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RESEARCH ARTICLE

Restoring Palmer's agave in a Lehmann lovegrass dominated grassland in southeastern Arizona

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Dryland restoration is becoming increasingly challenging in arid and semiarid regions, such as in the southwestern United States, due to rapid land degradation, the spread of non-native species, and climate change. The development of strategies to enhance restoration of native species, particularly culturally and ecologically important native plants like Palmer's agave (*Agave palmeri*), is particularly critical in southeastern arid lands where scarce rainfall, herbivory, and invasive species dominance pose unique challenges to land management. In a large field experiment in southeastern Arizona, U.S.A., we assessed the utility of several management techniques to promote restoration and revegetation outcomes for Palmer's agave survival and growth, including protection from solar insolation and herbivory, and reduction in the competitiveness of Lehmann lovegrass (*Eragrostis lehmanniana*). We found that the combination of herbivory protection and shade resulted in the highest survival of planted agaves, while the shade treatment alone resulted in the largest agaves. In fact, our results suggest that dense Lehmann lovegrass cover protects agaves from direct sunlight and predation. If land managers are challenged by widespread Lehmann lovegrass, they can opt to mechanically reduce it. However, if population recovery of Palmer's agave is a priority and fire hazard is minimal, our work suggests that stakeholders concerned with population recovery of Palmer's agave can forgo removing existing vegetation and plant agaves in a matrix of (and/or under the canopy of) existing vegetation.

Key words: ***Agave palmeri*, *Eragrostis lehmanniana*, javelina predation, restoration, revegetation, weed management**

Implications for Practice

- Restoration is an intricate process in arid lands, and explicit understanding and proper management of biotic and abiotic stresses are critical in improving restoration outcomes.
- The combination of protection from the weather (by providing shade), herbivory, and competition from neighboring invasive plants can boost restoration outcomes for slow-growing native succulents.
- Existing vegetation provides agaves with essential microhabitats. In areas with moderately low fire hazards, practitioners could forgo removing or displacing existing vegetation (at least initially for nurse effects) for newly planted agaves.
- Restoration practitioners could consider transplanting multi-aged agave plant cohorts so that prolonged replenishment of the food sources for the bats and pollinators is ensured.

Introduction

Dryland ecosystems cover approximately 40% of the earth's land surface (Reynolds et al. 2007). Globally, these ecosystems are being degraded at a rapid rate due to climate change and land use changes, which imperil long-term ecological, economic, and social services (Carrick et al. 2015). Restoring arid and semiarid areas is particularly complex due to scarce rainfall, often distinct floral diversity, and complex spatial and biological dynamics driven by stochastic events (Ellis 1995; Carrick & Krüger 2007). Because passive reestablishment of functional native plant communities takes a long time after disturbance, if it occurs at all (van der Merwe & van Rooyen 2011), active restoration techniques are critical for achieving native habitat restoration goals.

Protecting native habitats of a regionally common plant, Palmer's agave (*Agave palmeri*)—a slow-growing, cool-season crassulacean acid metabolism (CAM) plant—is of crucial conservation interest. It is an ecologically, culturally, and commercially significant native plant to arid and semiarid landscapes in the southwest United States. Palmer's agave is particularly

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important to southeastern Arizona as it is a primary food source for a federally protected migratory bat, commonly known as the Lesser Long-nosed bat (*Leptonycteris curasoae*) (Ceballos et al. 1997; Scott 2004). These bats typically reach southeastern Arizona in late summer and might be a critical pollinator for Palmer's agave (Howell & Roth 1981; Slauson 2000). However, several studies report decreased forage availability due to overharvesting nectar sources, recent human disturbances, and land management interventions that destroy the feeding sources at the roosting sites and migration corridors (Lowery et al. 2009; Russo et al. 2018) in Arizona, New Mexico, U.S.A., and the surrounding Sonoran and Chihuahua desert in Mexico (Pavliscak & Fehmi 2020).

Agave habitat destruction and exploitation are causing agave populations to decline. An example of large-scale agave habitat destruction was the border fence construction between the United States and Mexico in the southern boundary of Coronado National Memorial in 2008 (Buckley & Nabhan 2016), which destroyed approximately 3,172 Palmer's agave plants. This decline exacerbated the ongoing loss of Palmer's agaves due to historic overgrazing by cattle (>100 years, ending in the 1990s), which has reduced agave coverage by almost 98% (USFWS 2018). After such a drastic decrease in the population of Palmer's agaves, some active restoration and mitigation are required to reestablish the agaves and replenish food sources for bats (Pavliscak & Fehmi 2020). However, in addition to interventions and disturbances, Palmer's agave populations are further challenged by being susceptible to drought, unfavorable temperatures, frequent wildfires, juvenile plant mortality, competitive inadequacy, predation, and reductions in pollinator numbers (Turner et al. 1966; Nobel 1977; Jordan & Nobel 1979; Slauson 2002; Fehmi et al. 2004; Best et al. 2015) in southeastern Arizona.

Challenges to population recovery of juvenile and young Palmer's agave plants are particularly complex as they are more vulnerable to unfavorable environments and herbivory than the adult agave plants (Turner et al. 1966; Jordan & Nobel 1979). Much of the mortality experienced by agaves under extreme climate stress occurs in seedlings, which are much more vulnerable to biotic and abiotic stresses such as drought, heat leading to sunburn, and high surface temperatures (Nobel 1976; Jordan & Nobel 1979). This is typical in arid environments, where several studies have reported juvenile mortality as the most crucial limitation to vegetation restoration (Pyke 1990; James et al. 2011); where successful early demographic transitions (i.e. germination and survival after emergence) become a major bottleneck to population growth (Chambers 2000). In addition to highlighting a critical mechanism driving population growth rate, this body of work highlights the importance of assessing arid land plant species soon after they are planted, to capture this key transition. Indeed, Hagen and Evju (2013) suggested incorporating short-term monitoring data to base "sensible management" strategies for large-scale restoration projects in desert systems at a heavily disturbed site. This might be particularly important for agaves species, where initial seedling establishment and survival are crucial for restoration success (Jordan & Nobel 1979; Pavliscak et al. 2015; Pavliscak & Fehmi 2020).

Greater agave seedling mortality is expected in areas of high competition by invasive plants (Lindsay et al. 2011). Lehmann lovegrass (*Eragrostis lehmanniana*) is a non-native invasive grass species commonly found in southwestern U.S. grassland systems typically occupied by native plants like agaves (Anable et al. 1992; Lindsay et al. 2011). Lehmann lovegrass directly threatens agave seedlings through the extraction of resources, as well as indirectly through its high combustibility (Geiger 2006). Lehmann lovegrass is known to increase the frequency and intensity of fires, which, in turn, limits agave germination, growth, and flowering stalk production (Kupfer & Miller 2005; Geiger 2006; Lindsay et al. 2011). Lastly, herbivory in the wild is a prominent cause of the decrease in agave numbers, especially in the arid and the semiarid lands where succulents like Agavaceae and Cactaceae are prominent representatives. In North America, javelinas (*Pecari tajacu*), also known as collared peccary, are characteristically herbivores. They are present in southern Arizona and southwestern regions of New Mexico and Texas (Noon et al. 2003). Javelinas concentrate their feeding preferences on succulents and cacti, which provide nutrients and water. Palmer's agave can also be eaten are cattle, sheep, goats, white-tailed deer, jackrabbits, insects such as Sonoran bumblebees, and small rodents (Hawks 1997; Fehmi et al. 2004).

Considering the complexity of the biotic and abiotic factors that are critical for Palmer's agave survival and subsequent agave restoration success, a deeper understanding is needed about strategies that can mitigate agave stress and enhance short-term restoration outcomes. In this study, we tested how different management approaches might affect variables that are critical for agave restoration outcomes, including solar insulation, protection from javelina herbivory, and reduction in Lehmann lovegrass competition. We primarily aimed to address two questions: (1) How do treatments affect agave survival and growth? and (2) How effective are Lehmann lovegrass removal methods in controlling the Lehmann lovegrass competitive effects on agave growth (and vice versa effects, if any)? We expected that protection from solar insolation, Lehmann lovegrass competition reduction, and herbivory protection would favor successful agave establishment, and enhance its growth and survival rates, which could provide key avenues for successful agave restoration in wildlands.

Methods

In October 2018, a collaboration among Bat Conservation International, the Ancestral Lands Project, the National Park Service, and the University of Arizona supported a project to restore Palmer's agave population in the Coronado National Memorial in southeastern Arizona. The project involved the planting of 1,200 juvenile Palmer's agaves within the southeastern corner (57°36′04″ N, 34°67′269″ E) of the Memorial. The study site elevation is approximately 1,524 m and is situated less than 1 km away from the U.S.-Mexico border, falling within the "nectar corridor" of the migratory *Leptonycteris* bats (Burke et al. 2019), where the agave population was destroyed during fence construction. It is a moderately flat grassland dominated by Lehmann lovegrass with sandy loam-type soil and warm, low humidity summer weather (daytime temperatures = 32–37°C). The summer rainy season (monsoon) is between late June and early September (NPS 2020).

For the experiment, we purchased agave outplants from a native plant nursery, Borderland Restoration Network in Arizona in October 2018 grown from seeds collected from agave parent plants (4-year-old) in the Upper San Pedro watershed (31°46′ 08″ N, 110°02′32″ W), approximately 82 km from the Memorial. The nursery grew the agave outplants for a year in a standardized soil mixture—equal proportions of sand, compost, perlite, and composted mulch— for agave seedling growth and were watered every alternate day. The average (mean ± SE) total number of leaves per plant at the time of planting was 4.19 ± 0.06 for seedlings. We installed agave outplants at the site in six, 1-ha square plots. Each plot was composed of 10 rows, each row extending 95 m and located 10 m from the next row. Every row consisted of 20 agaves planted 5 m apart for a total of 200 plants per plot, and 1,200 plants installed across the entire experiment. Any two treatment plots (amongst the six) were at least 90 m apart from each other.

We tested three different variables that affected young agave's mortality and growth: (1) solar insolation; (2) javelina herbivory; and (3) competition with Lehmann lovegrass. We installed a shade cloth (providing a 50% reduction in solar radiation) to reduce solar insolation, by using wooden stakes buried into the ground and secured on all four corners by using (6 × 2 inches) earth staples. The shade cloth was attached to the top of the stakes approximately 5 cm above the agave plant. To provide javelina herbivory protection, we installed a sieved chicken wire enclosure (15 × 30 cm) and pinned it around the base of each agave plant using landscaping staples. We reduced Lehmann lovegrass competition by removing it in two ways from the immediate surrounding (1 m circumference) of the focal agaves: (1) hand-pulling and (2) weed-eating aboveground biomass. We left behind the removed Lehmann's lovegrass on the ground. All the treatments were deployed 1–4 days after agave installation.

The treatments were a combination of five single and five combination treatments, based on manager recommendations. The five single treatments included: (1) control (hereafter referred to as "C") where no treatment was applied; (2) shade cloth (hereafter referred to as "S"); (3) protection from javelinas (hereafter referred to as "J"); (4) reduced Lehmann lovegrass by weed-eating (hereafter referred to as "W"); and (5) reduced Lehmann lovegrass by hand-pulling (hereafter referred to as "H"). The rest of the five treatments were combinations, including (6) shade and weed-eating (S+W); (7) shade and hand-pulling (S+H); (8) herbivory protection and shade (J+S); (9) herbivory protection and hand-pulling (J+H); and (10) herbivory protection and weed-eating (J+W). Treatments were randomly assigned to rows within a plot (e.g. all plants within a row were exposed to the same treatment).

Data Collection

We collected agave survival and growth responses in September 2019, a year after planting. We collected data from every fourth plant in a row (a total of 5 plants per row, and 50 per plot) to accommodate the sampling schedule of park managers and collect a representative subset from the sample population. We quantified agave survival and agave growth as the total number of leaves per plant. In cases where the agave plant was dead or removed by herbivory, we sampled the agave outplants planted in the north direction (in the same row) of the originally anticipated individual. Re-selection of the agave plant is only applied to the agave growth data (determined by size, calculated by the number of leaves). We also assessed the cover of Lehmann lovegrass for each agave sampled. We used a 1 m square quadrat (centered on the planted agave) to estimate the aerial cover of the lovegrass surrounding the agave plants. Due to substantial vehicle damage to many of our rows in plot 6, we excluded this plot from the analyses.

Analysis

We conducted two analyses. First, we assessed Palmer's agave survival by treatment and agave size by treatment ($n = 250$). To assess the effect of treatment on agave survival, we used mixed-effects logistic regression, where agave survival was coded as a binary response (live or dead/predated) variable, treatment was a 10-level fixed effect, and each row was afforded a random intercept effect. Agave survival per treatment was reported by converting the percent survival probabilities per treatment. We modeled it as:

$$\text{Log}-\text{odds survival} = \beta_0 + \beta_1 \times \text{treatment} + b_0$$

where b_0 is the random intercept for the row. To test for an effect of treatment on agave size, data were restricted to the cases where there were live agaves and had a maximum of three agaves per row ($n = 74$). In this model, we modeled agave size as Poisson-distributed count data, treatment as a 10-level fixed effect, and row as a random intercept effect. The generalized linear regression model for this was:

$$\text{Number of leaves} = \beta_0 + \beta_1 \times \text{treatment} + b_0$$

where b_0 is the random intercept for the row.

We also assessed the effect of a subset of treatments and agaves on Lehmann lovegrass cover. We first tested for an effect of hand-pulling and weed-eating treatments on Lehmann lovegrass cover, as well as an effect of agave presence or absence ($n = 65$). Lehmann lovegrass cover was modeled as a binomial response variable ($0 \le y \le 1$), treatment was a three-leveled categorical predictor, agave presence was a binary predictor, and the row was included as a random intercept effect:

$$\begin{aligned}&\text{Proportion Lehmann lovegrass cover}\\&\quad = \beta_0 + \beta_1 \times \text{treatment} + \beta_2 \times \text{agave presence} + b_0\end{aligned}$$

Additionally, we investigated Lehmann lovegrass percent cover as a response to hand-pulling Lehmann lovegrass treatment (H) and agave size as the explanatory variables and using row as a random effect. We omitted weed-eating treatments (W) from the analysis since there was only a single observation of a live agave in the weed-eating treatments. This model also included the interaction effect of agave size and hand pulling treatment on Lehmann lovegrass cover. We modeled it as:

$$\text{Proportion Lehmann lovegrass cover} = \beta_0 + \beta_1 \times \text{treatment} + \beta_2 \times \text{number of leaves} + \beta_3 \times \text{treatment} \times \text{number of leaves} + b_0$$

where b_0 is the random intercept for a row. In all analyses where treatment was a predictor variable, we used the control treatment as the reference level; all treatment coefficients are thus compared to that of the control, so *post-hoc* pairwise comparisons between treatments were unnecessary. All mixed-effects models used maximum likelihood estimation. All analyses were performed with R software (version-3.6.2; R Core Team 2018) and the following packages: *broom. mixed* (Bolker & Robinson 2021), *car* (Fox & Weisberg 2019), *dplyr* (Wickham et al. 2021), *extrafont* (Chang 2014), *ggplot2* (Wickham 2016), *lme4* (Bates et al. 2015), and *stringr* (Wickham 2019). R code developed for analyses is available on GitHub (https://github.com/jcoliver/agave-growth).

Results

Treatment Effects on Agave

Agave plant survival in the javelina and shade treatment (J+S) had the greatest agave survival of 88.7% ($p = 0.003$; Table S1) and it was significantly higher than survival in the control row—which had 36.5% agave survival. In the remaining treatments, agave survival did not differ significantly from the control treatment. Likewise, agave survivorship per treatment also was highest in the J+S treatment (Fig. 1).

Agave size did not differ significantly amongst the treatments, except in the S, J+S, and J+W treatments ($p < 0.011$, 0.026, and 0.020 respectively, Table S2; Fig. 2). In terms of agave sizes across the treatments measured by the average leaf count, S resulted in the highest agave size for an average of 2.086 leaves per plant, while J+W and J+S resulted in an average of 2.045 and 2.016 leaves per plant respectively. The least

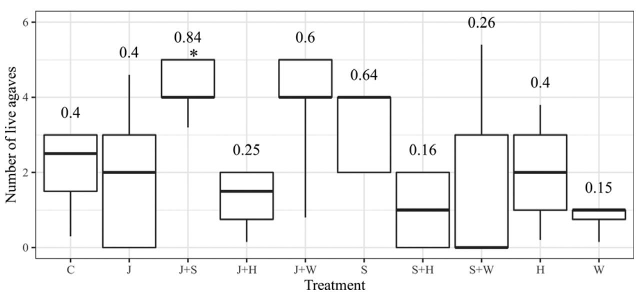

Figure 1. Boxplot of agave survival counted by the live number of leaves per treatment rows across all plots. The numerical values display agave survivorship (the proportion of agaves that survived per treatment over the experiment duration) across each treatment. Asterisk indicates the significant difference from the control treatment. We stratified agave survival by five plants per treatment row per plot; therefore, five is the maximum number of plants.

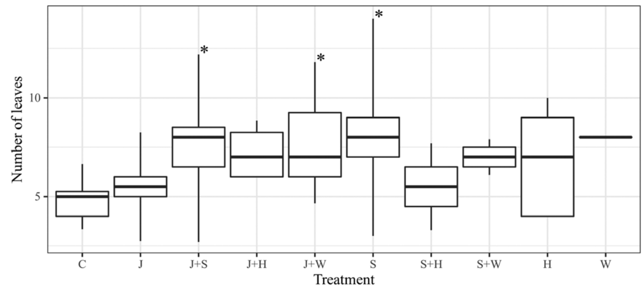

Figure 2. Box plot of agave size measured by the average number of live leaves per row per treatment plot. Asterisks indicate the significant differences from the control treatment.

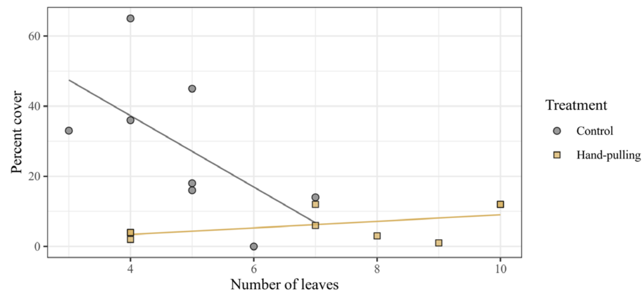

Figure 3. Percentage Lehmann lovegrass aerial cover to agave size (total leaf count, $N = 17$) for control and hand-pulling treatments.

number of agave leaves were found in the C treatment, having only an average size of 1.583 leaves per plant (Table S2).

Lehmann Lovegrass Cover Treatment

Lehmann lovegrass removal by hand-pulling (H) resulted in 71% less Lehmann lovegrass cover than the control treatment ($p < 0.001$; Table S3). Agave size alone appeared to reduce Lehmann lovegrass cover by only 10% for each agave leaf ($p < 0.001$; Table S3). The effect of agave size on the percent cover of Lehmann lovegrass was significantly different between treatments ($p < 0.001$; Table S3): the negative effect of agave size was restricted to control treatments, while agave size had a slightly positive effect on the percent cover of Lehmann lovegrass in other treatments (Fig. 3). The interactive effect of hand-pulling Lehmann lovegrass and agave size significantly increased Lehmann lovegrass cover ($p < 0.001$; Table S3; Fig. 3).

Discussion

Developing agave restoration techniques for population recovery is particularly challenging in arid land ecosystems due to extreme weather, competition with invasive species, and predation (Nobel 1976; Jordan & Nobel 1979). In this field study, we tested a set of 10 treatments to enhance agave survival and growth conditions in a restoration project. We found that the combination of shade and javelina protection improved agave survival and facilitated agave growth, while shade alone resulted in the largest agave size, on average, compared to the control treatment. This suggests that dense Lehmann lovegrass cover appears to protect agaves from direct sunlight and predation. We did not find a signature of a competitive effect of agave presence on Lehmann lovegrass, although our results suggest an inverse correlation between agave size and Lehmann lovegrass percent cover.

We found that the combination of shade and javelina protection facilitated agave growth and survival by providing a protective "nurse effect" against the extremities of the weather, sun, and predators. Several studies suggest that planting agaves into a matrix of existing vegetation will enhance restoration outcomes due to how existing plants provide "microenvironment" protection, which favors agave survival and growth (Jordan & Nobel 1979; Peters et al. 2008; Pavliscak et al. 2015). In a field experiment, Arizaga and Ezcurra (2002) reported that *Agave macroacantha* cohorts placed outside of the nurse plant canopy died within their first year of planting, in contrast to the cohorts that survived for more than 2 years under nurse plants. Several causes have been identified for this nurse effect. Studies suggest that succulents, including agaves, perform best when planted under the canopy of the prevailing vegetation, nurse rocks, or structures that obstruct direct sunlight (Peters et al. 2008). Shade and straw mulch/thatch also facilitate agaves seedling emergence and establishment by decreasing microsite soil temperatures, increasing moisture retainment and nutrient availability, and providing shelter from grazing and trampling (Jordan & Nobel 1979; Peters et al. 2008; Gill et al. 2022). Our results support these previous studies, demonstrating a strong relationship between shade-induced herbivory protections to improve agave survival potentially through a nurse effect. Our results indicate that dense monoculture of Lehmann lovegrass was beneficial for agave survival. Even though removing invasive Lehmann lovegrass decreased competitive pressure, the removal simultaneously deprived agaves of protection against solar insolation and visual protection against predation.

This surprisingly beneficial nurse effect would explain the positive trend between agave survival and Lehman lovegrass vegetation. Agave plant dependency on nurse plant facilitation to establish and survive might be more prominent in semiarid desert environments, which are characterized by high climatic fluctuations and summer drought stresses. These factors impede the natural growth and survival of young agaves. In this case, the surrounding Lehmann lovegrass biomass could have positively interacted with the agaves by improving microclimatic conditions through the shade. This has an important potential implication for the population recovery of Palmer's agave in wildlands, suggesting that managers should plant agaves in a matrix of (or under the canopy of) existing vegetation. Removing Lehmann lovegrass without further interventions—especially when agaves are planted in or near monocultures of Lehmann lovegrass—could deprive agaves of the vital nurse effect and limit agave growth and survival. We suggest that wildland managers refrain from clipping dense, neighboring vegetation surrounding agave plants if possible. By doing so, managers could enhance the conditions required for agave growth and survival while also saving labor and monetary resources. However, if removing Lehmann lovegrass that surrounds agave populations is a priority, then we suggest that wildland managers consider further interventions to ensure that agaves continue to benefit from a nurse effect (such as planting agaves under existing vegetation canopy or near other shading structures).

Interestingly, javelina protection and weed-eating also positively influenced agave size. This could be due to an unintended nurse effect (when coupled with herbivory protection). The weed-eating treatment activities included the clipping of the aboveground biomass of Lehmann lovegrass and leaving behind the clipped biomass in the plot. The clipped Lehmann lovegrass thatch on the ground could have acted similar to a surface mulch and/or a visual protection aid from predation for young (smaller) agave plants. As such, our results suggest that J+W and J+S acted similarly, sheltering young agaves from solar insolation, high surface temperatures, and herbivory. Moreover, both J+W and J+S as well could have enhanced soil water retention and surface cooling while reducing evaporation (Peters et al. 2008). García et al. (2000) reported a similar relationship between invasive shrubs and yew establishment, where the thorny, unpalatable shrub branches served as a fence that restricted ungulates from reaching juvenile yews. Re-planting or re-seeding desired native plant species in the dense, near monocultures of invasive Lehmann lovegrass, might be required as a control measure to keep the native species' habitat intact (US Forest Service 2012). Since dense Lehmann lovegrass appears to protect young agaves from predation and ameliorates the immediate growing conditions by providing shade and cooling, our results suggest that killing invasive species but leaving dead biomass on-site could provide the nurse plant dynamics that agaves need to thrive.

Although Lehmann lovegrass provides a protective matrix for agave seedlings, its potential for wide-scale invasion and aggressive conversion of natural landscapes to Lehmann lovegrass monocultures makes it problematic for land managers and restoration practitioners. Therefore, controlling Lehmann lovegrass biomass is a critical component of land management programs designed to protect and restore native vegetation. Some common Lehmann lovegrass control measures include herbicidal spraying, prescribed burning, and physical uprooting (Sumrall et al. 1991; US Forest Services 2012) all of which can be time and money intensive and lead to unintended consequences such as soil disturbance, untargeted foliar application in cases of herbicidal sprays (Benefield et al. 1999). Clipping or burning Lehmann lovegrass stands increases Lehmann lovegrass seed germination and subsequent plant recruitment (Sumrall et al. 1991). Hence, we recommend forgoing or at least postponing Lehmann lovegrass weed management if native plant restoration is a priority. However, this recommendation should be considered on a case-by-case basis as Lehmann lovegrass stands in wildlands can pose a direct threat to wildlife and human lives due to high combustibility and aggressive growing nature. Clearly, intervention to control this weed can be necessary to avoid fire disasters. In such instances, we recommend managers electrically mow the weed rather than physically uproot it.

For managers interested in re-establishing agave populations, we recommend transplanting multiple age classes of agave outplants and seedlings that are old enough to withstand solar extremities and competition from surrounding competitive plants (Gill et al. 2022). An integrated approach combining seeding, transplants, and conservation of intact populations is essential for the prolonged supply of goods and services that agaves offer, requiring a truly effective restoration plan for this long-lived native species. Of course, the challenges to such an approach are significant, including the high costs of native seeds and seedlings (Scasta et al. 2015).

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Supporting Information

The following information may be found in the online version of this article:

Table S1. Results of logistic regression of agave survival.
Table S2. Results of regression of agave size.
Table S3. Results of regression of Lehman lovegrass cover on treatment, agave size, and the interaction between treatment and agave size.

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