MODIFYING DRIVERS OF COMPETITION TO RESTORE PALMER'S AGAVE IN
LEHMANN LOVEGRASS DOMINATED GRASSLANDS

by

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A Thesis Submitted to the Faculty of the

SCHOOL OF NATURAL RESOURCES AND ENVIRONMENT

In Partial Fulfillment of the Requirements

For the Degree of

MASTER OF SCIENCE

In the Graduate College

THE UNIVERSITY OF ARIZONA

2020

THE UNIVERSITY OF ARIZONA
GRADUATE COLLEGE

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Acknowledgments

I would like to sincerely thank my graduate advisor, Dr. Elise S. Gornish & Fulbright Foreign Degree Program for providing the opportunity for me to complete my Master's in Science degree at the University of Arizona. Especially Dr. Elise S. Gornish, who provided constant support, mentoring, guidance throughout my thesis project. I would also like to thank my committee members, Dr. Jeffrey S. Fehmi and Dr. Mitchel McClaran, for their availability and support along the way. Huge call out to the Fulbright Program, International Institute of Education, National Parks Service, Bat Conservation International, & Ancestral Lands Crew for funding, collaborations, and data collection. Special thanks to Dr. Jeffrey S. Fehmi and Jeffrey C. Oliver for guidance with software and data analysis, and Albert Kline, Helen Fitting, Brooke Kubby, Mary Davis, and Angel Vega for the project. I am grateful for the support and guidance provided by the Gornish Laboratory throughout my time in Arizona. Finally, I thank my friends and family for their support and patience throughout this journey and my thesis project.

Amy Shamin Gill

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Abstract

Dryland restoration is becoming increasingly challenging in arid and semi-arid regions, such as the southwestern U.S., due to rapid land degradation, an increase of non-native species, and climate change. Encroachment of a non-native perennial grass species commonly known as Lehmann lovegrass (*Eragrostis lehmanniana*), is a particularly critical challenge for land managers of the region. Lehmann lovegrass threatens and outcompetes one of the Sonoran Desert's ecologically and socio-culturally significant plant species, Palmer's agave (*Agave palmeri*). Stakeholders in Southeastern arid lands are particularly challenged by scarce rainfall, limited land resources, invasive species dominance, and frequent predation posing unique challenges to land management. Unfortunately, mechanisms and drivers of Palmer's agave survival and growth patterns are not well understood, limiting our ability to design effective management strategies. In this study, we had a greenhouse experiment and a field study to explore survival and growth responses of transplanted Palmer's agave. For the greenhouse study, we measured agave growth and survival under a variety of manipulated conditions, both biotic (agave age and size class at planting, and simulated mowing of Lehmann lovegrass) and abiotic (simulated precipitation and surface mulch). In the field experiment in southeastern Arizona, U.S., we assessed the utility of several management techniques to promote restoration outcomes for Palmer's agave survival and growth, including protection from solar insulation and herbivory, and reduction in the competitiveness of Lehmann lovegrass. We found that the presence of thatch when combined with high and medium simulated precipitation levels significantly enhances agave biomass. However, we observed that Lehmann lovegrass biomass was indifferent to Palmer's agave presence, precipitation regimes, and thatch. 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. We conclude that stakeholders should use an integrated approach by using an additional artificial simulation of high and medium watering —especially in hot desert climates— with thatch as the surface mulch and shade provider to enhance agave growth and survival. For a long-term, large-scale restoration efforts, land

managers can forgo weed management and by planting agaves under nurse plants or existing vegetation canopy could save costs by providing the same shade benefits as thatch or surface mulch.

Chapter 1: Introduction

Non-native plant invasion is a concern worldwide (Davies, 2011). These plants jeopardize native floral establishment and biodiversity (Parker et al., 2006), alter resource cycling, and undermine ecosystem functioning (Tekiela & Barney, 2017). The United States alone has over 100 million acres of land infested with invasive plants leading to treatment costs exceeding 120 billion USD annually (Parker et al., 2006). For example, much of the rangelands in the arid and semi-arid Western U.S. have been subject to shifts in plant composition as a result of weed invasion, as dominant annual grass species are swiftly taking over the shrublands and desert grasslands (Abatzoglou & Kolden, 2011). The Nature Conservancy (2019) stated that invasive and alien plants are liable for almost 42% of the decline in endangered and threatened species of the United States. Therefore, in Arid lands, restoration of native habitats and plant communities can conserve the productive use and value of wild landscapes. With the continued habitat destruction caused by human actions and increasingly unfavorable climatic conditions, restoration in arid lands can be very challenging due to the intermittent and insufficient availability of the required growing conditions and resources for plant germination, establishment and sustenance (Bean et al., 2004; Bainbridge, 2007). Land managers seek adaptive management options and tools to restore and revegetate the degraded native plant habitat.

Invasive encroachment of one non-native perennial grass species, commonly known as Lehmann lovegrass (*Eragrostis lehmanniana*), is a particularly critical challenge for the stakeholders of arid landscapes in the southwestern U.S. Lehmann lovegrass was introduced to Arizona in the 1930s to control soil erosion and provide forage for cattle, but now the grass has spread far into non-seeded areas (Bock et al., 2007) causing various problems. It vigorously outcompetes native plants for both soil resources (nutrients, water, space) and light (Crooks, 2002; Rogstad et al., 2009) in low resource environments. The biomass of Lehmann lovegrass can be 4 times greater than the biomass of the native grasses (Anable et al., 1992).

One of the Sonoran Desert's ecologically significant plant species, *Agave palmeri* Engelmann (commonly known as Palmer's agave or Century Plant), is threatened by the presence of Lehmann lovegrass. Palmer's agave is a federally protected species that is native to Arizona, New Mexico, and Northwestern Mexico (Scott, 2004). On a global scale, Agaves species are commercially important as they are used to synthesize fiber and alcoholic beverages (FAO, 2010; Nobel, 1994). In the United States, *Agave americana* (also known as American Century plant) can be used as a potential commercial biofuel crop (Davis et al., 2016). The Agaves are designated as one of the 'keystone' species of the Sonoran Desert because they play a substantial role in maintaining biodiversity by supplying nectar and pollen to insects and other pollinators (Slauson, 2000). Palmer's agave is particularly critical for desert ecosystems as it is a prominent food source for a migratory nectar-feeding bat species, Lesser long-nosed bat (*Leptonycteris curasoe*). Co-existing Lehmann lovegrass obstructs Agave plants' growth and establishment largely at the seedling stage (Howell, 1981) by predominating the resource bank for the native plants. Lindsey et al (2011) studied the spatial effects of Lehmann lovegrass on the distribution and population abundance of Palmer's agave and found negative relationships between the two, i.e., low-density Palmer's agave areas were significantly associated with high Lehmann lovegrass abundance areas.

Lehmann lovegrass presence is a direct threat to the survival and sustenance of the native Palmer's agave plants. Lehmann lovegrass is considerably combustible which means that it can cause and change the frequency and intensity of the natural fire (Kupfer and Miller, 2005). Geiger (2006) reported that fire could alter Palmer's agave plant's germination, growth, abundance, in addition to the feeding behavior of pollinators. Fire directly interferes with the longevity and survival of agaves while indirectly reduces the number of the inflorescence which is a significant source of resources for pollinators in dryland habitats (Linsey et al., 2011). Additionally, the invasive grass indirectly affects pollinators by crowding out native plants such as Palmer's agave and reducing the availability of nectar sources and nesting sites (Lindsey et al., 2011). As a result, restoration attempts have focused on re-establishing Palmer's agave in Lehmann lovegrass invaded habitat.

It is hard to re-establish Palmer's agave populations in invaded habitats as several complex factors drive the successful establishment and survival of agave plants, especially in low resource environments such as desert grasslands of southeastern Arizona. In semi-arid areas, the sporadic availability of the required growing conditions and nutrients collude with the competitive dominance of the Lehmann lovegrass to the slow growth of Palmer's agaves. In invaded habitats, Palmer's agave population recovery is complex and includes factors such as exposure to extreme weather, competitive inadequacy, and predation of agave seedlings. Challenges to agave population restoration are further complicated by the non-uniform competitive interactions occurring among con and hetero-specific species in different age classes and size groups. For example, partial size and age symmetry among plants lead to unequal resource distribution which suppresses the growth of smaller plants (Schwinning and Weiner, 1997). Moreover, agave mortality can be unusually high due to stressful climatic conditions (frost in winters, sunburn in the summer). Several studies have shown that young plants, seedlings in general, are much more vulnerable to biotic and abiotic pressures (Gornish, 2014). This phenomenon is particularly true for semi-arid succulents like agaves which need multiple and consecutive years of favorable conditions to both germinate and establish (Nobel, 1979; Jordan and Nobel, 1979). Agaves—seedlings in particular— experience high mortality rates under extreme environmental and climatic stresses such as high surface temperatures and limited water availability, especially during the early growth years (Gentry, 1972; Jordan and Nobel; 1972; Nobel, 1977). Daehler (2003) reviewed studies that show that environmental growth conditions can influence a native plant's performance more than the growth rate and productivity of a neighboring competitor.

One way to enhance agave plants' growth and survival is to simultaneously manipulate dispersal, biotic, and abiotic community assembly filters of ecological restoration. Deploying community assemblage filters (dispersal, abiotic, and biotic interactions) simultaneously— instead of solely focusing on the biotic interactions—offer a better restoration framework for approaching land management (Hulvey & Aigner, 2014). Unfortunately, in our case, the profound underlying interactions that affect Palmer's agave growth

patterns and conditions in the presence of Lehmann lovegrass are not well understood. Thus, it is very helpful for the design of restoration practices if we understand the complex biotic and abiotic determinants of the growth conditions that improve the probability of restoring Palmer's agave plant population in the hostilities of invasion.

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Appendix A: <u>Drivers of competition between Palmer's agave and Lehmann lovegrass</u>

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Abstract

Encroachment of a non-native perennial grass species, commonly known as Lehmann lovegrass (*Eragrostis lehmanniana*), is a particularly critical challenge for land managers in the southwestern United States. Lehmann lovegrass is known to threaten and outcompete Palmer's agave (*Agave palmeri*), one of the Sonoran Desert's most ecologically and socio-culturally significant native plant species. Unfortunately, the drivers of Palmer's agave survival and growth patterns are not well understood, limiting our ability to design effective management strategies. We used a greenhouse experiment to explore survival and growth responses of transplanted Palmer's agave under a variety of manipulated conditions, including biotic (agave size at planting and simulated mowing of Lehmann lovegrass) and abiotic (simulated precipitation and surface mulch) treatments. Ten months after transplantation into the greenhouse, we measured agave survival, biomass, leaf length, and leaf number. For Lehmann lovegrass we measured biomass, tiller length, and total number of reproductive tillers. We found that high and medium watering treatments with thatch presence significantly enhanced agave biomass. We found that Lehmann lovegrass biomass was indifferent to Palmer's agave presence, precipitation regimes, and thatch. We conclude that managers should use an integrated approach by simultaneously using additional artificial simulation of high and medium watering (especially in hot deserts climates) with thatch as the surface mulch and shade to enhance agave growth and survival. For a long-term, large-scale restoration efforts, planting agaves under nurse plants or existing vegetation canopy could save costs by providing the same shade benefits as thatch or surface mulch.

Introduction

Habitat destruction by human actions and increasingly unfavorable climatic conditions have particularly affected arid lands, where intermittent and insufficient availability of required growing conditions and resources hinder plant germination, establishment, and survival (Bean et al., 2004; Bainbridge, 2007). Arid-land stakeholders seek adaptive management tools for the restoration of native habitats and plant communities to conserve the productive use and value of wild landscapes. Encroachment of one non-native perennial grass species, commonly known as Lehmann lovegrass (*Eragrostis lehmanniana,*), is a particularly critical challenge for land managers of the southwestern United States. Lehmann lovegrass was introduced to Arizona in the 1930s to control soil erosion and provide forage for cattle, but the grass has subsequently spread far into non-seeded areas (Bock et al., 2007), causing various problems. In southeastern Arizona, it is particularly widespread; by the 1980s it had doubled its extent and was predicted to potentially spread to over 7,000,000 ha under predicted climate change scenarios (Cox & Ruyle, 1986; Schussman et al., 2006; Huang & Geiger, 2008). Biomass of Lehmann lovegrass can be four times greater than the biomass of native grasses, and it vigorously outcompetes native plants for both soil resources (nutrients, water, space) and light in low resource environments (Anable et al., 1992; Crooks, 2002; Rogstad et al., 2009). Moreover, the distinctive combustibility of Lehmann lovegrass has been shown to increase the frequency and intensity of the natural fire cycle (Kupfer and Miller, 2005), exacerbating its ecological impact.

One of the Sonoran desert's most ecologically significant plant species, commonly known as Palmer's agave *(Agave palmeri)*, is threatened by the presence of Lehmann lovegrass. Palmer's agave is a federally protected plant that is native to Arizona, New Mexico, and Northwestern Mexico (Scott, 2004). Agaves play a substantial role in maintaining biodiversity in arid systems by supplying resources to insects (Slauson, 2000) and mammals (McColgin et al., 2003), notably including the federally protected migratory Lesser long-nosed bat (*Leptonycteris curasoe*) (Nassar, 2005). Unfortunately, the growth and establishment of agave, especially at the seedling stage (Howell, 1981), is obstructed by Lehmann

lovegrass (Lindsay et al., 2011), presumably due to the extraction of resources. This, in turn, indirectly affects pollinators by reducing the availability of nectar sources. Moreover, the disruptions to the fire cycle by Lehmann lovegrass could restrain germination, growth, flowering inflorescence production in Palmer's agave, and exacerbate these indirect effects on pollinators and their feeding behaviors (Geiger, 2006, Lindsey et al., 2011). As a result, restoration research has been directed towards understanding how to successfully re-establish Palmer's agave in Lehmann lovegrass invaded habitat.

Several complex factors drive the successful establishment and survival of agave plants, especially in low-resource environments, making it difficult to restore Palmer's agave populations in invaded habitats. For example, desert succulents, and particularly agave populations, need multiple consecutive years of favorable conditions to both germinate and establish (Nobel, 1976; Jordan and Nobel, 1979). Moreover, different competitive interactions occur among inter-and intra-specific plants across different age classes and size groups, typically involving larger plants suppressing the growth of smaller plants and with Lehmann lovegrass outcompeting agave (Schwinning and Weiner, 1997). Together, these variables interact with other factors, such as the sporadic availability of required growing conditions and nutrients, to reduce the resistance of Palmer's agave to invasion.

One way to enhance agave plant growth and survival is to simultaneously manipulate dispersal, biotic, and abiotic community assembly filters of ecological restoration. Most restoration studies that deploy community assembly filters have mainly concentrated on the biotic filter to change the biotic resistance in the restored communities (Funk et al., 2008; Hooper & Dukes, 2010; Cleland, Larios & Suding, 2013). But, Hulvey & Aigner (2014) suggest that land managers will have a better framework to undertake management actions and achieve restoration goals if they deploy the three common community assembly filters altogether, rather than just focusing on mitigating single factors alone.

Environmental factors can play a significant role in modifying biotic interactions, such as competition, that determine species-specific distribution and co-occurrence (Costanzo, Kesavaraju, & Juliano, 2005). Abiotic factors, such as precipitation, mulch, and shade (Jordan and Noble, 1979), along

with biotic interactions, determine the outcomes of competition, deciding the overall pattern and structure of plant communities (Yeaton, Travis, & Gilinsky, 1977). Environmental factors modify agave demographics, which likely play a role in competitive interactions. However, the complex interactions that affect Palmer's agave growth patterns and conditions within an invasion framework are not well understood. Thus, it is essential to identify the biotic and abiotic determinants of agave growth conditions in the presence and absence of a weedy competitor to design and deploy effective agave restoration strategies in invaded habitat. In this study, we examined the effects of several biotic and abiotic elements that are expected to modify the interactions between Palmer's agave and Lehmann lovegrass. The biotic filter consisted of inter- and intra-specific interactions among two size classes of Palmer's agave plants and Lehmann lovegrass. The abiotic filter consisted of manipulations of precipitation and surface mulch, as well as the reduction of the biotic filter by Lehmann lovegrass clipping.

This study aims to address two questions; 1) How does modifying the biotic and abiotic growth conditions help Palmer's agaves to yield greater biomass allocation? and 2) Will the induced biotic and abiotic modifications help Palmer's agave to withstand Lehmann lovegrass competition? We expected that modifying biotic factors through simulated mowing of Lehmann lovegrass and utilizing a larger size class of agaves, and abiotic factors through incorporating simulated precipitation and surface mulch would ameliorate agave growth and survival. We expected that using thatch and greater watering levels would improve agave growth and survival response to the competitive effect of Lehmann lovegrass.

Methods

In July 2018, a greenhouse study was set up at the University of Arizona, Tucson, Arizona for 10 months. The experiment investigated the growth and survival of Palmer's agave when exposed to the following treatments: 1) presence and absence of agaves of two different sizes (small and big); 2) presence of Lehmann lovegrass (none, clipped, unclipped); 3) presence of Lehmann lovegrass thatch (absent, present); and 4) watering frequency (low, medium, and high). Thirty-six distinct treatments ($2 \times 3 \times 2 \times 3$), each with ten replicates, were tested in a fully factorial, randomized complete block design. A total of 360

1L capacity pots were arranged in independent randomized blocks along the width of the greenhouse. The pots were filled with a standard potting mix (Sungro Horticulture Sunshine Mix #1/LC1) to 7 cm from the pot rim.

Plant Collection

Palmer's agave plants were purchased from the Borderlands Restoration Network Native Plant Nursery (BRN) in Patagonia, Arizona (65 miles south of Tucson). Two age classes of Palmer's agave, (typically used in regional restoration practices, as suggested by the Native Plant Material Program Catalogue, 2018) were purchased, i.e., tray-plugs seedlings (3-4 months old, hereafter referred to as 'small') and agave pups (1-year-old, hereafter referred to as 'big') grown from 4-year-old seedlings. Note that these terms are relative to the materials used, as adult agaves can grow to over 1.5m in height. BRN collected seeds (to grow seedlings and pups in the nursery) from plants in the Upper San Pedro watershed (31°46'8.7" N, 110°2' 32" W). We randomly allocated agaves to the specific age-class separated treatment (small and big) amongst the relevant treatment pots. At the time of planting, the average (mean ± SE) basal diameter was 6.07 ± 0.081cm for small agaves and 16.06 ± 0.720cm for big agaves. The average (mean ± SE) length of the longest leaf per pot was 3.79 ± 0.966 cm for small agaves and 6.75 ± 2.680 cm for big agaves. The average (mean ± SE) total number of leaves per pot at the time of planting was 4.19 ± 0.057 for small agaves and 5.16 ± 0.254 for big agaves.

We excavated Lehmann lovegrass plants from the Santa Rita Experimental Range (31°46′19" N, 110°53′26" W) by hand, while they were still alive and green. The soil type of the collection site was sandy loam. We kept the root ball intact to limit damage to excavated plants during transportation and immediately relocated the plants to the greenhouse. To reduce transplanting stress, we watered Lehmann lovegrass plants initially for four days before replanting them into treatment pots. At the time of planting, Lehmann lovegrass tillers were equally divided into two sets (i.e., 4 tillers each) and randomly allocated to treatment pots 5cm apart (e.g. all pots included in the Lehmann lovegrass treatment initially started with two grass tillers each). Each Palmer's agave plant was centrally positioned in the pot between the

two sets of Lehmann lovegrass. At the time of transplantation, the average length of the Lehmann

lovegrass tillers was 40.15 ± 12.488cm per pot, the average number of tillers was 2.85 ± 0.084 per pot

with 2.483 ± 0.106 number of reproductive tillers per pot. After plants were installed in pots, we deployed

the abiotic treatments.

Biotic treatments

Simulated mowing: To simulate Lehmann lovegrass mowing for the respective treatment plots, we

trimmed Lehmann lovegrass tillers on the first day of the experiment using hand clippers at an average

height of 3 to 5cm (Vigot, 1975) to imitate a standard mower trimming range. We removed the clipped

lovegrass tillers from the pots after trimming.

Abiotic treatments

Thatch: We used the excess dry and non-green Lehmann lovegrass from the field as thatch for pots

exposed to the thatch treatment after the agave and Lehmann lovegrass had been transplanted. We added

a single layer of excess, dried, and clipped Lehmann lovegrass thatch to cover the surface soil of the pot

(approximately 1.6g and 10-15cm deep).

Simulated Precipitation: The irrigation regime was set based on watering frequency rather than water

volume. We used watering treatment guidelines from local native nursery professionals (S. Plath, *pers*

comm. January 2020; J. Byrd, *pers, comm*. March 2020). We set our watering regime to a fixed volume of

120ml (precipitation equivalent = 4.93cm), as per suggestions and the trial-based watering requirements

for the pots. We confirmed that this volume was sufficient to provide moisture during the agave growing

stage. The precipitation regime was arranged based on low, medium, and high-water frequency treatments

(each having a fixed volume of 120 ml). Hence, during the Fall season (July to Mid-December), we

watered low watering treatment pots once a week; medium water treatment pots twice a week; high water

treatment pots three times a week (each week all pots received a fixed volume of 120 ml of water). Then,

during the Spring season (from January to May 2019), we reduced the watering frequency and employed

the following watering regime: low watering treatment pots were watered once every two weeks, medium

watering treatment watered once a week, and high watering treatment pots were watered twice a week (all pots received a fixed volume of 120 ml of water in each watering treatment).

Data collection

Throughout the experiment, growth and survival responses of both species were collected monthly. At the end of the experiment, we destructively sampled all plants to record biomass and the root/shoot length of both species, as well as the basal diameter of agaves. We gently washed the root balls of the plants for 15 seconds, to remove soil particles and then dried the root ball with a paper towel. We separated the shoot and the root and weighed them to find fresh weight. The plants were then oven dried at 70°C, until the bags reached constant weight (for 72 hours) and then reweighed to find the dry weight.

Statistical analysis

First, we examined Lehmann lovegrass effect on agave growth and survival by using analysis of variance ANOVA (Type II). Since the agave survival was very high for agave and Lehmann lovegrass across all the treatments, we did not investigate treatment effects on agave survival. We modeled Palmer's agave using agave dry weight (combined root and shoot weight) response to the singular and interactive effects of the presence of Lehmann lovegrass (clipped, unclipped, or none), size of the agave (small or big), presence of thatch and watering frequency (high, medium, and low). Data were log-transformed (v Shapiro-Wilk test, W = 0.9836, p = 0.0381) to conform to normality assumptions. Post hoc Tukey's Honest Significant Differences (HSD) tests were run to report pair-wise comparisons of means (p < 0.05). Second, we determined the effects of experimental treatments on Lehmann lovegrass by using analysis of variance ANOVA (Type II) on log-transformed (Shapiro-Wilk test, W = 0.9835, p = 0.0123) data of Lehmann lovegrass weight (combined root and shoot dried weight). Explanatory variables were agave size, the presence of thatch, simulated precipitation, and clipping treatment. All statistical analyses were performed in R: Language for Statistical Computing (version 3.5.2). Untransformed data and means are used in figures and reported in the text to enhance data interpretations.

Results

Agave biomass: There was a significant effect of the simulated precipitation, agave size, presence and of Lehmann lovegrass, and thatch on agave biomass (ANOVA, $p < 0.001$; Table A.1), compared to control (5.50 ± 0.39 g). Mean agave biomass varied significantly ($p < 0.001$) and ascendingly across simulated precipitation treatments levels, where it was smallest in the low watering level (3.80 ± 0.29 g), larger in medium (4.26 ± 0.33 g), and greatest in the high watering level (8.41 ± 0.60 g), as expected. Mean agave biomass varied significantly ($p < 0.001$) in small agaves (4.54 ± 0.26 g) was half of that of big agaves (9.35 ± 0.73 g), as expected. Across all the singular treatment levels of Lehmann lovegrass agave biomass varied significantly ($p < 0.001$); maximum agave biomass was found when Lehmann lovegrass was absent (6.81 ± 2.68 g), was second greatest with the unclipped levels (5.75 ± 2.57 g), and unexpectedly, the least with clipped Lehmann lovegrass (3.96 ± 2.26 g). Thatch significantly affected mean agave biomass ($p < 0.001$); thatch improved agave biomass by 63.6% compared to agaves that were not exposed to thatch (6.87 ± 0.42 g).

There was a significant effect of the interaction of simulated precipitation, thatch, and the simulated mowing of Lehmann lovegrass on agave biomass (ANOVA, $p < 0.001$; Table A.1), compared to control (5.50 ± 0.39 g). First, agave biomass was dissimilar across the interaction of simulated mowing of Lehmann lovegrass and simulated precipitation (ANOVA, $F = 4.69$, $p = 0.017$: Table A.1). Overall, average biomass across all the watering levels was highest when Lehmann lovegrass was absent with high watering treatment (11.09 ± 1.29 g), second highest when Lehmann lovegrass was unclipped with high watering treatment (8.80 ± 1.04 g), second lowest when Lehmann lovegrass was absent with medium watering (5.64 ± 0.62 g), and the least when Lehmann lovegrass was clipped with medium watering (3.01 ± 0.54 g: Table A.2).

Agave biomass significantly varied in the presence of an interaction between simulated precipitation and thatch (ANOVA, $F = 4.69$, $p = 0.010$: Table A**.**1). In the presence of the high watering level, agave biomass did not differ in the absence (7.02 ± 0.67 g) or presence (9.74 ± 0.98 g) of thatch.

However, in the low watering treatment and in the presence of thatch, agave biomass (5.02 ± 0.47 g) was twice as large as those not exposed to thatch (2.5 ± 0.24 g; Table A.3).

Effect	df	MS	F-value	P-value
Lehmann lovegrass	2	8.23	9.269	0.000166 ***
Simulated precipitation (water)	2	25.29	28.469	0.000000 ***
Size of agave	1	20.77	46.761	0.000000 ***
Thatch	1	22.45	50.546	0.000000 ***
Lehmann lovegrass × water	4	5.54	3.121	0.017055 *
Lehmann lovegrass × size	2	0.80	0.905	0.406878
Water × size	2	2.63	2.963	0.054950
Lehmann lovegrass × Thatch	2	2.17	2.448	0.090231
Water × Thatch	2	4.17	4.699	0.010598 *
size × Thatch	1	0.23	0.511	0.475926
LL× water × size	4	3.02	1.699	0.153560
LL × water × Thatch	4	4.66	2.623	0.037390 *
LL × size × Thatch	2	0.03	0.036	0.964851
Water × size × Thatch	2	0.56	0.635	0.531402
LL × water × size × Thatch	4	0.61	0.346	0.846631
Residuals (Error)	**139**	**641.73**		

Table A.1. ANOVA table for Palmer's agave biomass along with other treatments. Effects that are significant at $P < 0.05$ are marked with a single asterisk, and the ones significant at $P < 0.001$ are marked with triple asterisk.

Simulated Lehmann lovegrass	Simulated Precipitation			Grand Total
	Low	Medium	High	
None	3.65 ± 0.60	5.64 ± 0.62 *	11.09 ± 1.29 *	6.81 ± 1.02
Unclipped	4.32 ± 0.50	4.11 ± 0.51	8.80 ± 1.04 *	5.75 ± 0.79
Clipped	3.51 ± 0.40	3.01 ± 0.54 *	5.35 ± 0.45	3.96 ± 0.49
Grand Total	3.80 ± 0.50	4.26 ± 0.58	8.41 ± 1.04	5.50 ± 0.81

Table A.2. Mean Palmer's agave biomass (±SE) for the interactive effects of simulated mowing of Lehmann lovegrass and simulated precipitation.

Simulated Precipitation	No Thatch	Thatch	Grand Total
Low	2.5 ± 0.24*	5.02 ± 0.47*	3.80 ± 0.41
Medium	2.7 ± 0.37	5.81 ± 0.48	4.26± 0.47
High	7.02 ± 0.67*	9.74 ± 0.98*	8.41 ± 0.85
Grand Total	4.09 ± 0.53	6.87 ± 0.73	5.50 ± 0.66

Table A.3. Mean Palmer's agave weight (±SE) for the interactive effects of simulated precipitation and Thatch.

Thatch Presence	Lehmann lovegrass	Simulated Precipitation levels	Average agave weight ± Standard error (g)
No	None	High	6.81 ± 1.20
		Low	2.21 ± 0.45
		Medium	3.63 ± 1.07
	Clipped	High	3.66 ± 0.61
		Low	2.48 ± 0.74
		Medium	1.64 ± 0.69 *
	Unclipped	High	11.00 ± 2.17 *
		Low	2.77 ± 0.64
		Medium	2.85 ± 0.90
Yes	None	High	15.37 ± 2.93 *
		Low	4.74 ± 1.54
		Medium	7.65 ± 1.08 *
	Clipped	High	7.04 ± 0.84 *
		Low	4.44 ± 0.80
		Medium	4.38 ± 1.25
	Unclipped	High	6.82 ± 1.97
		Low	5.87 ± 1.06
		Medium	5.37 ± 1.14

Table A.4. Mean Palmer's agave weight for the interactive effects of simulated precipitation, simulated mowing of Lehmann lovegrass, and thatch presence.

The overall three-way interaction of simulated mowing of Lehmann lovegrass, simulated precipitation, and thatch treatments significantly affected agave biomass (ANOVA, F= 2.62, p =0.037: Table A.1). Across all the interactive combination effects of these three treatments, the absence of Lehmann lovegrass in combination with the high watering treatment and thatch resulted in the largest agave biomass (15.37 ± 2.92 g: Table A.4). The combined effect of unclipped Lehmann lovegrass, high watering level, and the absence of thatch resulted in second-highest agave biomass (11.00 ± 2.17 g: Table A.4). Next, the medium watering with thatch and no Lehmann (7.65 ± 1.08 g; Table A.4), and clipped Lehmann lovegrass, with high watering and thatch (7.04 ± 0.84 g: Table A.4) followed. Finally, the least agave biomass occurred in the presence of clipped Lehmann lovegrass, low watering treatment, and no thatch (1.64 ± 0.69 g: Table A.4).

The four-way interaction of the main effects did not affect agave growth significantly (ANOVA, F= 0.34, p =0.846; Table A.1). With thatch, the medium watering treatment with no Lehmann lovegrass affected the agave weight gain similar to high watering treatments with clipped Lehmann lovegrass (Figure A.1). Likewise, unclipped Lehmann lovegrass with thatch and high watering influenced agave weight just as clipped Lehmann lovegrass; with high water no thatch, medium, and low water with thatch (Figure A.1).
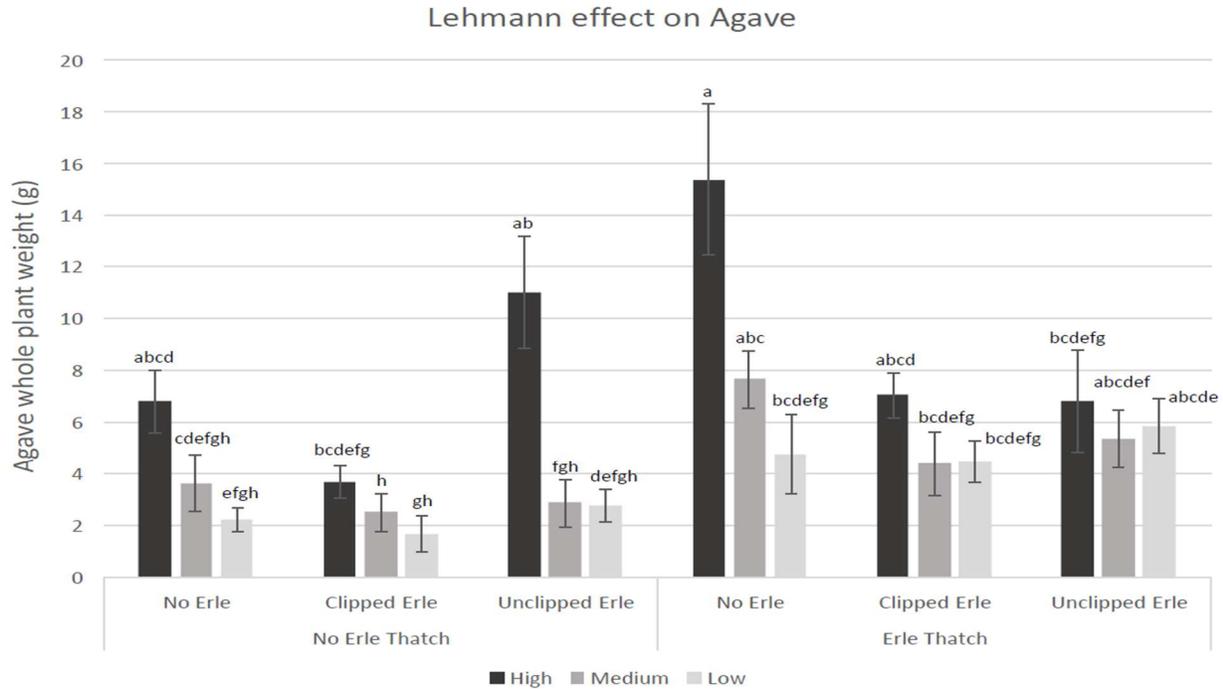
Figure A.1. Mean Palmer's agave biomass across all the treatment levels when estimated by whole plant dried weight. This graph uses the untransformed data with the error bars and Tukey's HSD letters (p<0.05). All the combinations are significantly different, except the ones that share at least one letter.

Lehmann lovegrass biomass: Lehmann lovegrass biomass did not vary significantly across the singular treatments, except in the simulated mowing treatment of Lehmann lovegrass (ANOVA, $F = 36.34$, $p < 0.001$, Table A.5), where the biomass decreased by 2.62 times more in clipped (0.90 ± 0.08g) versus in unclipped Lehmann lovegrass treatments (1.46 ± 0.08 g). Moreover, Lehmann lovegrass biomass did not vary significantly across the crossed treatments except in the four-way interaction of agave presence or absence, thatch, simulated precipitation, and simulated mowing of Lehmann lovegrass (ANOVA, $F= 3.124$, $p = 0.04$: Table A.5). In this four-way combination effect, mean Lehmann lovegrass biomass for thatched agaves across the overall precipitation treatment decreased by 1.91 times in clipped Lehmann lovegrass treatment (0.83 ± 0.09 g) versus the unclipped treatments (1.59 ± 0.14 g). Interestingly, mean Lehmann lovegrass biomass across the overall precipitation treatment with thatch, but no agaves, decreased by 1.37 times in clipped Lehmann lovegrass treatment (0.97 ± 0.13 g) versus in the unclipped

treatments (1.33 ± 0.09 g), suggesting that the presence of agave and thatch did not significantly reduce the Lehmann lovegrass biomass, but the clipping treatment did.

Effect	df	MS	F-value	P-value
Agave	1	8.23	0.090	0.763900
Simulated precipitation	2	25.29	0.942	0.391600
Lehmann lovegrass clipping	1	20.77	36.347	8.18E-09 *
Thatch	1	22.45	0.215	0.6433
Agave × water	2	5.54	0.884	0.4147
Agave × Lehmann lovegrass clipping	1	0.80	0.634	0.4269
Water × Lehmann lovegrass clipping	2	2.63	2.109	0.1241
Agave × Thatch	1	2.17	0.177	0.6746
Water × Thatch	2	4.17	0.859	0.4251
Lehmann lovegrass clipping × Thatch	1	0.23	0.281	0.597
Agave × water × Thatch	2	3.02	0.620	0.5388
Agave× Lehmann lovegrass clipping × Thatch	2	4.66	0.530	0.5898
water × Lehmann lovegrass clipping × Thatch	1	0.03	0.002	0.9618
Water × Lehmann lovegrass clipping × Thatch	2	0.56	0.141	0.8689
Agave × water × Lehmann lovegrass clipping × Thatch	2	0.61	3.124	0.0462
Residuals (Error)	194	102.34		

Table A.5. Means ANOVA **Table** Agave effect on the Lehmann lovegrass biomass. Significant effects at the $p < 0.001$ are marked with an asterisk.

Discussion

Deploying community assemblage filters (dispersal, abiotic, and biotic) simultaneously — instead of solely focusing on the biotic interactions — offer a better restoration framework for approaching land management (Hulvey & Aigner, 2014). In invaded habitats, implementing these community assemblage filters to long-term agave restoration requires a deeper understanding of the complexity and variability of favorable conditions for agave survival and growth. One common practice of incorporating dispersal filter is by re-vegetation and plant reintroduction by transplanting of nursery-grown seedlings to conserve

threatened species, especially in the wild (Maunder 1992; Godefroid et al. 2011). This greenhouse experiment attempted to understand the growth response of transplanted Palmer's agave against invasive Lehmann lovegrass by modifying biotic (size and simulated mowing by clipping Lehmann lovegrass) and abiotic growth conditions (simulated precipitation and surface mulch or thatch using dried Lehmann thatch). As expected, agave biomass was significantly higher in the treatments where Lehmann lovegrass competition was either reduced or absent with high and medium precipitation regimes and thatch facilitation. Conversely, Lehmann lovegrass biomass was indifferent to Palmer's agave presence, precipitation regimes, and facilitation by thatch (except only Lehmann lovegrass was clipped).

Daehler (2003) reviewed studies that show that environmental growth requirements can influence a native plant's performance more than the growth rate and productivity of a neighboring competitor. It is widely recognized that agave seedlings are particularly vulnerable to environmental growing conditions. Unlike mature plants, agave seedlings need multiple consecutive years of favorable conditions, especially during the first year of the growth, to establish, grow, and survive (Gentry, 1972; Nobel, 1977). High surface temperatures and limited water availability account for high agave seedling mortality rates and are the prime cause for stunted agave seedling growth in the Southwest U.S. (Nobel, 1979; Jordan and Nobel, 1979, 1982). Plant-water relationships are critical for plant growth and survival, especially in desert environments, where water availability is usually intermittent. Limited water availability impedes the growth of agave species in the Southwest U.S (FAO, 1989). Despite high growth response variation to water availability, some Southwestern U.S. agaves like *Agave weberi* were perform fairy productive under reduced water availablity but still not as productive as plants with high watering treatments (Bergsten and Stewart, 2014). The results of our watering treatments are consistent with these studies both in the singular and the combination treatments. Mean average biomass in the singular simulated precipitation effect ascends across the watering treatments; the least in the low watering and most in the high watering treatment, clearly highlighting the inhibitions reduced water availability can have on agave growth.

In addition to ample moisture availability, arid-adapted agaves species like Palmer's agaves benefit from growing in a matrix of existing vegetation besides a 'nurse' plant or under indirect sunlight exposure. The presence of thatch doubled the average biomass in the low watering treatments versus the cases where the thatch was missing. The highest mean agave biomass across all interactions in the experiment resulted from thatched, high watering treatments with no Lehmann lovegrass competition to hinder agave growth. Several studies have reported that shade and straw mulch/thatch facilitate agave seedling emergence and growth. Jordan and Nobel (1979) reported one such example as they found higher *Agave deserti* growth in habitats surrounded by nurse plants. Arizaga & Ezcurra (2002) reported that, in hot deserts, *Agave macroacantha* seedlings critically depend on the protective shade of the nurse plants for seedling establishment success, just as other succulents and cacti depend on nurse plants (Turner et al., 1966; Steenbergh and Lowe, 1969; Valiente-Banuet and Ezcurra, 1991). Likewise, Pavliscak et al. (2011) demonstrated that facilitation by shade and straw operates to enhance the establishment and survival of Palmer's agave, regardless of precipitation amount. Our results support these previous studies, suggesting that the presence of thatch and high and medium watering treatments enhanced agave biomass significantly amongst all the simulated precipitation and thatch treatments. Utilizing these precise additive strategies could help increase long term success by conditioning agave plants to cope with environmental stresses such as high surface temperature and limited water availability, regulating agaves to yield better trait values (leaf number, size and length, root and shoot biomass) and eventually grow bigger.

In semi-arid and invaded habitats, succulents —particularly Palmer's agaves —are further challenged by the non-uniform biotic challenges from surrounding vegetation along with the existing abiotic stresses that limit plant growth and persistence. Palmer's agaves are naturally slow-growing plants that are monocarpic in nature .i.e., they grow for about 35 years before blooming only once and dying (Gentry, 1982). Hence, Palmer's agaves are vulnerable to the neighboring competitive biotic stresses, where nonuniform inter-and intra-specific species interaction with various physiological, and physical

growing needs further complicate agaves' persistence. In such stressed environments, several studies suggest that bigger, more robust, and mature plants are physiologically and morphologically favored in acquiring more resources than smaller plants which comparatively assists them with better survival and establishment than juveniles when encountered by negative biotic interactions (Goldsmith, 1978; Keddy and Shipley, 1989; Mangla et al., 2011). Our results support these previous studies, as we found that higher age and size class agaves maintained a greater biomass than smaller ones, as expected according to the experiment design.

Throughout the experiment, agaves of both sizes demonstrated low and similar rates of mortality. This information should be valuable for the stakeholders who refrain from using agave pups or seedlings in restoration due to poor growth performance and survival. Our results suggest that mitigation of environmental stress by thatch, and simulation of precipitation, helped both sized agaves to withstand environmental and biotic stresses. Therefore, managers could consider recruiting relatively small sized agaves for restoration purposes. After all, even slightly larger agave plants are morphologically and physiologically better equipped at handling the biotic and the abiotic stresses (if planted under shade or nurse plants), so they can offset the gaps for small agave establishment and survival rate, especially in invaded habitats. Moreover, recruiting agaves from a series of age and size classes not only enhances agave population recovery, but can possibly increase the future continuous supply of associated benefits such as food resources for pollinator and nectivorous bats. Therefore, we recommend planting both agave sizes for restoration practices and implementing abiotic manipulations, wherever applicable and economically feasible. For a long-term, large-scale wildland restoration purpose, planting agaves under nurse plants or existing vegetation canopy could save cost against the prohibitively expensive installments of thatch or surface mulch for shade. This is particularly important for desert wildlands where meager resources, climatic adversity, predation, and several other causes complicate restoration processes, putting ecological biodiversity, species preservation, and associated benefits at risk.

One prominent threat to the persistence of Palmer's agave is the invasion of Lehmann lovegrass. Several studies report that Lehmann lovegrass dominates plant communities by establishing a near monoculture (Krzic et al., 2000; Wilsey and Polley, 2006), which can reduce species richness by half (Sanchez Munoz 2009; McClaran and Anable, 1992; McLaughlin and Bowers 2006). Since agaves are slow-growing succulents, Lehmann lovegrass can exact resources earlier and likely at a faster rate. We expected to find ameliorated agave growth response in the reduced Lehmann lovegrass competition (clipped Lehmann lovegrass). Unexpectedly, we found lower agave biomass in the clipped Lehman lovegrass treatments versus the unclipped, even when sufficient water and facilitation by thatch was available. Presumably, clipping Lehmann lovegrass deprived Palmer's agave from the shade and soil surface cooling that the standing Lehmann lovegrass plants provided. One possible explanation is the plant to plant density dependent interactions, where one plant and its relative density surrounding another plant can help ameliorate the drought stress and competition for the other dependent plant (Zhang & Tielbörger, 2020). This is an interesting result as it emphasizes that the abiotic factors such as surface temperature, shade, and water availability are play an even more critical role than biotic factors such as size and competition in initial growth of Palmer's agaves. This outcome highlights the value of using an integrated management approach by simultaneously using additional artificial simulation of high and medium watering (especially in hot deserts climates) with thatch when transplanting agaves. Alternatively, in the case of invasion, clipping Lehmann lovegrass would aid in maintaining the ecologically, economically, and culturally important threatened native plants like Palmer's agave by providing shade through fallen thatch.

This study identifies some key drivers of Palmer's agave performance and response to various biological and environmental stresses by testing what factors are important for limiting or enhancing agave survival and growth. Native plant restoration in arid lands is complex and is continually challenged by inadequate scientific knowledge, a lack of communication among stakeholders, contradictory policy and funding, and low supply and high cost associated with native seeds and plant collection and

restoration. Cumulatively, these challenges suggest a need to reconsider native plant restoration, where reseeding and/or transplantation likely requires additional understanding of managing native plants for production agriculture, ecological good and services, and other salient benefits.
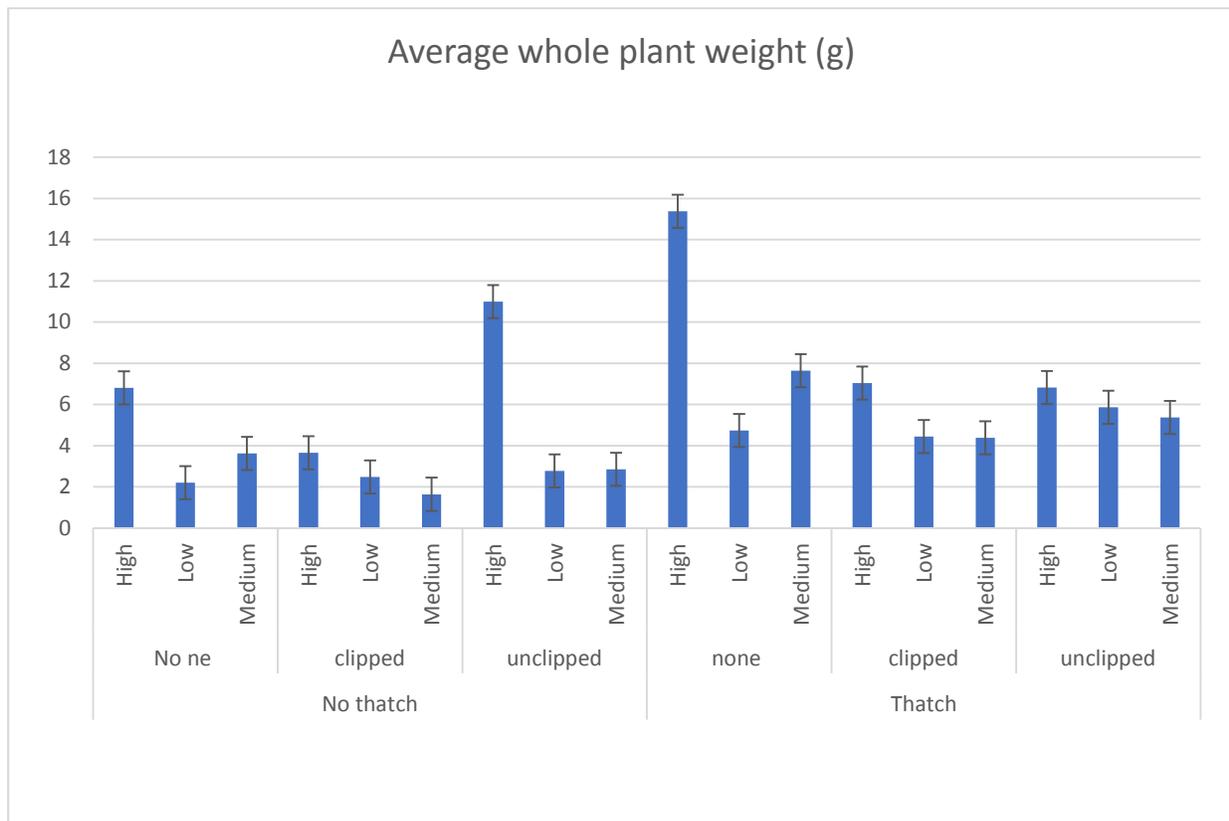
Supplementary Figure

Figure A.2. Agave whole Palmer agave biomass across all the treatment levels when estimated by whole plant dried weight. This graph uses the untransformed data with the error bars.

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Appendix B: <u>Restoring Palmer's agave in a Lehmann lovegrass dominated grassland in Southeastern Arizona</u>

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Abstract

Dryland restoration is becoming increasingly challenging in arid and semi-arid regions, such as the southwestern U.S., due to rapid land degradation, 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, USA, we assessed the utility of several management techniques to promote restoration outcomes for Palmer's agave survival and growth, including protection from solar insulation 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, this work suggests that stakeholders concerned with population recovery of Palmer's agave can forgo weed management and plant these species in a matrix of (and/or under the canopy) of existing vegetation.

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 benefits (Carrick et al., 2015). However, restoring arid and semi-arid areas is particularly complex due to scarce rainfall, often distinct flora diversity, complex spatial and biological dynamics driven by stochastic events (Ellis, 1994; Carrick & Krüger, 2007). Because passive re-establishment 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.

Palmer's agave (*Agave palmeri*) is a slow-growing, cool-season crassulacean acid metabolism (CAM) plant. It is an ecologically, culturally, and commercially significant native plant to arid and semi-arid lands in the Southwest United States. Palmer's agave species is particularly 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 curasoe*). These bats typically reach Southeastern Arizona in late summers following the seasonal flowering cycles in search of food which is primarily based on Palmer's agave nectar (Ceballos et al. 1997). In 2015, U.S. National Parks Service (NPS) reported in *Survey of an Endangered Bat Roost at Coronado National Memorial, Arizona* reported that the bat populations have been declining annually in the area due to reductions in forage availability for bats as a result of declined agave population among other reasons. One case of reduction occurred during the U.S. and Mexico border fence construction in 2008, about 3,172 Palmer's agave plants were destroyed near the Southern boundary of the Coronado National Memorial (Holt, 2017). Natural climatic stresses such as drought, sunburn from heat, and frequent wildfires (Monument fire in 2011) heavily damaged Palmer's agave contribute to a further decline in agave population (Holt, 2017). This decline exacerbates the ongoing loss of Palmer's agaves due to historic overgrazing by cattle (>100 years, ending in the 1990s) and then which has reduced agave coverage by almost 98% (NPS, 2015). After such a drastic decrease in the population

of Palmer's agaves, mitigating action was required to reestablish the agaves and replenish the food sources for bats (Holt, 2017).

Challenges to population recovery of Palmer's agave are complex and include factors such as exposure to extreme weather leading to drought, sunburn and frost freeze death, competitive inadequacy, and predation of agaves (NPS, 2017). Much of the mortality experienced by agaves under extreme climate stress is demonstrated by 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 and Nobel, 1979). Higher agave seedling mortality is also expected in areas of high competition by invasive plants (Howell, 1981). Lehmann lovegrass (*Eragrostis lehmanniana*) is a non-native invasive grass species commonly found in the southwestern U.S. grassland systems typically occupied by native plants like agaves (Anable et al., 1992; Lindsey 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, obstructs agave germination, growth, and flowering stalk production (Kupfer and Miller, 2005; Geiger, 2006; Lindsey et al., 2011). Lastly, herbivory in the wild is a prominent cause of the decrease in the agave number, especially in the arid and the semi-arid lands where succulents like Agavaceae and Cactaceae are prominent representatives. In North America, javelinas (*Pecari tajacu*), also known as collared peccary, are essentially 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 nutrition and water. Other forms of Palmer's agave herbivory are from cattle, sheep, goats, white-tailed deer, jackrabbits, insects like Sonoran bumblebees, and small rodents (Hawks, 1997; Fehmi, Danzer & Roberts, 2004).

Considering the complexity of 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 restoration efforts. In this study, we tested how different management

approaches might affect the variables that are critical for agave restoration outcomes, including solar insulation to prevent weather extremities such as sunburn, protection from javelina herbivory, and Lehmann lovegrass competitive dominance. We primarily aim to address two questions: 1) how do our treatments affect agave survival (measured by the number of live plants in a row) and growth (measured by the number of leaves from live plants); and 2) how do the Lehmann lovegrass competition removal by weed-eating and hand-pulling treatments affect agave growth and percent cover of Lehmann lovegrass? We expected that providing protection from solar insolation, removing Lehmann lovegrass competition, and herbivory protection would favor successful agave establishment on transplantation, and enhance its growth and survival rates which could provide key insights to strategize agave management practices for successful restoration in wildlands.

Methods

In October 2018, a collaboration amongst Bat Conservation International, the Ancestral Lands Project, the National Park Service, and the University of Arizona supported a project to restore plant Palmer's agave population in the Coronado National Memorial in southeastern Arizona. The project involved the planting of 1200 juvenile Palmer's agaves within the Southeastern corner (57°36'04" N, 34°67'269" E) of the National Memorial. The study site elevation is approximately 1524 m and is situated about less than 1 km away from the US-Mexico border. It is a moderately flat grassland dominated by Lehmann lovegrass with sandy loam type soil and warm, low humidity summer weather (daytime temperatures = 32-37C). The summer rainy season (monsoon) is between late June and early September (NPS, Weather Station Info Page, 2020).

For the experiment, we purchased agaves pups from Borderland Restoration Network (grown from seeds collected at the Memorial) and then planted them at the site in six one-hectare square plots in October 2018. Each plot is composed of ten rows, each row extending 95 m and placed 10 m from the next row. Every row consisted of twenty agaves planted 5m apart making a total of 200 plants per plot, for a

collective count of 1200 plants installed across the entire experiment. A different treatment was applied to each row of agaves within a plot. Any two treatments (amongst the six) were 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 used shade cloth (providing a 50% reduction in solar radiation) to reduce solar insolation. To provide javelina herbivory protection (and really, protection from any large herbivore), we installed a sieved chicken wire enclosure (15 x 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, a) hand-pulling and b) weed-eating above-ground mass from the immediate surrounding (1-m circumference) of the focal agaves. We left behind the removed Lehmann's lovegrass on the surrounding ground. All the treatments were deployed 1-4 days after the agave installation.

The treatments were a combination of five single and five combination treatments, based on manager recommendations. The five single treatments included: control, hereafter referred to as "C", was the reference point for comparison and had no other treatment applied to it, 2) shade cloth, hereafter referred to as "S", to provide weather protection from solar insolation, 3) protection from predation, hereafter referred to as "J", 4) reducing Lehmann lovegrass by weed-eating, hereafter referred to as "W", and 5) reducing Lehmann lovegrass by hand-pulling, hereafter referred to as "H". The rest of the five treatments were combination treatments, including 6) shade and weed-eating (S+W), 7) shade and hand-pulling (S+H), 8) herbivory protection and shade cloth (J+S), 9) herbivory protection and hand-pulling (J+H), and 10) herbivory protection and weed-eating (J+W). All ten treatments were randomly assigned to rows in each plot.

Data collection

We collected agave survival and growth responses in September 2019, a year after planting. We collected data from every 4th plant in a row (a total of 5 plants per row, and 50 per plot) to accommodate the sampling schedule of park managers. We quantified agave survival as a binary response (alive or dead)

and agave growth as the total number of leaves per plant. In cases where the agave plant died or was predated, we sampled the agave pup planted in the north direction (in the same row) of the originally anticipated individual. Re-selection of the agave plant 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 to estimate the aerial cover of the lovegrass surrounding the measured agave plants. Due to substantial vehicle damage to many of our treatments in plot 6, we excluded this plot from the analyses.

For agave measurements, we took agave survival per treatment was reported by converting the percent survival probabilities per treatment. We modeled it as; *Log−odds Survival = β_0 + β_1 × Treatment + b_0,* where b0 is the random intercept for plot. In this model, survival is treated as a binary response variable and a logistic regression model is applied (N = 250). Whereas, for agave size per treatment, we reported the average leaf count per treatment. In this model, individual agave size, measured by the number of leaves, is a continuous response variable in linear regression mixed-effects models. We modeled it as; *Number of Leaves = β_0 + β_1 × Treatment + b_0,* where b0 is the random intercept for the plot.

For Lehmann lovegrass measurements, we reported Lehmann lovegrass percent as a function of agave presence (if it had any effect at all) and treatments applied. We modeled it as; *Percent Lehmann lovegrass cover = β_0 + β_1 × Treatment + β_2 × Agave presence+ b_0,* where *Agave presence* is a binary predictor, indicating whether or not a live agave was present and *b*0 is the random intercept for plot. We also observed the effect on Lehmann lovegrass percent as a function of agave size, Lehmann lovegrass competition removal treatments (H and W only), and the treatments applied. We modeled it as *Percent Lehmann lovegrass cover = β_0 + β_1 × Treatment + β_2 × Number of Leaves + β_3 × Treatment × Number of Leaves*, where *b*0 is the random intercept for plot.

Statistical Analysis

We conducted two analyses. First, we assessed Palmer's agave survival by treatment and agave size by treatment. To assess the effect of treatment on agave survival, we used mixed-effect logistic regression,

where agave survival was coded as a binary response (live or dead/predated) variable, treatment was a 10-leveled fixed effect, and plot number was included as a random intercept effect. Whereas, for individual agave sizes, we recorded the number of the leaves (N= 74) as a continuous response variable by having treatments as the fixed effect and plot number as the random effect using a linear regression mixed-effects model. For agave size analysis, data were restricted to the cases where there were live agaves and had a maximum of three agaves per row. For both, agave survival and agave size models, the plots are taken as random intercepts.

We also assessed Lehmann lovegrass cover (measured as the estimated percentage aerial cover) as a function of Lehmann lovegrass control treatments, H only, and agave metrics of size and survival. For this analysis, all the other combination treatments such as J+H, J+W, S+W, and S+H were not included. We used linear regression to accommodate for the small sample size. Whereas, we used a mixed model to investigate the effect of Lehmann lovegrass control treatments (W and H) and presence or absence of an alive agave (N = 65) as binary predictor variable on the percent cover of Lehmann lovegrass as a response variable, and included plot number as a random intercept effect.

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 plot numbers 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. However, we included the interactive effect of agave size and hand pulling on the Lehmann lovegrass percent cover, unlike agave presence and H versus Lehmann cover. For Lehmann lovegrass, post-hoc tests were unnecessary since the H and W were compared to control treatment only. All analyses were performed with R software (version-3.6.2; R Core Team, 2020). R code developed for analyses is available on GitHub (https://github.com/jcoliver/agave-growth).

Results

Agave plant survival differed significantly from the control —which had 30.6% agave survival— among the following treatments: the javelina and shade treatment (J+S) had the greatest agave survival of 90.5% in this treatment ($p < 0.001$,; Table B.1), the javelina protection and weed-eating treatment (J+W) resulted in 71.9% agave survival ($p < 0.01$; Table B.1), and shade treatment (S) had 66.5% agave survival ($p = 0.04$; Table B.1). However, W alone treatment varied significantly with control, contributing to the least agave survival of only 7.5% ($p = 0.04$; Table B.1). Moreover, in J+S treatment, 3.07 ± 0.88 (Table B.1) more plants survived on average in comparison to control treatment. Whereas, in J+W and S, 1.75 ± 0.73 and 1.50 ± 0.74 more agaves survived on average than n control treatment (Table B.1). Agave survival did not differ significantly amongst the rest of the singular and combined treatments. Conversely, agave survivorship per treatment (the number of the agaves that survived in treatment over the experiment duration) conforms to the order of the treatment significance and percent survival (Figure B.1).

Predictor	Coefficient Estimate	Error	Survival percentage	P-value
C	-0.82	0.82	30.649	0.318
H	0.16	0.70	34.25	0.815
J	0.16	0.70	34.25	0.815
J+H	-0.86	0.77	15.78	0.263
J+S*	3.07	0.89	90.51	0.001*
J+W	1.76	0.74	71.96	0.017
S	1.51	0.74	66.58	0.042
S+H	-0.86	0.79	15.73	0.276
S+W	-0.76	0.68	17.09	0.261
W	-1.69	0.83	7.51	0.042

Table B.1. Agave survival by treatment. Tukey's HSD significant effect at $p < 0.05$ is marked with an asterisk. C represents the Control treatment.
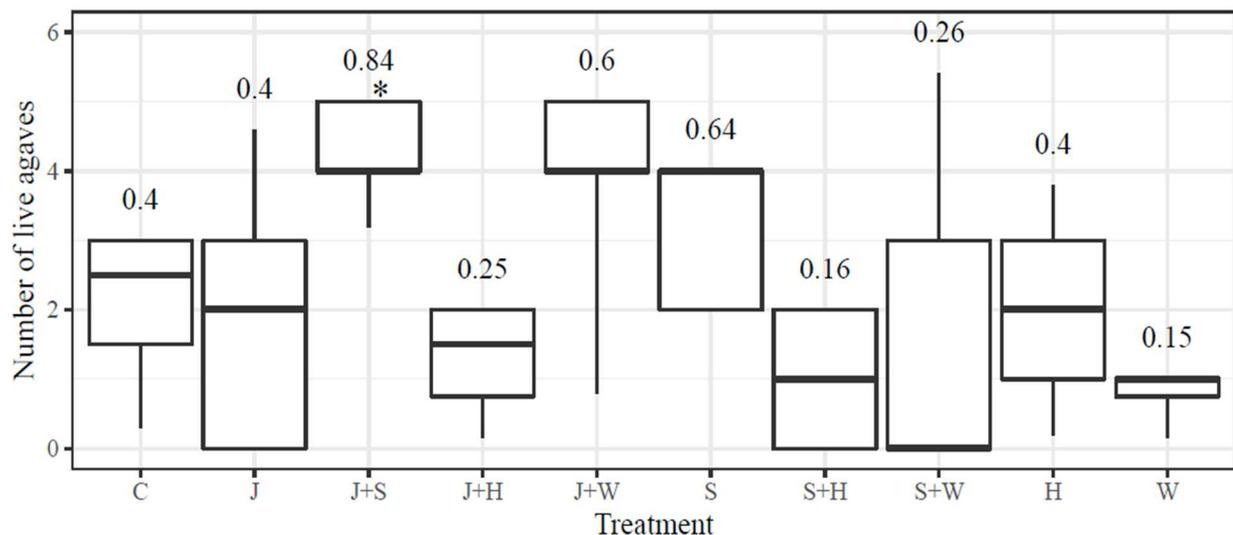
Figure B.1. Agave survival by treatment using linear regression. The boxplot shows the median, 25th and 75th percentiles (lower and upper box boundaries, respectively), and the lower and upper whisker at 5th and 95th percentiles, respectively. The numerical values display agave survivorship (the proportion of the agaves that survived in a treatment over the experiment duration) across each treatment. The supplemental data is available online on: https://github.com/jcoliver/agave-growth

Agave size did not differ significantly amongst the treatments ($p < 0.05$), except in the shade-alone (S), and javelina protection and shade treatment (J+S) ($p < 0.001$ and 0.03 respectively Table B.2). In terms of average agave sizes across the treatments measured by the average leaf count, S gave the highest agave size for an average of 8.04 leaves, J+S gave 7.27 leaves (Table B.2). Other, non-significant ($p > 0.05$) treatments, resulted in the following average agave size per treatment; S+W and W resulted in the same number of leaves 7.51, while J+H, H, and J+W resulted in 7.01, 6.95, and 6.91 leaves. The least agave size resulted in the Control treatment, having only an average size of 4.76 leaves.

Predictor	Coefficient Estimate	Error	Average Leave number	p-value
C	4.76	1.04	4.76	< 0.001
H	2.19	1.29	6.95	0.097
J	1.04	1.47	5.80	0.482
J+H	2.25	1.63	7.01	0.174
J+S	2.50	1.18	7.27	0.038 *

J+W	2.14	1.22	6.91	0.084
S	3.28	1.20	8.04	< 0.001*
S+H	0.71	1.66	5.47	0.673
S+W	2.75	2.13	7.51	0.202
W	2.74	2.84	7.51	0.338

Table B.2. Agave size by treatment using linear regression, where b_0 is the random intercept for plot. Significant effect at $P < 0.05$ is marked with an asterisk. In this table, the row listed as C represents the Control treatment.
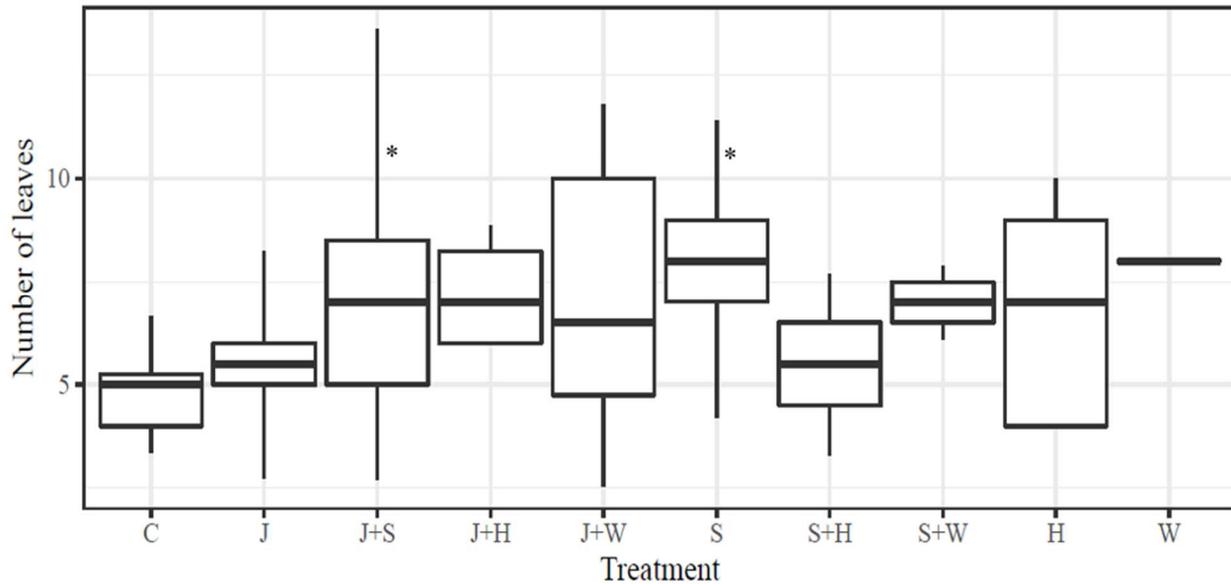

Figure B.2. Agave size by treatments using mixed-model linear regression. Box plot show median with upper and lower box boundaries at 25th and 75th quartiles, and the whiskers at 5th and 95th percentiles. The supplemental data is available online at: https://github.com/jcoliver/agave-growth

Percent Lehmann cover by agave presence

Treatments H and W resulted in at ($p < 0.001$) reduction of Lehmann lovegrass percent cover by 20.26 % and 23.24% respectively (Table B.3). The presence of agave did not affect Lehmann lovegrass cover ($p = 0.265$). As expected, control treatment accounted for the greatest (32.42 %) Lehmann lovegrass cover (Table B.3, Figure B.3).

Predictor	Coefficient Estimate	Error	*P*-value
Intercept	37.86	7.27	0.0031

Hand-pulling (H)	-20.26	3.78	< 0.001*
Weed-eating	-23.24	4.29	< 0.001*
Agave Presence	-4.20726	3.75	0.2659

Table B.3. Percentage Lehmann lovegrass aerial cover for the weed control treatments, H and W, and agave presence. Significant effect at $p < 0.05$ is marked with an asterisk. C represents the Control treatment.
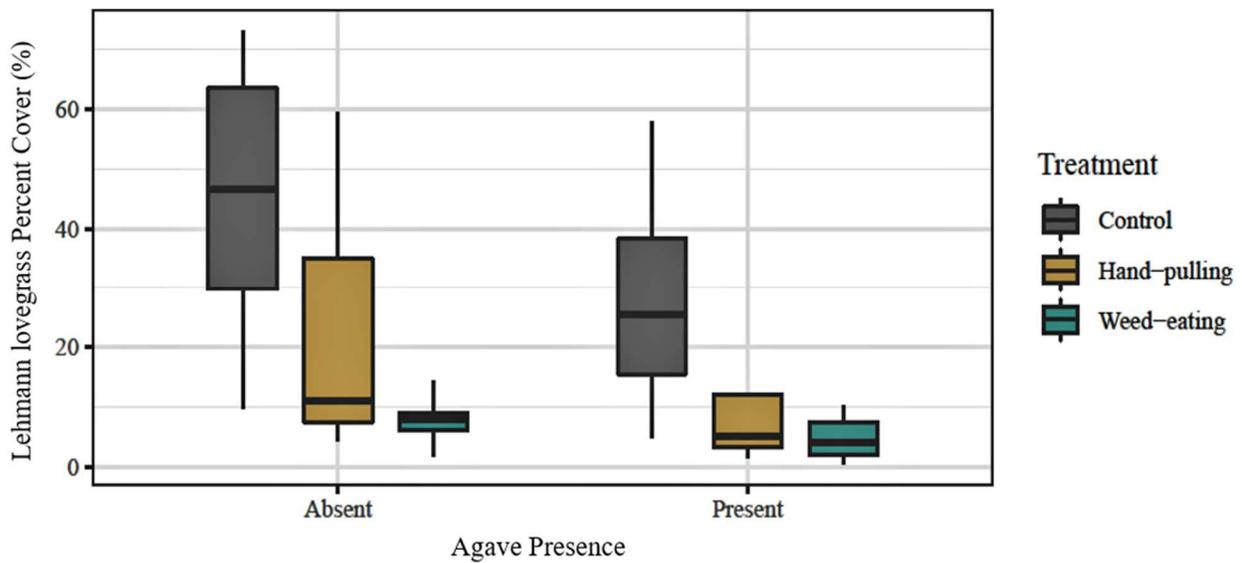

Figure B.3. Percentage Lehmann lovegrass aerial cover for the weed control treatments, H and W, and agave presence (the numbers of alive leaves, (N = 65). Box plot show median with upper and lower box boundaries at 25th and 75th quartiles, and the whiskers at 5th and 95th percentiles. Supplemental data is available online at: https://github.com/jcoliver/agave-growth

Lehmann lovegrass cover by agave size

Lehmann lovegrass removal by hand-pulling (H) resulted in 78% less Lehmann cover than the control treatment ($p = 0.001$; Table B.4). However, agave size reduced Lehmann lovegrass cover by only 10% than the control treatment ($p = 0.017$). Surprisingly, the interactive effect of hand-pulling Lehmann lovegrass and agave size gave 11% more Lehmann lovegrass cover than the control treatment (F = 7.294, $p = 0.018$). Our result suggests that the increase in agave leaf count moderated the percent Lehmann lovegrass cover (or vice versa); Figure B.4).

Predictor	Coefficient Estimate	Error	P-value
Control	77.97	18.69	0.001
Hand-pulling (H)	-78.32	22.68	< 0.001 *
Agave size	-10.17	3.73	0.017 *
H : Agave size	11.11241	4.11	0.018

Table B.4. Agave size by treatment using linear regression. Significant effect at *P* <0.05 is marked with an asterisk. We have reduced treatment to only two levels (Control and Hand-pulling), *post-hoc* tests are unnecessary.
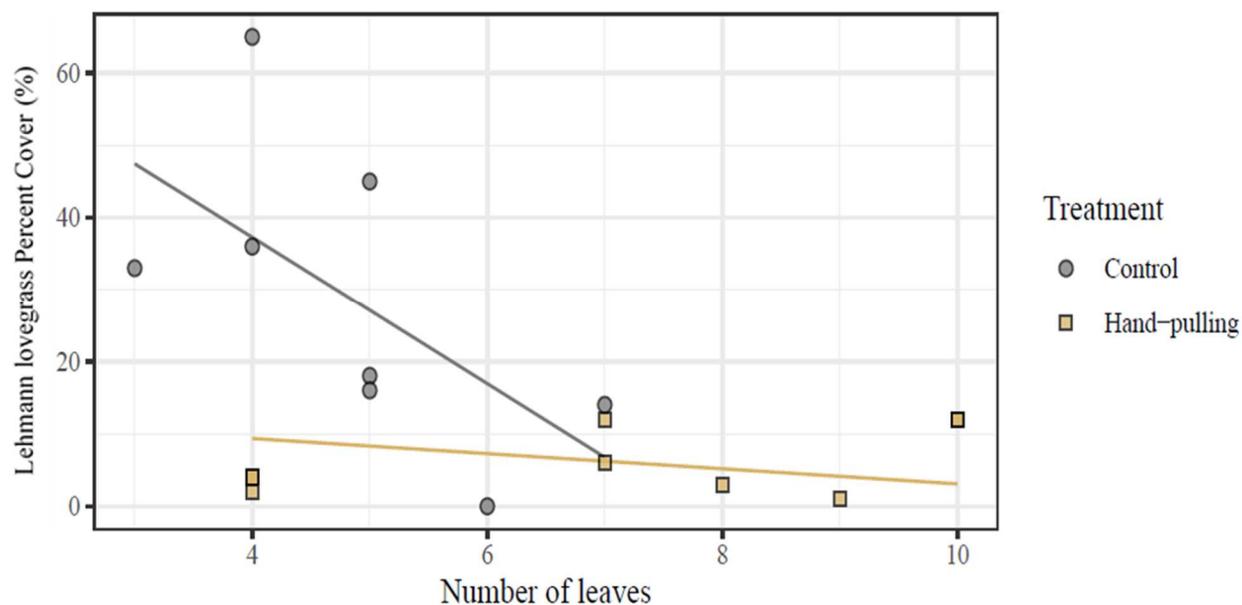

Figure B.4. Percentage Lehmann lovegrass aerial cover in relation to agave size for the Hand-pulling and Control treatments (total leaf count, N = 17). Supplemental data is available online at: https://github.com/jcoliver/agave-growth

Discussion

Developing agave restoration techniques for population recovery is particularly challenging in drylands ecosystems because of several factors including extreme weather, competition with invasive species, and predation (Nobel, 1976; Jordan and Nobel, 1979). In this field study, we tested a set of ten treatments to enhance agave survival and growth conditions in a new 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. We did not

find a signature of a competitive effect of agave presence on Lehmann lovegrass, our results suggest an inverse correlation between agave size and Lehmann lovegrass percent cover (or vice versa). Interestingly, we found that dense Lehmann lovegrass cover appears to protect agaves from direct sunlight and predation.

Several studies suggest that planting agaves into a matrix of existing vegetation has a nurse effect: it provides the growing natives with a 'microenvironment' protection, which favors agave survival and growth (Jordan & Nobel, 1979; Peters et al., 2008; Pavliscak et al., 2011). In a field experiment, Arizaga & Ezcurra (2002) reported that *Agave macroacantha* cohorts placed outside of the nurse plant died within their first year of planting, in contrast to the cohorts that survived for more than 2 years under the nurse plants. Several causes have been identified for this nurse effect. For one, Pavliscak et al. (2011) reported that surface mulch and shade significantly increased Palmer's agave establishment rates by protecting them from direct sunlight, irrespective of simulated precipitation levels. For another, others have reported that straw cut up as thatch not only provides light attenuation as a direct benefit but also prevents Lehman lovegrass regrowth as an indirect benefit, by photo-inhibiting the seedling germination, emergence, and establishment (Roundy et al., 1992). Finally, shade and straw mulch/thatch have also been shown to facilitate agaves seedling emergence and establishment by cooling down the soil surface, decreasing microsite soil temperatures, increasing moisture retainment and nutrient availability, and providing shelter from grazing and trampling (Jordan and Noble, 1979; Peters et al., 2008). Our results support these previous studies, providing a strong positive correlation between shade and agave survival. We found that the combination of shade and javelina protection (J+S) and shade alone (S) facilitated the agave growth and survival by providing the nurse effect against the extremities of the weather, sun, and predators.

This nurse effect would explain the surprising positive trend between agave survival and dense Lehman lovegrass existing vegetation. Our results indicate that dense Lehmann lovegrass vegetation surrounding the young agave succulent was beneficial for agave survival. Even though removing invasive Lehmann lovegrass decreased the biological invasion for agaves, the removal simultaneously deprived agaves of

protection against solar insolation and visual protection against predation. Agave plant's dependency on nurse plants facilitation to establish and survive might be more prominent in semi-arid desert environments which are characterized by high climatic fluctuations and summer drought stresses. Both of these limiting factors impede the natural growth and survival of agave species. In this case, the surrounding Lehmann lovegrass biomass could have positively interacted with the agaves by improving the essential microclimatic shade conditions. Other studies suggest that succulents, including agaves, perform best when planted either under the canopy of the prevailing vegetation, nurse rocks or structures that obstruct direct sunlight (Peters et al., 2008). This has an important potential implication for stakeholders concerned with population recovery of Palmer's agave should plant agaves in a matrix of –or under the canopy of –existing vegetation. This is especially important for managers attempting to replenish agave populations in wildlands: removing Lehmann lovegrass without further interventions— especially in or near monocultures of Lehmann lovegrass —could deprive agaves of the vital nurse effect and limit agave growth and survival. Our greenhouse study also conforms to this phenomenon where clipping neighboring Lehmann lovegrass resulted in lesser Palmer's agave biomass. So, we suggest that wildland managers refrain from clipping dense, neighboring vegetation surrounding agave plants when possible. By doing so, managers could enhance the conditions required for agave growth and survival and will be able to save the resources in terms of time, energy, and money but are also protecting the agaves. If the vegetation that surrounds agave consists of Lehmann lovegrass *and* removing Lehmann lovegrass is a priority, then we suggest that wildland managers consider further interventions to ensure that agaves continue to enjoy the nurse effect.

Interestingly, javelina protection and weed-eating (J+W) also positively influenced agave survival and size. We expect this to be a result of an unintended nurse effect. The weed-eating treatment activities included the clipping of above-ground biomass of Lehmann lovegrass in the absence of plant biomass removal. The clipped Lehmann lovegrass thatch on the ground could have acted like a surface mulch or a shade treatment. As such, the J +W treatment could have acted like an alternative J + S treatment,

sheltering young agaves from solar insolation, high surface temperatures, and herbivory. Similarly, Garcia et al (2000) reported a similar positive interaction between invasive shrub facilitation and yew establishment, where the thorny, unpalatable shrub branching served as a fence for ungulates to reach the 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 Services, 2012). Our results conform to similar positive agave survival and size outcomes with dense Lehmann lovegrass stands. Presumably, because of the dense Lehmann lovegrass density visibly protects young agaves from predation and ameliorates the immediate growing conditions by providing shade and cooling. which indicates that killing invasive species without removal of plant biomass (e.g. not by prescribed burning or herbicide—clipping and leaving dead biomass on site) could provide the nurse plant dynamics that these restoration species 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 from natural disasters like wildfires. Some commonly yet ineffectively practiced Lehmann lovegrass control measures include herbicidal spraying, prescribed burning, and physical uprooting (Sumrall et al., 1991; US Forest Services, 2012). Studies show that mechanical weed removal is a common, effective, and efficient weed management tool for the noxious range weeds if mowing is done in the late growth season (Benefield et al., 1999). Physical uprooting is another easy yet ineffective method that causes soil disturbances, providing more germinating sites for the Lehmann lovegrass seeds. In that case, mowing is a simplistic, economical, and time-efficient practice to control the noxious annual and some perennial range weeds (Benefield et al., 1999). Sumrall et al., 1991 suggest that clipping or burning Lehmann lovegrass stands increases Lehmann lovegrass seed germination and subsequent plant recruitment. We recommend forgoing Lehmann lovegrass weed management if native plant restoration is

a priority. Whereas, in majorly monocultured Lehmann lovegrass stands in wildlands like Coronado National Monument, Lehmann lovegrass poses a direct threat due to high combustibility and aggressive growing nature. Clearly, intervention to control this weed could be necessary to avoid fire disasters. In such instances, we recommend managers to electrically mow the weed than physically uproot Lehmann lovegrass. Our results support this as mowing Lehmann lovegrass reduced its percent cover significantly better in mowing treatments as compared to control or hand-pulling treatment.

Our results did not find any signature competitive effect of agaves on Lehmann lovegrass growth and cover, despite conditions that favored agave growth and survival as we expected. We found that the presence of agave was both non-significant and unexceptional for Lehman lovegrass (Figure B.3). On the contrary, we observed that an increasing agave leaf count resulted in a non-significant yet exceptional reduction in the percent Lehmann lovegrass cover in the untreated plot (or vice versa), as compared to the Hand-pulling treatment (H)(Figure B.4). By comparison, though, Lindsay et al. (2011) reported high percentage coverage areas of Lehmann lovegrass were significantly associated with the areas of low-density agaves, indicating that high Lehmann lovegrass abundance outcompete native flora. Together, our results and Lindsay et al.'s (2011) results suggest a complete one-way competitive and dominant (albeit partially protective) interaction of Lehmann lovegrass with Palmer's agave. Several attributes pertain to the aggressive and successful establishment of invaders like Lehmann lovegrass such as ease of establishment, high seed production, seed dormancy, aggressive reproduction, fast growth rate, dominant resource extraction, increased resistance to removal, and predators, and confers greater persistence to environmental stress. (Scasta et al., 2015). This competitive dominance becomes particularly crucial for naturally slow-growing succulents like Palmer's agaves especially during their early stages of growth where physiological, morphological, and environmental stresses limit their growth and survival (Nobel, 1976; Jordan and Nobel, 1979). Moreover, the minimum trait overlap between Palmer's agave and Lehmann lovegrass further complicates the invasion resistance dynamics.

Altogether, this indicates that recruiting small agaves for restoration purposes in semi-arid environments might not have high or any success. We recommend managers to transplant multiple age classes of agave pups and seedlings grown in nurseries until old enough to withstand wildland weather extremities. Moreover, to provide long-term agave restoration for uninterrupted annual foraging opportunities for bats, pollinators within the impacted habitat, would require a population with a spectrum of age classes, rather than a single-aged cohort resulting from a seeding effort. Therefore, an integrated approach combining seeding, transplants, and conservation of intact populations would be essential for the prolonged supply of goods and services that agaves have to 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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