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Techniques for Restoring Damaged Mojave and Western Sonoran Habitats, Including Those for Threatened Desert Tortoises and Joshua Trees
Scott R. Abella
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Roadside Enhancement of Creosote Bush (*Larrea tridentata*) in the Desert
David K. Lynch

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A journal devoted to broadening knowledge of plants indigenous or adapted to arid and sub-arid regions and to encouraging the appreciation of these plants.

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From the Editor

Welcome to the first fully digital issue of Desert Plants. We hope that the journal will continue to serve you by providing diverse and interesting articles related to plants from dry regions.

This issue features a detailed study examining ecological restoration in the Mohave Desert and western Sonoran Desert. Restoration work in this arid region is particularly challenging due to a variety of factors. The authors present results on the effectiveness of various techniques to accomplish restoration and thoughts on how climate change may influence future efforts. The second paper presented in this issue examines the density and size of creosote bush plants growing adjacent to roads in the Mohave Desert compared with plants in areas further from roads. This study found that plant density and size along roads are the result of factors that are more complex than might be apparent. I extend my sincere thanks to each of the authors for their work in preparing these manuscripts.

Thank you for your interest in Desert Plants journal.

Matthew B. Johnson
Editor, Desert Plants

Cover Photo: Western Joshua trees in diverse shrubland including native annual forbs in Joshua Tree National Park, southern Mojave Desert, California (S.R. Abella).

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Cresote located in Tucson, Arizona by Darci Parsley on Unsplash

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Techniques for Restoring Damaged Mojave and Western Sonoran Habitats, Including Those for Threatened Desert Tortoises and Joshua Trees

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Abstract

Ecological restoration has potential for contributing to conservation activities for threatened Mojave desert tortoises (*Gopherus agassizii*) and Joshua trees (*Yucca brevifolia*, *Y. jaegeriana*) and the Mojave and western Sonoran Desert ecosystems the species inhabit. To be effective, restoration actions deployed strategically need to halt and reverse habitat degradation, replenish or enhance resources used by both species (e.g., large shrubs for protection of tortoises and nurse plants facilitating recruitment of Joshua tree seedlings), and ideally foster resilience during likely future environmental changes. We synthesized restoration techniques and their effectiveness in the Mojave and western Sonoran Desert, provide estimated costs of candidate techniques, and anticipate future research needs for effective restoration in changing climates and environments. Over 50 published studies in the Mojave and western Sonoran Desert demonstrate that restoration can improve soil features (e.g., biocrusts), increase cover of native perennial and annual plants, enhance native seed retention and seed banks, and reduce risk of fires to conserve mature shrubland habitat. We placed restoration techniques into three categories: restoration of site environments, revegetation, and management actions to limit further disturbance and encourage recovery. Within these categories, 11 major restoration techniques (and their variations) were evaluated by at least one published study and range from geomorphic (e.g., reestablishing natural topographic patterns) and abiotic structural treatments (e.g., vertical mulching) to active revegetation (e.g., outplanting, seeding). For example, 16 outplanting studies assessed performance of 46 species to begin identifying top-performing species, associated treatments (e.g., protection from herbivory) required to aid outplant survival, and potential for outplants to trigger formation of self-sustaining populations. Creosote bush (*Larrea tridentata*), a shrub that tortoises use for cover and that serves as a nurse plant for Joshua tree recruitment, achieved at least

50% survival in five of eight studies. Estimated costs for restoring desert habitats varied primarily with the severity of the disturbance, site factors including the diversity of vegetation that was lost, logistical factors such as accessibility of sites (influencing transportation costs), and the cost-effectiveness of the restoration techniques chosen. The review highlights six major research and adaptive management needs for advancing desert habitat restoration. These needs include: 1) continued development of innovative techniques and bet-hedging approaches to provide managers with "tool boxes" of candidate treatments to deploy in dynamic environmental and management conditions, 2) identifying how to optimize spatial deployment of limited restoration resources, 3) developing practical techniques for reducing non-native annual grasses across spatial scales, 4) improving linkages between habitat enhancements and short- and long-term indicators of tortoise usage and responses and Joshua tree population sustainability, 5) mitigating multiple, interacting stressors with cumulative impacts, and 6) integrating biotic (e.g., seeding) and abiotic (e.g., fencing, shade structures) treatments to complement each other at site and landscape scales in dynamic climates and environments. It is possible that bet-hedging approaches employing multiple treatment types (or phased treatments across years) and greater incorporation of abiotic treatments, which are less sensitive to timing of precipitation compared with biotic treatments, will become increasingly important under future climates projected to be drier and more variable. Existing research suggests that restoration can be deployed effectively even under adverse climatic conditions, but success requires identifying suitable techniques tailored to dynamic environments.

Introduction

Studies of recovery of topographic features, soils, and vegetation after disturbances have a multi-decadal history in the Mojave and western Sonoran Desert. For example, Webb (1983) conducted research on recovery of soils and vegetation following human disturbances, Elvidge and Iverson (1983) evaluated recovery of desert pavement, and Heede (1983) examined rehabilitation of rills and gullies created by off-road vehicle traffic. Substantial attention was devoted to research on natural recovery of vegetation after different types of disturbances (e.g., Johnson et al. 1975, Vasek et al. 1975a, 1975b, 1979/1980, Lathrop and Archbold 1980a, 1980b, Lathrop 1983, Brum et al 1983, Lovich and Bainbridge 1999, Anderson and Ostler 2002). More recently, Hereford (2009) discussed recovery of landscape disturbances caused by old military camps. Abella (2010) reviewed and summarized findings on estimated times for recovery of various species of plants. These and other works indicate that from decades to centuries can be required for natural recovery of composition and diversity of soils, shrubs, native grasses, and annual forbs (e.g., Berry et al. 2015, 2016). As understanding of recovery on disturbances progressed, recognition of the complexity of desert ecosystem processes was the first of many steps in moving toward research focusing on ecological restoration for accelerating recovery in degraded ecosystems. Kay et al. (1977) and Kay (1979) outlined the physiological and ecological requirements for growing species of native shrubs and bunch grasses for revegetating disturbed areas along a Los Angeles aqueduct, a major pipeline traversing 160 km in the western Mojave Desert. They experimented and described the characteristics of several species of shrubs and grasses common in the Mojave Desert and their potential use in revegetating disturbed soil. The studies ranged from collecting and evaluating survival of seeds to survival rates of seedlings and shrubs after planting (Kay and Graves 1983; Kay 1988). The investigators also experimented with revegetating soils covering the buried aqueduct pipeline, seeded several different species, and compared those areas with controls. Bainbridge et al. (1995) outlined planning considerations for desert restoration projects, such as understanding ecosystem processes, selecting reference sites perceived as high-quality habitat to assist with establishing restoration goals, and procedures for obtaining plant materials. Subsequently, Bainbridge (2007) presented a manual discussing ideas and techniques for a variety of revegetation, soil rehabilitation, and hydrological restoration applications. Abella and Newton (2009) followed with a review of published information on the performance of revegetation efforts. Weigand and Rodgers (2009) summarized revegetation efforts in Joshua Tree National Park and provided a list of candidate plant species for effective revegetation.

Given often slow natural recovery, there continues to be interest in restoring habitat quality on degraded sites in the Mojave and western Sonoran Desert, including in national park units, protected areas, and where fires have reduced cover and diversity of native shrubs (e.g., Abella et al. 2021). Two of the most recent stimuli for research on developing techniques for restoring topographic features, soils, and native vegetation include: the precipitous decline in the herbivorous Mojave or Agassiz's desert tortoise (*Gopherus agassizii*; herein desert tortoise; Figure 1), found primarily in the Mojave and western Sonoran deserts and peripherally in the ecotone between the Mojave and Great Basin deserts; and the decline and loss of the geographic range for the western Joshua tree (*Yucca brevifolia*), the

Figure 1. Mojave desert tortoise in Lake Mead National Recreation Area, eastern Mojave Desert, southern Nevada (S.R. Abella).

iconic tree found in the western and southern Mojave and southern Great Basin deserts (Figure 2), and the eastern Joshua tree (*Y. jaegeriana*) in the eastern and northeastern Mojave and western Arizona deserts (Lenz 2007; Berry and Murphy 2019; Hess and Baldwin 2022a, 2022b). These species are under siege from multiple anthropogenic-related activities, triggering loss and degradation of habitat and reduced geographic ranges (e.g., Berry and Murphy 2019, Wilkening et al. 2020, Berry et al. 2021, California Department of Fish and Wildlife 2022; Figure 3).

Desert tortoise populations were listed in the state of California in 1989 as threatened and federally listed under the U.S. Endangered Species Act as threatened north and west of the Colorado River in 1990 (California Department of Fish and Wildlife 2022, U.S. Fish and Wildlife Service [USFWS] 1990). A recovery plan and critical habitat designations were prepared in 1994 and updated in 2011 (USFWS 1994a, 1994b, 2011). The tortoise could be along a trajectory toward extinction, with most populations by 2014 having declined below viability (USFWS 2015, Allison and McLuckie 2018, Berry and Murphy 2019). In 2021, the International Union for the Conservation of Nature placed the desert tortoise on the Red List as a critically endangered species (Berry et al. 2021). The western Joshua tree became a candidate for California's list of endangered and threatened plants in 2020 and remained under consideration in June 2022 (California Department of Fish and Wildlife 2022).

Figure 2. Western Joshua trees in diverse shrubland including native annual forbs in Joshua Tree National Park, southern Mojave Desert, California (S.R. Abella).

The USFWS conducted a status assessment of both the western and eastern Joshua trees in response to a 2015 petition for federal listing as threatened (Everson 2019). Although the assessment concluded that listing was not warranted in 2019, the assessment reinforced identification of wildfires, non-native plants, habitat loss, and rapid climatic changes as the primary known threats to Joshua trees (Everson 2019).

Both the desert tortoise and Joshua tree are emblematic species of the Mojave and western Sonoran Desert and

Figure 3. Top photo: comparison of structure between unburned (left) and burned (right) habitat persisting 14 years after the 2005 Loop Fire in Red Rock Canyon National Conservation Area, eastern Mojave Desert, southern Nevada. Creosote bush is a major species that tortoises utilize for cover and thermal protection and as a location for constructing burrows. While some creosote bushes have resprouted, they remain smaller and 90% lower in numbers in the burned area. Bottom photo: example of relatively undisturbed habitat with abundant nurse shrubs, herbaceous perennials including desert globemallow, and annual plants. The site is west of the Newberry Mountains, eastern Mojave Desert, southern Nevada. Photos by S.R. Abella in October 2018 (top) and April 2017 (bottom).

primarily found there. They occupy roles of keystone, flagship, and umbrella species. For keystone species, we use the definition of Cottee-Jones and Whittaker (2012): "… a species that is of demonstrable importance for ecosystem function." The tortoise and Joshua tree fulfill the definition of flagship and keystone species because of their large geographic distributions, threatened or endangered status, central roles in desert ecosystems, recognition regionally, charisma, and cultural significance (Bowen-Jones and Entwistle 2002). The tortoise and Joshua tree are also umbrella species, either in whole or in part because their "…conservation confers protection to a large number of naturally co-occurring species" (Roberge and Angelstam 2004, Branton and Richardson 2010). The burrows of tortoises, for example, provide food, nesting, cover, and many other habitat features for invertebrates, reptiles, birds, and mammals (e.g., Woodbury and Hardy 1948, Roberge and Angelstam 2004, Walde et al. 2009, Agha et al. 2017). Further, the tortoise is an ecological engineer because it modulates the availability of resources for other species with construction and use of burrows (e.g., Jones et al. 1994, Pike and Mitchell 2013). Several species of animals are associated with Joshua trees, and some may depend on them: desert night lizard (*Xantusia vigilis*), desert spiny lizard (*Sceloporus magister*), ladder-backed woodpecker (*Dryobates scalaris*), Scott's oriole (*Icterus parisorum*), cactus wren (*Campylorhynchus brunneicapillus*), loggerhead shrike (*Lanius ludovicianus*), American kestrel (*Falco sparverius*), white-tailed antelope ground squirrel (*Ammospermophilus leucurus*), and desert wood rat (*Neotoma lepida*; Miller and Stebbins 1964, Borchert and DeFalco 2016). Swainson's hawk (*Buteo swainsoni*) nested in Joshua trees in the past (Riseborough et al. 1989), and common ravens (*Corvus corax*) also perch and nest in the branches.

The USFWS, as part of recovery efforts for tortoises, established regional Recovery Implementation Teams to accelerate recovery efforts. The teams ranked restoration of habitat as a high priority for aiding conservation efforts for tortoises (e.g., Darst et al. 2013). With this ranking for tortoises coupled with pending consideration of state listing for western Joshua trees, we emphasized the requirements of these species in summarizing projects to restore their habitats and ecosystems in the Mojave Desert and adjacent ecotones with the Great Basin and western Sonoran deserts (Tables 1, 2).

Often associated with the desert tortoise and Joshua tree, the creosote bush (*Larrea tridentata*), is a foundational species that structures habitat in the Mojave and western Sonoran Desert (Rundel and Gibson 1996, Reynolds et al. 1999). Gibson et al. (2004) summarized one of creosote bush's important characteristics: "Its coppice mounds are the largest in the desert scrub community and harbor many animal burrows, and as fertile islands, these shrubs serve as an important nutrient base for a desert community." It is more long-lived than tortoises or Joshua trees—potentially in the thousands of years where large clones have formed (Vasek 1980, Bolling and Walker 2002, McAuliffe et al. 2007). Vasek (1983) wrote that "creosote bush communities are very old, mature communities of shrubs"; and that "…annuals comprise an integrated and adapted component of very old communities." Vasek (1983) further noted that "…annuals, or at least some constellations of annual species, may be members of stable old communities and therefore probably have evolved intricate highly integrated adaptations for long persistence in stable desert conditions." Native annuals often utilize the shaded, nutrient-enriched soils, termed fertile islands, below creosote bushes and other shrubs (Abella and Smith 2013). In turn, native annual forbs are generally the most

Table 1.
Characteristics and requirements of Mojave desert tortoises for consideration when restoring habitat in the Mojave and western Sonoran Desert

Topic	Relevant subject matter for restoration of habitat	Key references
Geographic range	Current range: North and west of the Colorado River Grand Canyon complex in the Mojave and western Sonoran Desert. States: southern deserts SE California north to Owens Valley; S Nevada N to Beatty; SW Utah in Mojave Desert; NW Arizona and a limited population in a hybrid zone in NW Arizona where Mojave Desert vegetation meets Sonoran Desert vegetation.	1, 2, 3
Current distribution	Loss of habitat in many valleys and hills (e.g., Antelope, Apple, Lucerne, Fremont, Indian Wells, Lanfair, Ivanpah, Las Vegas, Virgin River) to agricultural, mining, urban, military, and energy development. Current distribution is truncated from distributions shown in maps of the former geographic range (Nussear et al. 2009, Berry and Murphy 2019, Berry et al. 2021). Tortoises are not found in severely degraded habitats with loss of vegetation and compacted soils.	2, 4, 5, 6, 7
Elevational range	Generally from 190 to ~1300 m, but can be found almost anywhere due to release of captives.	2, 8
Critical habitat	Designated critical habitat has also lost land to expansion of military bases in the central and southern Mojave Desert, with more anticipated losses with the western expansion of the National Training Center, Ft. Irwin, California.	6, 9
Connectivity between critical habitats and populations	Some potential valuable areas exist for maintaining connectivity between desert tortoise populations in critical habitats and are described. However, key areas of connectivity in the western and northwestern Mojave were not included, e.g., connecting areas between the Fremont-Kramer critical habitat unit through the El Paso Mountains into Indian Wells Valley and Rose Valley to designated wilderness areas along the foothills of the eastern Sierra Nevada.	10, 11
Plant communities	Many different plant community types in the western Sonoran Desert of California, throughout the geographic range in the Mojave Desert and the ecotone with the Great Basin Desert. Absent from areas at low, dry elevations where shrubs are sparse and forage is limited. In the western Sonoran Desert, typical plants include trees found in microphyll woodlands in ephemeral stream beds, e.g., ironwood (*Olneya tesota*), palo verde (*Parkinsonia florida*), and smoke trees (*Dalea spinosa*). On adjacent alluvial fans and valleys are ocotillo (*Fouquieria spendens*) and teddy-bear cholla (*Cylindropuntia bigelovii*), mixed with creosote bush (*Larrea tridentata*) communities. In the Mojave and western Sonoran deserts, saltbush or members of the Chenopodiaceae (*Atriplex*) communities commonly occur near some playas, often in association with creosote bush and white bursage (*Ambrosia dumosa*) communities with few to many species of shrubs and native perennial grasses; these communities are common and widespread throughout the geographic range of the desert tortoise. At mid-elevations in the Mojave Desert, plant communities include western or eastern Joshua trees (*Yucca brevifolia, Y. jaegeriana*, respectively), other species of yuccas (Y. *schidigera, Y. baccata*) and cacti (e.g., members of the *Cactaceae*). In southwestern Utah in the ecotone with the Great Basin, creosote bush communities transition into sand sage (*Artemesia filifolia*) and blackbrush (*Coleogyne ramosissima*). Desert tortoises are absent from pinyon-juniper woodlands, but occur with junipers and Joshua trees.	2, 7, 8, 12, 13, 14, 15, 16
Topography	Once common to frequent in many valleys, alluvial fans, rolling hills, boulder and rocky outcrops, base of mountain ranges. Absent from high elevations (> 1300 m) in mountain ranges, cliffs, and steep slopes.	13, 15
Surficial geology and soils	Rare to absent on talus slopes and rocky habitat with large rocks or dense cobbles and rocks. Tortoises of all sizes must be able to walk or travel easily, without risk of overturning and being trapped between cobbles or rocks. Soils must be suitable for digging burrows without collapsing. Sandy loam, loam, and loamy fine sands with some clay are suitable for supporting burrows and native wildflowers. Soils should be free of elemental toxicants present in some mining districts.	17, 18, 19, 20, 21, 22
Ephemeral stream channels	Ephemeral stream channels of different sizes, depending on location in the hydrological system of valleys, hills, and mountain ranges, provide important sources of cover because of increased density and diversity of vegetation, forage, locations for travel, and burrows. Axial ephemeral stream channels are generally wide with rapidly flowing water during storms, whereas secondary, tertiary, and quaternary drainage systems are generally more important for use (travel) and specialized forage species that grow in stream channels.	15. 21, 22, 23
Temperature constraints	Tortoises cannot tolerate the heat typical of mid-late spring, summer, and early autumn days. They retreat to shade at body temperatures between 37° and 38°C. Overheating occurs at 39.5°C and death at internal temperatures between 39.5° and 43.0°C.	24, 25

Requirements for cover and underground retreats	Tortoises spend most of their lives in the shelter of burrows, dens, rock shelters, and caves—an estimated 98% of the time underground. Time underground enables avoiding extremes of temperature, water loss, and predators. Not all underground retreats are equal: tortoises have multiple burrows but generally only a few are sufficiently deep to withstand the extremes of temperature.	21, 22, 26
Types of cover for adults and juveniles	With few exceptions, most burrows constructed by adults and smaller tortoises are under shrubs with greater shade-giving canopies such as catclaw (*Acacia greggii*), Mojave yucca (*Y. schidigera*), and creosote bush. At a southern Nevada site, 72% of burrows were under such shrubs. At multiple sites in California, 79% of burrows used by juvenile and immature tortoises were under canopies of large live or dead shrubs with creosote and white bursage as common species. In situations where tortoises use dens and caves in wash banks, the sites may not be associated with a shrub. In a multi-year study of released head-started juvenile tortoises, juveniles placed burrows under large creosote bushes, limbs of downed Joshua trees, and Cooper's thornbush (*Lycium cooperi*).	20, 21, 27, 28, 29
The importance of coppice mounds	Coppice mounds beneath large and usually older shrubs (i.e., creosote bushes) are composed of soil and detritus from the shrub itself, dead annual plants, and windblown sand. They are rich in nutrients, rodent and other animal holes, and provide easy digging for juveniles and all sizes of tortoises. Importantly, they are locations for nests within burrows and on the mounds or opening of burrows. Coppice mounds are easily damaged by livestock grazing, off-road vehicle use, and other disturbances.	30, 31, 32, 33
General statements about feeding and forage	Tortoises are primarily herbaceous, feeding on native winter annual forbs and herbaceous perennial subshrubs from late winter through spring and grasses in summer. They have been observed to consume bones, dead lizards, and caterpillars. Winter annuals are important foods from late winter through spring, and grasses in summer. Green, succulent plants are preferred to dry foods.	21, 26, 34, 35
Avoidance of plants high in potassium	Tortoises do not eat leaves, stems or other parts of shrubs, because shrubs in general are high in potassium. Similarly, many species of annual plants are also high in potassium and are not eaten. Potassium requires free water to process and free water is rarely available. The concept of potassium excretion potential, known as PEP, is important to understand when studying choice of plant foods by the desert tortoise.	21, 26, 36, 37
Selection and timing of foods	Tortoises are highly selective in choice of plant foods, drawing on different annual and herbaceous perennial plants by phenology. They also consume some species of cacti. In general, native annual plants are preferred to non-native, except for the forb, filaree (E*rodium cicutarium*). Plant families with preferred species include *Asteraceae, Boraginaceae, Cactaceae, Fabaceae, Malvaceae, Nyctaginaceae, Onagraceae*, and *Plantaginaceae*. However, not all plants are eaten in these families, only a select few.	34, 35, 38, 39
Sizes and types of selected food plants dependent on size of tortoise	The size of tortoise and the size and strength of the beak determine the diet. Juvenile tortoises have limited reach and small, delicate beaks. They are unable to bite through cactus pads or well-developed leaves of such species as desert globemallow, which adults can consume. Juveniles are limited to plants with delicate leaves, e.g., desert dandelion (*Malacothrix* spp.), desert plantain (*Plantago ovata*), and some species in the borage family (*Cryptantha* spp.).	36, 40
Non-native annual grasses are undesirable forage and are harmful	The Mojave Desert and ecotones with the Great Basin and western Sonoran Desert have several species of non-native grasses in the genera *Schismu*s and *Bromus*. These and native grasses are undesirable forage when they are the sole source of the diet, because they cause nutrient losses and require water to digest. In experimental studies, juveniles fed exclusively grasses do not thrive and have high death rates. In addition, the awns of grasses may become imbedded in the jaws, causing infection.	41, 42, 43, 44, 45
Requirements and sources of free water	Tortoises require free water and emerge from burrows, caves, and dens to drink during rain, if dehydrated. They will travel to sites where water collects such as at the base of rocks or on boulders, or tortoises will construct water catchments.	46, 47
Consumption of soil at soil licks	Tortoises consume soil at licks, a common activity of ungulates. They may be obtaining needed minerals; the minerals sought may be calcium or other nutrients. Use of licks was observed in the walls of washes and on areas of selected desert pavement.	48

Notes:
References: (1) Murphy et al. 2011, (2) Berry and Murphy 2019, (3) Edwards et al. 2015, (4) von Seckendorff Hoff and Marlow 2002, (5) Nussear et al. 2009, (6) U.S. Fish and Wildlife Service 2010, (7) Berry et al. 2013, (8) U.S. Fish and Wildlife Service 1994a, (9) U.S. Fish and Wildlife Service 1994b, (10) Averill-Murray et al. 2013, (11) Averill-Murray et al. 2021, (12) McLuckie et al. 2002, (13) Berry et al. 2006, (14) Berry et al. 2014a, (15) Berry et al. 2014b, (16) Berry et al. 2020a, (17) Weinstein 1989, (18) Selzer and Berry 2005, (19) Chaffee and Berry 2006, (20) Burge 1978, (21) Woodbury and Hardy 1948, (22) Mack et al. 2015, (23) Jennings 1997, (24) Brattstrom 1961, (25) Brattstrom 1965, (26) Nagy and Medica 1986, (27) Berry and Turner 1986, (28) Rautenstrauch et al. 2002, (29) Berry, K.H. personal observations based on 2012-2022 observations and use of burrows by juvenile and small immature tortoises, (30) Webb and Stielstra 1979, (31) Rundel and Gibson 1996, (32) Reynolds et al. 1999, (33) Gibson et al. 2004, (34) Avery and Neibergs 1997, (35) Jennings and Berry 2015, (36) Oftedal 2002, (37) Oftedal et al. 2002, (38) Burge and Bradley 1976, (39) Turner et al. 1984, (40) Morafka and Berry 2002, (41) Nagy et al. 1998, (42) Medica and Eckert 2007, (43) Hazard et al. 2009, (44) Hazard et al. 2010, (45) Drake et al. 2016, (46) Medica et al. 1980, (47) Henen et al. 1998, and (48) Marlow and Tollestrup 1982.

Table 2.
Characteristics and requirements of western and eastern Joshua trees (*Yucca brevifolia, Y. jaegeriana*, respectively) to consider for restoring habitat in the Mojave Desert and ecotones with the southern Great Basin Desert. When reviewing the literature described here and elsewhere, note that not all authors separate Joshua trees into the two different species. For each study reported here, we assigned each species to the appropriate taxon according to location of the study area.

Topic	Relevant subject matter for restoring habitats with Joshua trees	Key references
Taxonomic considerations	Authors have distinguished two species with several differences in morphology and structure of trunks and branching, leaf length, floral characters, and pollinators. Phenotypic differences in the two species are best explained by differences in pollinator species.	1, 2, 3, 4
Geographic distributions of the two species	*Y. brevifolia*: southern, western, and northern Mojave Desert in California and northern Mojave Desert in Nevada. *Y. jaegeriana*: northwest and western Arizona, eastern California, southern to central Nevada, and extreme southwestern Utah. The species have separate distributions but grow together in the Tikaboo Valley of Lincoln County, Nevada.	1, 4
Elevations	*Y. brevifolia*: 200-2300 m; *Y. jaegeriana*: 700-2000 m in CA; NV, AZ, UT.	4
Plant communities	Many regions and plant communities, depending on whether *Y. brevifolia* or *Y. jaegeriana*. *Y. brevifolia:* southern and eastern slopes of Sierra Nevada, Tehachapi Mountains, to the western and southern Mojave Desert. Occurs in creosote bush, mixed desert scrub, blackbrush (*Coleogyne ramosissima*), sage brush (*Artemesia tridentata*), to lower-elevation ponderosa pine (*Pinus ponderosa*) forests. *Y. jaegeriana*: from the Sonoran Desert, AZ, to the ecotone with the Mojave-Great Basin deserts in similar plant zones. Precipitation is relatively evenly distributed throughout the year.	1, 4, 5
Topography	Valleys, flats, hills, and mountainous slopes.	4
Soils and surficial geology	Rich valley soils with abundant underground water; sandy and gravelly soils; soils of loam that retain moisture; plains, desert pavements covering fine clay soils, hard-packed clay; and pebbly surfaces of volcanic origin. Mesas, alluvial fans, and bajadas.	1, 6, 7
Reproduction: rosettes, growth of underground rootstocks, seeds	Plants may develop rosettes and shoots from rhizomes and on the stem or trunk. Rosettes were observed on all age classes for *Y. brevifolia*, but only on the stem for *Y. jaegeriana*. Reproduction from rosettes may be treated as a mixed cohort. However, few plants died during the 20-year study, and most were in the young classes.	1, 7
Reproduction from seeds	Few seedings survive due to browsing by lagomorphs and rodents; germinability of seeds remaining in soils was reduced after 12 month and declined to < 3% after 40 months. Rodents disperse and cache seeds.	1, 7, 8, 9
Importance of nurse plants for seedling survival	In a Nevada study on transects spanning elevations from creosote bush to pinyon-juniper communities, 93% of Joshua tree seedlings occurred below canopies of woody shrubs; 16 species of plants nursed *Y. jaegeriana*. Blackbrush was the most frequent nurse. Pima rhatany (*Krameria erecta*), white bursage (*Ambrosia dumosa*), and spiny hopsage (*Grayia spinosa*) nursed more seedlings than expected at one study area. Microhabitat associated with the nurse plants was also important (east vs. west sides of shrubs), influencing soil moisture and nutrients beneath canopies. In another study, seed survival was greater under creosote bush (*Larrea tridentata*) than in the open. In a study of seed caching by rodents, caches were usually close to or under blackbrush, Nevada ephedra (*Ephedra nevadensis*), Anderson thornbush (*Lycium andersonii*), and creosote bushes.	5, 7, 10, 11
Production of fruit, dispersal of seeds, and consumption of seeds	Production of fruit is highly variable. Yucca fruit consumed by yucca larvae, horses, feral burros, mule deer, Scott's orioles (*Icterus parisorum*), Mohave ground squirrels (*Xerospermophilus mohavensis*), white-tailed antelope squirrels (*Ammospermophilus leucurus*), and rodents. Production of fruits and seeds varies by year, high in some years, low in others. Seeds are dispersed by seed-caching rodents.	9, 10, 12, 13, 14
Importance of microhabitat to growth of seedlings and seedling survival	Seedlings are defined as plants < 25 cm in height. At one-month post-germination, most seedlings have a single cotyledon, occasionally 1 or 2 primarily leaves and were ≤ 7 cm tall; at one year, seedlings grew to ≤ 8 cm tall, with 1, 2, 3, or rarely 4 leaves. More seeds in shade emerged. Mortality was high from rodents. Timing of rainfall is important in germination, growth, and survival. Drought contributes to losses of juveniles < 1 m tall, from rodents and black-tailed hares (*Lepus californicus*).	8, 12, 13, 14
Variation in growth rates by location and year	Growth rates depended on location, microhabitats, and precipitation. Growth between 1975-1995 was evaluated for both species. In the southern part of the range, *Y. brevifolia* grew 5.8 and 5.1 cm/year, depending on decade, for stems before branching began, but growth rates were lower for plants that had branched. In the northern part of the range, growth rates were 3.8 and 2.2 cm/year for total height depending on decade. For *Y. jaegeriana*, growth in total height was 3.4 and 4.1 cm/year depending on decade. In another study in Utah, growth rates were 3.8 cm and 3.6 cm/year.	7, 15

Time to first flowering or reproduction, may be site-dependent	*Y. brevifolia*: Yucca Flat, Nevada: at 2.1 m in height; < 30 years.	7, 14, 16
Sizes of Joshua trees	Largest known *Y. brevifolia* was in Antelope Valley, California, and was 24 m until set on fire. In 2007, the largest tree of this species occurred in remote parts of Joshua Tree National Park. Height: typically 6-9 and to 16 m, branching at 1 to 3 m above plant base. *Y. jaegeriana* height: typically 3 to 6 and up to 9 m, branches < 1 m above base.	1, 4, 15, 17
Population recruitment and survival	Low for germinating seeds and young *Y. brevifolia* at one site in the southern range, also low in the north over 20 years; none for one site in the western range for *Y. jaegeriana* in a 20-year period. In a Utah study of trees ranging from 2 to 150 or more years old, the annual per capita survival probability was 0.896 for 1987 to 2001; the authors estimated 50% will survive to reach 100 years.	7, 15
Generation time	30 or more years.	14
Life span	*Y. brevifolia*: 100 years, and some likely much older. *Y. jaegeriana*: oldest known of 383 years from southwestern Utah, with an estimated 5% reaching this age.	15
Factors limiting survival	Pocket gophers (*Thomomys bottae*), black-tailed hares (*Lepus californicus*), and woodrats (*Neotoma* spp.) gnawed the periderm and stems of *Y. brevifolia* in dry years, contributing to tree death. Other species of rodents harvested the fruits. Urban and agricultural development, fire, livestock grazing, off-road vehicle use, and climate warming contribute to reduced survival. *Y. brevifolia*: modelling predicted reduction of southern geographic range in Joshua Tree National Park.	12, 16, 18, 19

Notes:
References: (1) Lenz 2007, (2) Yoder et al. 2013, (3) Smith et al. 2021, (4) Hess and Baldwin 2022b, (5) Brittingham and Walker 2000, (6) Hunning and Peterson 1973, (7) Comanor and Clark 2000, (8) Bryant et al. 2012, (9) Borchert and DeFalco 2016, (10) Vander Wall et al. 2006, (11) Reynolds et al. 2012, (12) Miller and Stebbins 1964, (13) Lenz 2001, (14) Esque et al. 2015, (15) Gilliland et al. 2006, (16) Wilkening et al. 2020, (17) McElvey 1938, (18) Cole et al. 2011, and (19) Barrows and Murphy-Mariscal 2012.

important group of forage plants for desert tortoises (Jennings and Berry 2015).

Restoration of desert habitats that contain features required for supporting viable populations of conservation-priority species can be a long, slow process and require multiple stages. The amount of time and effort to restore a local area depends on initial condition of the site and objectives, whether the intent is to restore soils, soil crusts, and topography; provide cover of native shrubs and trees or cover and composition of shrubs and trees comparable to undisturbed areas; or to restore annual and herbaceous perennial species similar to their former cover, composition, and diversity. Many steps can be involved ranging from project planning and obtaining plant materials, to applications of treatments in one or more stages, followed by monitoring and maintenance. An important issue is that both the tortoise and Joshua tree require long periods to reach reproductive maturity: 17 to 20 years for tortoises (Medica et al. 2012) and possibly 30 or more years before first flowering of Joshua trees (Esque et al. 2015). Both species are long-lived, with the eastern Joshua tree estimated to live over 300 years, and tortoises over 60 to 80 years (Gilliland et al. 2006, Berry and Murphy 2019). All three species exhibit low survival of juveniles (DeFalco et al 2010, Bryant et al. 2012, Esque et al. 2015, Berry and Murphy 2019, Berry et al. 2020c). As a result, developing early indicators of restoration success for these species may be important, together with recovering habitat features to foster long-term resilience during changing climates and environments.

Ecological restoration can serve as a potential tool for hastening ecological recovery and enhancing availability of resources for conserving these priority species. The objectives of this review include: 1) synthesizing major and emerging restoration techniques and their effectiveness in the Mojave and western Sonoran Desert, including how restoration could interact with the threatened desert tortoise and Joshua tree; 2) providing estimated costs of candidate restoration treatments; and 3) anticipating future restoration needs in changing climates and environments and identifying additional research needs for effective habitat restoration in this dynamic environment. We begin by presenting the geographic scope of the review, summarizing the types of disturbances in which restoration is conducted, and discussing factors limiting recovery in deserts that restoration must overcome. This is followed by synthesizing techniques and their effectiveness for the restoration of topographic patterns, soils, and native vegetation in habitats supporting desert tortoises and Joshua trees.

GEOGRAPHIC SCOPE

This review focuses on the geographic range of Joshua trees in the Mojave Desert and on the range of the federally listed Mojave desert tortoise population. Mojave desert tortoise habitat primarily includes hot desert habitat north and west of the Colorado River. This habitat encompasses most of the 124,000-km^2 Mojave Desert occupying parts of Arizona, Utah, Nevada, and California, as well as the western Sonoran Desert in southeastern California (Berry and Murphy 2019). The Mojave Desert receives much of its rainfall from November through April, during winter and spring (Rowlands et al. 1982). Annual precipitation averages 10-20 cm at low/middle elevations below 1,500 m where most desert tortoise habitat occurs. Topography includes mountain ranges, low hills, washes (ephemeral stream channels), and valleys. Soils include those derived from several rock types (e.g., basalt, limestone) and depositional material from erosion (Rautenstrauch and O'Farrell 1998, Berry et al. 2006, Mack et al. 2015). Geological history and soil age are key factors affecting biota, such as old surfaces of desert pavement compared to young soils in ephemeral stream channels (McDonald et al. 1995).

Dominant vegetation within the desert tortoise's range is shrubland (Rundel and Gibson 1996). Creosote bush and white bursage (*Ambrosia dumosa*) predominate across extensive low elevations, blackbrush (*Coleogyne ramosissma*) and succulent woodlands containing Joshua trees at mid-elevations from 1,300 to 1,800 m, and coniferous woodlands and forests at the higher elevations. Desert tortoises are most abundant in the low- and mid-elevation creosote bush and mixed shrublands, and are sparse to absent in higher-elevation woodlands and forests (Berry et al. 2006, Rautenstrauch and O'Farrell 1998, Nussear et al. 2009). In years with sufficient rainfall, most annual plants in the desert shrubland germinate in winter, grow through spring, and senesce by May (Beatley 1974, Smith et al. 2014). The eastern Mojave and western Sonoran have more summer annuals, stimulated by summer monsoonal storms (Jennings 2002). Annual plants are typically most abundant below canopies of shrubs that form the fertile islands of shaded, nutrient-enriched soil (Brooks 2009). Some annual species, however, are most abundant in interspaces between shrubs (Abella and Smith 2013). The spatial variation in the distribution of different shrub species and interspaces creates heterogeneity in the annual plant community, which may be important for diversifying the forage available to tortoises (Schamberger and Turner 1986, Jennings and Berry 2015). The amount and timing of rainfall are highly variable among years and across the landscape within a year (Hereford et al. 2006). Some years or locations have essentially no annual plants, while others support 50 species of annual plants within a km^2 (Brooks and Berry 2006). Non-native annual grasses are now the predominant component of annual plant communities across much of the ranges of the desert tortoise and Joshua tree (Brooks 2009, Barrows and Murphy-Mariscal 2012).

DISTURBANCES, LIMITING FACTORS, AND CONTEXT FOR DESERT RESTORATION

A variety of past and recent anthropogenic disturbances fragment and degrade habitat of desert tortoises and Joshua trees and remove or compromise resources (e.g., shrubs for cover) required by these species. Examples of the numerous past and recent disturbances include clearing for agriculture and townsites, mining activities, road-building, off-road vehicle use, military activities (including World War II and contemporary training activities), livestock grazing as well as disturbance from feral horses and burros, energy transmission corridors, renewable energy developments, and wildfires in part fueled by non-native plants (Lovich and Bainbridge 1999, Chaffee and Berry 2006, Brooks et al. 2018, Berry et al. 2020b).

Although in some cases after disturbance a "do nothing" approach may be the most ecologically and cost-effective (e.g., if most top-killed native perennials do re-sprout rapidly), a large body of research in the Mojave and Sonoran deserts has shown that plant and soil recovery after disturbance is slow or essentially non-existent without restoration. In a synthesis of 47 published studies in the Mojave and Sonoran deserts, the time estimated for the full reestablishment of perennial plant cover after disturbances (clearing such as for pipeline right of ways, wildfires, and road disturbances) averaged 76 years (Abella 2010). Recovery rates of perennial species richness (number of species per unit area) were highly variable among studies, ranging from full recovery within 3 years to projections of 152 years to full recovery. Recovery of species composition (species present and their relative abundance) to that typical of nearby undisturbed areas was estimated to require an average of at least 215 years, assuming that recovery would continue along a linear trajectory. A recent study further highlighted slow recovery after wildfires, which are degrading increasingly large cumulative areas of desert habitat. After 32 wildfires dating back to 1980 in the eastern Mojave Desert, perennial plant cover was forecasted to require decades to recover while species composition (including for mature shrubs needed by desert tortoises and by Joshua trees as nurse plants) was projected to require centuries at many sites (Abella et al. 2021). Species composition of mature creosote bush communities required an estimated 82 years to full recovery akin to composition of nearby, undisturbed sites. Blackbrush shrublands required even longer: 550 years to full recovery. In both communities, the time to recovery actually lengthened between measurements made in 2007 and 2016, implying that instead of recovery, species composition of the burned sites was diverging from that of nearby undisturbed communities. This implied that species composition on burned sites, if unassisted by active restoration, may not be capable of recovering naturally to that resembling unburned sites in ambient environmental conditions. Recovery of native annual plant species composition may similarly require decades to centuries and be contingent on recovery of native perennials providing nutrient-enriched fertile islands conducive to recruitment of many annual species (Berry et al. 2015, 2016).

These long recovery times are significant to desert tortoise and Joshua tree conservation efforts for several reasons. First, these types of disturbances (e.g., wildfire) already cover vast areas of tortoise and Joshua tree habitats and are continuing to increase (Brooks et al. 2018). Second, even if some plant recovery occurs (e.g., cover increasing over time), the species may not necessarily be those that were originally present, so their benefit to tortoises or Joshua trees may be comparatively lower. An example is that early colonizing perennial plants tend to be smaller-statured species, too small to cover an adult tortoise, rather than the larger shrubs tortoises favor for cover and burrow-construction locations (Abella et al. 2021). Severe disturbances can become even less hospitable to tortoises if some of the early colonizing herbaceous perennials that serve as food plants decline after their initial colonization (Drake et al. 2015). Third, the long recovery times imply a cumulatively increasing "recovery debt," whereby increasing portions of the landscape spatially and temporally are not in a mature habitat condition. These observations underscore the potential for restoration to accelerate ecological recovery on existing disturbances while also contributing to efforts to curtail new anthropogenic disturbances.

Ecological restoration is not intended to contribute to all recovery actions for the desert tortoise and Joshua tree but has high potential to aid overall recovery. For example, instead of restoration, management activities or policies may be most appropriate for limiting tortoise exposure to disease, but restoration activities to enhance forage quality could improve resistance of tortoises to some diseases (Jacobson et al. 2014). Restoration can likely make three main contributions to improving tortoise and Joshua tree habitat quality: i) ameliorating or reversing stressors to the species; for tortoises, such as poor-quality forage, exposure to toxicants, or lack of cover plants, and for Joshua trees, replenishing nurse plants facilitating recruitment and reducing non-native grasses that threaten the trees with competition and wildfires; ii) expanding or connecting habitat useable or favorable to the species, such as revegetating denuded areas otherwise avoided by tortoises; and iii) limiting further degradation of habitat, such as through lowering wildfire risk by reducing non-native plants (Abella and Berry 2016). Restoration can thus serve as a major tool along with other management and policy activities seeking to contribute to conserving tortoises and Joshua trees and their habitats (Averill-Murray et al. 2021).

Research has demonstrated that enhancing habitat quality on disturbances is feasible in the Mojave and western Sonoran Desert, even when environmental conditions are adverse, but that it is difficult and restoration projects must generally implement sound practices to be successful in this environment. Three of the overarching general restoration goals common in deserts include ameliorating propagule limitations as barriers to plant recruitment, stabilizing and repairing soils to limit further soil degradation, and reestablishing the fertile islands associated with mature perennial plants (Wallace et al. 1980, Abella 2017b). To meet these goals, typical challenges desert restoration commonly must overcome include low and erratic precipitation and hot, desiccating summers; infertile, shallow, or damaged soils after disturbance; often intensive levels of herbivory by ungulates, squirrels, and rodents at restoration project sites given limited natural forage and herbivores targeting planted species enriched in nutrients from propagation processes in greenhouses; limited availability of native plant materials for restoration; and competition or fire hazards stemming from non-native plants (Bainbridge 2007). Compared to moister regions, these issues are heightened challenges in drylands where plant regeneration even under undisturbed conditions is relatively infrequent, precisely a reason why plant cover in drylands is low naturally. Moreover, forecasts for continued warming and frequency of drought conditions in the desert Southwest suggest that environmental conditions will remain challenging (e.g., Mankin et al. 2017, Overpeck and Udall 2020, Williams et al. 2020, 2022). Restoration is arguably even more relevant during times of rapid climatic change such as the present. Reducing as many stressors as possible via habitat restoration is likely to provide species with the greatest chance for successfully accommodating environmental change, as compared with species facing these changes in a weakened state in compromised habitat (Longshore et al. 2003, DeFalco et al. 2010). Restoration techniques discussed in the remainder of this paper can increase chances that restoration can successfully overcome limitations to recovery of desert habitats.

LITERATURE SYNTHESIS METHODS

To obtain restoration literature for the review, we performed systematic searches using the databases AGRICOLA, BioOne, GoogleScholar, JSTOR, Scopus, ScienceDirect, SpringerLink, Web of Science, and Wiley Online Library. Article titles, abstracts, and key words were searched for the following terms: Mojave, Sonoran, restoration, revegetation, rehabilitation, outplanting, seeding, transplanting, propagation, soil, invasive plants, exotic plants, non-native plants, control, treatment, management, and recovery. These searches focused on peer-reviewed journal articles, book chapters, and conference proceedings, collectively the primary holdings of the databases. U.S. Government serial publications (e.g., U.S. Forest Service technical reports, U.S. Geological Survey open-file reports) were also searched. We extracted data and summarized results from published articles meeting the criteria of occurring in the Mojave and western Sonoran Desert and reporting results of one or more restoration treatments. Nomenclature and classification of species by growth form (e.g., annual forb) follow Natural Resources Conservation Service (2022).

OVERVIEW OF RESTORATION TECHNIQUES

Eleven restoration techniques in three categories (restoration of site environments including soil, topography, and structure; revegetation; and restorative management actions) have been examined in at least one published study in the Mojave and western Sonoran Desert. These techniques can help repair topographic features, rehabilitate soils, and reintroduce missing propagules of native plants, with potential benefits for the desert tortoise and Joshua tree. Each technique is detailed in ensuing sections.

RESTORATION OF SITE ENVIRONMENTS

Topsoil Salvage and Replacement

Although information is limited for the Mojave Desert, re-applying topsoil is likely to be among the most ecologically effective strategies for restoration where salvaging topsoil is feasible and appropriate (Allen 1995, Abella et al. 2015b, Rowe et al. 2022). This conclusion is based on three lines of evidence: ecological studies of soil properties and biota, limited but highly successful examples of restoring topsoil, and more extensive research with topsoil salvage in other deserts. Nutrient pools and

Figure 4. Plant recovery on an area receiving salvaged topsoil (right side of gray line) after disturbance from re-alignment of Northshore Road, Lake Mead National Recreation Area, eastern Mojave Desert, southern Nevada. The photo was taken five years after disturbance (S.R. Abella).

root matter can be held in deep (e.g., > 50 cm) soil layers in some desert soils, but generally organic matter and nutrients are concentrated in the upper 30 cm of soil (Koyama et al. 2019). Most seeds, often at least ~90% of the total, occur in the upper 5 cm of desert soil (Guo et al. 1998). Soil biota, including constituents of biocrust, are also often concentrated in surface soils (Williams et al. 2012). These observations suggest that salvaging the upper 5 cm of soil has potential to encompass much of the stored plant propagules and soil resources. In one of the few studies of influences of salvaging topsoil for Mojave Desert restoration, planting of salvaged native perennials on salvaged topsoil doubled survival compared with planting on non-topsoil surfaces (Abella et al. 2015b; Figure 4). The benefit of topsoil (without irrigation) to plants was nearly equivalent to irrigating them. More extensive research in other drylands, such as in Australia, has highlighted that re-applying topsoil can speed ecological recovery while retaining local genetics and species composition, if donor and recipient sites are matched well (Waryszak et al. 2021).

To maximize benefits of topsoil for restoration, careful planning can aid salvage operations (e.g., Ghose 2001, Scoles-Sciulla and DeFalco 2009, Abella et al. 2015b). Present knowledge suggests that ideal salvage procedures for desert soils include: 1) avoiding areas infested by non-native plants or soil contaminants; 2) consistently salvaging the upper 5-10 cm when a goal is to maximize soil seed bank density; and 3) timing salvage to occur in summer from May through September (and later into autumn if it is a dry year) to capture winter annual seeds dispersed the previous spring, but before seedlings emerge in autumn/winter. Illustrating how mixing subsoil with topsoil can dilute seed bank resources, Scoles-Sciulla and

DeFalco (2009) found that germinable seed density was 86% lower in the upper 4 cm of soil (the most important for seedling emergence) when this upper layer was mixed with salvaged soil 30 cm thick (Figure 5). In the future, space required to store soil might be reduced by examining benefits of strategically salvaging “fertile island” soil below the driplines of canopies of shrubs to increase efficiency of nutrient and seed capture (Abella et al. 2015b, Rowe et al. 2022). Salvaging some interspace soil could also be wise to ensure capture of seeds of annual plants primarily growing in the open (Guo et al. 1998). If topsoil cannot be transferred directly from donor to recipient sites, topsoil needs to be stored carefully to maximize biotic and nutrient retention. Topsoil should be stored as briefly as possible before reapplication. Practical constraints typically result in some storage time being required, and this unavoidably creates some loss of biotic components (Ghose 2001). If soils must be stored, storage time ideally would not exceed 6-12 months (Ghose 2001, Scoles-Sciulla and DeFalco 2009). For storage of long durations, treatments could potentially extend longevity of biotic components. Some possible treatments may include transplanting vegetation (such as native cactus pads) on top of the piles to potentially enhance longevity of soil microorganisms. These types of treatments have not been tested extensively and should be considered experimental. Also, height of stockpiles should be as low as possible, preferably no more than 45-60 cm tall, because the deeper the pile, the more likely biotic components will be lost. If limits on storage space require deeper piles, periodically turning the soil can be considered. Stored soil should be protected, such as via tackifier, from wind erosion or other damage.

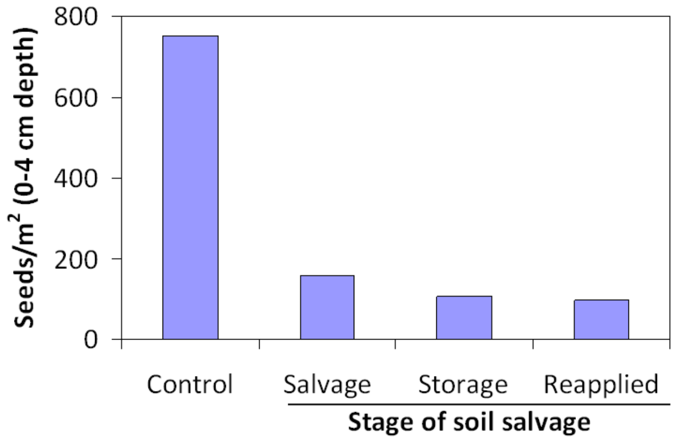

Figure 5. Loss of germinable seed during three stages of topsoil salvage, relative to the 0-4 cm soil layer of undisturbed desert, in Lake Mead National Recreation Area, eastern Mojave Desert, southern Nevada. Most (79%) of the seed loss occurred during the salvage operation itself, likely because subsoil (to a depth of 30 cm) was mixed with topsoil. The topsoil was stored for four months. Data from Scoles-Sciulla and Defalco (2009).

Geomorphic and Microtopographic Treatments

On disturbed sites targeted for restoration, treatments to shape land surfaces and roughen soil have potential to deter soil erosion from water and wind, retain seeds and biotic material, and to improve favorability of soil conditions for plant colonization by concentrating soil resources and offering microsites for regeneration (Weigand and Rodgers 2009, Fick et al. 2016). Bainbridge (2007) discussed numerous possible surface treatments, such as roughening (e.g., pitting, imprinting, ripping; Figure 6); constructing water catchments, check dams and fences; use of fabrics or organic mats; and horizontal and vertical mulches. Not all treatments nor their variations (e.g., different materials of organic mats or spatial configurations) have been tested extensively yet for their effectiveness at improving site conditions or for cost-benefit assessments.

Some geomorphic treatments were evaluated in the Mojave or Sonoran deserts or are currently being tested. On eroding, abandoned agricultural land in the western Mojave Desert, constructing a network of parallel wind fences (10 m between fences) perpendicular to prevailing winds reduced fugitive dust emissions by 64% from a height of 0.2-2 m above ground (Grantz et al. 1998c). Plastic cones (61 cm tall) and wire cages (91 cm tall) distributed at a density of 460 structures/ha across the site reduced dust emissions by 6-fold at a height of 0.2 m above the ground and by 25% at a height of 1 m (Grantz et al. 1998c). Revegetation generally reduced dust emissions more (91-99% at a height of 1 m) than fences or distributed smaller structures, but revegetation was not successful every year (Grantz et al. 1998a). With additional examples discussed in the outplanting and seeding sections of this paper for how surface treatments can influence revegetation, DeFalco et al. (2012) illustrated how tillage (creating 3-cm wide, 5-cm deep furrows) increased formation of soil seed banks by 55% after seeding in the central Mojave Desert. Soil pitting, producing a rough soil surface with many depressions, retained moisture, trapped seeds, and increased survival of outplants (Bainbridge 2000). Although ripping can de-compact soils, Caldwell et al. (2009) cautioned that additional research be directed toward developing ripping techniques for reducing soil compaction to avoid undesirable effects such as raising salts from subsoils into the rooting zone. In the Sonoran Desert, ripping to restore habitat on decommissioned trails reduced soil compaction and increased water infiltration but increased non-native plant cover (Rowe et al. 2022).

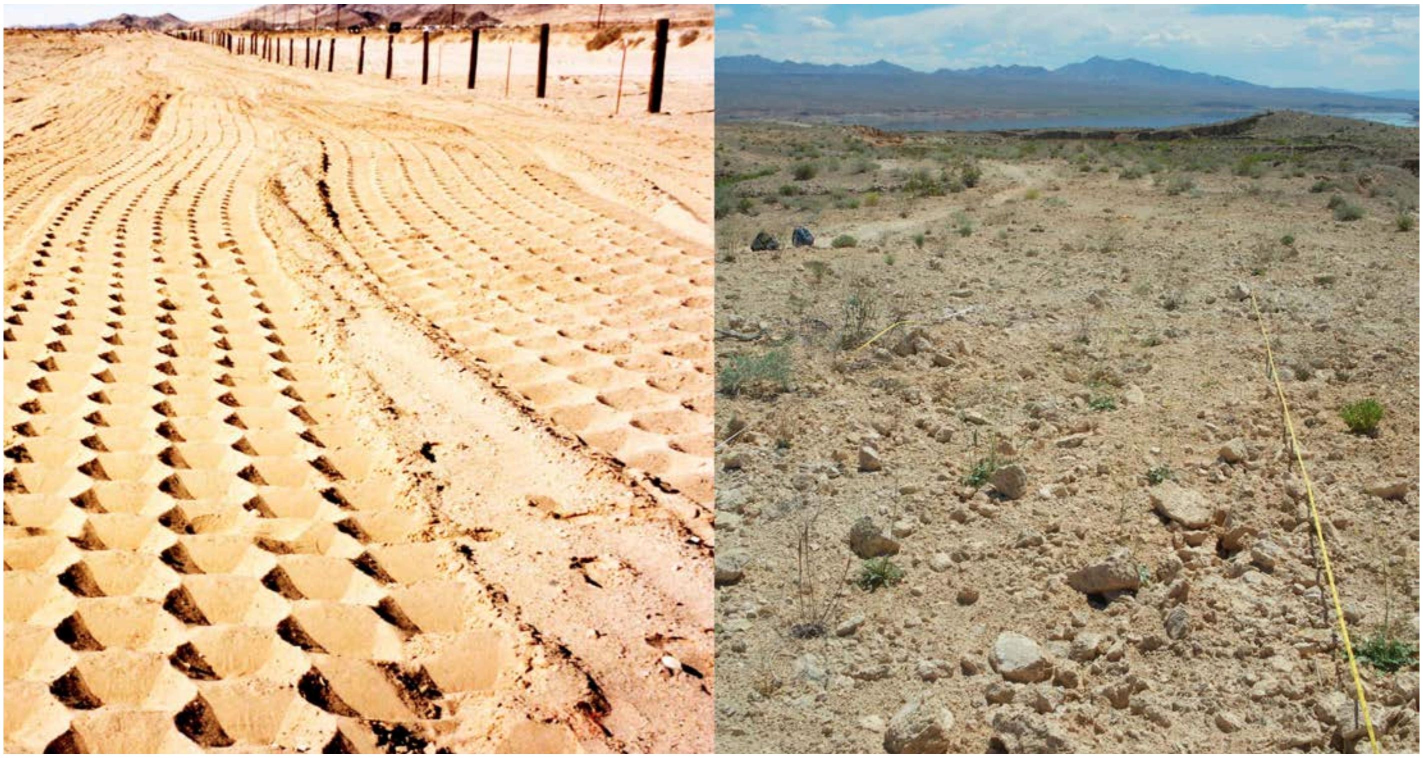

Figure 6. Examples of geomorphic restoration treatments for encouraging recovery on compacted and disturbed soils. Left photo: Imprinting intended to roughen the surface of compacted soil to deter erosion, retain nutrients and biotic resources, and create favorable conditions for native plant establishment (photo courtesy of D.A. Bainbridge). Right photo: Ripped road designed to de-compact soil and promote plant establishment on gypsum soil, Lake Mead National Recreation Area, eastern Mojave Desert, southern Nevada (S.R. Abella).

Recent studies evaluated minimal-input techniques for constructing pits/catchments and distributed roughening treatments in desert tortoise habitat, with mixed success. Rader et al. (2022) found that constructing depressions using hand tools undesirably increased cover of non-native grasses (while not benefiting natives; Figure 7). However, the depressions resulted in some soil accumulation (0.1 cm/year) compared to a loss of 0.4 cm/year of soil without treatment. In an ongoing follow-up study, creating distributed patches of roughened soil enhanced native annual plant cover and species richness (Figure 8). In addition to significantly reducing soil compaction, the roughening treatments doubled soil moisture from 2% to 4%, likely partly via increasing water infiltration.

Restoring Soil Features: Biocrust, Desert Pavement, and Desert Varnish

Biocrusts, defined as soil surface layers including bacteria, cyanobacteria, algae, mosses, liverworts, fungi, or lichens, can be major components of undisturbed desert ecosystems on sites suitable for biocrust establishment (Belnap et al. 2001). In addition to adding diversity via their own constituents of species, biocrusts can limit soil erosion, increase accumulation of soil organic matter and nutrients, and interact (positively or negatively) with vascular plants (Bowker 2007). Biocrust functions can vary with biocrust composition (e.g., lichen- compared with cyanobacteria-dominated crust) or cover, structure and thickness of biocrust layers, variation in precipitation, and other components of habitats such as composition of vascular plants (Pietrasiak et al. 2013). Well-developed biocrust layers can require decades to recover after severe disturbance (Kidron et al. 2020).

Research on techniques to restore biocrusts has expanded across drylands globally particularly in the last 10-15 years, including in the Mojave Desert, but is still considered in the early stages (e.g., Antoninka et al. 2020). Bowker (2007) outlined three main stages for restoring biocrusts: 1) stabilizing soil to enable favorable surfaces for biocrust colonization and growth; 2) resource manipulations such as changing water or nutrient availability to favor biocrust growth; and 3) inoculation-based techniques, such as salvaging or propagating biocrust organisms and re-applying them as dry powders, slurries, or outplants similar to outplanting vascular plants. Most of these variations in treatment have not been tested extensively in the Mojave Desert, but two studies evaluated potential for salvaging and transplanting biocrust material. Cole et al. (2010) evaluated transplanting the dominant biocrust moss *Syntrichia caninervis*. All transplanted sections of moss survived after 27 months, although

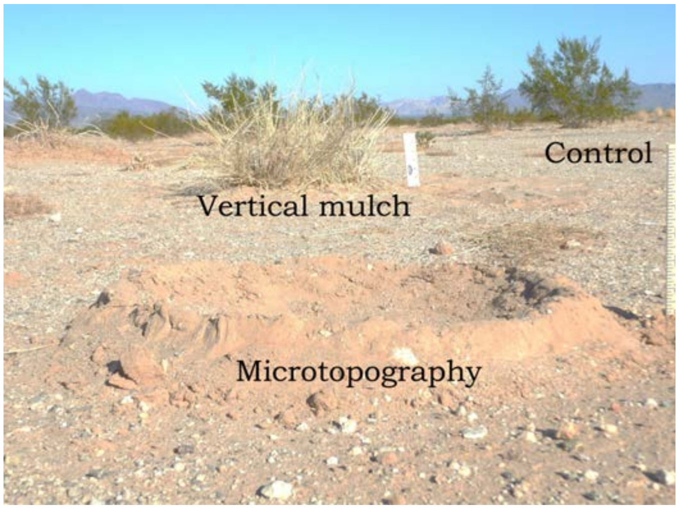

Figure 7. An experiment examined how constructing microtopographic structures (50-cm outer diameter, 10 cm tall), compared with vertical mulch and no treatment (control), influenced plant recruitment and soil properties on disturbances along an energy transmission corridor (Rader et al. 2022). The photo was taken just after treatments were implemented. The site is near the Chuckwalla Critical Habitat Unit for the desert tortoise in the western Sonoran Desert, southeastern California.

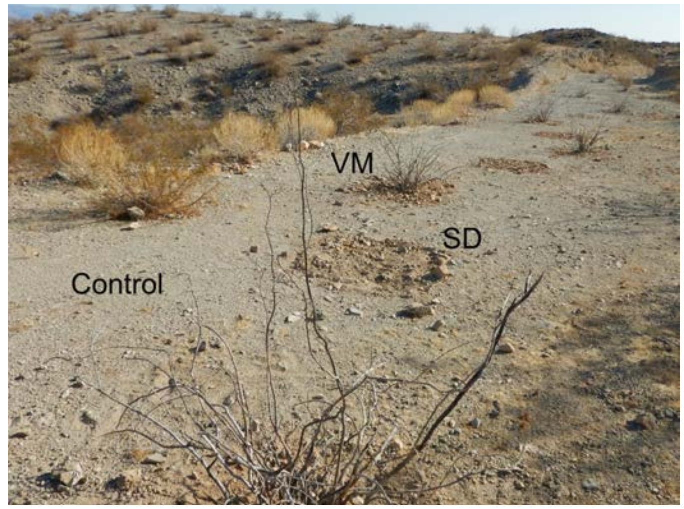

Figure 8. An experiment examined influences of surface de-compaction (SD) compared with vertical mulch (VM) and control (no manipulation) treatments designed to promote revegetation on an abandoned road in the eastern Mojave Desert, southeastern California. The SD treatment entailed de-compacting the upper 5-10 cm of soil using rock hammers and hand rakes in 1 m × 1 m patches. The photo was taken in December 2017 when treatments were implemented (L.P. Chiquoine).

moss cover declined 20-52% (relative to initial cover) and shoot density declined 26%. The authors suggested avoiding transplanting source material derived from shaded (below shrub) microsites to an open site, comparable to recommendations to match orientation toward the sun when transplanting cacti (Smith et al. 2012).

To restore severely disturbed, decommissioned road sites in the eastern Mojave Desert, Chiquoine et al. (2016) tested effects of applying biocrust inoculation (salvaged and stored dry for two years), salvaged topsoil, an abiotic soil amendment (wood shavings), and outplanting white bursage. Eighteen months after treatment, only plots receiving biocrust inoculum contained lichen and moss cover. Plots receiving inoculum also recovered 43% of the cyanobacteria density found on undisturbed controls. In addition to inoculation, applying salvaged topsoil increased cyanobacteria density. Wood shavings and white bursage plants had no significant effect on lichen and moss recovery but did influence cyanobacteria composition and soil fertility. Plots receiving biocrust inoculum also had enhanced soil stability, likely important to retain biotic material and reduce soil erosion. The study concluded that while it may not always be possible to salvage (or store) biocrust material, being able to do so can accelerate recovery of biocrusts. Moreover, the results suggested that if even small amounts of donor biocrust material are available, they can serve as inoculation sources to enhance biocrust recovery over time.

Ongoing research with biocrusts in the Mojave and in other deserts has further illustrated potential for restoring biocrusts, such as by establishing greenhouse production facilities to grow biocrust material (e.g., Antoninka et al. 2016). It is possible that lichens and mosses can be propagated in greenhouses, then outplanted in restoration sites (Ballesteros et al. 2017). Inoculates of cyanobacteria could similarly be prepared and re-introduced to restoration sites accompanied by treatments to potentially enhance growth.

Desert pavement is a stone-covered geomorphic surface, consisting of angular or rounded, densely packed stones, usually one or two layers thick and set in or overlaying a matrix of fine-grained soil material, on generally flat terrain (Haff and Werner 1996). Desert pavements are typically ancient surfaces, commonly exceeding 10,000-100,000 years old (Seong et al. 2016). Desert pavements cover appreciable area within the ranges of desert tortoises and Joshua trees, including the generally flat valleys representing extensive tortoise habitat (Wood et al. 2005). Although plant cover on desert pavement is sparse, a native annual forb (desert plantain, *Plantago ovata*) of pavement is a tortoise food plant (Oftedal et al. 2002, Jennings and Berry 2015). Additionally, because water infiltration is minimal on pavements and thus runoff is high, desert washes and drainages in landscapes with pavement can contain abundant vegetation, including forage plants (Jennings 1997). Topography atop hills and mesas and the tops of steep-walled ephemeral stream channels often have pavement. Tortoises use dens and burrows in these channel walls (Berry et al. 2006).

Desert pavements take many millennia to form but can be readily disrupted or destroyed via disturbances such as off-road vehicles (Elvidge and Iverson 1983). An experiment in the western Mojave Desert found that small disturbances "healed" naturally through repositioning of displaced stones over time (Haff and Werner 1996). Small, 10-cm^2 disturbed plots became "repaved" at a rate of 10% per year, resulting in recovery in a decade. Recovery of larger but still small plots declined sharply, with a "repaving" rate of 1% per year on 40-cm^2 plots. In retrospectively assessing 40-year-old displaced boulder locations, Haff and Werner (1996) found that the locations had filled with material, but the infilled stones were half the diameter (1 cm compared with 2 cm) of stones found on nearby, undisturbed desert pavement. These observations suggest that natural processes can repair small disturbances in desert pavement, but that larger disturbances are likely to require decades to many centuries (or even millennia) for the pavement surfaces to heal (Haff and Werner 1996).

Restoration techniques are not well developed for desert pavements and are complicated by the fact that pavements represent an integrated geomorphic landform of both the surface stone layer and underlying vesicular soil horizon of fine-grained material which forms on time scales of millennia (Haff and Werner 1996). However, it is possible that treatments such as applying stones (or re-arranging stones such as through raking), salvaged or synthesized fine soil material, or applying adhesives (e.g., to conglomerate rocks or bind them to soil) could begin to provide some functions of pavement surfaces or to conceal the disturbance (Abella et al. 2007; Figure 9).

Desert varnish is often associated with desert pavement and can be disturbed with disruption of pavement surfaces or rocks in other topographic settings, such as hillslopes. Desert varnish is a thin brownish, orange to black coating on rock surfaces in arid regions and consists of manganese, iron, clay particles, and various trace elements such as magnesium (Dorn and Oberlander 1982). Millennia are required to create well-developed desert varnish, which can be quickly disrupted when rocks are scraped, dislodged (exposing non-varnished surfaces), or removed (Haff and Werner 1996). Improving aesthetics to humans is a main reason to mitigate damage to desert varnish for visual restoration, including to attempt to limit further disturbance. However, while poorly understood, it is possible that mitigating damage to desert varnish could also have ecological influences such as with light reflectance and soil temperatures, potentially affecting biota (Abella et al. 2007). Little formal testing to evaluate ecological effects has been performed with techniques for mitigating damage to desert varnish, but techniques such as raking to adjust rock configuration and applying artificial coloring amendments to simulate the chemical composition and appearance of varnish may have potential (Abella et al. 2007).

Figure 9. Disturbed area without (left) and with restoration (right) in Lake Mead National Recreation Area, eastern Mojave Desert, southern Nevada. Restoration involved outplanting creosote bushes and raking and applying coloring treatments to simulate desert pavement and desert varnish. The disturbance occurred in 1998 and the photo was taken in 2006, nine years after restoration (S.R. Abella). Before disturbance, the site contained a mature creosote bush shrubland with extensive desert pavement.

Restoring Structure: Vertical and Horizontal Mulch

Considerable interest exists in ascertaining to what extent non-living stems and branches can provide ecological functions comparable to live perennial plants, because dead plant materials could be cheaper and logistically easier than active revegetation (Li et al. 2017). Moreover, using dead branches and stems would not be time sensitive nor contingent upon variable precipitation compared with timing of seeding and outplanting. The structures, once placed, would be present and available to assist with recovery across years regardless of amounts of precipitation (Grantz et al. 1998b). Although dead branches and stems would not produce litterfall and all the functions of live plants, these structures could partly or fully provide some functions such as shading and trapping windblown sand, litter, and seeds. These functions could foster accumulating soil nutrients and facilitating recruitment of plants, some of which may be used by desert tortoises. Dead shrubs are

Figure 11. Restoration site in Joshua Tree National Park, California, that received vertical mulch, such as shown in the bottom left of the photo and in the lower center of the 2 m × 20 m sample plot. Vertical mulch structures supported greater annual plant growth than did interspaces but less than below live shrubs. Photo taken in April 2017 (S.R. Abella), nine years after the vertical mulch was installed.

used by tortoises as sites to construct burrows; fallen limbs of Joshua trees are also sites for constructing burrows (KHB, personal observation).

Vertical mulch consists of dead plant material (e.g., branches) placed upright in the ground (Figure 10; Bainbridge 1996). To evaluate whether vertical mulch could serve as “nurse objects” that facilitate recruitment of plants for restoration in Joshua Tree National Park, Abella and Chiquoine (2019) compared plant communities over nine years among vertical mulch, outplant, and interspace microsites (Figure 11). In general, across years, plant cover around and below vertical mulch structures was intermediate between that below outplants and in interspaces. This suggested that vertical mulch could benefit native plant communities, including annual forbs, many of which are important forage plants for tortoises. However, non-native annual grasses also benefited from vertical mulch. The study suggested that treatments

Figure 10. Vertical mulch structures, shown in the bottom right of the photo and in the center-right (to the left of the top of the wilderness sign), as part of restoration on a decommissioned road in the Dead Mountains Wilderness Area, eastern Mojave Desert, southeastern California. The vertical mulch was constructed from collecting dead branches of creosote bush and arranging them vertically in the soil to mimic structure of a creosote bush shrub (albeit without live foliage). Photo taken in November 2016 by S.R. Abella.

targeting non-native plants may need to be paired with vertical mulching (as well as outplanting) to enable native plants to receive more of the benefits of vertical mulching. Additionally, the study indicated that while some vertical mulch structures could degrade or be knocked over (such as by humans or winds), most structures persisted through the nine-year study. Studies of decomposition of wood suggest that, due to aridity, the decomposition process is slow in southwestern deserts, and vertical mulch is likely capable of persisting for decades (Ebert and Ebert 2006).

Another recent study, in the western Sonoran Desert near the Chuckwalla Critical Habitat Unit for desert tortoises, illustrated how vertical mulch could succeed and serve as a bet-hedging restoration approach during severe droughts when revegetation failed (Rader et al. 2022). After outplanting was implemented along a disturbed energy transmission line corridor, the initial growing season (2018) was the driest of the last 47 years. Despite some irrigation and plant care, all outplants died during this drought. As outplanting failed, vertical mulch increased abundance of native shrub seedlings at the driest site and reversed soil erosion across sites by increasing the soil accumulation rate by 6× to 2 cm/year. These restoration benefits occurred across two years despite the drought conditions. The study illustrated a key point in that while it may be possible to conduct phased outplantings or seedings across years to bet hedge that at least one year will have favorable precipitation, it can be logistically difficult to propagate or store plant materials across multiple years and to mobilize resources to implement active revegetation annually. In contrast, the one-time treatment of establishing the vertical mulch structures enabled them to be present for stimulating restoration benefits. Including some abiotic structural treatments along with active revegetation may be a prudent bet-hedging strategy in case active revegetation fails.

Mulch, such as straw, wood materials, or gravel, placed horizontally and often covering more of sites than vertical mulch, has had inconsistent and generally limited restorative effects. As detailed in the ensuing outplanting and seeding sections, results of horizontal mulch applied in combination with active revegetation were inconsistent and benefits were minimal. Ostler et al. (2003) found that three mulches (gravel, cellulose fiber, or wood bark material), but not straw mulch, enhanced early emergence of seeded species, but no mulch type resulted in seedlings persisting the second year (Caldwell et al. 2009). In that study, the bark and cellulose fiber mulches reduced soil moisture, possibly because the materials absorbed water,

Table 3.
Eleven major restoration techniques placed in three categories (restoration of site environments, revegetation, and restorative management actions) examined in at least one published study in the Mojave and western Sonoran Desert. Some studies evaluated multiple treatments.

Technique	No. of studies
Restoration of site environments	
Topsoil salvage and replacement	2
Geomorphic and microtopographic treatments	6
Restoring soil features (biocrust, pavement, varnish)	3
Vertical and horizontal mulching	8
Revegetation	
Outplanting	16
Salvaging and transplanting	3
Cuttings	3
Seeding	13
Assisted natural regeneration	1
Restorative management actions	
Fencing, protection, and herbivory management	3
Reducing non-native plants and fire risk	4

reducing water available to seeds and plants (Caldwell et al. 2009). Winkel et al. (1995) concluded that wheat straw mulch crimped into soil did not benefit early seedling emergence. When applied around outplants, Grantz et al. (1998b) reported that straw and bark mulch did not improve plant vigor. In other studies, Walker and Powell (2001), in examining mining disturbances, found that when applied to mining waste heaps, rock mulch improved water retention but not when applied to an abandoned road. For restoration of former road locations, Chiquoine et al. (2016) reported that wood shavings incorporated into soil did not improve lichen and moss recovery as components of biocrust but did increase density of cyanobacteria and soil fertility.

Supporting results from the Mojave Desert, studies in other deserts similarly reported inconsistent benefits of mulching. For example, in the Sonoran Desert, mulch of bark did not improve survival or growth of outplanted honey mesquite ((*Prosopis glandulosa*; Bainbridge et al. 2001). Wheat straw mulch did not enhance establishment of seeded plant species (Banerjee et al. 2006). In contrast, Beggy and Fehmi (2016) found that wheat straw increased establishment of seeded species and tempered soil erosion. Using rock mulch, Fehmi (2018) found that plant cover was 12× lower in mulched plots, indicating highly detrimental effects of mulch. Also indicative of potential negative effects, grass mulch did not increase establishment

Figure 12. Outplants intended to initiate recovery at a disturbed site in Joshua Tree National Park, California. Outplants are enclosed in wire cages (affixed to rebar) to deter herbivory. The photo was taken in June 2008 following outplanting that spring (S.R. Abella).

of seeded species and instead appeared to increase cover of non-native grasses (Woods et al. 2012).

An overall appraisal of the science suggests that vertical mulch has benefited native plant recruitment (though potential benefits to non-natives as well is a concern), while horizontal mulch has rarely benefited native plants and in some cases resulted in negative effects. The literature indicates that the type (e.g., various organic sources, rock) and perhaps thickness (Fehmi 2018) of the mulch material can influence effects of horizontal mulch (Kay 1978). Further exploring these types of variables, as well as examining whether horizontal mulch could produce benefits (e.g., slowing soil erosion, replenishing soil organic matter over time, possibly trapping naturally dispersing seeds), beyond those associated with active revegetation (Bainbridge 2007), is likely warranted to advance understanding of the benefits of horizontal mulch relative to costs.

REVEGETATION

Outplanting

Outplanting is planting nursery-propagated seedlings or cuttings at field sites (Figure 12). A main advantage of outplanting is that by propagating plants in nurseries, it bypasses a need at field sites for seed retention in suitable microsites, successful germination, and early survival of seedlings, all of which are rare in field settings in deserts (Bean et al. 2004). Compared to seeding, outplanting is intended to represent a greater investment through nursery care in each propagule (seed or cutting) to result in a higher percentage of propagules producing a persistent plant. Outplanting is typically deployed to revegetate small disturbances (e.g., < 10 ha), to strategically establish vegetated islands within large disturbances, or to serve as enrichment plantings to diversify species composition (Hulvey et al. 2017). In addition, outplanted shrubs, depending on species, could act as nurse plants to Joshua trees (Esque et al. 2015). While the outplants themselves may rapidly provide habitat functions such as shading or floral resources, reproduction by outplants or facilitation of reproduction for other species could enable outplants to revegetate larger areas over time than were originally planted (Abella et al. 2012a, Devitt et al. 2020).

Outplanting can produce direct and indirect benefits for ameliorating degraded habitat. Reestablishing native perennials can limit soil erosion, conserving site productivity and limiting exposure of tortoises to fugitive dust potentially containing harmful substances (Grantz et al. 1998d, Jacobson et al. 2014, Kim et al. 2014). Outplanting shrubs, if sufficiently large, may provide protective structures to offer tortoises resting locations and sites to construct burrows to escape temperature extremes (Henen et a. 1998, Drake et al. 2016). Outplanting cacti, such as beavertail (*Opuntia basilaris*) and herbaceous perennials, such as desert globemallow (*Sphaeralcea ambigua*) and wishbone bush (*Mirabilis laevis*), can increase food available to tortoises. Forage-supplying perennials can be particularly important to tortoises during dry years when few annuals bloom (Medica et al. 1985). Indirect benefits of outplanting shrubs to tortoises can include enhancing production and biomass of native annual plants used as forage via formation of fertile islands below perennials and increasing habitat resources needed by other organisms in tortoise habitat (e.g., pollinator communities utilizing floral resources of outplants).

Sixteen published studies in the Mojave and western Sonoran Desert collectively assessed survival of 46 outplanted native perennial species for at least one year after outplanting (Table 4). Although many species were not assessed in more than one study to enable evaluating consistency of their performance, the data enabled identifying nine species exhibiting ≥ 50% survival in at least two studies. These top performers are shrubs and trees and include white bursage, fourwing saltbush (*Atriplex canescens*), allscale saltbush (*Atriplex polycarpa*), Nevada jointfir (*Ephedra nevadensis*), cheesebush (*Hymenoclea salsola*), creosote bush, Anderson thornbush (*Lycium andersonii*), honey mesquite, and Mojave yucca (*Yucca schidigera*).

Table 4.
Summary of percent survival of 46 perennial species outplanted in the Mojave and western Sonoran Desert in 16 published studies that reported and evaluated survival at restoration field sites for at least a year. Highlighted species were the best performers with survival of at least 50% in at least two studies. A range of survival percentages is shown if multiple treatments were applied to outplants in a study.

	Study															
Species	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**
Grass																
Achnatherum hymenoides				0-20												
Achnatherum speciosum				0-0												
Aristida purpurea	0															
Distichlis spicata								0-33								
Muhlenbergia porteri	5															
Sporobolus airoides	3			50-67				0-2								
Forb/subshrub																
Artemisia ludoviciana															56-75	
Baileya multiradiata	0															
Penstemon bicolor	3															
Salvia sonomensis											0-0					
Sphaeralcea ambigua	55															
Stephanomeria pauciflora											0-0					
Cactus																
Opuntia basilaris												100				
Shrub																
Acacia greggii							88-91					0				
Ambrosia dumosa	23	0-45	11	50-67		82-90				42-54	33-44	0		8-75	0-50	
Artemisia cana				0-33												
Artemisia frigida				0-33												

Artemisia tridentata				0-33							0-33				17-100	
Atriplex canescens				100-100						12-28	50-67				0-100	3-100
Atriplex confertifolia				80-80												
Atriplex lentiformis				33-50												
Atriplex nummularia				50-67												
Atriplex parryi								0-0								
Atriplex polycarpa				67-100		44-67				0-31						
Atriplex torreyi				50-67												
Baccharis sarathroides				100-100												
Cleome isomeris						74-81										
Coleogyne ramosissima											0-100		4			
Encelia farinosa	0					78-86										
Encelia virginensis					10-43											
Ephedra nevadensis				67-100		82-96							61			
Ephedra viridis				67-100												
Ericameria nauseosa				67-100											33-33	
Eriogonum fasciculatum	28			33-50												
Grayia spinosa				0-0							0-0				8-60	
Hymenoclea salsola		0-90				64-82										
Krascheninnikovia lanata			0								0-40				0-67	
Larrea tridentata	23		2	75-100		89-92				0-12	50-69	92			50-100	
Lepidospartum squamatum										0-8						
Lycium andersonii				33-50							20-67				0-33	
Lycium pallidum											0-0					
Prosopis glandulosa						33-82			10-62							
Salazaria mexicana											0-0					
Sarcobatus vermiculatus								0-22								
Yucca brevifolia											0-50				29-44	
Yucca schidigera											0-60				0-67	

Notes:
Studies include: (1) Abella et al. 2012a, (2) Bainbridge and MacAller 1996, (3) Brum et al. 1983, (4) Clary and Slayback 1983, (5) Devitt et al. 2020, (6) Edwards et al. 2000, (7) Fidelibus and Bainbridge 1994, (8) Fisher 1984, (9) Grantz et al. 1998c, (10) Graves et al. 1978, (11) Hunter et al. 1980, (12) Newton 2001, (13) Scoles-Sciulla et al. 2015, (14) Walker et al. 2001, (15) Wallace et al. 1980, and (16) Yamashita and Manning 1995. Studies evaluated outplant survival for 1-5 years after outplanting among studies.

Many of these top-performing shrubs and trees are favored by tortoises for resting and sites for constructing burrows, suggesting that outplanting can enhance availability of these key habitat resources. Furthermore, although many of the studies assessed outplant survival for a relatively short duration (one to three years after outplanting), the few longer-term studies reported persistence, growth, and flowering of outplants. Clary and Slayback (1983), for example, reported that most outplanted species alive after two years persisted five years after outplanting in the central Mojave Desert. Although not included in Table 4 as the study reported a cover metric rather than survival, Abella (2017a) found that outplants persisted at least six years in a semi-natural environment in the eastern Mojave Desert. Presumably, outplants persisting for these five- to six-year periods may be established in the habitat, and their longer-term survival could be comparable to naturally established individuals subject to mortality events from droughts and other factors (Miriti et al. 2007).

In burned desert tortoise habitat, height growth of surviving outplanted shrubs was rapid, with average heights of 49, 42, and 26 cm respectively for eastern Mojave buckwheat (*Eriogonum fasciculatum*), creosote bush, and white bursage three years after outplanting (Abella et al. 2012a). Desert tortoises generally construct burrows beneath larger plants with spreading canopies, underscoring the importance of outplant height (Burge 1978). Highlighting production of floral resources and potential for outplants to reproduce, an average of 86% of desert globemallow, 73% of eastern Mojave buckwheat, 33% of creosote bush, and 22% of white bursage flowered within three years after outplanting (Abella et al. 2012a). For relatively short-lived species, such as desert globemallow, reproducing or replenishing soil seed banks can be essential to population persistence (Drake et al. 2015).

Treatments associated with outplanting can be critical to success. However, treatments add cost and complexity, suggesting that cost-benefit analyses are necessary to compare any treatment-facilitated increases in plant performance with an alternative, such as simply planting more plants and accepting lower survival. In cases where few seeds are available for propagation or for species difficult to propagate in nurseries, then treatments to maximize survival of each propagule may be appropriate, even if treatments are costly. Resources may be optimally allocated when the most effective treatments and the species most reliant on such treatments to establish successfully are identified.

Eleven different treatments associated with outplanting were evaluated in 13 published studies (Table 5). These treatments include: cages for protection from herbivory, shelters to ameliorate microclimates and deter herbivory, chemicals to repel herbivores, different types of irrigation, construction of water catchments around outplants, fertilization, manipulating fertile islands at planting locations, treatments of non-native plants to reduce potential competition, and three treatments associated with outplanting procedures (seedling transport, planting methods, and planting at low or high density). Thus far, it is difficult to extract conclusions from the literature on effectiveness of most treatments because most have been tested in two or fewer studies, results were species- and context-specific, treatments can be contingent and interactive with each other, and there are numerous variations to treatments (e.g., the frequency or amount of water delivered for irrigation) that could further influence their effectiveness. With consideration to this variability and a need for further studies to optimize application of treatments where and when they are most needed, the existing literature offers insight into potential effectiveness of the more commonly applied treatments and ideas for further innovations.

Some type of physical barrier to mammalian herbivory, either a wire cage or shelter (typically a plastic cone or cylinder; Figure 13) enclosing outplants, has consistently enhanced outplant survival among treatments evaluated in at least two studies. All five studies testing cages or shelters reported that they have at least nearly doubled outplant survival (Table 5). In one study (Bainbridge and MacAller 1996), no unprotected outplants survived. In two studies of outplant survival in shelters compared with cages,

Figure 13. Outplanted creosote bush that grew to a height of 130 cm and flowered within three years after outplanting to revegetate a burned site in the eastern Mojave Desert, southern Nevada. Shelters protecting outplants in this study doubled outplant survival. Photo taken in May 2011 (S.R. Abella).

survival was 1.5 (Grantz et al. 1998c) and 2.3× (Bainbridge and MacAller 1996) greater in shelters. This could be because shelters provided both protection from herbivory and ameliorated microclimates, whereas cages only provided protection from herbivory. Two reasons that some form of protection from herbivory was often a key to outplanting success included 1) the intensive levels of herbivory occurring in deserts with naturally low amounts of palatable forage (potentially exacerbated at disturbed sites with little vegetation where outplanting is often performed) and 2) greenhouse-propagated seedlings may be enriched in nutrients and therefore attractive to herbivores.

Superficially, we might assume that enhancing moisture via such treatments as irrigation or construction of water catchments in depressions around outplants would increase plant survival in deserts. However, the effects of moisture-enhancing treatments on outplant survival have

Table 5.
Summary of treatment effectiveness associated with outplanting native perennials in the Mojave and western Sonoran Desert. Studies assessing one or more treatments and that reported outplant survival percentages for at least a year after outplanting are included. Treatment effects are shown as the ratio of percent survival in the treatment compared to no treatment (or shelter compared to cage for that comparison). Positive effects (+) indicate that a treatment increased survival, whereas negative effects (-) indicate that a treatment reduced survival. The symbols ++ and - - indicate that ratios were not calculated because all outplants died in either the no-treatment control (++, indicating treatments were crucial to plant survival) or treatment (- -). As an example of the ratios, outplant survival in cages was 40% in Devitt et al. (2020; numbered study 4) compared with 10% survival without cages, resulting in a ratio of +4.0.

Treatment	Effects (survival ratio)	Study
Protection		
Cage	+4.0, +1.8, +1.8	4, 9, 12
Shelter	+1.9, (++)	1, 2
Shelter: cage	+2.3, +1.5	2, 7
Herbivore repellent	(- -)	2
Moisture enhancement		
Irrigation	+1.9, +1.1, 1.0, 1.0, 1.0, +2.4	1, 3, 4, 8, 10, 13
Water catchment	+1.1	5
Nutrient enhancement		
Fertilization	-1.1	13
Fertile island	+1.4	11
Reduce competition		
Manage non-natives	-1.1, +1.3	10, 13
Planting procedures		
Seedling transport method	1.0	6
Planting method	+2.6	7
Planting density	+1.2	13

Notes:
Studies are numbered as follows: (1) Abella et al. 2012a, (2) Bainbridge and MacAller 1996, (3) Clary and Slayback 1983, 1984, (4) Devitt et al. 2020, (5) Edwards et al. 2000, (6) Fidelibus and Bainbridge 1994, (7) Grantz et al. 1998c, (8) Graves et al. 1978, (9) Hunter et al. 1980, (10) Scoles-Sciulla et al. 2015, (11) Walker et al. 2001, (12) Wallace et al. 1980, and (13) Yamashita and Manning 1995.
- The fertile island treatment in (11) Walker et al. 2001 tested outplanting in a fertile island microsite where a mature shrub had been removed.
- The seedling transport method in (6) Fidelibus and Bainbridge 1994 compared container with jelly rolled seedlings.
- Planting method in (7) Grantz et al. 1998c compared digging holes with an auger or pick axe.
- Planting density in (13) Yamashita and Manning 1995 compared planting at low or high density.

been inconsistent. Three of six studies testing irrigation (either as a slow-release gel or directly introducing water) found that irrigation increased outplant survival. The other three studies found no benefit of irrigation. Similarly, water catchments described by Edwards et al. (2000) produced minimal benefit, with 84% outplant survival with catchments and 74% survival without. There could be several reasons for inconsistent benefits of moisture treatments, such as 1) difficulties with delivering sufficient quantities, 2) timing of water delivery to appreciably influence outplant survival, or 3) effects of other factors, such as herbivory or soil erosion, overwhelmed the influences of moisture availability.

Other treatments may have promise but were not evaluated for their influence on outplant survival for at least a year in sufficient numbers of studies to evaluate their reliability. For example, based on the observation that non-native annual plants reduce fitness of mature shrubs (Rodríguez-Buriticá and Miriti 2009), reducing potential competition experienced by outplants could enhance outplant survival, particularly at sites with appreciable non-native annuals. Herbicide treatments designed to reduce non-native annuals enhanced outplant survival in one study (Yamashita and Manning 1995) but slightly reduced outplant survival in another (Scoles-Sciulla et al. 2015). Benefits to outplant performance of treating non-native plants could be contingent on factors such as the competitiveness of the particular non-native species at sites, interactions with other treatments, climate, and whether non-native annuals are sufficiently abundant to threaten outplant survival by increasing wildfire risk. Furthermore, potential exists for selecting native perennials that provide functions for tortoises and Joshua trees and that are also competitive with non-native annuals (Abella et al. 2011, 2012b).

Logistical challenges of outplanting vary with factors such as degree of difficulty of obtaining seed, availability of nursery facilities, type and size of containers in which plants are propagated, the number of outplants produced and desired planting density at restoration sites, ease of transporting outplants to field sites, and associated treatments applied to outplants (e.g., shelters, irrigation). Species-specific survival can also be a key factor, although species with lower survival may still be worth outplanting if they provide key functions, even if the cost per surviving plant is high. This highlights how additional research identifying ways to cost-efficiently enhance propagation techniques and outplant survival in the field has potential to substantially lower costs. Cost estimates for outplanting are presented in the restoration finances section of this paper.

Salvaging and Transplanting Plants

Transplanting entails moving plants from a donor to a recipient site. It often occurs in the context of salvaging plants before a planned disturbance, then using the salvaged plants to revegetate another site or to revegetate the original donor site in the case of a temporary disturbance (McMahon et al. 2008). After plants are salvaged, they may be moved directly to a recipient site or undergo a period of storage and nursery care before redeployment to other sites (Weigand and Rodgers 2009). Transplanting can be viewed as a three-phase "survival budget" including survival of the initial salvage operation, the period of transport or nursery care, and the post-planting period at revegetation sites (Abella et al. 2015b). While each of these phases can result in plant attrition, germination and sprouting of propagules in donor soil associated with salvaged plants can produce additional plants that can be separated and used in restoration. As with the preparation of outplants, the type and size of container (including the possibility of bare-root methods) is important for salvaging and caring for plants (Landis et al. 1990). As research continues on the numerous potential permutations of containers for propagating Mojave Desert species, a reasonable strategy balances salvaging as much root volume as possible with constraints on transport and storage of large volumes of soil and root mass (Smith et al. 2012). Salvaging small- to medium-sized perennials commonly employs 4-L or 16-L pots (Abella et al. 2015b). Salvaging the largest perennials, such as Joshua trees, was accomplished using heavy equipment to move large soil and root volumes, in addition to the heavy aboveground material (McMullen 1992, Weigand and Rodgers 2009).

Three studies demonstrated that salvaging and transplanting native perennials can commonly achieve survival rates > 25-50% cumulatively across all phases of salvage and > 50% specifically after transplants surviving earlier salvage phases were placed at restoration sites (Table 6). A total of 44 species were evaluated for amenability to transplanting and 25 of them achieved at least 50% survival (Table 6). Cacti appeared particularly amenable to transplanting: all nine species examined achieved 57-100% cumulative survival. Several shrubs and trees also performed well in at least one study, such as catclaw acacia (*Acacia greggii*), white bursage, creosote bush, desert almond (*Prunus fasciculata*), Mojave yucca, and Joshua tree. Only one study included herbaceous perennials, of which at least one (desert globemallow; Abella et al. 2015b) is consumed by desert tortoises (Esque et al. 2021).

Figure 14. Top: temporary field nursery established in a fenced area near a ranger station, which had a water source, in a plant salvage and transplanting project in Lake Mead National Recreation Area, southern Nevada. Bottom: transplants placed at one of the restoration sites. All transplants were enclosed in cages to deter herbivory and some were planted on salvaged topsoil and with or without two types of irrigation (hand watering or slow-release gel). Top photo by L.P. Chiquoine; bottom photo by S.R. Abella.

A study in desert tortoise habitat in the eastern Mojave Desert in Lake Mead National Recreation Area illustrated variation in transplant success among perennial species and effects of treatments (Abella et al. 2015b). The study involved salvaging 2105 individuals of 23 perennial species before construction activities that re-routed a park road, storing and caring for the plants for 16 months in a temporary field nursery near future restoration sites, placing plants at restoration sites after construction activities ceased (with the restoration sites being removed segments of the old road), and monitoring survival for 27 months at the restoration sites (Figure 14). Immediately after plants were salvaged, several treatments were evaluated for their ability to enhance plant survival: a root-stimulating hormone, a gel polymer added to soil to slowly release water

Table 6.
Summary of survival of plants salvaged and transplanted to restoration sites in three studies in the Mojave and western Sonoran Desert. Survival is the percentage of transplants placed back out in the field that survived at restoration sites for 2-3 years among studies.

	Study				
Species	**1**	**2**	**3**	**Total**	**≥ 50%**
	— Survival % (no. plants transplanted) —				
Grass					
Pleuraphis rigida	14 (29)			1	0
Forbs/subshrubs					
Astragalus preussii	3 (33)			1	0
Baileya multiradiata	30 (104)			1	0
Enceliopsis argophylla	17 (18)			1	0
Eriogonum inflatum	27 (89)			1	0
Gutierrezia sarothrae	25 (4)			1	0
Sphaeralcea ambigua	50 (105)			1	1
Stephanomeria pauciflora	47 (55)			1	0
Suaeda moquinii	50 (26)			1	1
Cactus					
Cylindropuntia acanthocarpa	67 (6)			1	1
Cylindropuntia echinocarpa			49 (332)	1	0
Cylindropuntia ramosissima			64 (202)	1	1
Echinocereus engelmannii			57 (7)	1	1
Echinocereus triglochidiatus			77 (75)	1	1
Echinomastus johnsonii	100 (8)			1	1
Ferocactus cylindraceus	100 (5)	85 (20)		2	2
Grusonia parishii			70 (27)	1	1
Opuntia basilaris	93 (103)		83 (23)	2	2
Shrub					
Acacia greggii	0 (3)		75 (148)	2	1
Ambrosia dumosa	60 (360)			1	1
Atriplex canescens			0 (5)	1	0
Atriplex confertifolia	54 (28)			1	1
Atriplex hymenelytra	47 (17)			1	0
Coleogyne ramosissima			29 (94)	1	0
Encelia farinosa			82 (33)	1	1
Encelia virginensis	36 (14)			1	0
Ephedra californica			100 (4)	1	1
Ephedra nevadensis			57 (60)	1	1
Ephedra torreyana	36 (22)			1	0
Eriogonum fasciculatum			61 (23)	1	1
Grayia spinosa			51 (98)	1	1
Hymenoclea salsola	19 (21)		100 (5)	2	1
Isocoma acradenia	38 (16)			1	0

Larrea tridentata	53 (73)		0 (1)	2	1
Lycium andersonii			9 (11)	1	0
Lycium cooperi			10 (10)	1	0
Prunus fasciculata			79 (34)	1	1
Psorothamnus fremontii	14 (14)			1	0
Salazaria mexicana			78 (9)	1	1
Tetradymia spinosa			0 (3)	1	0
Yucca schidigera		39 (459)	84 (478)	2	2
Chilopsis linearis			100 (4)	1	1
Juniperus californica			0 (1)	1	0
Yucca brevifolia			54 (782)	1	1
Total	**23**	**2**	**25**	**44**	**25**

Notes:
Studies are numbered as follows: (1) Abella et al. 2015b, (2) McMullen 1992, and (3) Weigand and Rodgers 2009.

to roots, and soaking roots in water. These post-salvage treatments had no statistically significant effect on plant survival of salvage and the 16 months of nursery residence. However, treatments applied to transplants placed back in the field at restoration sites affected transplant survival. Transplants placed on sites receiving salvaged topsoil (upper 20 cm of soil) exhibited 56% survival at 27 months, more than twice the 25% survival of transplants placed on sites without topsoil. The benefits of planting on salvaged topsoil (without irrigation) were nearly equivalent to irrigating plants at a 63% augmentation of the site's average rainfall of 16 cm/year. Irrigation increased transplant survival by 1.6×, but the type of irrigation affected species differently. White bursage, for example, responded similarly to hand watering or a slow-release gel affixed near roots in soil. In contrast, for reasons that were unclear, desert globemallow only responded to hand watering. Although herbaceous perennials as a group did not perform as well as shrubs or cacti across the treatments applied, including herbaceous perennials in salvage operations may be warranted to diversify species composition and provide unique ecological functions.

Studies further illustrated logistical considerations for reintroducing salvaged plants to restoration sites. For re-planting salvaged cacti, Smith et al. (2012) suggested the potential importance of orienting transplanted cacti in the same direction at restoration sites as they had originally grown. Cactus tissue can become acclimated to the direction of the most intense sunlight. When feasible, salvaging topsoil along with salvaging plants appears beneficial to both provide a substrate for increasing transplant survival at restoration sites and likely other benefits too (e.g., restoring soil microorganisms). The finding in Abella et al. (2015b) that both topsoil and some type of irrigation similarly increased overall transplant survival illustrated a potential tradeoff where salvaging topsoil represents a major up-front effort but may save effort later if less care of transplants is required. Research to date suggests that transplanting can be an effective restoration tool for desert perennials when donor sites are available and may be especially important for restoring taller individuals (such as Joshua trees) otherwise requiring decades to grow to maturity.

Cuttings

Propagating plants using cuttings from stems, branches, rhizomes, or roots avoids a need for collecting and successfully germinating seed. However, propagating from cuttings requires donor plants and the ability of cuttings to root. At least four studies reported techniques for propagating cuttings from material collected from the Mojave or Sonoran deserts.

For example, using stem cuttings collected in the northern Mojave Desert, Wieland et al. (1971) presented optimal treatments (among combinations of applying concentrations of rooting hormones and greenhouse care techniques) for 16 species of shrubs and trees (Table 7). With the exceptions of stem cuttings from Utah juniper (*Juniperus osteosperma*) and little-leaved ratany (*Krameria erecta*), which failed to root under any treatment, stem cuttings from 14 species rooted. Applying a root-stimulating hormone (1H-indole-3-butanoic acid; IBA) enhanced rooting in nine of the species, while five species did not need IBA to stimulate rooting. Further research would be required to evaluate the performance of the rooted cuttings in field settings and how the performance of the cuttings may compare with outplants, transplants, or seedlings originating from seeding.

Table 7.
Results of treatments to stimulate rooting of stems cut from 16 species of native shrubs common in the northern Mojave Desert (Wieland et al. 1971). IBA is the root-stimulating hormone 1H-Indole-3-butanoic acid.

Species	Results
Ambrosia dumosa	Stem cuttings readily rooted with 0.3% IBA
Atriplex canescens	Stem cuttings from seedlings rooted without IBA
Atriplex confertifolia	Stem cuttings from seedlings or juveniles rooted without IBA
Atriplex hymenelytra	Stem cuttings from seedlings rooted without IBA
Atriplex lentiformis	Stem cuttings rooted with 0.8% IBA
Bassia americana	Stem cuttings rooted without IBA
Ephedra viridis	Stem cuttings from seedlings rooted without IBA
Grayia spinosa	Stem cuttings rooted with 0.3% IBA
Juniperus osteosperma	Stem cuttings failed to root
Krameria erecta	Stem cuttings failed to root
Krascheninnikovia lanata	Vigorous shoots of any age rooted; 0.3% IBA improved rooting
Larrea tridentata	Juvenile plant shoots rooted; 0.8% IBA stimulated rooting
Lycium andersonii	Stem cuttings readily rooted with 0.3% IBA
Lycium pallidum	Juvenile plant shoots rooted; 0.3% or 0.8% IBA stimulated rooting
Lycium shockleyi	Juvenile plant shoots rooted; 0.3% or 0.8% IBA stimulated rooting
Thamnosma montana	Stem cuttings readily rooted; 0.3% or 0.8% IBA stimulated rooting

Using material collected from near Palm Springs, California, Chase and Strain (1966) reported that brittlebush (*Encelia farinosa*) and white bursage had at least 33% of their stem cuttings successfully root in at least one treatment. The treatments examined included various rooting hormone solutions, immersion in Hoagland's nutrient solution, and using vermiculite as a rooting medium. In contrast to Wieland et al. (1971), creosote bush cuttings did not root in any treatment. Chase and Strain (1966) further suggested that the ability of cuttings to root could vary among individuals within species. As a result, the authors began randomly selecting individuals from which to obtain cuttings and raised the possibility of identifying traits of individuals potentially most amenable to propagation.

In the western Sonoran Desert, Chiquoine et al. (2022) examined not only rooting ability of plants, but also their subsequent performance in different planting locations at a restoration field site. The study focused on beavertail, a cactus which provides food for adult tortoises and is also an important species for pollinators (Esque et al. 2021). Cuttings (single pads) were obtained from a donor site, placed in pots in a greenhouse for root development for six months; 83% of pads survived and rooted during this period (Chiquoine et al. 2022). At a disturbed field site, the propagated cuttings were placed either in the open or in the interior of a circle of "nurse rocks" to provide protection (Figure 15). In the first 15 months after planting, during which precipitation was average, survival of cacti did not differ between microsites, but only individuals planted within nurse rocks flowered. Nurse rocks subsequently became even more important during extreme drought. Twenty-seven months after planting, twice as many cacti with nurse rocks survived compared to those without. Results highlighted the potential importance of selecting or creating favorable microsites for planting locations to increase plant survival and therefore maximize use of plant material. Furthermore, results highlighted that studying plant distributions in reference sites (where beavertail were largely restricted to growing near rocks) can help guide planting locations and arrangements at restoration sites. The study demonstrated that propagating and planting cuttings in suitable microsites can restore beavertail populations, even during extreme drought, and that individuals can flower and reproduce vegetatively on site within about a year.

The three studies above, along with Rowe et al. (2020) who found that most cuttings (pads) of *Cylindropunti*a and *Opuntia* spp. survived for at least five years at restoration sites when moved directly from donor plants in the Sonoran Desert, suggest that propagating species from cuttings is a promising restoration tool. Furthermore, bypassing a need to obtain viable seed for propagating plants and instead using cuttings, could become increasingly useful if droughts become more severe in coming decades and curtail viable seed production. Further research to advance propagating plant material from cuttings could include screening more species for rooting ability of their different parts (e.g., stems or rhizomes), identifying if variation among individuals in rooting ability is predictable, continuing to test treatments for cost-effectively stimulating rooting either in greenhouse or field settings, examining effects of collecting material from donor plants to minimize potential damage to wild source populations, and assessing performance of plants derived from cuttings at restoration sites.

Figure 15. Beavertail, grown from pads propagated in a nursery, enclosed in a "nurse rock" treatment at a restoration site in the western Sonoran Desert, southeastern California. Cacti placed within nurse rock shelters had higher flowering frequency and greater survival during drought than plants without nurse rocks (Chiquoine et al. 2022).

Seeding

Outcomes of seeding were highly variable among 13 Mojave Desert studies that included a total of 44 native species and that monitored establishment of the plants for ≥ 1 year (Table 8). Seeding in some projects failed to result in establishment of most or all species, whereas in other studies, some species became established at least in the short-term.

Identifying the consistently best-performing species is difficult, because most species were seeded in ≤ 2 studies, seed viability and seeding rates varied among species, and measures of plant establishment differed among studies (Table 8). However, some qualitative trends appear evident for species seeded in at least two studies. The perennial sand ricegrass (*Achnatherum hymenoides*) became established in three of four studies in which it was seeded, similar to James' galleta (*Pleuraphis jamesii*) which became established in two of three studies. Among herbaceous perennials, Palmer's penstemon (*Penstemon palmeri*) became established in both studies in which it was seeded, while desert globemallow became established in only one of five studies. Top-performers among shrubs included white bursage (establishment in three of six studies), four-wing saltbush (all five studies), allscale saltbush (all three studies), Mojave Desert buckwheat (three of five), and winterfat (*Krascheninnikovia lanata*; two of four). *Atriplex* performed well, as all five species in the various studies in which they were seeded exhibited some establishment in each study. Creosote bush was the poorest-performing shrub seeded in at least two studies, with establishment in only one of seven studies. Brittlebush (establishment in one of three studies) and cheesebush (establishment in one of four studies) also performed poorly in seeding.

Precipitation exceeded long-term averages in the post-seeding monitoring period in 62% (8 of 13) of studies, which may relate to why at least some seeded species became established in most studies (Table 8). However, some plant establishment also occurred for at least one seeded species in at least one site in four studies in which precipitation was below average, ranging from 33-85% of average precipitation (Graves et al. 1978, Grantz et al. 1998a, Jones et al. 2014, Suazo et al. 2013). The seeding study occurring in the driest conditions, with 33% of average rainfall, found that seeding failed to result in any plant establishment at most sites, but some species did become established at one site (Grantz et al. 1998a).

Table 8.
Summary of seeded species performance in 13 published studies in the Mojave and western Sonoran Desert that evaluated post-seeding plant establishment for at least a year. Studies used different measures to quantify seedling establishment. Measures of seeded species performance are abbreviated as: seedlings/m^2 (/m^2), % of seeds producing a seedling (% S), and % plant cover (% C).

	1	2	3	4	5	6	7	8	9	10	11	12	13	Total
Species	**/m²**	**/m²**	**% S**	**/m²**	**% C**	**% S**	**/m²**	**/m²**	**% S**	**% S**	**/m²**	**% S**	**/m²**	
Grass														
Achnatherum hymenoides					10		2.0				1.2		0	**4**
Achnatherum speciosum					0									**1**
Aristida purpurea	0													**1**
Elymus elymoides							1.1							**1**
Pleuraphis jamesi							<0.4				0.1		0	**3**
Sporobolus cryptandrus											0.1			**1**
Forbs/subshrubs														
Baileya multiradiata	0											0	2.7	**3**
Eschscholzia californica					0									**1**
Linum lewisii													0	**1**
*Lupinus sparsiflorus**													0	**1**
Penstemon bicolor	0							9.4				0		**3**
Penstemon palmeri											1.9		6.7	**2**
*Phacelia parishii**								3.6						**1**
*Plantago ovata**		5-48												**1**
Sphaeralcea ambigua	0	0					<0.4					0	0	**5**
Sphaeralcea grossulariifolia											0.1			**1**
Sphaeralcea rusbyi								0.3						**1**
Xylorhiza tortifolia													0.4	**1**
Shrub														
Ambrosia dumosa	0		0.5			4				0		0	0.8	**6**
Artemisia tridentata				0.1										**1**
Atriplex canescens				0.6	12, 0	62	<0.4				0.2			**5**
Atriplex confertifolia							0.6							**1**
Atriplex lentiformis				0.2										**1**
Atriplex polycarpa				4.2	10, 0	12								**3**
Atriplex spinifera			1.1											**1**
Bebbia juncea	0													**1**
Brickellia incana													0	**1**
Cleome isomeris				0.8										**1**
Coleogyne ramosissima									1-22			21		**2**
Encelia farinosa	0			0.2								0		**3**
Encelia virginensis													0.1	**1**
Ephedra nevadensis							0.6							**1**
Ephedra viridis							<0.4							**1**
Ericameria nauseosa					0		<0.4							**2**
Eriogonum fasciculatum	0			0.2	8, 0		<0.4					0		**5**
Grayia spinosa							<0.4							**1**
Hymenoclea salsola	0	0					<0.4					0		**4**
Krascheninnikovia lanata		0	0.3				0.4				0			**4**
Larrea tridentata	0		0.1		0	0				0		0	0	**7**
Lepidospartum squamatum						8								**1**
Lycium andersonii							<0.4							**1**
Sarcobatus vermiculatus							<0.4							**1**
Total	**10**	**4**	**4**	**7**	**8**	**5**	**15**	**3**	**1**	**2**	**7**	**9**	**12**	**42**

Notes:
Studies are numbered as follows: (1) Abella et al. 2012a, (2) Abella et al. 2015c, (3) Brum et al. 1983, (4) Clary and slayback 1983, (5) Grantz et al. 1998a, (6) Graves et al. 1978, (7) Hall and Anderson 1999, (8) Hiatt et al. 1995, (9) Jones et al. 2014, (10) Ostler et al. 2003, Caldwell et al. 2009, (11) Ott et al. 2011, (12) Suazo et al. 2013, and (13) Walker and Powell 1999.

- Species with asterisks are annuals; the rest are perennials.
- In (2) Abella et al. 2015c, the range of seedling densities in different treatments is provided.
- In (5) Grantz et al. 1998a, numbers separated by commas represent plant cover in two separate trials within the study.

The longest-term study, monitored for 14 years (1993-2007) after seeding in the northeastern Mojave Desert for revegetating mine sites, showed how abundance of seeded species fluctuated through time with variation in seasonal and multi-year precipitation trends (Ott et al. 2011). For example, sand ricegrass peaked at a density of 2.2 plants/m^2 in 1997 following multiple wet periods but declined to 0.2 plants/m^2 by 2007 after two years of generally below-average precipitation. In another example, the herbaceous perennial, Palmer's penstemon, exhibited no or minimal establishment (≤ 0.1 plants/m^2) until four years after seeding. Density was then 2-3 plants/m^2 in 1997-1998 (five and six years post-seeding) during a wet period, dropped to 0.1 plant/m^2 in the dry 2002, increased to 0.7 plants/m^2 in the wet 2005, and was absent in the dry 2007. Four-wing saltbush was consistently present in all study years between 1993 and 2005, but it too disappeared by 2007.

The long-term data for abundance of seeded species suggested four conclusions: 1) conditions in any particular year of monitoring could have a major influence on perception of seeding effectiveness, 2) establishment in years soon after seeding did not necessarily mean that seeded species became persistent components of the community, 3) "progressions" and "retrogressions" may exist within restoration communities at achieving revegetation goals, and 4) it is possible that seeding (or subsequent reproduction of seeded individuals) can promote replenishment of seed banks and thus have beneficial effects even during periods when seeded species are sparse aboveground. Additionally, Ott et al. (2011) highlighted that communities of seeded species on restoration sites may be subject to fluctuations in densities of seedlings and mature plants across variation in annual and multi-year precipitation periods, similar to mature desert communities.

Twelve studies, including two not in Table 8 because they evaluated plant establishment for < 1 year, assessed treatments associated with seeding. Success was mixed within and among treatments (Table 9). Pelletizing seed, by enclosing seeds in a protective coating, negatively affected seedling emergence for blackbrush (Jones et al. 2014). In another study, pelletizing seed of three perennial species did not improve emergence (compared to bare seed) in the first year and failed to result in any live plants by the second year (Abella et al. 2015c). In contrast, pelletizing seed of desert plantain, a native forb comprising tortoise forage, tripled in cover through at least two growing seasons after seeding (Abella et al. 2015c). Protecting seeds from mammalian granivory or herbivory using wire exclusion cages or fences consistently enhanced seedling emergence and establishment. In total, authors of four of five studies reported that protection enhanced plant establishment for at least some species (Table 9). In comparison, irrigation improved seedling establishment in only two of six studies. Brum et al. (1983) reported that at least 46 of 47 surviving seedlings across two years were in irrigated plots, but survival of seedlings was low overall with only 47 of 13,818 seeds (0.3%) producing a seedling after two years. In Hall and Anderson (1999), only a spring irrigation, when combined with seeding on replaced topsoil, improved seedling establishment. Irrigating in both spring and autumn or without topsoil did not improve establishment. This was possibly because benefits of irrigation were highly contingent upon conditions at the time the irrigation treatment occurred and that other ecological conditions were not amenable to germination during autumn irrigation.

Manipulations of ground surfaces and use of soil amendments coupled with seeding also displayed mixed success for aiding seedling establishment (Table 9). DeFalco et al. (2012) found that tillage (3-cm wide, 5-cm deep furrows, which were then seeded) improved seedling emergence four months after seeding. Tillage also increased seed retention on site, enabling potential formation of soil seed banks from seed that did not initially germinate. The only other study reporting that a surface or amendment treatment produced a benefit was Winkel et al. (1995). In that study, which examined emergence of short-term seedlings for five months after seeding, water catchments consisting of sloping areas to collect water enhanced emergence of seeded shrubs. In a study where surface manipulations negatively affected establishment of seedlings, Grantz et al. (1998a) reported that broadcast seeding without disturbing the soil was the most effective treatment, possibly because the sites contained the least cover of competitive, non-native annual plants, compared with seeded sites receiving ripping and furrowing. Furthermore, drill seeding was generally less effective than broadcast seeding. Mulches (e.g., straw, gravel, or wood bark material) and tackifier (designed to stabilize soil) did not improve seedling establishment in the three studies in which they were tested (Table 9). Although it is possible that treatment of ground surfaces and amendments such as mulches could have other benefits beyond aiding seedling establishment, they also increase the cost and complexity of restoration and thus may fail a cost/benefit analysis with respect to improving seeding effectiveness (Table 9).

Seeding rates varied among studies, and uncertainty exists as to whether varying seeding rates could have changed seeding outcomes. For example, seeding

Table 9.
Summary of whether treatments aided establishment of seeded species in 11 published studies in the Mojave and western Sonoran Desert. Symbols illustrate whether treatments benefited (+), did not affect (0), or negatively affected (-) seedling emergence and establishment. For studies with a treatment symbolized as +,0, outcomes of treatments varied among groups of species or with variations of the treatment.

Study	Duration (yrs)	Precip. (%)	Pelletize	Protection	Irrigation	Surface	Catchment	Mulch	Tackifier
1	3	103		0	0				
2	2	103	+, 0	+, 0	0				
3	2	146		+	+				
4	0.3	273				+			0
5	3-5	33-76				-			
6	2	76			0				
7	2	167			+, 0				
8	2	85	-	+					
9	1	82						0	
10	2	81		+					
11	0.4	150			0	0	+	0	

Notes:
-Studies are numbered as follows: (1) Abella et al. 2012a, (2) Abella et al. 2015c, (3) Brum et al. 1983, (4) DeFalco et al. 2012, (5) Grantz et al. 1998a, (6) Graves et al. 1978, (7) Hall and Anderson 1999, (8) Jones et al. 2014, (9) Ostler et al. 2003, Caldwell et al. 2009, (10) Suazo et al. 2013, and (11) Winkel et al. 1995.
-Duration is how long a study monitored seedling establishment after seeding.
-Pelletize represents placing seeds in protective coatings. Protection entailed protecting seeds or seedlings from granivory and herbivory, such as seeding within small fences. Irrigation included delivering water to seedlings using various methods. Surface treatments are those typically seeking to create topographic microheterogeneity or to de-compact soils, such as soil roughening. Catchments were small depressions, intended to retain seeds and collect water and organic material. Mulch was placing various materials (e.g., straw) horizontally on the ground. Tackifier was designed to stabilize soil by adding substances to hold soil together.

local areas at high rates could attract unusually high numbers of granivorous ants, mammals, or birds, but protective treatments could limit removal of seeds and damage to seedlings. Seeding at high rates did not assure establishment of seedlings; instead high seeding rates could simply result in more seeds failing to produce persistent seedlings. For example, Abella et al. (2015c) seeded at a high density of 5000 (cheesebush), 1700 (winterfat), and 13,000 seeds/m^2 (desert globemallow). However, no seedlings of these three perennials persisted after two years. In contrast, in a study where seedlings established, Grantz et al. (1998a) observed that doubling the seeding rate approximately doubled the number of seedlings produced.

Although complicating identifying general conclusions from the literature to date, the diversity of seeding rates, seeded species, treatments, timeframes of monitoring, and contexts (e.g., precipitation, variability in source genetics and viability of seed) helps illustrate numerous considerations associated with seeding and highlights opportunities for future research. For example, the different timeframes of studies, ranging from monitoring seedling establishment for four months to 14 years post-seeding, illustrate the significance of differentiating emergence versus persistent seedling establishment. Short-term studies are valuable for ascertaining species and treatments that result in emergence as an initial restoration step, while identifying that seeding protocols that result in emergence but not seedling establishment can detrimentally forestall opportunities for formation of seed banks in the soil. If short-term emergence does not occur and viable seeds persist on site, then projects seemingly initially unsuccessful could at least potentially maintain propagule sources. Thus, it may be appropriate to evaluate effectiveness of seeding projects as three stages consisting of ability to produce emergence, seedling establishment, and either persistent plants or replenished seed banks.

The existing research further illustrates that project and treatment success are likely contingent on selection of species. For example, seeding failed to augment perennial species used by tortoises for cover in Abella et al. (2015c) but it did enhance availability of an annual food plant, desert plantain. Annual species were rarely included in seed mixtures among studies. Evaluating more annual species is warranted, especially given the importance of annual forbs in forming the bulk of diets of desert tortoises (Jennings and Berry 2015).

Illustrating how treatments need to be tailored to species-specific needs, pelletizing reduced emergence of blackbrush but enhanced emergence in desert plantain (Jones et al. 2014, Abella et al. 2015c). Various permutations to treatments like irrigation can also affect outcomes, such as the finding by Hall and Anderson (1999) that irrigating only in spring provided benefits. Varying the amount and timing of irrigation could affect seeded species differently and in different years varying in precipitation, along with potentially interacting with soil surface conditions.

Further screening a diversity of plant species for their amenability to seeding, evaluating different treatments (with cost-benefit analyses), and developing tools to match seeding to conditions for success are likely to be productive for generating useful restoration techniques. It would also be useful to test seeding using the same sets of species and seed sources but across multiple years to work towards pinpointing the types of years in which different species can be successfully seeded. While it may be assumed that moist years would be most favorable, these years can also have the most competition from non-native and non-seeded plants. Additionally, factors other than precipitation, such as temperature, can affect emergence of seedlings (Beatley 1974).

From a practical management perspective, existing research can help identify species amenable to either or both seeding and outplanting, highlights potential in using "bet-hedging" approaches to operational projects, and indicates the utility of protection treatments (Tables 4, 8). *Atriplex* exemplify species that performed well in both seeding and outplanting. White bursage performed at least moderately well in both seeding and outplanting. In contrast, creosote bush and cheesebush performed well in outplanting but poorly in seeding. These observations suggest that employing both seeding and outplanting as a bet-hedging approach may be prudent to increase the chance that at least some plants will become established. Interestingly, protection treatments (e.g., cages or shelters to deter damage to plants) have thus far most consistently aided plant establishment for both outplanting and seeding among all the treatments tested. While cages or fencing may be infeasible, particularly for broad-scale seedings, exploring other procedures for protecting seeds, such as using decoy seeds to attract the focus of granivores (Longland and Bateman 1998), may have potential for aiding seeding.

Owing to the usual limitation of availability of native plant seed and to the potential influence of seed source on outcomes of projects, the question of whether to use locally collected seed (and if so, how local) is commonly raised for restoration projects. This issue is unresolved and the subject of ongoing research. Combining analyses of genetics and plant performance are required to determine how successful particular seed sources are in different present and anticipated future environments. Given frequent local adaptation of plants, the current consensus is that seeds for restoration projects should be collected as locally as possible, unless specific reasons exist to expect that genotypes from elsewhere will perform better (Johnson et al. 2010). In an example of local adaptation in the Mojave Desert, Shryock et al. (2015) identified genetic differentiation in desert globemallow populations along environmental gradients of water stress and seasonality of temperatures.

Assisted Natural Regeneration

Assisted natural regeneration (ANR) is a restoration and management technique for enhancing the natural recruitment of desired species (Abella et al. 2020). Unlike outplanting, transplanting, and seeding which assume that humans must reintroduce propagules for successful restoration, ANR focuses on enhancing recruitment from existing on-site propagules or aiding natural processes to increase propagule availability on site. This approach has the potential advantages of favoring local genetics, avoiding resource-intensive preparation and transport of plant material, and lowering costs. However, uncertainties in applying ANR include whether natural regeneration can be effective, which methods produce successful ANR, and how ANR compares with active revegetation techniques, such as outplanting.

Much of the existing ANR research and application has occurred in forests with tree seedlings, with less focus in drylands. The technique may have both challenges and opportunities as a restoration tool in deserts. For example, successful recruitment of desert perennials under natural conditions is generally highly episodic, and while it may not be uncommon for thousands of seedlings to appear at a site some years, few to none of the seedlings survive across multiple years (e.g., Sheps 1973). Thus, while ANR may only be feasible in years with seedlings, techniques that increase survival of seedlings by even small percentages could substantially increase plant recruitment in years with mass germination.

To test ANR methods, an initial study in the eastern Mojave Desert located 72 creosote bush seedlings (1-2 years old) in 2017 on a decommissioned road where restoration was desired (Abella et al. 2020). Treatments chosen to assist seedlings in overcoming the limitations of herbivory and lack of moisture included providing slow-release irrigation gel and enclosing seedlings in plastic tree shelters (Figure 16). The irrigation gel did not significantly affect survival or growth. After two years, and in contrast

Figure 16. Sheltered creosote bush seedling (shown in the inset with the shelter removed) receiving slow-release irrigation gel from the brown tube in an assisted natural regeneration study in the Dead Mountains Wilderness Area, eastern Mojave Desert, southeastern California. Irrigation gel did not increase survival or growth. Shelters reduced survival but tripled height growth of surviving seedlings. Photo by field botanists with the University of Nevada Las Vegas.

to expectations, only half as many sheltered as unsheltered seedlings remained alive. However, surviving sheltered seedlings grew 3× faster and taller than surviving unsheltered seedlings. Over the longer term, the benefit of the shelter treatment would hinge on whether the taller plants have advantages (e.g., out of reach of some herbivores, more rapid flowering) and whether the treatment was worth the cost. The shelters cost $3 each. Labor equated to 15 minutes/plant and included transporting shelters on foot 1.5 km to the project site in a wilderness setting, installing and checking shelters, and removing them at the end of the experiment. As the lower foliage on seedlings within shelters died, problems with shelters could have been excessive heat buildup, too little sunlight, or inadequate gas exchange (Oliet et al. 2019). Further research would be needed to test different colors or types of shelters which can function differently, making ventilation holes in shelters, or using other materials and designs.

Although results were mixed for this ANR study, they highlighted that further research exploring other species and other techniques is warranted to determine whether potential benefits could be realized for ANR to become another restoration tool. The study also highlighted a possible contrast, where the treatments of irrigating gel and shelters did not improve survival in ANR but substantially increased survival of greenhouse-grown creosote bush seedlings in outplanting. It is possible that treatments aiding outplants are not the same as those that could aid natural seedlings in ANR.

MANAGEMENT ACTIVITIES TO LIMIT DISTURBANCE AND PROMOTE RECOVERY

Fencing and Protection

Fencing and other practices to limit disturbance can benefit desert tortoises, Joshua trees, and other sensitive and imperiled species through improving habitat resources (e.g., forage quality and quantity for tortoises and nurse plants for Joshua trees) and potentially through reducing stressors such as subsidized predators and vandalism by humans (Berry et al. 2020a). Strategically deploying fenced exclosures to limit access by domestic or feral animals (or otherwise removing the animals) has improved forage conditions and plant cover for tortoises (Brooks 1995). Overlap in forage preferences exists among desert tortoises, domestic livestock (cattle and sheep), and feral burros, particularly in the forb component heavily utilized by all the herbivores (Nicholson and Humphreys 1981, Avery and Neibergs 1997, Berry et al. 2014a, Jennings and Berry 2015). In seven studies across the Mojave Desert, for example, desert plantain comprised the greatest percentage (11%) of feral burro diets (Abella 2008). Based on bite counts of juvenile desert tortoises, this native annual forb also formed 23% of tortoise diets in the central Mojave Desert (Oftedal et al. 2002). Constructing exclosures and removing feral burros has led to (Abella 2008) or correlated with (Abella et al. 2019) increases in native plants.

Long-term research in the Desert Tortoise Research Natural Area provides an example of the potential benefits of fencing for protection from sheep grazing, off-road vehicles, and other anthropogenic disturbances (Figure 17). During a 34-year study of habitat conditions and tortoise populations inside the fenced natural area (tortoises were able to pass beneath the fence) compared with conditions outside the fence, perennial plants used by tortoises for cover and native annual plants used for forage were more abundant inside the fence than outside (Brooks 1995, Berry et al. 2020c; Figure 18). Density of common ravens, a predator of tortoises, was lower inside the fence during several years (Berry et al. 2020c). By the end of the study in 2012 after 34 years of protection, tortoise densities were

Figure 17. Views of habitat outside (left photo) and inside (right photo) the fenced Desert Tortoise Research Natural Area, western Mojave Desert, Kern County, California. Habitat outside the fence, shown in 2012, was once comparable to the diverse creosote bush community found inside the fence but has been degraded by off-road vehicle use and sheep grazing. It is typical of many sites in the western, central, and southern Mojave Desert where off-road vehicle use occurs and livestock graze or have historically grazed. Inside the fence, habitat was protected from recreational vehicle use and sheep grazing from 1980 through the present. The Natural Area was protected by the U.S. Congress in 1980 and encompasses 100 km^2 of protected land for the Mojave desert tortoise. Both photos, taken in 2012, were from a long-term study (1979-2012) of demography and habitat of desert tortoises and is in a diverse creosote bush community (Berry et al. 2020c). A desert tortoise appears in the bottom left of the photo on the right.

2.5× greater inside the fence compared with outside (Berry et al. 2020c). Limiting anthropogenic impacts, whether via fencing or other management strategies, appears to significantly alleviate some of the threats facing tortoises and may begin reversing habitat deterioration (Brooks 1995, Berry et al. 2014a, Berry et al. 2020c). It is possible these benefits could be further accelerated or accentuated by strategically deploying restoration or non-native plant treatments within the protected area.

Reducing Non-Native Plants and Risk of Wildfires

Non-native plants, particularly annual grasses and Sahara mustard (*Brassica tournefortii*), are degrading habitat for desert tortoises, Joshua trees, and many other native species. Non-native annuals produce deleterious effects in two principal ways: reducing quality of the native annual plant communities (lowering diversity and quantity of native food plants available to tortoises) and heightening risk of wildfire, harming tortoises, Joshua trees, and the broader ecosystem (Berry and Murphy 2019, Wilkening et al. 2020). Presence and increase in the biomass of Sahara mustard correlated with reduced native forbs, some of which were food plants for desert tortoises in the western Sonoran Desert (Berry et al. 2014b). Risk of fire in invaded desert habitats is correlated with the amount and continuity of non-native annual grass fuel (Brooks 1999, Rao et al. 2010, Abella 2020). Non-native annual grasses, such as Mediterranean grass (*Schismus* spp.) and red brome

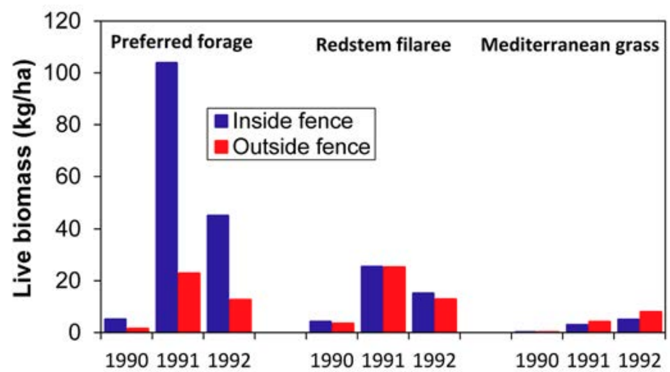

Figure 18. Biomass of preferred forage plants and non-native redstem filaree (generally better forage than non-native grasses but less preferred by tortoises than some native forbs) and non-preferred Mediterranean grass (a non-native annual) inside and outside fencing at the Desert Tortoise Research Natural Area, western Mojave Desert, Kern County, California. Data, from Brooks (1995), are shown for three years varying in rainfall.

(*Bromus rubens*), also compete with native perennials that tortoises utilize for cover and with native annual forage plants (Holzapfel and Mahall 1999, Brooks 2000, Rodríguez-Buriticá and Miriti 2009). Fire also reduces large-statured native perennial plants for at least decades to centuries, limiting the fertile islands that native annuals, including tortoise food plants, require for recruitment (Wilkening et al. 2020, Abella et al. 2021). Joshua tree seedlings also use shrubs for nurse plants: 93% of seedlings grew below canopies of shrubs (Brittingham and Walker 2000).

When non-native annuals are reduced, native annuals, including high-quality tortoise food plants, have generally responded positively. For example, Brooks (2000) found that thinning *Schismus* via cutting doubled density of native annuals in a wet year. Some of the increasing natives were bristly fiddleneck (*Amsinckia tessellata*) and other forb species that Jennings and Berry (2015) identified as forage favored by tortoises. Native annuals also remained green two weeks later in spring on *Schismus*-thinned plots, which could allow tortoises to forage longer (Brooks 2000).

Carefully timed herbicide applications have reduced non-native plants while increasing native annuals. On a burned site in the western Mojave Desert, Steers and Allen (2010) found that applying the post-emergent herbicide Fusilade early in the growing season reduced non-native grasses as well as the non-native forb redstem filaree (*Erodium cicutarium*). Species richness and cover of native annuals were up to 3× greater in treated compared to untreated areas. Glyphosate and some other herbicides were effective in reducing or eliminating germination of another non-native annual forb, Sahara mustard (Abella et al. 2013). These studies further illustrate that treatment outcomes can be influenced by many nuances related to treatment application, such as timing, weather any given year, treatment type, secondary invasion by other non-native species, and differential responses among native plants. This suggests that further work is necessary to identify treatment strategies effective under a range of conditions.

Effects of herbicide on the desert tortoise are unclear, but early timed herbicide applications, exploiting the accelerated phenology of non-native compared to native plant species (Marushia et al. 2010), could generally occur when adult tortoises are inactive (Esque et al. 2014). For example, Steers and Allen (2010) applied herbicide in January. Adult tortoises generally remain in burrows until mid-February in some years, depending on the part of the geographic range (Burge 1977, Rautenstrauch et al. 1998). Juveniles, however, may be active from November through February when local temperatures are warm (Wilson et al. 1999). The California Invasive Plant Council (2015) published best-management practices to reduce non-target effects of herbicides to fauna, while controlling non-native plants damaging to wildlife populations, that may be useful in desert tortoise habitats. Potential negatives of non-native plant treatments must be balanced against the positives of curtailing deterioration of tortoise habitats by non-native plants and the threat wildfires pose to both tortoises and Joshua trees.

In addition to established non-native plants such as red brome, new invasions of harmful plants are an omnipresent threat to desert tortoises, Joshua trees, and the habitats they occupy. This is especially noteworthy given increasing disturbance and vectors for introductions of new, non-native species. A central tenet of invasive species science is that the early detection and removal of new invaders is more cost effective than attempted eradication of established infestations (Davis 2009). Roads and trails can be prime locations for introductions of non-native plants to invade interior lands (Brooks 2009; Berry et al. 2014b). An example of surveying for and treating incipient populations of non-native plants in desert tortoise habitat was the “Weed Sentry” program collaboratively performed by the University of Nevada Las Vegas and National Park Service (Abella et al. 2009). This early detection program surveyed 3,300 km of roads between 2009 and 2011 in the eastern Mojave Desert and removed over 37,000 non-native plants in incipient populations, potentially forestalling invasions (Abella et al. 2009). It should be noted that in addition to new invaders, surveying for expanding populations in the interiors of habitats for regionally established non-native species may also help conserve high-quality habitats for native species (Abella et al. 2009). As a result, roads should be incorporated into broader landscape strategies for non-native plant management, because many firmly established non-native plants are not, or at least are no longer, distributed only along roadsides (Craig et al. 2010). For example, ephemeral stream channels (washes) could also be part of landscape-scale detection programs, because ephemeral stream channels facilitate the spread of Sahara mustard (Berry et al. 2014b, Berry and Murphy 2019). Decommissioning un-needed backcountry roads would be expected to reduce vectors for non-native plant spread, in addition to reducing fragmentation of tortoise and Joshua tree habitats (DeFalco and Scoles-Sciulla 2011).

Non-native plants pose top threats to sustainability of desert tortoise habitat and to the health of tortoises (Brooks and Matchett 2006; Hazard et al. 2009, 2010; Drake et al. 2016), as well as to Joshua trees (Wilkening et al. 2020). Further research exploring potential improvements in habitat quality from treating non-native plants, developing effective treatment strategies to optimize benefits while minimizing negative tradeoffs, and developing innovative techniques and monitoring their effectiveness across scales (e.g., strategically treating fuel breaks in priority locations to expanding to landscape-scale treatments) is a top priority for recovering native desert habitats (Reed et al. 2009, Darst et al. 2013, Tuma et al. 2016). Exemplifying the type of work needed to identify treatment strategies and tradeoffs, Chiquoine et al. (2020) found that addition of carbon in the form of sucrose, designed as an alternative to herbicide, successfully reduced non-native plants but had the previously unreported negative tradeoff of severely damaging soil biocrust in tortoise habitat in the eastern Mojave Desert. Whether other forms of carbon can help ameliorate nitrogen enrichment from atmospheric pollution (Brooks 2003) and be applied at meaningful spatial scales to reduce non-native plants without undesirable tradeoffs remains unclear (Steers et al. 2011). Controlled experiments and associated projects with monitoring designed to change as the situation warrants could help assess a range of treatment scenarios with goals of reducing risk of fires, protecting and promoting growth of perennial plants for tortoises and Joshua trees, and enhancing quality of native annual plant communities for meeting tortoise nutritional needs.

FINANCES AND LOGISTICS OF DESERT HABITAT RESTORATION

Estimated costs for restoring desert habitats vary primarily with the severity of the disturbance coupled with factors such as accessibility of sites (influencing transportation costs), site factors including the diversity of vegetation that was lost, and the cost-effectiveness of the restoration techniques chosen based on the desired degree and speed of recovery. Estimated costs for restoring damaged desert plant communities, including topographic and soil restoration where necessary as a first step to enable plant establishment, are summarized in Table 10. The cost estimates shown are as provided by the source publications in the year studies occurred and are not adjusted for inflation or deflation. While energy, some materials, and labor costs may have increased, certain materials (including some plant materials) may now be more widely available and proportionately less costly. Moreover, use of drones and other technology could save some energy or labor costs in the future. Published cost estimates include those typical across North American deserts (Bainbridge 2007) and as project-specific estimates illustrating some of the variation in costs among site conditions and restoration goals. Considerable overlap exists in cost estimates among projects and regions. This is not surprising because the general restoration practices (e.g., outplanting) are similar and fixed costs are generally similar among projects. For example, the cost of outplanting is generally similar across regions, because outplanting in all regions similarly involves the costs of collecting seed, propagating seedlings in nurseries, transporting plants to field sites, and the activities of planting and maintaining plants. One of the standard pot sizes for propagating seedlings of desert perennials in nurseries is 4 L, which can be ordered for similar costs across the United States. In general, project-specific costs, such as related to the severity of disturbance or how far restoration sites are from maintained access roads and the resulting transportation costs, may be anticipated to produce as much or more variability in costs within as among desert regions.

Table 10.
Summary of published cost estimates for at least partially restoring damaged or destroyed desert habitats generally in the Southwest and specifically for the Mojave and Sonoran deserts.

Region	Cost per hectare	Context	Reference
General	$49,420-123,550	Intensive restoration	Bainbridge 2007
General	$12,355-49,420	Moderate-intensity restoration	Bainbridge 2007
General	$7,413-12,355	Low-intensity restoration	Bainbridge 2007
General	$2,471	Minimal-input restoration	Bainbridge 2007
Mojave	$9,225	Includes seeding, outplanting, and irrigation	Brum et al. 1983
Mojave	$12,355-24,710	Includes site preparation, soil amendment, outplanting	McMahon et al. 2008
Mojave	$1,651	Outplanting, protection, irrigation; $34-55 per surviving plant	Devitt et al. 2020
Sonoran	$26,834	Outplanting and plant care; $64 per surviving plant	Abella et al. 2015a
Sonoran	$4,430	Includes site preparation, outplanting, irrigation	Bean et al. 2004

Notes:
- Costs are as provided for the year of the study and are not adjusted for inflation nor potential deflation for some materials. For example, if seeds and nurseries focusing on growing native desert plants become more widely available, costs for obtaining native desert plants may proportionally decrease.
- The general costs for restoration of damaged desert habitats in Bainbridge (2007) span a gradient of restoration intensity from the highest and costliest including activities such as salvaging soil and plants, amending soils, and performing both outplanting and seeding with species-rich mixtures, to low-intensity, cheaper restoration including limited site recontouring and low-diversity, minimal seeding and outplanting. Note that these are generalized activities and costs, and not all activities may be appropriate or necessary depending on site conditions, disturbance severity, and restoration resources available.
- Protection in Devitt et al. (2020) consisted of caging outplants to deter herbivory.

Bainbridge (2007) presented cost estimates for restoration of severe disturbance in hot deserts, based on four tiers of restoration intensity. Intensive restoration cost an estimated $49,420 to $123,550/ha, moderate-intensity restoration $12,355 to $49,420/ha, and low-intensity restoration $7,413 to $12,355/ha. The least intensive restoration, using minimal-input techniques, cost an estimated $2,471/ha. Costs for intensive restoration included salvaging soils and plants and re-applying them later to that or another restoration site, recontouring sites (e.g., ripping soils to ameliorate de-compaction), amending soils (e.g., applying mulch or inoculating them with biocrust organisms), seeding at least 10 species, intensive outplanting at a density of 25,000 plants/ha, caring for outplants such as through supplemental watering, and maintaining and monitoring sites such as treating non-native plants. An emerging intensive disturbance, unauthorized cannabis grow sites covering hectares, could similarly be a high-cost situation as they can require remediation of contaminated soil and altered hydrology. Bainbridge (2007) described moderate-intensity restoration as including site recontouring, seeding 3-10 species, outplanting at a lower density of 2500 plants/ha, caring for outplants, and limited maintenance and monitoring. Low-intensity restoration included limited site recontouring (e.g., erosion control structures), some seeding with a low-diversity mixture (e.g., ≤ 3 species), limited outplanting at a low density of 500 plants/ha including some plant protection and irrigation, and some maintenance of the site (e.g., continuing to water surviving outplants). The least expensive tier, a minimal-input approach, included a basic site recontouring (e.g., ripping), applying an abiotic surface treatment such as vertical mulch in lieu of major active revegetation, and application of a minor revegetation technique such as a simple seed mixture.

Other restoration projects in the Mojave and Sonoran deserts that reported cost estimates are near or within the range of the Bainbridge (2007) generalized estimates. Using outplanting, seeding, and irrigation to revegetate disturbed powerline right-of-ways, Brum (1983) provided a cost of $9,225/ha. To restore native desert plants to Mojave Desert sites disturbed by construction activities (which altered surface soils and removed vegetation), McMahon et al. (2008) provided costs of $12,355 to $24,710/ha. Restoration activities in the McMahon et al. (2008) study included salvaging topsoil, recontouring, planting perennials, seeding, and managing sites to limit damage by unauthorized off-road vehicle use. To revegetate a burned site in the Mojave Desert through outplanting, Devitt et al. (2020) estimated a cost of $1,651/ha, or $34-55 per surviving plant. These costs included plant propagation in a greenhouse, the activity of outplanting, and providing protection from herbiory (wire cages around each plant) and supplemental irrigation across two years. In the Sonoran Desert, Bean et al. (2004) estimated a cost of $4,430/ha to restore denuded sites using outplanting. Bean et al.'s (2004) detailed budget included activities such as installing temporary irrigation, treatments for non-native plants, and the cost of outplantings. Also in the Sonoran Desert, Abella et al. (2015a) provided an estimated cost of $26,834/ha to revegetate roadside sites disturbed by construction activities. This cost included outplanting and plant care and totaled $64 per surviving plant. Revegetation sites in the Abella et al. (2015a) study were small and widely dispersed, which may be more costly in aggregate to restore than a single larger site such as described in Bean et al. (2004). Numerous small, dispersed sites could incur high travel costs and have limited "economy of scale" compared to fewer, larger sites.

Another approach to estimating restoration costs is to compile prices for native plants available from nurseries. In national parks or other settings where use of in-park genetic sources is usually important, the nurseries would need to propagate seeds made available from within the park. An example of a cost estimate is available from the Nevada Division of Forestry's state nursery in Las Vegas, which offers a variety of native shrub and perennial forb species growing in desert tortoise and Joshua tree habitats. A typical cost of a native desert perennial in a 4-L pot is $7. Cost estimates of transporting the plants, planting them, applying any amendments, and plant care would then need to be added. Any additional soil or site restoration practices for preparing sites for restoration would also require computation, such as using the Bainbridge (2007) four-tiered estimates.

Published research further highlighted costs and logistical considerations of transplanting. If salvaged plants can be transported directly to their recipient site and re-planted without nursery care, this may substantially reduce costs but the effects on plant performance remain uncertain (McMahon et al. 2008). A period of nursery care could help plants overcome potential negative effects of the salvage operation, but nursery residence and the additional transport event from the nursery to the restoration site is another opportunity for mortality. Other than Weigand and Rodgers (2009) noting that large Mojave yucca and Joshua tree can cost up to $425 each to salvage, cost estimates of salvaging plants in the Mojave Desert were unavailable. It seems likely that costs are similar to outplanting for small- and medium-sized perennials, as the salvage operation may be similar in cost to seed collection and meeting germination requirements needed to prepare outplants.

Treating non-native plants is often required as part of desert restoration activities to ensure native species are the beneficiaries or to ensure restoration efforts are not negated by wildfires facilitated by non-native plants. Moreover, treating non-native annuals is likely to generally improve forage conditions for desert tortoises if native forbs respond positively (Brooks 2000, Steers and Allen 2010). In the Mojave Desert, Brooks et al. (2006) reported that treating the non-native annual forb Sahara mustard (*Brassica tournefortii*) cost $811/ha/year using mechanical treatment (hand tools) and $384/ha/year using herbicide. Brooks et al. (2006) noted that treatments would need to continue for several years to deplete the soil seed bank and to remove any newly germinated seedlings.

ANTICIPATED EFFECTS OF CHANGING LANDSCAPES AND CLIMATES

Three of the several ongoing or anticipated habitat changes include continued disturbance and/or fragmentation, non-native plant invasions, and changes in climate. Wildfires and non-native plants were covered earlier. Another ongoing disturbance anticipated to continue affecting habitat of the threatened desert tortoise and possibly Joshua trees is renewable energy development, specifically solar and wind. A review of the effects of renewable energy developments on tortoises and their habitats is beyond the scope of this paper, and to summarize, ongoing energy developments have replaced and fragmented habitat (Lovich and Ennen 2011, Hernandez et al 2015). Energy developments can also alter nearby habitats, by changing microclimates and hydrology, or creating disturbances facilitating non-native plants (Moore-O'Leary et al. 2017). Although some energy developments retained some vegetation and may be able to support a few local tortoises individually, the long-term viability of such limited populations is uncertain, and the developments contribute to cumulative anthropogenic disturbance and fragmentation of habitat (Lovich et al. 2014, 2018).

The climate changes projected for desert tortoise and Joshua tree habitat in upcoming decades include warmer temperatures and increased frequency, duration, or severity of droughts (Lovich et al. 2014, Guida and Abella 2020). The lower average precipitation could also be accompanied by shifts in the timing, frequency, or amount of rainfall per event (Knapp et al. 2008). Although future climate projections (especially for precipitation variables) have uncertainty, the recent conditions of warming temperature and long-term drought during the past 20+ years (Mankin et al. 2017, Williams et al. 2020, 2022) are already thought to have negatively affected desert tortoise populations and recruitment windows for Joshua trees (e.g., Nagy et al. 2002, Longshore et al. 2003, Medica et al. 2012, Lovich et al. 2015, Barrows and Murphy-Mariscal 2012). Protracted drought is likely to increase shrub mortality and limit recruitment, reducing density and cover of shrubs (Miriti et al. 2007, McAuliffe and Hamerlynck 2010). The losses of shrubs reduce thermal protections for desert tortoises (Woodbury and Hardy 1948, Burge 1978, Berry and Turner 1986, Bulova 2002, Mack et al. 2015). Loss of shrubs also reduces nurse plants important to growth and protection of Joshua tree seedlings (Comanor and Clark 2000, Reynolds et al 2012).

As noted earlier, tortoise populations are already in severe declines in most parts of the geographic range, and few places remain where densities of adults are likely to support viable populations (USFWS 2015, Allison and McLuckie 2018, Berry et al. 2020a, 2021). Climate change including warming temperatures with less predictability and reductions in rainfall, lower food supply, and potentially lower moisture content of soils on the surface and in burrows are additional, life-threatening stressors. For the tortoise, every aspect of life is affected by timing and amounts of precipitation and resulting production and availability of forage and environmental temperatures—for health, growth, daily and seasonal activities, movements, home range sizes, reproduction, and ultimately survival (Brattstrom 1961, 1965, Nagy and Medica 1986, Henen 1997, Henen et al. 1998, Christopher et al. 1999, 2003, Duda et al. 1999, Berry et al. 2002, Longshore et al. 2003). Although tortoise populations persisted through past droughts in the last several thousand years, conditions then did not include today's pervasive anthropogenic degradation and fragmentation of habitats and accentuation of multiple stressors (Morafka and Berry 2002, Berry et al. 2013, Berry et al. 2021).

Joshua trees have faced reductions in the geographic range since the late Pleistocene (22,000-13,000 BP) in the southern part of the geographic range and possible expansions northward (Cole et al. 2011). Modeling indicates continued losses in the southern part of the range and up to a 90% reduction of suitable habitat in Joshua Tree National Park if a 3°C increase in mean July maximum temperatures occurs (Cole et al. 2011, Barrows and Murphy-Mariscal 2012). Changing climates could similarly affect the southern part of the geographic range of desert tortoises (Barrows 2011). In modeling effects of potential climate changes on desert tortoises in Joshua Tree National Park, Barrows (2011) described a reduction in the southern part of the range and at lower elevations. With climate warming, tortoises are likely to spend more time deep in burrows, because the lower lethal deep body temperature is 39.5°C and currently occurs in late spring and summer (McGinnis and Voigt 1971). If shelters are inadequate and tortoises are exposed to full sun and elevated temperatures, hyperthermia may occur with death following (Brattstom 1961, 1965). Climate warming is likely to alter daily and seasonal activities: less time would be spent above ground in spring, summer and early autumn, and more time in late autumn and winter. Rapid movement of the range northward would be difficult; to what extent this can or will occur is uncertain. Loss and fragmentation of habitat in the north could limit tortoise movement, and cooler, moister, upper elevations are generally not considered tortoise habitat (Averill-Murray et al. 2013, Barrows et al. 2016). If climatic changes result in fewer years supporting populations of native annual forbs, effects on tortoise forage quality and quantity could be profound. Drought years with little forage and drinking water have correlated with low growth, reduced reproduction, indicators of poor health, and elevated mortality (Henen 2002; Berry et al. 2002; Christopher et al. 1999, 2003; Longshore et al. 2003; Medica et al. 2012). Presumably, more severe shortages of food plants would accentuate these deleterious trends. Reduced precipitation and warming temperatures could increase, decrease, or have minimal influence on fire activity. Drought could curtail fuel production and therefore fire activity. Conversely, fire activity could increase if periodic wet years with copious fuel production are followed by dry conditions promoting fire.

From the perspective of conserving and restoring vegetation during warmer, drier climates, a first effort is to limit future disturbances to retain as much native vegetation as possible. Restoration can assist the tortoise and Joshua tree by conserving/enhancing perennial cover for thermal protection. Restoring native annual and herbaceous perennial food plants, while reducing non-native annual grasses, will likely continue to be a challenge at landscape scales and could benefit from further research attention. A major concern is that many non-native annuals may now disproportionately benefit from rain events by occupying the most favorable microsites (i.e., nutrient-enriched, shaded locations below shrubs; Abella and Smith 2013). This could become a positive feedback, reinforcing the trend whereby non-natives preferentially reproduce and replenish seed banks in favorable microsites while natives do not. Reducing non-native plants to enable natives to better utilize rainfall and to offer tortoises appreciable forage in more years, including in climatically marginal years, is likely to be a priority.

RESEARCH FOR ADAPTIVE MANAGEMENT

Of many potential research priorities to advance desert habitat restoration, we describe six strategic, programmatic areas that may improve soil and vegetation restoration for desert tortoises, Joshua trees, and Mojave and western Sonoran ecosystems generally.

1) To build on the few dozen existing restoration studies in the Mojave and western Sonoran Desert, continuing to test species performance and treatments for cost- and ecologically effective soil rehabilitation and revegetation techniques and on how to integrate treatments to maximize bet-hedging in variable environments could further advance the science. Our review has highlighted that prior studies started the process of identifying top-performing plant species and the types of treatments required to enable successful growth and survival at restoration sites. However, only dozens of native perennials and fewer annuals have yet been examined in even one study for their revegetation potential. Many species tortoises could use for cover or food and that could serve as nurse plants for Joshua trees have yet to be evaluated for their restoration potential and needs. As examples for desert tortoise food plants, attention could focus on the commonly eaten species, in such genera as *Lupinus, Astragalus, Acmispon, Camissonia, Malacothrix, Prenanthella*, and members of the Malvaceae and Boraginaceae. Some species grow primarily in or on edges of ephemeral stream channels and could be placed in such situations (e.g., widow's milkvetch [*Astragalus layneae*], an herbaceous perennial species, and Booth's evening primrose [*Eremothera boothii*], an annual forb). Wishbone bush, an herbaceous perennial, produces leaves even in dry periods and is favored early in the season by tortoises in the western Mojave Desert. Germination, propagation, and restoration requirements of these types of species may enhance the ability of restoration to enhance tortoise food quality. For treatments, testing variations to different candidate restoration techniques in different conditions can help provide practitioners with information on expected treatment reliability, a "tool box" of potential treatments to choose among to deploy, and improved matching of treatments to conditions in which they are expected to provide the greatest chance for success.

2) Research on how to effectively deploy restoration resources spatially is likely to be beneficial. For example, if funds are available for 3,000 outplants to revegetate a disturbance, how are the outplants best deployed? Should they be evenly spaced to potentially stimulate recovery into coalescing patches? Or, should they be planted in clusters as revegetated islands that could expand while serving as thermal refugia, enabling tortoises to move through and utilize a recovering habitat sooner? Or, in terms of recovering Joshua trees, what is the best arrangement for nurse plants?

3) A major research program is needed to develop local and landscape-scale approaches to improve the condition of annual plant communities by reducing non-native annual grasses (in turn reducing hazardous fuels) while promoting native herbaceous food plants for tortoises and limiting hazardous fuels around Joshua trees.

4) Research that improves the linkage between habitat enhancement activities and short- and long-term indicators of desert tortoise health and population traits is likely to be beneficial. This represents a next step from previous research that correlated extant environmental features with tortoise health (e.g., correlating tortoise growth with forage availability; Medica et al. 2012) and in studies advocating for the benefits that habitat restoration may bring for improving tortoise health (Reed et al. 2009, Darst et al. 2013). The opportunities in this realm for collaborations among tortoise biologists, plant ecologists, and restoration ecologists seem extensive. Existing literature provides indicators of tortoise health that can be used for assessing changes in health during and after restoration activities (Christopher et al. 1999, Berry and Christopher 2001, Nagy et al. 2002). Similarly, research that links how restoring habitat resources (e.g., nurse plants) and ameliorating stressors may improve Joshua tree demographics could clarify roles restoration can play in conserving Joshua trees.

5) The desert tortoise and Joshua tree have been experiencing multiple stressors, most of which are anticipated to persist or intensify with cumulative impacts. A research priority is exploring whether comprehensive habitat restoration is capable of reversing short-term indicators of declining health of tortoises and longer-term population declines. This topic may best be examined within a protected landscape (*sensu* Berry et al. 2020c) as an adaptive management experiment. With minimization of as many threats as possible (e.g., anthropogenic disturbance, subsidized predators, presence of disease), comprehensive restoration could be implemented, including but not limited to enhancing cover of perennial plants, reducing non-native plants and promoting high-quality native forb forage plants, and reconstructing hydrology as needed. Such an experiment may require several years to implement multiple restoration phases and to measure short- and long-term indicators of tortoise health and population status. Until the types of research in priorities #4 and #5 are implemented, it will be difficult to accurately understand the potential role that habitat restoration could have in aiding tortoise recovery efforts. A similar restoration approach at sites where Joshua trees have been lost could assess the potential for restoration activities such as facilitating nurse plants, reducing non-native plants, and augmenting Joshua tree seed availability and seedling establishment to recover Joshua tree populations.

6) Given forecasts for warming temperatures and increasing drought, or at least more variable precipitation, research attention on bet-hedging approaches (by incorporating multiple treatment types or implementation across years), assisted natural regeneration, and using abiotic treatments could help restoration strategies adapt to the changing environment. For example, effectiveness of abiotic treatments can be less contingent on timing of rainfall than are outplanting or seeding, which can incur costly failures if drought occurs after their implementation. Climatic changes of warming temperatures and drought may underscore the importance of restoring as much habitat as possible and improving habitat condition for reducing other stressors to desert tortoises, Joshua trees, and associated native species to foster potential resilience to future climatic changes.

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Roadside Enhancement of Creosote Bush (Larrea tridentata) in the Desert

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Figure 1. Scotty's Castle Road in the Mojave Desert crossing an alluvial fan, looking northwest. Enhanced creosote growth on the sidecast banks is evident.

Introduction

Have you ever noticed how relatively lush creosote *(Larrea tridentata*) grows on either side of paved desert roads? (Figures 1-4)

This surprising situation is called an *edge effect* (Edge Effects 2022; Delgado García 2007) and it occurs in transitions between two habitats: the road and the undisturbed surrounding landscape where creosote growth is sparse. Such gradations are called *ecotones* (Vanderplank et al. 2014). Biological diversity is usually greater in ecotones as members of each habitat mix and adjust to the transition.

The reason roadside growth is enhanced seems obvious: rainwater flows off the pavement so plants grow better where water accumulates, right? Yes, but there is more to the story: road building itself plays a crucial role.

Figure 2. Panamint Valley Road in the Mojave Desert south of CA 190, looking north down an alluvial fan.

ROAD BUILDING

It starts by bulldozing a path through ancient desert floor that is has become well-compacted over thousands of years. Scraping loosens it to a crumbly mixture of rock fragments (*clasts*), soil and roots. This material is pushed to the side (*sidecast*) forming a bank a few feet above grade (Figures 4 and 5). Many desert roads are on *alluvial fans* which may contain many different kinds of rocks from the surrounding mountains with a wide range of chemical compositions: basalt, granite, gneiss, feldspars, limestone, quartz, etc. The road is then prepped with several layers of compacted gravel to support vehicles and then paved, always with a slight camber to facilitate runoff.

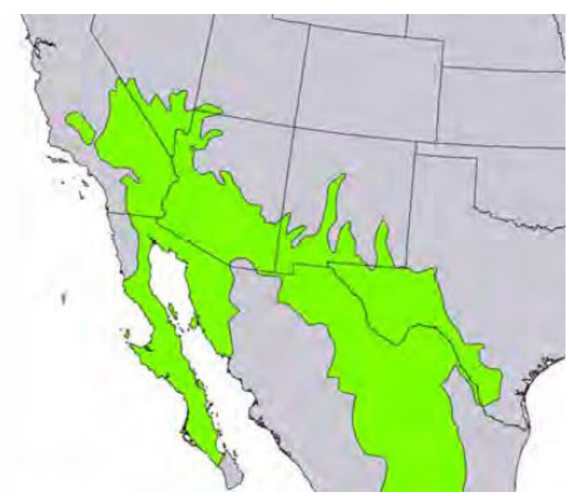

Figure 3. Range of Larrea tridentata (US Forest Service).

Figure 4. CA190 in Death Valley National Park looking east. Shown here are the paved road, ditch and sidecast bank with strong creosote growth. This section of road crosses an alluvial fan with many clasts and cobbles.

PLANT GROWTH ON SIDECAST

Rainwater naturally runs off the pavement to the roadside because asphalt and concrete are impervious to water. On sloping surfaces like alluvial fans, runoff will also collect on the uphill side of the uphill sidecast because it too impedes flow (Figure 6). This is especially effective during a deluge when *sheet flow* (Sheet Erosion 2022) moves over poorly drained soil. Both processes enhance moisture immediately next to and paralleling the road. More soil moisture means better plant growth. However, two more properties of sidecast greatly promote plant growth: porosity and chemical weathering.

The loosened sidecast is more porous than the unperturbed soil it came from and contains many small cracks and air pockets (Figure 5a). Porosity allows both air and water to more easily penetrate. Being elevated, the sidecast is more likely to catch a windblown seed or one blowing across the ground. If lodged in a crevasse, the seed will find an ideal location to begin life. Evaporation in the crack will be slower than in the sunlit surface so more moisture from rain and condensation will remain longer. Being somewhat protected, the seed and young plant will suffer less from the extreme heat and cold of the desert.

Water percolating into the sidecast will also promote chemical weathering. With a relative abundance of oxygen, water and air, rocks can break down readily into a wide variety of secondary minerals, i.e., nutrients. This is especially true when desert pavement clasts are present (Figure 5b). Thus, sidecast enhances the necessary ingredients for plant growth: CO_2, water, nutrients and relatively mild temperatures.

If growing conditions are so good in sidecast, why don't all plants populate them with equal vigor? The answer comes from the Spanish name for creosote: *gobernadora,* which translates as "governess" or "governor". Creosote

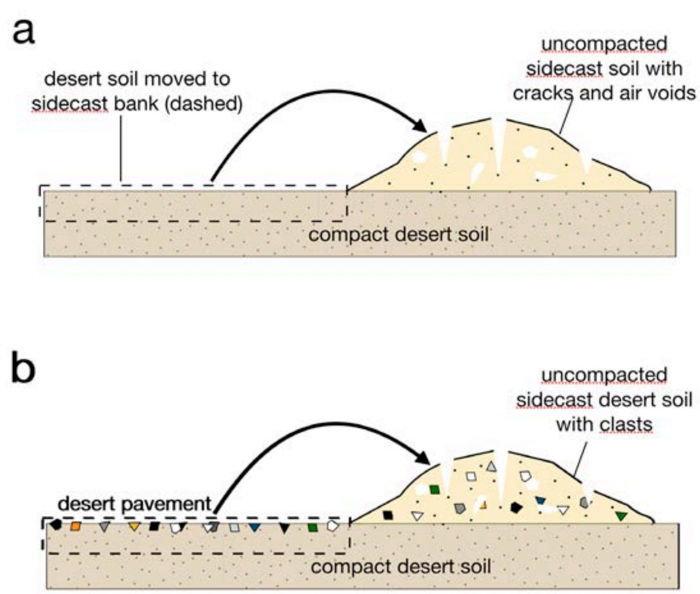

Figure 5. Sidecast origin and structure (sketch).

Figure 6. Google Earth image of small section of Scotty's Castle Road crossing a fan. Surface flow direction is from top to bottom. Note the enhanced creosote growth on both sides of the pavement from runoff. It is stronger on the uphill sidecast where runoff from the fan ponds into standing water as the numerous small white alkali areas show uphill of the road. Such areas are not seen downhill of downhill sidecast because there is no barrier to surface flow.

roots efficiently collect moisture from the surrounding soil and prevent other plants from growing: creosote starves them of water. Thus the roots "govern" the water supply in their favor. Creosote bushes compete with themselves too, and tend to be separated by roughly the same amount (40 - 80 ft in the Mojave). It is not known how many adjacent creosote bushes are clones. If they are, their ramet spacing may be more complicated than competition for water but very likely involves water in some way.

ENJOY THE HEALTHY ROADSIDE GROWTH BUT REMEMBER....

Despite the vigorous greenery lining desert roads, it's not all good news. Any road - especially when elevated like a highway or railroad track - creates habitat fragmentation, runoff diversion and other conditions that damage the ecology far beyond the road's vicinity (Porensky and Young 2013; Johnson, Vasek and Yonkers 1975; Abella 2010; Watson 2005; Meier et al., 2018).

"Roads scare the hell out of ecologists." said William Laurance, a biology professor at James Cook University "You can't be in my line of business and not be struck by their transformative power." (Nijhuis 2015).

So as you drive along a desert road and enjoy the lush roadside growth, keep in mind that this lovely greenery comes with a price.

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