

Broadcast Seeding Fails to Enhance Native Plant Recovery 17 Years after a Mojave Desert Wildfire

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ABSTRACT

Increasing wildfire activity, partly associated with invasion of fuel-producing, non-native grasses, has stimulated interest in developing ecological restoration strategies to accelerate native plant recovery after wildfire in western North American deserts. Using plant community assessments from 1–3 (2009–2011) and 16 years (2024) after seeding, we examined effects of broadcast seeding five native species across 40 ha after the 2007 Bonnie Springs Fire (southern Nevada, Mojave Desert). Seeding did not increase the density or cover of seeded species in any year, nor did we detect many seeded species in soil seed banks (only one occurrence of one species). Moreover, there was little evidence that the activity of seeding influenced non-seeded, native or non-native species composition. By 2024, 17 years post-fire and 16 years post-seeding, native plant cover and species richness (100 m²) in the burned area, irrespective of seeding, remained only half the amount in unburned reference habitat while non-native cover was 2–3 times higher. Despite including locally sourced, readily germinable seed, selecting species capable of being initial post-disturbance colonizers, and receiving above average rainfall in two of the first three post-seeding years, seeding did not enhance native species establishment. Developing timely, reliable practices for seeding after desert wildfires may require further work regarding the degree to which seed availability limits recovery (relative to other factors such as site conditions), whether natural early colonizers are best for seeding, factors that influence germination ecology of candidate species, and if pairing other treatments with seeding can increase effectiveness.

Keywords: disturbance early colonizer, soil seed bank, species selection, vegetation change

Undesired or unnaturally severe wildfires (e.g., via human-induced changes in fuels) can reduce native plant cover, trigger soil erosion, and alter habitat quality and ecosystem functions (Brooks and Chambers 2011, Munson et al. 2015, Lee et al. 2024). Seeding is among the ecological restoration options for accelerating recovery of native plant communities (Palma and Laurance 2015, Shackelford et al. 2021, Davies et al. 2025). However, post-wildfire seeding has varied in establishing seeded species and in ecological outcomes and is considered controversial for many ecosystems (e.g., Beyers 2004, Peppin et al. 2010, Knutson et al. 2014). For example, in western North America where much of the continent's wildfire activity is occurring, systematic reviews of seeding projects in forests

(Peppin et al. 2010), cold deserts (Pyke et al. 2013), and hot deserts (Abella et al. 2023) have revealed examples where seeded species have failed to establish or conversely have become major portions of persistent communities. Beyond the seeded species, some investigations have found that seeding interferes with natural recovery and does not reduce or even promotes non-native plant invasions (Peppin et al. 2010, Pyke et al. 2013, Davies et al. 2025). Other investigations have instead found that seeded species can serve as nurse plants that facilitate recruitment of other native plants and that they suppress non-native plants (Taylor et al. 2014, Ott et al. 2019). These examples highlight a role for further restoration studies to determine when seeding is most likely to be an ecologically and economically effective strategy and to identify the timeframes and factors influencing its success.

In this case study, we examined three questions regarding 1) post-wildfire seeding related to short- and long-term effectiveness, 2) whether seeded species form soil seed banks, and 3) how seeding influences plant community change. The timeframes of when seeding is effective and how long seeding influences plant communities are

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variable. For example, early results can suggest seeding failure while later results suggest effectiveness, or vice versa (Munson et al. 2015, Ott et al. 2019, Farrell et al. 2021). If seeding enables seeded species to augment soil seed banks, it could promote persistence of seeded species or indicate longer-term seeding effectiveness even if seedlings do not quickly appear (DeFalco et al. 2012). Seeding could have a variety of influences on the plant community including on non-seeded native and non-native species. However, these influences, or how long they persist in post-disturbance communities, are not well understood (Peppin et al. 2010, Pyke et al. 2013, Shackelford et al. 2021).

Our study system was the Mojave Desert, USA, where fires at low-mid elevations are thought to have been rare and limited by sparse fuel historically. Wildfire activity has been increasing in recent decades in part from non-native grasses increasing fuel load and connectivity (Brooks and Chambers 2011). Without restoration, recovery of native perennial plant cover after severe disturbances in this desert can require decades and, for species composition, potentially centuries (Abella 2010). Coupled with the cumulatively increasing burned area and loss of mature desert shrublands, developing effective restoration techniques for burned areas is a priority (Esque et al. 2021). In our multi-decade case study of restoration seeding on a Mojave Desert wildfire, we asked: 1) How effective was broadcast seeding at increasing abundance of seeded species in the short- (first three years) and longer-term (16 years) after seeding? 2) Did seeded species form germinable soil seed banks? and 3) Did plant community changes after wildfire vary with seeding?

Methods

Study Site

We conducted the study in the Mojave Desert, a hot desert with low (typically < 20 cm/year) and variable among-year rainfall in the southwestern United States. Shrubland predominates, often with *Larrea tridentata* (creosote bush) at the lower elevations and mixed species such as *Coleogyne ramosissima* (blackbrush), *Krameria erecta* (littleleaf ratany), and *Yucca schidigera* (Mojave yucca) at mid-elevations. Annual plants appear in years with suitable precipitation-temperature combinations. Many sites primarily have winter annuals triggered to germinate by autumn or winter rains and flower in spring (Beatley 1967). Although hundreds of native annual species occur in the Mojave Desert, annual communities in many contemporary sites are dominated by non-native species such as the forb *Erodium cicutarium* (redstem stork's bill) and the grasses *Bromus rubens* (red brome) and *Schismus* spp. (Brooks and Chambers 2011, Jurand and Abella 2013, Lee et al. 2024). These non-natives invade minimally disturbed

desert as well as disturbed sites. When mature shrublands of long-lived species are disturbed, such as after wildfires, non-native annuals and native perennial forbs, grasses, and shrubs with shorter life spans (typically decades rather than centuries) often initially colonize (Abella et al. 2021).

Our study site was the 158-ha Bonnie Springs Fire (36°6'7"N, -115°26'29"W), within the 80,000-ha Red Rock Canyon National Conservation Area, administered by the U.S. Bureau of Land Management (BLM), 15 km west of Las Vegas, Nevada (Figure 1). Ignited on July 2, 2007, the wildfire was contained by July 4, 2007. The fire was primarily fueled by a mixture of senesced non-native annual plants and native shrubs in a mid-elevation, mixed-shrub community including *C. ramosissima* (Figure 2). A weather station 5 km away recorded an average of 18 cm/year of precipitation (1991–2024), 67% falling from October through March (Figure 3).

Seeding Treatment

A study of 32 wildfires since 1980 in the eastern Mojave Desert surrounding our present study site indicated that cover of native perennial plants (though not necessarily comprised of pre-fire species) in burned *C. ramosissima* communities required an average of 40–50 years to fully recover to levels found on unburned areas (Abella et al. 2021). With a goal of increasing and accelerating recovery of native plant cover, the BLM organized a restoration seeding after the Bonnie Springs Fire using native species from the local flora that prior research showed are capable of being early post-disturbance colonizers (Abella 2010, Vamstad and Rotenberry 2010). The BLM purchased 300 kg of pure live seed (\$63,000 in 2008 USD) in total of five native species collected from wildlands within Clark County, Nevada (the county containing our study site). The seed vendors were Comstock Seed (Gardnerville, NV), Native Seed (Park City, UT), and Granite Seed (Lehi, UT). The species included a perennial grass (*Aristida purpurea* [purple threeawn]), two perennial forbs (*Baileya multiradiata* [desert marigold] and *Sphaeralcea ambigua* [desert globemallow]), an annual forb (*Salvia columbariae* [chia]), and a shrub (*Hymenoclea salsola* [cheesebush]). In 40 ha of the wildfire BLM prioritized for restoration, the seeding was implemented in November 2008 with field personnel using hand-held seed spreaders to broadcast the seed mix of the five species at pure live seeding rates in Table 1. The November timing was chosen to enable potential exposure of the seeds to autumn and winter-spring rains for emergence and growth during the 2009 and subsequent growing seasons. We obtained a random sample of 120 seeds each for four of the five seeded species on which to conduct a laboratory germination test. The test revealed that 20–100% of the pure live seed was readily germinable under laboratory conditions when seeding occurred (Table 1).

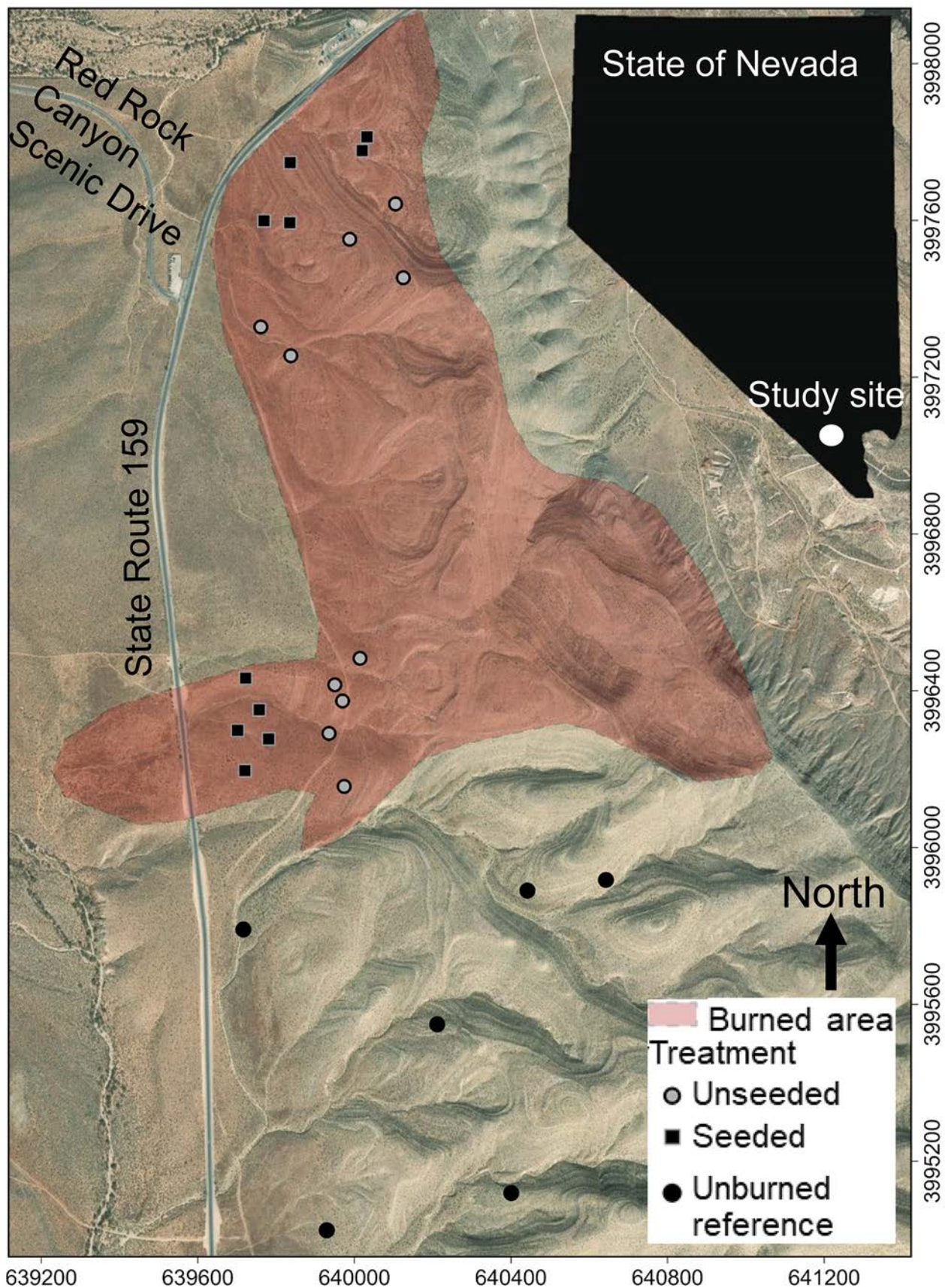


Figure 1. Location of the 2007 Bonnie Springs Fire in Clark County, NV, USA and the distribution of seeded and unseeded plots in the burned area and unseeded plots in unburned reference habitat. Map coordinates are North American Datum 1983, Universal Transverse Mercator, Zone 11N. The inset shows the general location of the fire within the state of Nevada.

Burned/seeded 2011



Burned/unseeded 2011



Burned/seeded 2024



Burned/unseeded 2024



Unburned reference 2024



Unburned reference 2024



Figure 2. Examples of plots sampled to examine post-wildfire seeding of native plants on the 2007 Bonnie Springs Fire, Mojave Desert, southern Nevada. Photos of the example burned/seeded and burned/unseeded plots were taken from the same locations in 2011 (four years post-fire and three years post-seeding) and 2024 (17 years post-fire and 16 years post-seeding). Two different example plots are shown in unburned reference habitat.

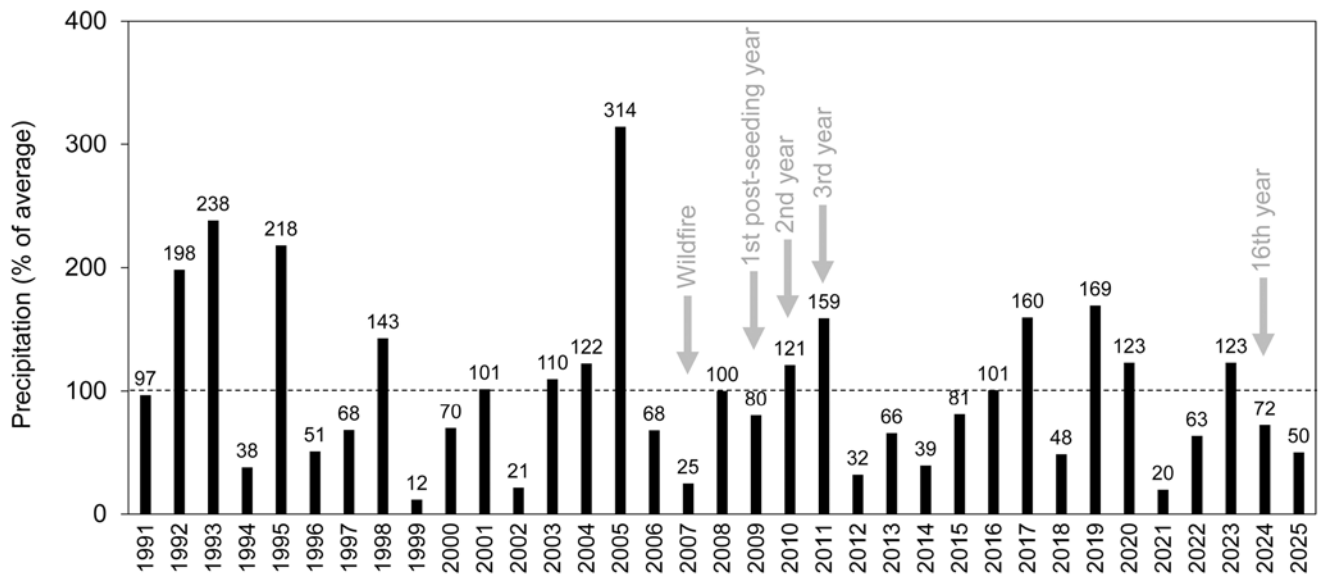


Figure 3. Autumn through spring (October through March) growing-season precipitation expressed as percent of the 12-cm average (out of 18 cm for all 12 months) from 1991 to 2025 for a weather station near the Bonnie Springs Fire, Mojave Desert, southern Nevada. Arrows mark the fire year and our sampling years starting the first growing season after the November 2008 seeding. Precipitation data were recorded at station 4324 (Red Rock Canyon Visitor Center), maintained by the Clark County Regional Flood Control District, Las Vegas, Nevada.

Table 1. Summary of five native plant species seeded on the Bonnie Springs Fire, Mojave Desert, southern Nevada.

Feature	<i>Aristida purpurea</i>	<i>Baileya multiradiata</i>	<i>Hymenoclea salsola</i>	<i>Salvia columbariae</i>	<i>Sphaeralcea ambigua</i>
Growth form	Perennial grass	Perennial forb	Shrub	Annual forb	Perennial forb
Pure live seeds/100 m ²	4400	13,600	2200	16,600	12,300
Seed weight (mg) ^a	0.7	0.5	3.9	— ^c	1.0
Germination (%) ^b	100	70	20	—	30
Average plant density/100 m ² ± SEM (% frequency ^d)					
Seeded 2009	2 ± 2 (10)	51 ± 26 (100)	2 ± 2 (30)	0 ± 0 (0)	92 ± 35 (100)
Seeded 2010	1 ± 1 (20)	33 ± 20 (90)	1 ± 1 (20)	20 ± 20 (20)	43 ± 10 (90)
Seeded 2011	1 ± 1 (20)	34 ± 17 (100)	1 ± 1 (10)	0 ± 0 (0)	28 ± 5 (100)
Seeded 2024	14 ± 6 (60)	79 ± 27 (100)	1 ± 1 (20)	0 ± 0 (0)	55 ± 7 (100)
Unseeded 2009	10 ± 7 (20)	29 ± 11 (80)	1 ± 1 (20)	2 ± 2 (10)	182 ± 67 (90)
Unseeded 2010	1 ± 1 (20)	10 ± 4 (100)	1 ± 1 (20)	0 ± 0 (0)	76 ± 22 (100)
Unseeded 2011	1 ± 1 (20)	11 ± 4 (90)	2 ± 1 (40)	8 ± 8 (10)	40 ± 9 (100)
Unseeded 2024	14 ± 9 (70)	39 ± 12 (100)	3 ± 1 (50)	0 ± 0 (0)	61 ± 12 (100)
Reference 2024	0 ± 0 (0)	8 ± 5 (83)	3 ± 3 (17)	0 ± 0 (0)	37 ± 13 (100)

^aAverage weight of air-dry, individual seeds we measured from samples of seed lots used for the post-wildfire seeding.

^bUsing 120 seeds/species randomly selected from seed lots, we assessed germination (radicle protrusion) by placing seeds on moistened paper towels in Petri dishes at room temperature for six weeks in a laboratory lighted from outside windows.

^cNot available.

^dFrequency is out of 10 plots each for seeded and unseeded areas on the burn and for six plots in unburned reference habitat. Plant densities are provided by measurement year (2009–2011, 2024). For the species (*B. multiradiata*, *S. ambigua*) with sufficient detection, average density did not vary with seeding ($p > 0.05$), but *S. ambigua* varied across years ($F_{3,72} = 14.6$, $p < 0.001$).

Data Collection

We randomly located 10 plots in the seeded portion and 10 plots in a similar-sized area in an adjacent unseeded portion of the burn. Environmental features of plots on the seeded and unseeded areas were similar. Elevation averaged 1192 m on seeded plots and 1177 m on unseeded plots. Slope gradients narrowly ranged from 3–13% among plots, and

slope aspects were generally south- and west-facing. Soils were mapped as the Zeheme-Potosi and Bludiamond-Diamondhill associations classified as Haplocalcids-Torriorthents and Petrocalcids-Argidurids (Lato et al. 2006). These well-drained soils, derived from limestone and sandstone, are shallow with bedrock or a petrocalcic horizon typically within 25–75 cm of the surface (Lato et al. 2006).

We sampled plots near peak plant cover annually in spring (mid-April to May) from 2009–2011 (2–4 years post-fire and 1–3 years post-seeding) and 2024 (17 years post-fire and 16 years post-seeding). In each 10 m × 10 m (100 m²) plot, we visually categorized the aerial cover of each vascular plant species using cover classes: trace, > 0.1 < 1, ≥ 1 < 2, ≥ 2 < 5, ≥ 5 < 10, ≥ 10 < 15, ≥ 15 < 25, ≥ 25 < 50, and ≥ 50–100% (with 0.1% for trace and the category mid-point percentages used for analyses). For the major non-native annual grass (*B. rubens*) generating fuel for wildfires (Brooks and Chambers 2011), we categorized cover separately for live and dead plant parts. We also counted the number of individuals on each plot for each seeded species. Additionally in 2024, we inventoried six, 100-m² plots using the same methods and randomly located in adjacent, unburned reference habitat for comparison with seeded and unseeded burned habitat. Nomenclature and classification of species' growth forms (e.g., annual forb) and nativity to the U.S. follow Natural Resources Conservation Service (2025).

In October 2009 and 2010, to represent the persistent seed bank available for potential germination during autumn–winter rains, we collected soil samples of the upper 5 cm of soil (mostly or all mineral soil) from the 10 seeded and 10 unseeded burned plots. We collected the samples from open areas (few to no shrubs remained alive post-fire) at each of the four corners of each plot. Each of the four subsamples per plot were 200-mL cores (7 cm in diameter), and we combined them into one homogenized sample per plot.

We used the emergence method to assay seed bank samples within a month of sample collection. For the 2009 collection, we prepared two samples per plot. Each 235-mL sample was spread evenly on top of 400 mL of sterilized potting soil (Black Gold cactus mix, Sun Gro Horticulture Distribution, Inc., Bellevue, WA) in plastic, 12 cm × 12 cm pots. We randomly arranged pots on a bench in a greenhouse (University of Nevada, Las Vegas) and randomly applied one of two protocols to samples from each plot. These protocols were either watering samples twice daily to field capacity or the method detailed in DeFalco et al. (2009). This method included four alternate wetting (each three weeks) and drying (each three weeks) cycles, then applying potassium nitrate and gibberellic acid intended to stimulate germination. We ran the assay for one year, with samples remaining under natural lighting in the greenhouse. As seedlings matured and were identified, we pulled seedlings from pots. For the samples collected in 2010, we followed the same greenhouse procedures, except that we applied only the first protocol (consistent watering twice daily). There was little difference in species detection between the protocols (e.g., 12 total species detected via consistent watering and 14 species in the wet-dry-amendment protocol in 2009), so we combined data on a plot basis. As we detected only one occurrence of a

seeded species in seed banks, we did not apply inferential statistics to the seed bank data and report the descriptive statistics of mean seed density and frequency.

Data Analysis

In addition to cover and density (plants/100 m²) of seeded species, we calculated 11 univariate plant community variables: native annual and perennial cover and species richness and in total for all native species, non-native annual forb and grass cover (no non-native perennials inhabited plots), cover and species richness of native food plants for desert tortoises (*Gopherus agassizii*), and *B. rubens* biomass as fuel. We included forage quality for desert tortoises as a functional outcome metric for two reasons: 1) a seeded species (*S. ambigua*) is favored forage, and 2) how restoration activities may affect habitat for the desert tortoise is noteworthy because of its listing as threatened under the U.S. Endangered Species Act in the Mojave Desert (Jennings and Berry 2015). We classified plants as desert tortoise food plants based on tortoises preferentially feeding on them relative to a plant species' availability using data in Jennings and Berry (2015). To estimate fuel loads of *B. rubens* from live and dead cover, we used the allometric equation in Abella (2020) from the Goodsprings Fire, near (within 15 km) the present study site.

We performed three sets of statistical analyses on the vegetation data including: 1) on the univariate variables comparing seeded and unseeded burned plots among years, 2) on the univariate variables for 2024 comparing seeded and unseeded plots with unburned reference habitat, and 3) multivariate community analyses. First, we analyzed average plant density of the most abundant seeded species (*B. multiradiata* and *S. ambigua*) and total density and cover of all five seeded species along with the other univariate community variables in a generalized linear mixed model (PROC GLIMMIX) in SAS v. 9.4 (SAS Institute, Cary, NC). This model included seeding (present or absent), year (2009–2011, 2024), their interaction, and plot as a repeated measures subject. Response variables were either Box-Cox transformed to approximate a normal distribution or were negative binomial (species richness as count data). If main effects or their interaction were significant ($p < 0.05$), we used Tukey-Kramer tests to compare means. Second, to compare the univariate variables across seeded and unseeded burned areas and the unburned reference habitat in 2024, we used a one-way generalized linear model. Third, we compared community composition based on relativized cover (cover of species/ Σ cover of all species on a plot) between seeded and unseeded areas (and with unburned reference habitat in 2024) within years using multi-response permutation procedures (Sørensen distance and $n_i/\Sigma n$ group weighting). We displayed compositional differences using non-metric multidimensional scaling (Sørensen distance, random starting coordinates, and 250 runs each with real

Table 2. Variation in seeded species and plant community metrics on the Bonnie Springs Fire, Mojave Desert, southern Nevada.

	Analysis Factors ^A			Measurement Years ^B			
	Treatment (T)	Year (Y)	T × Y	2009	2010	2011	2024
Native species	F^C (p)			Mean ± SEM			
Seeded species (plants/100 m ²)	0.1 (0.768)	11.5 (< 0.001)	0.7 (0.577)	180 ± 45 ^a	92 ± 20 ^{bc}	63 ± 10 ^c	132 ± 16 ^{abc}
Seeded species cover (%)	0.1 (0.899)	6.6 (0.001)	0.2 (0.910)	2 ± 1 ^a	3 ± 1 ^{ab}	3 ± 1 ^a	5 ± 1 ^b
Annual cover (%)	0.9 (0.368)	24.3 (< 0.001)	0.3 (0.861)	0.5 ± 0.1 ^a	1.5 ± 0.3 ^b	0.4 ± 0.1 ^a	0.5 ± 0.1 ^a
Perennial cover (%)	1.9 (0.188)	38.1 (< 0.001)	0.5 (0.687)	6 ± 1 ^a	11 ± 1 ^b	11 ± 1 ^b	19 ± 2 ^c
Total cover (%)	1.6 (0.224)	40.1 (< 0.001)	0.4 (0.779)	6 ± 1 ^a	13 ± 2 ^b	11 ± 1 ^b	20 ± 2 ^c
Tortoise food cover (%)	0.1 (0.911)	2.2 (0.105)	0.2 (0.867)	2.5 ± 0.5	3.4 ± 0.7	2.2 ± 0.4	3.1 ± 0.3
Annual species/100 m ²	0.8 (0.386)	21.7 (< 0.001)	0.5 (0.720)	3.9 ± 0.5 ^a	7.4 ± 0.7 ^b	2.8 ± 0.3 ^a	2.5 ± 0.2 ^a
Perennial species/100 m ²	8.6 (0.008)	7.3 (0.001)	0.3 (0.830)	12 ± 1 ^{ab}	13 ± 1 ^{ab}	12 ± 1 ^a	14 ± 1 ^b
Total species/100 m ²	2.0 (0.176)	27.0 (< 0.001)	1.2 (0.325)	16 ± 1 ^{ab}	20 ± 1 ^c	15 ± 1 ^b	17 ± 1 ^a
Tortoise food species/100 m ²	1.0 (0.339)	11.5 (< 0.001)	0.7 (0.563)	4 ± 1 ^{ab}	5 ± 1 ^c	4 ± 1 ^{bc}	3 ± 1 ^a
Non-native species							
Annual forb cover (%)	0.2 (0.661)	27.5 (< 0.001)	3.0 (0.039)	2.3 ± 0.6	6.6 ± 1.4	1.9 ± 0.4	0.5 ± 0.2
Annual grass cover (%)	0.1 (0.753)	33.8 (< 0.001)	2.5 (0.068)	1 ± 1 ^a	8 ± 2 ^b	15 ± 3 ^c	18 ± 3 ^c
<i>Bromus rubens</i> mass (g/m ²)	0.1 (0.887)	33.2 (< 0.001)	2.1 (0.112)	10 ± 2 ^a	51 ± 10 ^b	85 ± 13 ^c	89 ± 12 ^c

^ATreatment represents presence or absence of seeding on the burn area. Year represents the study years of 2009–2011 (2–4 years post-fire and 1–3 years post-seeding) and 2024 (17 years post-fire and 16 years post-seeding).

^BMeans within a row without shared letters differ at $p < 0.05$. Because of the interaction, non-native annual forb cover has no letters.

^CF-statistics in bold have $p < 0.05$. Degrees of freedom (DF) for the F-statistic vary with the model data distribution and covariance matrix. Models using the normal distribution and autoregressive covariance had ca. 1, 22 DF for treatment; 3, 54 for year; and 3, 54 for treatment × year.

and randomized data). We then performed indicator species analysis (Dufrêne and Legendre 1997) to identify individual species associated with treatments. We implemented the community composition and indicator species analysis in PC-ORD 7.10 (MjM Software Design, Gleneden Beach, OR).

Results

Seeded Species in Vegetation

There was little evidence in any of our analyses that post-wildfire seeding increased seeded species during our study including the first three (2009–2011) and 16 years (2024) after seeding. Individual seeded species either had low density and occurrence among burned plots with no trend for greater abundance with seeding (*A. purpurea*, *H. salsola*, and *S. columbariae*) or were common but had no significant differences between seeded and unseeded plots (*B. multiradiata* and *S. ambigua*; Table 1). For the five seeded species considered together, average density and cover of seeded species did not vary ($p > 0.05$) with seeding, instead varying only with year (Table 2). In 2024, density of seeded species in both the seeded and unseeded burned areas was higher than in unburned (and unseeded) reference habitat (Table 3). Likewise, using cover in indicator species analysis, no seeded species in 2024 were more prevalent in the seeding treatment (Table 4). The four seeded species still present in 2024 (*S. columbariae* was absent) were primarily associated with burned habitat, independent of seeding, when compared with unburned habitat.

Seeded and Non-seeded Species in the Soil Seed Bank

We detected only one of the five seeded species in soil seed bank samples collected in both 2009 and 2010 (2–3 years post-fire and 1–2 years post-seeding; Table 5). The only seeded species we detected was *S. columbariae*, occurring in seed banks of only one of the 10 seeded plots.

Including *S. columbariae* as the only seeded species detected, native species dominated seed banks in terms of the number of species (16 of 20 total species, 80%). However, non-native species dominated in terms of seed density, comprising 87–93% of all detected seeds (Table 5). The non-native annual grass *B. rubens* and the annual forb *E. cicutarium* in sum had densities averaging 1213–5436 seeds/m². Although with sharply lower densities always averaging < 106 seeds/m² for individual species, the predominant native species we detected in seed banks were annual forbs such as *Lepidium lasiocarpum* (shaggyfruit pepperweed), *Phacelia fremontii* (Fremont's phacelia), *Plantago patagonica* (woolly plantain), *Plantago ovata* (desert plantain), *Cryptantha* spp., and *Amsinckia tessellata* (bristly fiddleneck).

Post-fire Change in Plant Communities in Seeded and Unseeded Areas

In comparing variation in seeded and unseeded burned areas across years (2009–2011 and 2024 spanning 1–3 and 16 years post-seeding), most (10 of 13, 77%) of the univariate vegetation variables differed only through time and not with seeding nor its interaction with year (Table 3).

Table 3. Variation in seeded species and plant community metrics with seeding treatment in burned areas compared with unburned reference habitat around the Bonnie Springs Fire, Mojave Desert, southern Nevada. Data are for 2024, 17 years post-fire and 16 years post-seeding.

	Seeded	Unseeded Mean $\pm$ SEM ^A	Reference	F _{2,23} (p) ^B
Native species				
Seeded species (plants/100 m ²)	148 $\pm$ 27 ^b	117 $\pm$ 18 ^b	48 $\pm$ 14 ^a	10.8 (< 0.001)
Seeded species cover (%)	5 $\pm$ 1 ^b	4 $\pm$ 1 ^{ab}	2 $\pm$ 1 ^a	4.4 (0.024)
Annual cover (%)	0.5 $\pm$ 0.1	0.5 $\pm$ 0.2	0.9 $\pm$ 0.4	0.7 (0.486)
Perennial cover (%)	18 $\pm$ 2 ^b	20 $\pm$ 2 ^b	32 $\pm$ 4 ^a	6.2 (0.007)
Total cover (%)	18 $\pm$ 2 ^b	21 $\pm$ 2 ^b	33 $\pm$ 4 ^a	6.8 (0.005)
Tortoise food cover (%)	3 $\pm$ 1	3 $\pm$ 1	5 $\pm$ 4	0.1 (0.906)
Annual species/100 m ²	2 $\pm$ 1	3 $\pm$ 1	4 $\pm$ 1	1.9 (0.170)
Perennial species/100 m ²	13 $\pm$ 1 ^b	16 $\pm$ 1 ^b	22 $\pm$ 1 ^a	8.4 (0.002)
Total species/100 m ²	15 $\pm$ 1 ^b	19 $\pm$ 1 ^b	26 $\pm$ 2 ^a	10.2 (< 0.001)
Tortoise food species/100 m ²	3 $\pm$ 1	3 $\pm$ 1	4 $\pm$ 1	1.3 (0.291)
Non-native species				
Annual forb cover (%)	0.8 $\pm$ 0.3 ^b	0.1 $\pm$ 0.1 ^a	0.1 $\pm$ 0.1 ^a	8.5 (0.002)
Annual grass cover (%)	21 $\pm$ 5 ^b	16 $\pm$ 3 ^{ab}	7 $\pm$ 2 ^a	4.5 (0.022)
<i>Bromus rubens</i> mass (g/m ²)	98 $\pm$ 20 ^b	79 $\pm$ 14 ^{ab}	40 $\pm$ 8 ^a	3.8 (0.037)

^AMeans within a row without shared letters differ at $p < 0.05$.

^BF-statistics in bold have $p < 0.05$.

Table 4. Indicator species analysis of associations with seeding treatment in burned areas compared with unburned reference habitat around the Bonnie Springs Fire, Mojave Desert, southern Nevada. Data are for 2024, 17 years post-fire and 16 years post-seeding. All seeded species are shown along with 10 non-seeded species with the highest indicator values.

				Comparison					
	Seeded : unseeded			Seeded : reference			Unseeded : reference		
	Seeded	Unseeded	p	Seeded	Reference	p	Unseeded	Reference	p
Seeded species ^a									
<i>Aristida purpurea</i> (PG)	46 ^b	16	0.401	60	0	0.052	70	0	0.026
<i>Baileya multiradiata</i> (PF)	63	37	0.632	86	12	0.004	78	18	0.072
<i>Hymenoclea salsola</i> (S)	3	33	0.289	6	12	0.844	27	6	0.471
<i>Salvia columbariae</i> (AF)	0	0	1.000	0	0	1.000	0	0	1.000
<i>Sphaeralcea ambigua</i> (PF)	52	48	0.789	72	23	0.041	71	25	0.017
Non-seeded species									
<i>Ambrosia dumosa</i> (S)	0	20	0.470	0	67	0.008	4	53	0.083
<i>Astragalus nuttallianus</i> (PF)	2	15	0.491	1	94	< 0.001	3	84	0.002
<i>Bromus rubens</i> (AG)	53	47	0.532	73	27	0.002	70	30	0.002
<i>Coleogyne ramosissima</i> (S)	4	49	0.072	1	95	< 0.001	11	82	0.003
<i>Dasyochloa pulchella</i> (PG)	67	33	0.084	90	8	0.002	82	15	0.015
<i>Eriogonum deflexum</i> (AF)	26	63	0.188	70	0	0.022	100	0	< 0.001
<i>Eriogonum inflatum</i> (PF)	11	69	0.057	8	70	0.040	35	51	0.628
<i>Krameria erecta</i> (S)	9	43	0.172	6	68	0.049	22	53	0.334
<i>Menodora spinescens</i> (S)	1	17	0.474	0	82	0.002	1	77	0.007
<i>Yucca schidigera</i> (S)	0	40	0.084	0	83	0.002	6	71	0.026

^aAF, annual forb; AG, annual grass; PF, perennial forb; PG, perennial grass; S, shrub. All species are native except *B. rubens*.

^bIndicator values range from 0 (no association with a group) to 100 (maximum association). Values with $p < 0.05$ are in bold.

Table 5. Soil seed bank composition in seeded and unseeded areas of the Bonnie Springs Fire, Mojave Desert, southern Nevada. Data are for seed bank samples collected in 2009 and 2010, representing 2–3 years post-fire and 1–2 years post-seeding.

	2009		2010	
	Seeded	Unseeded	Seeded	Unseeded
Native	Seeds/m ² (% frequency) ^b			
<i>Amsinckia tessellata</i> (AF) ^a	11 (10)	21 (20)	0 (0)	0 (0)
<i>Astragalus nuttallianus</i> (PF)	0 (0)	11 (10)	0 (0)	0 (0)
<i>Bouteloua barbata</i> (AG)	0 (0)	43 (20)	0 (0)	0 (0)
<i>Chaenactis fremontii</i> (AF)	0 (0)	0 (0)	21 (10)	0 (0)
<i>Chamaesyce</i> spp. (PF)	0 (0)	11 (10)	21 (10)	21 (10)
<i>Cryptantha</i> spp. (AF)	32 (20)	21 (20)	21 (10)	0 (0)
<i>Descurainia pinnata</i> (PF)	11 (10)	0 (0)	0 (0)	0 (0)
<i>Gilia</i> spp. (AF)	64 (20)	11 (10)	0 (0)	0 (0)
<i>Lepidium lasiocarpum</i> (AF)	85 (50)	85 (40)	43 (10)	106 (40)
<i>Linum lewisii</i> (PF)	0 (0)	21 (10)	0 (0)	0 (0)
<i>Phacelia fremontii</i> (AF)	11 (10)	21 (20)	0 (0)	64 (10)
<i>Phacelia</i> spp. (AF)	11 (10)	0 (0)	0 (0)	0 (0)
<i>Plantago ovata</i> (AF)	0 (0)	0 (0)	21 (10)	64 (20)
<i>Plantago patagonica</i> (AF)	96 (30)	32 (20)	0 (0)	0 (0)
<i>Poa secunda</i> (PG)	11 (10)	0 (0)	0 (0)	0 (0)
<i>Salvia columbariae</i> (AF)	22 (10)	0 (0)	0 (0)	0 (0)
Native total	351	277	128	255
Non-native				
<i>Bromus rubens</i> (AG)	1383 (90)	2479 (100)	766 (80)	3064 (90)
<i>Erodium cicutarium</i> (AF)	2787 (100)	2957 (100)	447 (100)	809 (90)
<i>Salsola tragus</i> (AF)	0 (0)	21 (10)	0 (0)	0 (0)
<i>Schismus arabicus</i> (AG)	43 (20)	43 (40)	0 (0)	0 (0)
Non-native total	4213	5500	1213	3872

^aAF, annual forb; AG, annual grass; PF, perennial forb; PG, perennial grass. Of the five seeded species, we detected only *S. columbariae* in seed bank samples.

^bSeed bank densities are for the 0–5 cm mineral soil. Frequency is out of 10 plots each for seeded and unseeded areas.

Among the other three variables, cover of desert tortoise food plants did not vary significantly with seeding or time. Non-native annual forb cover (dominated by *E. cicutarium*) varied with a seeding $\times$ year interaction overall, though none of the seeded-unseeded comparisons differed within years. Lastly, native perennial species richness was the only variable to differ with the seeding main effect, but perennial richness was lower (12 ± 1 species/100 m², mean $\pm$ standard error of mean) in seeded compared with unseeded areas (14 ± 1 species/100 m²).

In 2024 comparisons of seeded and unseeded burned areas with unburned reference habitat, the 13 univariate vegetation variables either did not differ across the habitats or generally just differed between the burned (irrespective of seeding) and unburned habitat (Table 4). An exception was non-native species variables (annual forb and grass cover and *B. rubens* biomass), which were higher only in the burned, seeded areas than in the unburned reference habitat.

In multivariate analyses, burned seeded and unseeded areas never differed ($p > 0.05$) in community composition in any study year. Both seeded and unseeded burned

areas, however, differed from unburned reference habitat in 2024 (Figure 4). In follow-up indicator species analysis, no seeded or non-seeded species were associated with seeding in 2024 comparisons between seeded and unseeded burned areas (Table 5). When compared with unburned reference habitat, several species were associated with burned areas irrespective of seeding, such as the native perennial forb *S. ambigua* (a seeded species), perennial grass *Dasyochloa pulchella* (low woollygrass), annual forb *Eriogonum deflexum* (flatcrown buckwheat), and the non-native annual grass *B. rubens*. Other native species, such as the shrubs *C. ramosissima* and *Y. schidigera* and the perennial forb *Astragalus nuttallianus* (small-flowered milkvetch), were associated with unburned reference habitat.

Discussion

Potential Factors Limiting Seeding Effectiveness

As a restoration strategy, broadcast seeding is based on an assumption that viable seed availability limits recovery and that augmenting seed availability increases plant

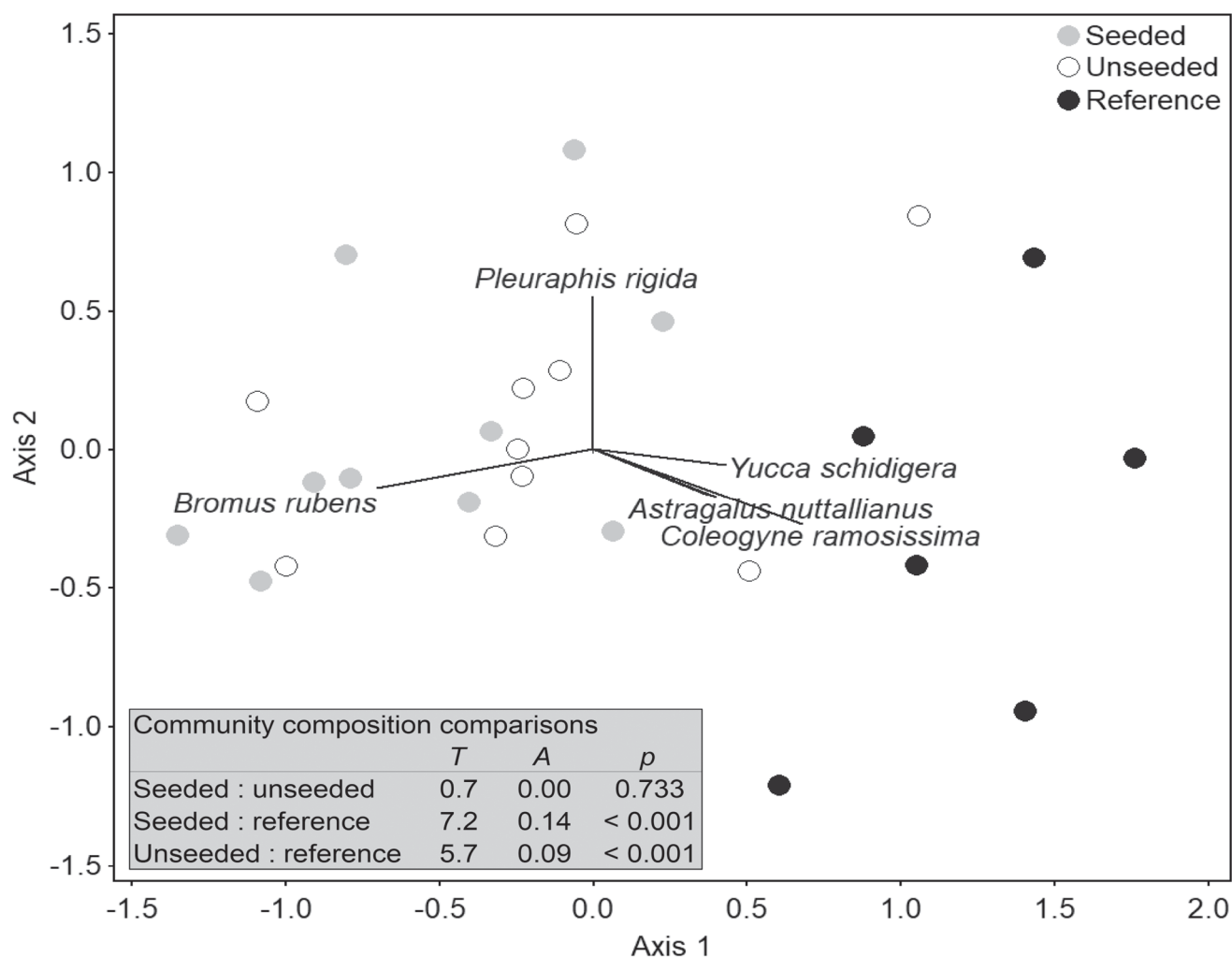


Figure 4. Non-metric multidimensional scaling ordination of 2024 plant community composition in seeded and unseeded burned areas and unburned reference habitat around the 2007 Bonnie Springs Fire, Mojave Desert, southern Nevada. Each point, symbolized by treatment, represents a sample plot ($n = 10$ each for seeded and unseeded burned areas and $n = 6$ for unburned reference habitat). Species correlated ($r^2 > 0.30$) with community variation are shown as vectors and all are native except *B. rubens*. The ordination had a stress of 16 and represented 82% of the variance (64% for Axis 1 and 18% for Axis 2) in the community matrix. The inset shows multi-response permutation procedure tests of the null hypothesis of no difference in 2024 community composition between seeded and unseeded burned areas and the unburned reference habitat (*T*, test statistic; *A*, chance-corrected within-group agreement).

establishment (Shackelford et al. 2021). Seeding failed to increase plant establishment in our study despite using locally collected seed, evaluating the seed lot for viability and ensuring some seeds were readily germinable, seeding species capable of colonizing disturbances, and receiving above average rainfall in two of the first three post-seeding years.

There could be several reasons why broadcast seeding did not increase native plant establishment. Although the commercially purchased seed was locally collected within the county containing our study site, it cannot be ruled out that seed was nevertheless ill-suited to site conditions. Even subtle among-population variation, such as tolerance to longevity of freezing temperatures, could result in seeding

failures (Shryock et al. 2022). The question of “how local is local” or how closely environments must be matched between seed source and restoration sites is unresolved and under active research (Erickson and Halford 2020). Although our total seeding rate was 491 pure live seeds/m², much seed can be moved to unfavorable microsites or consumed by granivores (Suazo et al. 2013). For example, 16 weeks after broadcast seeding in the Mojave Desert, only 22% of seeds remained (DeFalco et al. 2012). Given these potential losses, it could be hypothesized that even higher seeding rates should have been used in our study (Shackelford et al. 2021). However, this might raise logistical concerns such as financial costs, seed availability, and labor expenditure, still with uncertain prognosis of success.

Although the second (2010: 121% of average October through March precipitation) and third (2011: 159%) years after seeding had above average precipitation, the first year after seeding (2009: 80%) was below average and was the fourth consecutive year of below average precipitation. Similarly, our 2024 sample year (16 years after seeding) was dry (72%) and was the third year in a four-year period with below average precipitation leading up to 2024. It is possible that protracted wet periods are required for broadcast seeding to be more reliable in the Mojave Desert, as the more consistent seeding effectiveness reported in wet periods in the 1970s–1980s has been difficult to replicate in the generally drier decades since the late 1990s (Abella et al. 2023). As all five of our seeded species occurred on the burn irrespective of seeding, clearly soil conditions were not so prohibitive as to exclude these species. However, it is possible that availability of suitable microsites, rather than availability of seed, limited plant recruitment and thus hindered seeding from augmenting plant recruitment.

Soil Seed Banks

Our results did not support the idea that seeded species formed readily germinable, persistent soil seed banks. Emergence but death of seedlings before they reproduce can be a major depletion process of soil seed banks (Beatley 1967). Since we did not observe mass appearance of seedlings of seeded species during our study nor their readily germinable seeds in the soil, what was the fate of the seeds after seeding? Although resolving this question requires seed-fate studies, several possibilities exist. As mentioned previously, granivores could have removed and consumed appreciable seed (DeFalco et al. 2012). Seed also could have moved off-site via wind or water, failed to lodge in suitable microsites for retention on-site or for germination, or become desiccated or non-viable on the soil surface. Surficial plant litter, important for trapping seed (DeFalco et al. 2009), is minimal after desert wildfires (Abella and Engel 2013). Seeds may have been too sparse for detection in our soil sampling or they could have lost viability. Seeds also could have entered dormancy after seeding following our determination that at least some of the seeds were readily germinable when seeding occurred. Further work on the species' germination ecology may aid detection of seeds (if present) in the emergence method of seed bank assay and whether any type of pre-conditioning treatment could prime seeds for germination under post-seeding field conditions (Ostler et al. 2003). For *S. ambigua*, for example, Dunn (2011) found that commercially purchased seed exhibited 18% germination (compared with 30% in our study), which doubled after scarifying the seed coat with sandpaper and further increased with a 30-day, moist stratification.

Our results were consistent with prior research in burned Mojave Desert habitats showing that non-native species typically dominate readily germinable soil seed banks after

wildfires (Abella et al. 2009, Esque et al. 2010, Jurand and Abella 2013, Lee et al. 2024). Our data indicate that seeding did not discernably augment native seed banks.

Broadcast Seeding as a Restoration Strategy

Our results add to seeding literature that may enable identifying patterns in seeding outcomes in the Mojave Desert and contribute more broadly to restoration practices in drylands. In our previous review of 13 seeding studies in the Mojave Desert that evaluated outcomes for ≥ 1 year and were published between 1978–2023, 11 studies reported that at least one seeded species increased while two studies found no increase of seeded species (Abella et al. 2023). In addition to our present study being the third in which seeding did not enhance species establishment, three other trends seem noteworthy. First, the four perennial species seeded in our study commonly recruit naturally after disturbances, yet have been among the poorest performers in Mojave Desert seeding projects. Seeding outcomes in prior studies for these species in the Mojave Desert were as follows: *A. purpurea* (increased after seeding in 0/1 studies), *B. multiradiata* (1/3), *S. ambigua* (1/5), and *H. salsola* (1/4; Abella et al. 2023). This suggests that capability for natural colonization of disturbances and amenability to seeding (at least simple broadcast seeding) may not correlate. Second, although it is difficult to ascribe disturbance type as a casual factor in seeding effectiveness because other factors (e.g., climate) have also varied among studies, this is the third Mojave Desert study to report minimal effectiveness of seeding after wildfire. The others found that none of 10 (Abella et al. 2012) or only one of nine seeded species became established (Suazo et al. 2013). Third, long-term studies of seeding effectiveness are rare. Our results extending to 16 years and the results of Ott et al. (2011) extending to 14 years post-seeding in the northeastern Mojave Desert show contrasting patterns. After mining disturbance, Ott et al. (2011) found that different individual or groups of seeded species appeared, disappeared, or re-appeared at different times including at year 14. Thus, early results did not necessarily portend later results in Ott et al. (2011). This contrasts with minimal early seeding effectiveness being prescient of no seeding effect at year 16 in our study.

Conclusion

Despite using seemingly sound practices for seeding (e.g., ensuring germinability of seed) and the major effort and expense involved, broadcast seeding did not enhance post-wildfire recovery of native plant communities in our case study. We offer the following lessons learned and suggested future directions. Because operational-scale seedings across large areas can involve considerable expense and labor, we suggest that there is an important role for experimental seeding trials in small plots and germination investigations to attempt developing reliable seeding

practices before seeking to upscale across large areas. The four perennial species seeded in our study have shown minimal establishment through seeding in the Mojave Desert at any scale from small plots (e.g., 4 m²; Abella et al. 2012) to 40 ha in the present study. Pinpointing causal factors for seeding failure or success and identifying candidate seeding practices (e.g., treatments paired with seeding such as pelletizing seed or adding mulch) in experiments in small areas could be considered a first step before upscaling to large, expensive projects. This proactive development of candidate seeding practices, or assessing their reliability for deployment, is likely especially important for large, unplanned disturbances such as wildfires where urgent action may be expected and require restoration practices already well-tested.

Our results also suggest that the idea of selecting species for seeding based on their ability to recruit naturally after disturbance should be re-examined. The ability to colonize disturbances naturally and amenability to augmentation through seeding may not be correlated. Alternatively, further work may be required to understand the germination ecology and practices that can make seeding effective for these species.

Our case study further raises questions regarding the potential role of bet-hedging approaches to restoration such as applying treatments across multiple years or implementing multiple treatment types to reduce risk of complete project failure (Rader et al. 2022). Although increasing project complexity, adding treatments such as pelletizing some seed, strategically outplanting nursery-grown seedlings, incorporating assisted natural regeneration, or deploying abiotic treatments to ameliorate site conditions could be considered for spreading risk away from a single treatment such as broadcast seeding (Abella et al. 2023). Identifying if or which candidate seeding practices exist for reliable restoration on wildfires in western North American drylands likely requires further work on factors such as limitations to plant establishment, species most amenable to seeding, and context-dependency of seeding effectiveness.

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