SOIL SEED BANKS: PRESERVING NATIVE BIODIVERSITY AND REPAIRING DAMAGED DESERT SHRUBLANDS

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Vascular plants in California's Mojave and Sonoran deserts produce seeds that withstand inhospitable conditions in the soil for months or years. Viable seeds that accumulate in the top inch of soil comprise the "seed bank." Often underappreciated, seed banks represent future plant populations and comprise the species that may persist in a changing climate.

In 1949 botanist and ecologist Fritz Went (1949) gathered surface soils at then-named Joshua Tree National Monument that revealed distinct annual floras hidden below ground. He discovered a flora that germinates in summer when soil temperatures are warm and a different flora in winter when soil temperatures are cold. In the Coachella Valley, Lloyd Tevis (1958) snatched seeds from harvester ants as they foraged near their nests and observed how granivores could change the species composition of desert vegetation. Since these early efforts, awareness has grown about the importance of seed banks as well as their role in revegetating disturbances throughout the deserts.

ABOVE: Understanding seed banks commonly starts in the greenhouse by subjecting field-collected soils to alternating wetting-drying cycles until all seeds germinate and seedlings are identified and counted. This process takes up to nine months. TOP: Native seeds of perennial shrubs such as white bursage (*Ambrosia dumosa)* are rare in the seed bank compared to annual species. All photographs by Lesley A. DeFalco unless otherwise noted.

THE EXPOSED SEED AND STRATEGIES FOR PERSISTENCE

Ripened seeds are vulnerable from the time they fall to the ground and settle into the seed bank until the right weather conditions trigger germination. Precipitation is unpredictable in California's deserts, and seasonal rains that promote germination are often followed by dry periods that stress or kill developing seedlings before they reproduce and replenish the seed bank. Many species cope with the possibility of mass seedling mortality by maintaining a portion of their seed bank in a dormant state for successive years, a strategy known as "bet hedging."

Seeds need specific environmental conditions to overcome dormancy. For example, heavy rains wash away chemical inhibitors in the seed coat, and hot or cold soil temperatures initiate physiological changes for germination (Baskin and Baskin 1998). Various strategies of seed dormancy promote species coexistence and high biodiversity in desert shrublands. This biodiversity is important at a time when extreme and fluctuating climate patterns present strong selective pressures for adaptation.

Birds, small mammals, and ants distribute seeds to locations that are favorable for seedling establishment (Tevis 1958, Nelson and Chew 1977), but they also consume copious amounts of seeds. Perennials known as "masting" species produce extraordinarily large seed crops in some years. These large crops during "mast years" overwhelm seed harvesters by producing more seeds than can be consumed or stored. For example, Joshua tree (*Yucca brevifolia*) produces large seed crops only once or twice a decade. Because seeds rapidly lose viability in the soil, the opportunity for seed germination and seedling establishment is urgently timed to coincide with summer rains that closely follow seed dispersal (Reynolds et al. 2012).

THREATS TO NATIVE SEED BANKS

Seed banks are vulnerable to human-caused disturbances that impact desert soils. Concentrated vehicle use has cascading impacts on seed banks: vehicles crush and kill seed-bearing shrubs, and they compact soils or destabilize soil aggregates so that soil, litter, and seeds are exposed to wind and water erosion. In a study at Fort Irwin, California's National Training Cen-

ter near Barstow, military training reduced the number of species in the seed bank by half and the number of seeds to one-sixth those of undisturbed areas (DeFalco et al. 2009). Excavation of trenches for tank exercises diminished the abundance of perennial seeds, burying them too deep for seedlings to emerge when the trenches were refilled. These disturbances resemble those common throughout the desert associated with recreation, construction of aqueducts, power lines, and pipelines. Comparable impacts to seed banks are expected as urban areas expand and alternative energy projects increase.

Fire and invasive species also threaten desert seed banks. The increasing incidence and size of wildfires in recent decades is paralleled by the invasion and dominance of exotic annual grasses at middle (cheatgrass, *Bromus tectorum*) and low elevations (red brome, *B. madritensis* ssp. *rubens*; Mediterranean grass, *Schismus* spp.). In contrast to California coastal scrub, many Mojave and Sonoran shrubland species do not readily resprout after injury by fire. Whereas new seedlings typically arise from the seed bank following natural disturbances, a recent study found that fire killed 55%–80% of seeds in a Mojave Desert seed bank of northern Arizona (Esque et al. 2010). Two exotic species, one with small seeds that filtered into soil cracks (Mediterranean grass) and another with a self-drilling appendage (stork's bill, *Erodium cicutarium*) helped them escape lethal temperatures.

Comparing seed banks in recovering burned and unburned shrublands, we found seed densities of the dominant native annual grass (six-weeks fescue, *Festuca octoflora*) declined by more than 70% and native forbs by more than 50% due to wildfire. In contrast, exotic annual grass and forb seed densities were two- and six-times higher, respectively, than their native counterparts. Furthermore, burned sites had one-third the number of native species than adjacent unburned areas, signaling a significant loss of plant diversity.

Small mammals such as kangaroo rats (*Dipodomys* sp.) and harvester ants (*Pogonomyrmex rugosus*) collect seeds of most shrub species. Rodents gather seeds and store them in shallow caches, and seedlings emerge when seeds are forgotten. Also pictured is a Joshua tree seedling (*Yucca brevifolia*). Harvester ant and Joshua tree seedling photographs by Todd C. Esque.

Air pollution associated with urban development, particularly from the Los Angeles basin, is making its way into desert wildlands. Nitrogen emissions are blown inland and enrich the ordinarily infertile desert soils. Exotic annual grasses are well-suited to nitrogen pulses for growth and reproduction compared with native species. A study at Joshua Tree National Park showed that sites with the lowest nitrogen deposition had the highest seed bank species richness (Schneider and Allen 2012). Continued nitrogen exposure is expected to reinforce exotic dominance in the seed bank, thereby reducing native species diversity.

A PRESCRIPTION FOR REPAIR

Rehabilitating degraded shrublands depends in part on minimizing further disturbances, developing methods for suppressing aggressive exotics, and replenishing native seed banks. We have found across multiple sites that pre-emergent herbicides (applied before the arrival of fall and winter rains) are effective at not only suppressing exotic annuals by 50–95% up to three years after application, but also at reducing their seed bank in as many years. Furthermore, native annual species—six weeks-fescue in particular—increased in shoot mass and seed bank density following herbicide treatments. Seed dormancy may play a role in protecting native seed populations from herbicide impacts, whereas exotic species such as red brome that lack dormancy can be gradually reduced in infested areas.

In a related study, herbicide application in combination with native seeding increased the density of early-colonizing species six-fold, including desert marigold (*Baileya multiradiata*) and desert globemallow (*Sphaeralcea ambigua*). Larger areas of treatment may exclude exotic annuals for longer periods of time and restore native species' ability to accumulate in the seed bank. Limited herbicide use is intended to accelerate native species establishment so that the plant

Landscape-scale disturbances such as concentrated vehicle areas (above) and areas burned by desert wildfires (below) kill seed-bearing shrubs and disrupt vulnerable surface soils where seeds reside, making vegetation recovery difficult.

community can resist reinvasion and rebound from future disturbances. However, the impacts of herbicides to soil microbes and to the animal populations in larger treatment areas are unknown.

Based on supplemental seed studies, ants and rodents can collect more than 80% of the seeds broadcast during revegetation (DeFalco et al. 2012). We are exploring methods to encapsulate seeds and shield them from granivores until suitable conditions promote establishment. One method has been to use "seed balls," a mixture of seeds, clay, and organics. When dried, the marble-sized pellets are durable when scattered across large disturbances. However, initial evaluation of seed balls using native desert species proved less successful than expected, so we are adjusting the recipe to improve seedling emergence and assessing plant establishment at a variety of sites.

Despite our progress using restoration methods on small experimental plots, seed availability for restoration projects is limited because desert species do not reliably produce enough seed from one year to the next. Seeds purchased from commercial collectors are expensive and not always representative of local ecotypes, or may even have been collected outside the desert ecoregion. Since 2010, federal and state agencies, universities, arboreta, and botanic gardens have cooperated to acquire local populations of native species (see the Seeds of Success Program, nps.gov/plants/sos).

Spring 2013 was a unique mast year for a variety of species including Joshua tree, Nevada joint-fir (*Ephedra nevadensis*), and blackbrush (*Coleogyne ramosissima)*. In fact, blackbrush reproduced across its entire range in the Mojave Desert and the Colorado Plateau. These mast events are opportunities to collect the seeds of multiple populations across species' ranges for use in restoration, and when properly stored, the seeds remain viable for up to 20 years (Kay et al. 1988). However, collecting seeds cannot, alone, keep pace with the growing need caused by increasing disturbances. Seed production of native species by farmers distributed across the desert ecoregion may eventually provide a reliable and abundant source for wildland seedings and at reasonable prices.

Even when seed production is sufficient, preserving and restoring vulnerable topsoil layers is essential for revegetating degraded desert lands. Surface soil not only holds the seed bank but also holds organic litter and microbes important for plant mineral nutrition. Topsoil collection and replacement (using heavy equipment) has potential application for severe disturbances (for example, bladed sites for solar arrays, wind farms, and geothermal facilities). Large-scale seed bank conservation is difficult, however, because conventional equipment collects soil below a 1–2 inch depth, often mixing deeper seedless soil fractions with seed-rich topsoil. This mixing dilutes seed numbers in the stored soil and upon redistribution, buries seeds too deeply for seedling emergence (Scoles-Sciulla and DeFalco 2009).

Traditional approaches to rehabilitate degraded shrublands, in addition to seed bank conservation, aim to replace ecosystem components destroyed by disturbances and include transplanting seedlings, providing structure through vertical mulch, and improving soils before reseeding, to name a few. Although restoration ecologists are working on solutions to reverse the degradation of disturbed shrublands, minimizing disturbances and promot-

Experimental application of herbicide in late fall (blue dye) has been effective at diminishing exotic annuals in the seed bank of repeatedly-burned areas.

Reseeding with natives in combination with herbicide applications promotes native establishment, as pictured here for desert marigold (*Baileya multiradiata*) on small experimental plots in the eastern Mojave Desert.

ing shrubland function is the first priority.

Importantly, our progress in developing rehabilitation solutions does not justify the continuing degradation of California's desert lands, because plant community composition does not readily recover for many decades to centuries. Limiting human activities to areas already disturbed and protecting areas with minimal disturbance is the best strategy for preserving our unique desert shrublands and the plants and animals that depend upon them.

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Laboratory trials with "seed wafers," an improvement over seed balls, have shown that encapsulating seeds in a soil matrix improves water status and increases seedling emergence over unprotected seeds. Field trials are ongoing to determine if wafers reduce the need for high seeding densities, thereby reducing costs.

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