do resprout after fire can have increased reproductive output and growth rates compared to unburned plants (Molinari et. Al. 2019). In a study of a fire in the western Colorado Desert, creosote bush stands regained their pre-burn cover within five years (O'Leary and Minnich 1981). A study in the Mojave Desert found that a layer of hydrophobic soils developed under burned desert shrubs, including creosote bush, and this soil layer prevented the establishment of vegetative cover on shrub hummocks compared to open areas (Adams et al. 1970). After wildfires in the Mojave Desert, creosote bush communities can take over 25 years to recover perennial plant cover and 50 years to recover species composition comparable to unburned sites (Abella et al. 2021).

Ethnobotany.

Creosote bush has a deep cultural history and is utilized by several tribes such as the Cahuilla, Diegueno, Hualapai, Pima, Mahuna, and Yavapai, to name a few (NAEB 2023). It has several medicinal uses as well as some antimicrobial and sun-blocking properties. Examples of use include treating stomach cramps, pain, aches, skin sores, and respiratory problems (NAEB 2023). Additionally, it is used as a disinfectant and deodorant, and the sticky resin has some tool-making applications (NAEB 2023). For more information, see the North American Ethnobotany Database.

Horticulture.

Creosote bush is a common addition to xeriscape gardens and yards due to its drought tolerance and attractiveness to an abundance of pollinators (Calscape 2023). It can attract beneficial bees, act as a privacy screen and is deer resistant. It is recommended to grow creosote bush in full sun and in rocky or sandy fast-draining soils (Calscape 2023). It is sometimes available from retail nurseries as a container plant (Calscape 2023).

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 creosote bush. 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.

See Chromosome Number for information about intraspecific ploidy variation in creosote bush and implications for seed sourcing.

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.

Creosote bush does not appear to be commonly available for purchase from large-scale commercial seed vendors. When available, 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. There have been no conservation plant releases of creosote bush.

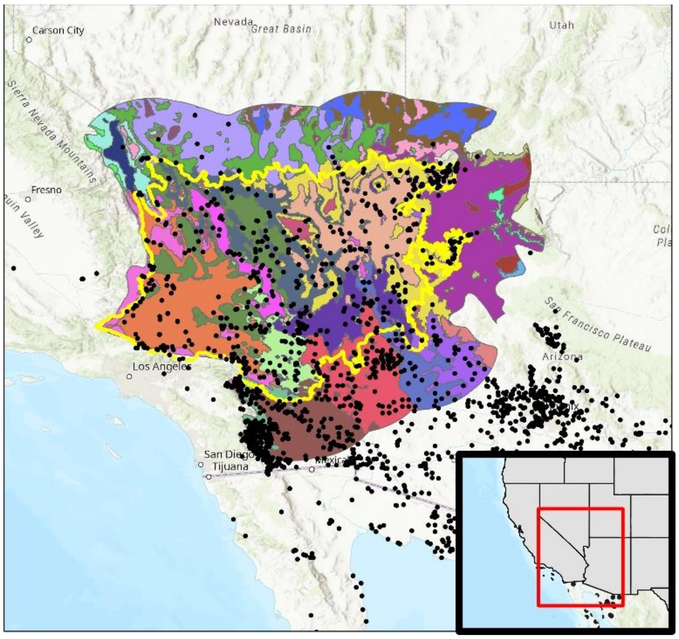

Figure 6: The distribution of creosote bush across the Desert Southwest Provisional Seed Zones (Shryock et al. 2018). Occurrences (black dots) are based on georeferenced herbarium specimens and verified observations (SEINet 2023). The Mojave Basin and Range Level III ecoregion (yellow outline) is buffered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

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.

In the Mojave Desert, creosote bush is typically collected between May through August with the majority of collections occurring in June (BLM SOS 2022).

Collection Methods.

Seed can be collected by hand by plucking fruits from the shrub, one at a time. Seed collectors with the Chicago Botanic Garden have collected creosotebush using badminton rackets and butterfly nets. To do so, they first taped up the heads of the rackets so the strings wouldn't get tangled in the creosote branches. Then, they swatted the ripe seeds off the bush, catching as many seeds as possible in the net. Lastly, they gathered the seed into large bins and removed sticks and leaves by hand (Lisak 2024, personal communication). No specific methods for collection were described in the literature or through personal communication.

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).

Treating creosote bush seeds with insecticide via fumigation or dusting is recommended (Busing 2008).

Figure 7: Collected seed material from creosote bush; scale shown in cm. Photo: BLM SOS CA930A

Seed Cleaning.

Creosote bush seed is relatively difficult to clean. The fruit can be gently rubbed over a #12 or #10 sieve or rubber mat to break the nutlets from the fruit segments. Then, a blower can be used to separate chaffy material and non-viable seed (Wall and MacDonald 2009). The hull can also be removed using a hammermill, however a hammermill can cause higher rates of seed damage and abnormal seedlings (Burgess et al. 1977). A belt harvester, which is used to shell alfalfa, is also successful at hulling creosote bush seed (Graves et al. 1975).

Seed Storage.

Creosote bush seed is orthodox (SER SID 2023). Seeds have been shown to maintain viability after 7 years of storage at room temperature and 9 years of storage at -15 °C (5 °F) (Kay et al. 1988, SER SID 2023).

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 pure seed unit-- a combined unit of seed and attached structures that is classified as pure seed as opposed to inert material —for creosote bush is defined by AOSA as an "intact fruit segment (with or without seed), piece of broken fruit segment larger than one-half the original size (unless there is no seed), seed (with or without seed coat), and a piece of broken seed (with or without seed coat) larger than one-half the original size (AOSA 2016).

An AOSA tetrazolium test protocol for the Larreaa genus may be followed to assess creosote bush seed viability (AOSA 2010). The tetrazolium test protocol for Larrea seed viability assessments first involves preconditioning seed by soaking overnight at 20-25 °C. After soaking, seeds are cut longitudinally, leaving seed within the carpel. Seeds are then placed in a 0.1 % tetrazolium solution overnight or for up to 24 hours at 30-35° C. Viability can then be quantified by assessing the percentage of seeds where the entire embryo is evenly stained (AOSA 2010).

Wildland Seed Yield and Quality.

Wild-collected creosote bush seed is generally of fairly high quality, with an average of 72% fill, 94% purity and 74% viability indicated by tetrazolium tests across 39 Seeds of Success collections (BLM SOS 2022, Table 2). Wild collections contain an average of over 168,000 PLS/lb (BLM SOS 2022, Table 2).

Table 2: Seed yield and quality of creosote bush 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)	2.48	0.21-6.68	39
Clean weight (lbs)	0.48	0.04-1.19	39
Purity (%)	94	85-99	39
Fill (%)	72	15-99	39
Viability (%)	74	20-93	39
Pure live seeds/lb	168,735	19,416-3,855,514	39

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

Large scale commercial seed producers are not eager to grow creosote bush due to its slow-growth rate, relatively low seed output, and likely difficulty of mechanical harvest (Winters 2023, personal communication; Hagman 2023, personal communication). Most shrubs are not considered cost-effective for large scale seed increase (Hagman 2023, personal communication). Wildland populations are extensive and produce seed regularly, reducing the need for agricultural seed increase of this species.

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 pre-variety germplasm certification standards for creosote bush seed in the states where it occurs.

Isolation Distances.

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

Table 3: Crop years and isolation distance requirements for pre-varietal germplasm crops of outcrossing perennial species in Utah. 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 sowing or transplanting creosote bush seeds or plugs. 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).

Seed Pre-treatments.

Removing creosote bush seeds from the hull can improve germination compared to unhulled seeds (Graves et al. 1975). See Seed Cleaning for information on how to hull seeds. Soaking or leaching seeds in water for 12 to 48 hours prior to sowing can remove germination inhibitors and promote imbibition (Graham 2022, personal communication; Wallace 2023, personal communication; Plath 2023, personal communication; Johnson 2023, personal communication). One procedure that works well for leaching is placing the seeds in a nylon stocking in a bucket with water with a fountain pump to aerate and cycle the water, changing the water as often as possible over a 24-to-48-hour period (Plath 2023, personal communication). Similarly, soaking seeds in a leach bucket with charcoal and an aquarium aerator is effective (Asbell 2023, personal communication). Adding a gibberellic acid solution to an overnight soak can further enhance germination rates (Wallace 2023, personal communication).

Seeding Techniques.

Little information is available on seeding techniques. Plug plantings may result in better establishment. See Wildland Plantings for information on planting practices that may be applicable to agricultural settings.

Establishment and Growth.

No information is available on the establishment and growth of creosote bush in agricultural settings.

Weed Control.

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

Pest Management.

No information is available on pest management for creosote bush in agricultural settings.

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).

No recommendations for pollinator management specific to creosote bush were described in the literature or through personal communications. However, it's attractiveness to a diverse guild of pollinators (see Pollination) indicates it may not require special pollination management actions.

Irrigation.

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.

There is no information on harvesting creosote bush seed in agricultural settings.

Seed Yields and Stand Life.

There is no information on seed yields and stand life for creosote bush in agricultural settings.

NURSERY PRACTICE

Creosote bush can be propagated easily from seed. See Seed Pre-treatments for further information on germinating creosote bush seed in nursery settings. Germination typically occurs within 48 hours after sowing and will continue for 6 to 7 days (Graham 2022, personal communication). Creosote bush does not propagate well from cuttings (Sturwold et al. 2022, personal communication; Sale and Perez 2023, personal communication).

Creosote bush plants are often slow growing in nursery containers and can stop growing altogether if they become root constricted (Wallace 2023, personal communication; Asbell 2023, personal communication). If plants are started in a smaller container, they may need to be transplanted after reaching 2" in height (Asbell 2023, personal communication). However, plants can exhibit signs of stress after transplanting (Asbell 2023, personal communication).

Overhead watering is not recommended for creosote bush since it can leach protective residue from the leaves (Graham 2022, personal communication; Wallace 2023, personal communication). Placing pots under drip irrigation or watering by hand allows for water to be delivered directly to the base of the plant (Graham 2022, personal communication; Wallace 2023, personal communication).

The propagation protocol for creosote bush at Joshua Tree National Park is as follows:

After a 24-to-48-hour soak, seeds are sown into open flats in a growing medium of 2 parts sand, 1 part mulch and 2 parts perlite (Graham 2004). After about 2 to 3 weeks, seedlings are transplanted into newspaper cylinders (29 cm tall and 7.5 cm in diameter) held in plastic food wrap. After another 8 to 12 weeks, the plants are transplanted along with their newspaper cylinders (minus the plastic wrap) directly into 2-gallon PVC pots, their final container for restoration outplantings. An Osmocote™ time release fertilizer is incorporated into the medium. Prior to delivery to a restoration site, plants undergo four to eight weeks of hardening off where irrigation frequency and duration is gradually reduced, and plants are moved into an open growing area. This whole process, including time for plants to develop sufficient roots for wildland restoration outplanting typically lasts about 12 months (Graham 2004).

REVEGETATION AND RESTORATION

Creosote bush is an ecologically foundational species and is useful in revegetation and restoration projects to stabilize soil, accelerate ecological functions, and support a diverse pollinator community. As a nurse plant, creosote bush can help facilitate vegetation recovery after disturbance (Badano et al. 2016). Planting nursery grown, containerized stock seems to be more effective and commonly practiced compared to direct seeding in revegetation and restoration efforts.

Wildland Seeding and Planting.

Wildland Seedings.

There is limited information on seeding practices for wildland revegetation and restoration.

Creosote bush was used in a seeding study to assess methods for reducing granivore-driven seed loss from restoration sites in the Mojave Desert (DeFalco et al. 2012). Seed was sourced commercially, though the origin of the source collection is not stated. Creosote bush was seeded in plots at a rate of 117 ± 3 seeds per square meter. They found that seed loss was mitigated by applying a tackifier (a water-soluble latex polymer typically used to reduce dust emissions), although the benefit of tackifier was reduced at 16 weeks after sowing seed. Harrowing prior to seed application to break up soil compaction and increase safe sites for seeds was also effective at reducing seed loss (DeFalco et al. 2012).

Wildland Plantings.

Creosote bush consistently exhibits relatively high survival rates (>50%) when planted from container stock (Abella and Newton 2009). To increase establishment success, plantings should be protected from herbivores such as jackrabbits either by fencing the planting area or using protective structures around individual plants (Clary and Slayback 1984, Abella et al. 2012).

Creosote bush was used in a study of roadside revegetation techniques in the Mojave Desert where researchers found that container plants were more effective than direct seeding for this species (Clary and Slayback 1984). Seed to propagate container plants was purchased from local seed collectors, but the specific source location relative to the planting area was not mentioned. Two irrigation treatments were applied: no irrigation and one gallon of water per plant administered monthly from May to October. Creosote bush plants had 100% survival in irrigated areas and 75% survival in non-irrigated areas five years after planting (Clary and Slayback 1984).

Another study in the Mojave Desert compared outplanting to seeding, as well as a test of herbivory protection and irrigation techniques, to establish several native plant species, including creosote bush (Abella et al. 2012). Seeds for both the direct seeding and container propagation were collected locally for the project. Container plants (1-gallon pots) were either sheltered from herbivores with wire mesh cages or not, and either irrigated or not. Seeding was not successful and did not result in establishment of any seeded species. Creosote bush was one of the most successful species with container outplanting and had up to 28% survival one year after the planting. The protective shelters and irrigation significantly increased establishment survival rates across all species, though information on the relative influence of herbivory protection and irrigation is not provided for creosote bush specifically (Abella et al. 2012).

In the Chihuahuan Desert, creosote bush seedlings were planted in plots that received three different treatments: irrigated, irrigated and fertilized, and not amended (Whitford et al. 2001). Plots were in one of three vegetation communities: ungrazed black grama grassland, creosote bush shrubland, and overgrazed grassland. Seeds were locally collected within the watershed area and propagated for one month in soil flats prior to being transplanted. No seedlings survived in the grassland or shrubland two years after planting, regardless of irrigation or fertilizer treatments. Seedlings survived in the overgrazed grassland and were present up to 15 years after the planting. This suggests that creosote bush prefers to establish in areas of bare ground found in the overgrazed grassland (Whitford et al. 2001).

Another study investigated the survival of salvaged native perennials (including creosote bush) in the Mojave Desert in Lake Mead National Recreation Area (Abella et al. 2015). Plants were hand-excavated from future construction sites within the park, with minimal soil retained. Plants were treated with a rooting hormone and/or a watering treatment. After treatment, plants were placed in temporary nursery with a 1:3 mulch-to-sand mix. To prepare the field site, salvaged topsoil was added to a thickness of 5 cm. Each plant was given 1 liter of water and potting soil during planting, along with a mesh anti-herbivore cage. Survival was recorded at 27 months. After 27 months in the field, creosote bush showed 53% survival (Abella et al. 2015).

In a study to assess methods for assisted natural regeneration (ANR) in the Mojave Desert, researchers applied irrigation and herbivory shelters to naturally occurring creosote bush seedlings (Abella et al. 2020). They found that irrigation did not improve seedling survival or growth. Herbivory shelters reduced survival by 31% but tripled height growth of surviving seedlings. These results suggest these ANR practices may not be beneficial to creosote bush (Abella et al. 2020).

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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/

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COLLABORATORS