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FINAL REPORT

Developing Appropriate Restoration Practices for Arizona Sonoran Desert Uplands Invaded by Buffelgrass

Project title:

Developing Appropriate Restoration Practices for Arizona
Sonoran Desert Uplands Invaded by Buffelgrass

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Developing Appropriate Restoration Practices for Arizona Sonoran Desert Uplands Invaded by Buffelgrass

EXECUTIVE SUMMARY

Milestones

This project included several related components all aimed at providing information support for furthering development of effective management strategies for buffelgrass in Saguaro National Park. In collaboration with Dana Backer and Saguaro National Park personnel, we conducted literature reviews, three field studies, and two syntheses and analyses of existing data collected by Saguaro National Park.

This document reports on:

1. Literature review on overall ecology of buffelgrass and its management, *completed in 2010*.
2. Literature review on vegetation restoration projects in the Sonoran Desert, *completed in 2011*.
3. Field study of ecological characteristics (vegetation, soil, and soil seed bank) at sites invaded and not invaded by buffelgrass within Saguaro National Park, *completed in 2011*. This effort was published in *Invasive Plant Science and Management* in 2012.
4. Field study of a condition assessment of sites previously treated for buffelgrass by Saguaro National Park and including condition of vegetation, soil, and the soil seed bank, in addition to current level of buffelgrass infestation, *completed in 2012*. This effort was published in *Environmental Management* in 2013.
5. Field study of soil seed bank composition across a buffelgrass treatment gradient and uninvaded sites using two seed bank assessment methods, *completed in 2013*. In addition to information contained in this report, a manuscript from this effort is under development.
6. Synthesis of passive transect data collected by Saguaro National Park, *completed in 2013*.
7. Synthesis of existing restoration data along Cactus Loop Drive collected by Saguaro National Park. This effort is 'in press' with *Natural Areas Journal* with a publication date of early 2015.

Project Summaries and Implications

Summary of Revegetation Publications in the Sonoran Desert

There are not many papers on revegetation using native Sonoran Desert species. The handful of papers that do exist often are limited with how the methods and data are described and reported, such as few species tested or short monitoring time periods. Some general conclusions that could be tentatively drawn include species selection is important, with some species establishing better than others, establishing some native species through seeding appears feasible even without supplemental irrigation in the Sonoran Desert upland subdivision, and irrigation has shown mixed results in enhancing seeding and planting projects. With some exceptions, irrigation has generally not been effectively evaluated. Most of the critical questions central to planning revegetation projects in the Sonoran have been little evaluated. Existing literature is valuable for illustrating some of the considerations about revegetation projects but is generally not able to directly address key questions that Saguaro National Park has about revegetating sites disturbed by buffelgrass. Existing literature can help new research avoid some of the problems of the older research to maximize information gained. New original studies are needed for screening a variety of native species for their ability to become established in disturbed sites and promote the recovery of indigenous ecosystems containing minimal amounts of exotic species.

Passive Colonization Following Buffelgrass Treatment, and Summary of Outplanting Effectiveness for Revegetation at Saguaro National Park

This report summarizes data provided by Saguaro National Park on (i) passive colonization along transects following buffelgrass treatment and (ii) outplanting effectiveness for establishing native species along the Cactus Forest Drive. Results from (i) suggest that treating buffelgrass achieved a greater reduction in the volume occupied by buffelgrass than it did the density of buffelgrass, although there was still a 3-fold reduction in buffelgrass density. Results from (ii) conclude that the project met management goals of reestablishing a 1:3 lost: restored ratio of tree density required for habitat restoration of an endangered owl species and of reestablishing a range of native species for aesthetic and vegetation structural restoration. Budget estimates indicated a cost per plant of approximately \$55 from grow-out in a nursery through plant maintenance in the field. This cost included supporting activities of site preparation, exotic plant control, and effectiveness monitoring. The monitoring data, combined with longer term observations, suggest that the National Park Service's revegetation strategy effectively established a range of native plant growth forms and met habitat restoration targets.

Soil, Vegetation, and Seed Bank of Buffelgrass-Invaded Sites

This study reviewed current site conditions of buffelgrass invaded sites and identified factors which may provide insight to how buffelgrass impacts the environment. Information from this study provides several considerations for the management of buffelgrass infested sites related to the potential long-term ecological effects of buffelgrass, the timing of management treatments, and post-treatment site management. The data indicated that soil nutrients (e.g., $\text{NO}_3\text{-N}$) were concentrated in buffelgrass patches, which should actually enhance soil fertility in these patches similar to the fertile island effects of native perennials, and that native plant cover but not species richness were reduced in buffelgrass patches at the current stage of invasion. These findings suggest that (i) the early treatment of buffelgrass patches while native plant species still persist might promote re-colonization by native vegetation of treated sites; (ii) soil nutrient status should not be unfavorable for native plant re-establishment on post-treatment buffelgrass sites; and (iii) while the overall native species richness and composition of buffelgrass patches did not differ from non-buffelgrass patches, two native species of conservation concern were significantly reduced in buffelgrass patches.

Soil, Vegetation, and Seed Bank of a Sonoran Desert Ecosystem along an Exotic Plant Treatment Gradient

This study reviewed treatments of buffelgrass along a gradient implemented by the National Park Service in Saguaro National Park. The data indicated that no negative consequences of removing buffelgrass were evident based on our analysis of native vegetation, soil, and seed banks. Our findings suggest that (i) treatments effectively reduced buffelgrass while resulting in post-treatment ecological conditions largely indistinguishable from those of areas not invaded by buffelgrass; (ii) treatments reduced the potential for risk of buffelgrass-fueled wildfire and longer term negative impacts of buffelgrass; and (iii) continuation of treatments by the National Park Service in Saguaro National Park to reduce exotic plants will meet park management goals of maintaining ecological communities dominated by native species.

Characterizing soil seed banks in invaded and treated buffelgrass stands in the Sonoran Desert

This study focused on the predictive power of soil seed bank assessments to assess the extent of treatment required to reduce or exclude buffelgrass presence from the seed bank, identify site potential for natural recovery, and compare seed bank assessment method results and observe if results lead to concurrent or conflicting conclusion. Our results suggest that (i) all treatments reduced buffelgrass seed compared to control, and this was evident in both the soil seed bank assessment methods used; (ii) extraction identified greater buffelgrass seed densities compared to emergence within some treatments, suggesting that a longer treatment regime may be necessary to successfully remove buffelgrass; (iii) neither the length of time of buffelgrass treatment nor time since treatment had a negative impact on native diversity indicating the potential to recover to similar composition as uninvaded sites, however treatment length may have impacted native seed densities due to reduced accumulation of native seeds; and (iv) extraction was more representative of the above-ground vegetation and may be more reliable for predicting future recovery of native vegetation.

Implications for the Future

In addition to information contained herein, this effort can help lay groundwork for further investigation to gain a greater perspective on effectiveness of buffelgrass removal and revegetation by native species. While any study has limitations, including this study, valuable insight into several aspects of buffelgrass ecology, treatment, and response of native ecosystems to buffelgrass treatments in Saguaro National Park was derived from this study. Moreover, the dry conditions that occurred during our study may become relatively typical for at least the near future, according to some climate projections. Thus, the study period might be quite representative. While temporal sampling was limited, inclusion of the soil seed bank throughout this research helps provide a cumulative, long-term assessment of the plant community and seed availability at the field sites.

Project Limitations

Our results indicate that buffelgrass can leave a legacy of change in the above-ground vegetation and seed bank. However, we only sampled one season within one year along a buffelgrass treatment gradient, which limits the information available for estimating seed bank impacts on future species composition, particularly annuals. Several studies provide evidence that buffelgrass seeds can remain viable in the soil seed bank resulting in an extended impact even after treatment. Additionally, it is unclear which native species also remain viable in the soil seed bank for extended time periods or which species may provide the best effort to compete with buffelgrass under future projected climate conditions. Native species cover may have been reduced with buffelgrass infestation. Within our sampling time native composition within the above ground community and within seed banks were retained during buffelgrass infestation and after treatment, indicating a high potential of native recovery. We also did not sample after the buffelgrass main active growing season in the summer, and did not capture cover of seasonal annuals which were more likely to be present during the time. Results suggests a potential for native species recovery once buffelgrass is removed, however these conclusions may fluctuate depending upon the year and season of sampling.

Future Research Needs

Several future research objectives have been identified to build on our existing knowledge of buffelgrass long-term impact on site ecology.

1) Continue vegetation and seed bank sampling of treated buffelgrass plots to provide further insight into temporal dynamics of vegetation at buffelgrass management sites. There are several questions which can be addressed with continued monitoring. It would be useful to management to determine recruitment potential from seed banks post-treatment and if management could stimulate native seed bank but not buffelgrass germination. Also, sampling during multiple growing seasons will capture seasonal variations in above-ground vegetation and seed banks. Several species, including brittlebush, potentially flower twice each year depending upon seasonal weather conditions, forming transient seed banks which can influence estimates of soil seed banks at different times within a year. Other species require particular conditions to germinate and establish and may not persist across seasons or years. Estimating species' contributions to the seed bank over several seasons and correlating residual effects in the above-ground emerging vegetation can provide evidence for the length of time required to reduce negative impacts due to buffelgrass residence and for native species recovery. Continued monitoring will additionally identify the potential for re-invasion by detecting viable buffelgrass seed within soil seed banks.

2) Buffelgrass may exhibit greater competition if provided suitable conditions. Several studies have results that suggest buffelgrass competes with native species due to earlier emergence, may have allelopathic effects on natives, and may over time cause unsuitable conditions, even for itself. It is uncertain, however, how many seeds individual plants can produce and how long buffelgrass seeds remain viable in Sonoran Desert conditions. Further investigations into buffelgrass seed production, viability (surface and subsurface influences; dry storage), and competition at different levels (seeding rate, germination, seedling, and adult competition) with native Sonoran species will elucidate which species, if any, have the most potential to endure buffelgrass infestation and treatment or have the potential to compete with buffelgrass. Paired with seed bank assessments, this information can assist with estimating the likelihood and severity of reinvasion, and potentially provide a list of native species which can be facilitated by managers to reduce the risk of reinvasion or extensive buffelgrass cover.

3) Buffelgrass seeds can remain viable in soil seed banks, but the longevity of buffelgrass seed banks may not exceed that of many native species. This suggests that there may be opportunities for exhausting buffelgrass soil seed reserves through management activities. It may be useful to management to identify potential persistence ability of native seed in existing treated and untreated buffelgrass patches. Additionally, typical across ecosystems, seed species important in the vegetation were not detected in the soil seed bank. An additional resource to managers would be a compilation of germination requirements for native species, growth requirements for native species, and active collections and/or propagation of native species. An additional external benefit would be to develop modifications to existing seed bank assessment methods to improve detection techniques.

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INTRODUCTION

Buffelgrass (*Pennisetum ciliare* (L.) Link) is a priority invasive, exotic species for managers of conservation lands in Australia, Mexico, and the United States because it can alter fire regimes and reduce native biodiversity. Since its introduction to the United States in the early 1900s, buffelgrass has shifted from a “wonder” grass for vegetating rangelands to a species of extreme concern due to its potential to compromise integrity of natural habitats (McIvor et al. 2000; Firn and Buckley 2010; Fehmi et al. 2010). Buffelgrass is particularly a concern for Saguaro National Park (Park) and southern Arizona because buffelgrass may alter ecosystem functioning by competition for space and resources, increased fire potential, and changing nutrient cycling. Since recognizing that the increasing spread of non-native grasses (Schmid and Rogers 1988), particularly buffelgrass, could result in future fire problems, managers at the Park have thus far established successful treatments of buffelgrass with the use of herbicides and pulling (Backer and Foster 2007; Backer and Hannum 2009). Three buffelgrass growth stages were identified by the Park for monitoring and treatment purposes: 1) seedling, 2) basal growth or re-sprouting of already established plants, and 3) plants going dormant, with approximately 50% green biomass (Backer and Hannum 2009).

Buffelgrass (*Pennisetum ciliare*) is a native African grass inhabiting arid and semiarid landscapes. It was first introduced to the United States in the early 1900's as a forage grass for cattle. The USDA Soil Conservation Service, Plant Materials Center developed several cultivars which would be more amenable for the US southwest environment (Halvorson and Guertin 2003). Buffelgrass is a C₄ herbaceous perennial graminoid that has a high genetic variability (Downton 1975; Van Devender et al. 1997). Individuals can reach up a height of 20-80 cm and have a thick robust root system which can be deep within soils up to 2.4 m. Plants often form dense thickets (Chambers and Hawkins 2002). Plants can establish throughout the year with an increase in survival with an onset of a wet season (Duke 1983) and can grow rapidly under appropriate air and soil temperatures and precipitation. Standing dormant mature plants begin to flourish when soil temperatures reach above 24°C, although limited by soil moisture, and leaf development can occur when temperatures are above 15°C with adequate soil moisture. Without precipitation, buffelgrass dies back and resumes vegetative growth when water becomes available. Above-ground vegetation dies back to the stem nodes to enable the plant to rapidly reinitiate growth response to precipitation (Van Devender et al. 1997).

The primary mode of reproduction is apomixes (or asexual reproduction), with lower levels of sexual reproduction (Williams and Baruch 2000). Pollination is still required for endosperm development of seed. It is not known how much seed is produced by buffelgrass individuals. Buffelgrass seed has a chemical and physical seed coat dormancy, which has to be terminated before germination can occur (Winkworth 1963). Dormancy is decreased with an increase of maturation temperature and fertility and can increase with water stress when imposed during maturation (Sharif-Zadeh and Murdock 2000). Studies have shown that buffelgrass seed can remain viable up to three years (Winkworth 1963) and if conditions remain dry, maybe longer (Parihar and Rai 1985).

The most opportunistic times to herbicide buffelgrass are during active photosynthesis during the hotter months (Duke 1983). Due to the potential of buffelgrass to re-invade or other non-native species to invade recently treated buffelgrass areas, it is important to understand the effects of buffelgrass on the ecosystem to assist in ecosystem recovery.

It is not definitive whether buffelgrass infestations leave a “legacy” of changed site properties within Sonoran systems even after buffelgrass has been treated, although our studies suggests buffelgrass does impact above-ground vegetative cover and soil seed banks. More information is required to make informed decisions on how buffelgrass impacts natural, undisturbed systems and how to restore native vegetation, if action is required, to areas infested by buffelgrass and where buffelgrass has been treated. To fill in some of these informational gaps, we investigated the influence of treated and untreated buffelgrass on soil properties, above-ground vegetation composition, and on the native seed bank of uncultivated areas that were invaded.

Project components:

To specifically assess associations of buffelgrass with Sonoran Desert communities and the potential of buffelgrass site “legacies,” we developed and implemented a study plan for evaluating the potential relationships of buffelgrass with soils and the native soil seed bank. This included evaluating vegetation and soil properties in (i) *a priori* identified patches of established buffelgrass infested and paired non-infested sites, (ii) patches identified at different levels of manual and herbicide treatment, and (iii) examining the soil seed bank in both of these studies. Additionally, included are several literature reviews and syntheses: (i) passive colonization along transects following buffelgrass treatment and (ii) outplanting effectiveness for establishing native species along the Cactus Forest Drive.

How to use this report:

This report presents investigations in order of the completion of operations. In the following report sections, each represents independent progress reports, with sections III through VI serving as preliminary manuscript drafts for publications. Additionally, sections build upon each other. Part III represents conditions in existing buffelgrass stands, while Part V represents treatments of buffelgrass along a treatment gradient and provides comparisons between buffelgrass invaded, treated, and uninvaded sites. Part VI further identifies buffelgrass residence and treatment impacts on the native soil seed bank, while comparing seed bank assessment methods results and their potential conflicting conclusions and impacts on land management decisions.

Products

The above noted studies resulted in three manuscripts published in *Invasive Plant Science and Management* in 2012, *Environmental Management* in 2013, and *Natural Areas Journal* (in press) in 2015, and additional seed bank analyses that are currently being worked into manuscript for journal publication. These manuscripts provided insight to the potential influences on soil properties, impacts to above-ground vegetation composition and to the soil seed bank, which has a direct impact on estimating the potential of recovery post-buffelgrass removal. The following report provides details about each part of our investigation as well as management recommendations and suggestions for future research.

Manuscripts

Abella, SR, LP Chiquoine, DM Backer. 2012. Ecological characteristics of sites invaded by buffelgrass (*Pennisetum ciliare*). *Invasive Plant Science and Management*, 5(4), 443-453.

Abella, SR, LP Chiquoine, DM Backer. 2013. Soil, vegetation and seed bank of a Sonoran Desert Ecosystem along an exotic plant (*Pennisetum ciliare*) treatment gradient. *Environmental Management*, 52, 946-957.

Abella, SR, KL O'Brien, MW Weesner. 2015. Revegetating disturbance in national parks: reestablishing native plants in Saguaro National Park, Sonoran Desert. *Natural Areas Journal* (In press).

Working title: Two soil seed bank assessment methods applied along an exotic plant (*Pennisetum ciliare*) treatment gradient and method implications on management decisions.

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PART I. Preliminary Report: Developing Appropriate Restoration Practices for Arizona Sonoran Desert Uplands Invaded by Buffelgrass

Submitted 31 January 2011, *Revised for final report*

Introduction

With its introduction to the United States in the early 1900s, buffelgrass (*Pennisetum ciliare*) was regarded as a “wonder” grass for vegetating rangelands. However, there is now extreme concern that buffelgrass may damage the ecosystems to which it has been introduced due to its potential to alter ecosystem functioning by competition for space and resources, increased fire potential, and changing nutrient cycling. This is particularly a concern for Saguaro National Park (Park) and southern Arizona because of the potential for buffelgrass to compromise the integrity of natural habitats (McIvor et al. 2000; Fim and Buckley 2010; Fehmi et al. 2010). Since recognizing that the increasing spread of buffelgrass could result in future fire problems, managers at the Park have thus far established successful treatments of buffelgrass with the use of herbicides and pulling (Backer and Foster 2007; Backer and Hannum 2009). Three buffelgrass growth stages were identified by the Park Service for monitoring and treatment purposes: 1) seedling, 2) basal growth or re-sprouting of already established plants, and 3) plants going dormant, with approximately 50% green biomass (Backer and Hannum 2009). The most opportunistic times to herbicide buffelgrass are during active photosynthesis.

Due to the potential of buffelgrass to reinvade or other exotic species to invade recently treated buffelgrass areas, it is important to understand the effects of buffelgrass on the ecosystem to assist in ecosystem recovery. It is not well established whether buffelgrass infestations definitively leave a “legacy” of changed on site properties even after buffelgrass has been treated. Key information required to support the restoration of native communities on buffelgrass sites include: the potential influence of buffelgrass on soil properties of uncultivated areas and on the native seed bank, the longevity of buffelgrass seed in uncultivated Sonoran Desert landscapes, and buffelgrass susceptibility to competition by native Sonoran Desert plants.

To specifically assess associations of buffelgrass with Sonoran Desert communities and the potential of buffelgrass site “legacies,” we developed study plans for evaluating the potential relationships of buffelgrass with soils and the native soil seed bank. The first study plan concentrated on impacts of buffelgrass invasion on soils, seed bank, and above-ground vegetation (Part III). We included *a priori* identified patches of established buffelgrass by Park personnel, and acquired soil samples from infested and paired non-infested sites, analyzed soil nutrients and bulk density, and examined the influences on the native seed bank. Soil seed bank samples for seed bank analysis were also acquired at the time of soil sampling. The second study plan observed the impacts of buffelgrass invasion and treatment along a gradient. We also used *a priori* identified patches of established and treated buffelgrass to examine soils, soil seed banks, and above-ground vegetation (Part V and VI).

Our investigations described in proceeding sections of this report indicate that buffelgrass does have impacts on native vegetation (Part III and V) and seed banks (Part III and VI), however not on uncultivated soils. There are several studies that examine soil properties under the influence

of buffelgrass; however, all but one study are from areas that are or have been under cultivation or were prepared seedbeds. Most of these studies focus on how soil characteristics influence buffelgrass germination, growth, and spread, and do not focus on the influence of buffelgrass on soil properties or on changes of soil properties over time, while under the influence of buffelgrass. Our investigation specifically look at buffelgrass-invaded areas and soil chemical and physical properties (Part III) and the impacts to soil properties due to buffelgrass invasion and treatments (Part V). There are only a couple of studies on buffelgrass influence on soil seed banks. Most seed bank studies have been conducted outside the Americas, used different cultivars of buffelgrass, and/or concentrated on cultivated landscapes. Most literature on buffelgrass competition concentrates on the ability of buffelgrass to suppress germination and growth of other species or on allelopathic effects of buffelgrass. A few studies have findings that suggest a possible competitive ability of native/resident species with buffelgrass, particularly with buffelgrass seedlings. There are several studies that examine the longevity of buffelgrass seeds; however, field-based studies concentrate on cultivated sites. These observations indicate that the Park and the Park Service can be a leader in understanding critical aspects of the ecology and management of buffelgrass in wildland settings, where it has received little study.

Literature Review

Changes in Soil Properties Due to Established Buffelgrass

There are few studies that assess soil property changes due to the influence of buffelgrass. Ibarra-Flores et al. (1999) sampled soils under buffelgrass stands more than 10 years old on 29 sites in 3 major climate regions in Mexico to assess soil properties against adjacent non-buffelgrass rangelands. Soil samples were obtained from 0-10 cm near the crown of the grass, or in interspaces from non-buffelgrass areas. This study found that long-term buffelgrass establishment had the most effect on soil in southeast Mexico, where the climate is wetter and warmer than other regions of Mexico. In this region, soils contain higher percent total nitrogen (0.6%) and mean organic carbon (6.7%) and a higher cation exchange capacity (CEC) compared to the soils from the other two regions in this study. In the southeast region there was a decline in soil organic carbon and total nitrogen by about 40% and a decline in exchangeable Ca^{2+} by 21% in buffelgrass pastures compared to paired uncultivated sites. In the northwestern region, Mg^{2+} declined by 36% in buffelgrass areas compared to paired uncultivated sites. Buffelgrass areas were cultivated prior to seeding, and cultivation increases potential declines in organic carbon and total nitrogen (Tiessen et al. 1982; Aquilar et al. 1988; and Woods and Schuman 1988), which could also be a factor in declines.

Interestingly, Ibarra-Flores et al. (1995) designed a survey to study survival, climatic characteristics, and soil characteristics for buffelgrass for sites in North America and Kenya, its region of origin. They found that only total soil nitrogen and organic carbon differed among three survival regions. Buffelgrass spread in areas where total soil nitrogen and organic carbon concentrations were least (total N = 0.1%, organic C = 0.9%), intermediate concentrations occurred where buffelgrass simply persists (total N = 0.3%, organic C = 2.6%), and the greatest concentrations occurred where the grass died (total N = 0.5%, organic C = 4.4%). Because reference sites or uncultivated sites were not included in the study, these survey data do not

provide enough information on a causal relationship between soil differences and buffelgrass presence.

Other studies concentrate on soil nutrient content influences on buffelgrass; however, they do not concentrate on how buffelgrass alters soil properties. Christie (1975) found in a study conducted in Queensland, Australia, that the growth of buffelgrass on sandy red soils was delayed when available phosphorous (0.01 N H₂SO₄ extractable) was less than 25mg kg⁻¹. Hacker (1989) found that when buffelgrass is planted with a legume, either siratro (*Macropodium atropurpureum*) or finestem stylo (*Stylosanthes guianensis*), populations of buffelgrass generally maintain high density as long as the legume persists. If the legume fails to persist, the buffelgrass gradually dies out. It is possible that for these particular locations, there was not an adequate phosphorous or nitrogen supply to support buffelgrass persistence.

Christie (1975) found that in semi-arid Queensland, Australia, in *Acacia* and *Eucalyptus* woodlands with red earth soils, buffelgrass readily establishes beneath tree canopies and has limited spread in adjacent inter-tree areas. This is believed to be a result of the greater availability of phosphorous in soils beneath mature trees (Christie 1975). Bishop et al. (1974) also found that trees and downed logs provided a more favorable microhabitat than open areas. Rasmussen et al. (1986) found that regardless of the addition of tebuthion, a broad spectrum herbicide used to control weeds, the average height and shoot weight of buffelgrass seedlings were greater when they were grown in soil that was collected from underneath honey mesquite canopies as compared to soils collected from interspaces. This suggested greater nutrient concentrations in the soils beneath these species.

It appears no studies have been done on soil property changes under the influence of buffelgrass without the additional influence of cultivation or a prepared seedbed with or without nutrient additions. Most studies that tested for soil properties focused on the properties of soils under the influence of buffelgrass and cultivation or that measure the deficiencies related to buffelgrass cultivation requirements without a comparison of the direct effects of buffelgrass on soil properties (Humphreys 1967, Brzostowski 1962, Christie 1975, Cox et al. 1988, Graham et al. 1981, Mutz and Scifes 1975, and Peake et al. 1990).

Susceptibility of Buffelgrass to Competition

There is not an extensive literature that presents data on successfully suppressing buffelgrass germination, growth, or spread through plant competition. In many cases, buffelgrass has shown to be more competitive as an established plant. Table 1 displays experimental studies on buffelgrass competition. Table 2 summarizes results of observational studies on buffelgrass relationships with other species in ecosystems. Several studies indicate that buffelgrass has an overall negative effect on native plant communities (Sands et al. 2009; Clarke et al. 2005; and Daehler and Carino 1998); however, buffelgrass has a tendency to decline after several years of growth (Bishop et al. 1974; Ball 1964; and Cook 1984). This may enable early native colonizers to establish and compete for space and resources. Once other species have a chance to establish, it may be difficult for buffelgrass to once again become vigorous. There are a few tantalizing studies in Table 1 that suggest that further examining competitive suppression (by giving native or resident species competitive advantages) as a management option for buffelgrass is warranted.

There are some studies that demonstrate that previously established plants, particularly grasses, appear to be competitive with buffelgrass. McIvor (2003) presents evidence that suggests other species may be able to compete with buffelgrass seedlings during early buffelgrass establishment. McIvor suggests that factors affecting the spread of buffelgrass are twofold: soil fertility and competition with other plants. He hypothesized that buffelgrass is strongly competitive as an established plant, but may be only weakly competitive as a seedling. Tests were run by comparing the survival of buffelgrass seedlings with and without competition, and the results showed that with the removal of above ground competition, buffelgrass seedlings had a much greater survivability than buffelgrass seeded in sites with above ground competition. Also, in competition treatments, buffelgrass individuals mostly remained as a single tiller and none of them flowered, while plants free from competition produced multiple tillers and flowered.

Cook and Dolby (1981) found that when buffelgrass was broadcast into untreated and mown native pastures in Queensland, Australia, it experienced competition with native vegetation. Competition increased over time in pastures treated with herbicide prior to seed broadcast and in cultivated seedbeds, mostly from two volunteer species consisting of speargrass (*Heteropogon contortus*), a native to Australia, and natal grass (*Rhynchelytrum repens*), not native to the region.

Two studies by Stevens and Fehmi (2009a and 2009b) provide information on competition between buffelgrass and the native Sonoran grass, Arizona cottontop (*Digitaria californica*). Stevens and Fehmi (2009a) found that buffelgrass, as an established seedling, reduced the aboveground biomass production of Arizona cottontop by 69% compared to control plants and reduced the reproductive output of Arizona cottontop. Also, Arizona cottontop grown with buffelgrass experienced significantly lower water-potentials compared to control plants. Arizona cottontop did not have a significant neighbor effect (only 22% reduction) on the aboveground biomass accumulation of buffelgrass compared to buffelgrass control plants; and buffelgrass had a 35% reduction in biomass accumulation due to intraspecific neighbor affect.

Stevens and Fehmi (2009b) tested the competition between buffelgrass and Arizona cottontop at different times of emergence and establishment for Arizona cottontop. Buffelgrass has been known to germinate earlier than native species in introduced habitats and has a greater emergence response to relatively low precipitation, contributing to its resource acquisition success (Ward et al. 2006), making it a vigorous competitor. Since buffelgrass may emerge earlier than Sonoran Desert natives plants it may have a physiological advantage for resource acquisition. However, if natives can establish prior to buffelgrass emergence and establishment, they may become more competitive. Buffelgrass neighbors of the same age and older caused declines in Arizona cottontop biomass production and reproduction. However, with a 21-day advantage, Arizona cottontop was effective at reducing the competitive effect of buffelgrass neighbors on Arizona cottontop after 80 days of growth. When Arizona cottontop plants were the same age or younger than buffelgrass, the buffelgrass caused an 87% and a 97% reduction in Arizona cottontop aboveground biomass, respectively. The aboveground biomass of Arizona cottontop plants was reduced by 97% by older buffelgrass plants, but reduced 79% by older Arizona cottontop plants, suggesting that interspecific competition is more intense than

intraspecific competition. This scenario is reverse for buffelgrass competition. Also, younger buffelgrass plants showed reductions up to 86% in biomass only with older buffelgrass neighbors.

A few studies demonstrate the ability for other plant species to invade cultivated buffelgrass areas. In Cook and Dolby (1981), cultivated seedbeds with buffelgrass experienced invasion by speargrass and natal grass. Ball (1964) observed in a cultivation and seed sowing study in the rangelands of Texas that buffelgrass spread rapidly, but native grass species would begin to re-establish and fill in the gaps after two years. Eventually, the introduced grasses declined in relative abundance compared to the native grasses. Mayeux and Hamilton (1983) conducted studies on the response from fire and soil-applied herbicides in buffelgrass pastures on common goldenweed (*Isocoma coronopifolia*), a small native subshrub in the southwestern U. S. that occurs only on the Rio Grande Plains of southern Texas and northwestern Mexico. Common goldenweed has a tendency to infest buffelgrass dominated rangelands, and rangeland researchers were trying to investigate with use of fire and herbicides how to eradicate the species. Without treatment, the common goldenweed stands thickened over a 3 year period competing for space with buffelgrass.

The competition factors are not thoroughly accounted for in these correlative observations, and study areas were either cultivated or were a prepared seedbed. Several studies suggest that initially buffelgrass is a stronger competitor and establishes rapidly. However, over time due to competition with itself and other species, and possible the release of allelopathic chemicals, which also may be a factor unaccounted for in the above studies; buffelgrass may hinder or exclude itself after several years of establishment. Older buffelgrass stands have required continued cultivation and reseeding due to reduced vigor (Bishop et al. 1974; Cook 1984). In addition, residual effects of formerly infested buffelgrass may remain until inhibitory chemicals are leached out of soils.

Hussain et al. (1982) conducted several germination and growth experiments that suggest allelopathy may be responsible for the initial success of buffelgrass, then its decline, in Pakistan rangelands. Buffelgrass and *Bothriochloa pertusa* were both mutually suppressed when planted alone with five other common Pakistan range plants, with each other (Buffelgrass $\times$ *Bothriochloa pertusa*), and when with themselves. In addition, both in pot and field experiments, the growth of other grasses that were growing in soils that contained or previously contained buffelgrass or *Bothriochloa* decreased compared to controls. A previous study by Akhtar et al. (1979) found that toxic root exudates and water extracts contained substances that showed an inhibitory effect on *Chrysopogon aucheri*, another introduced range grass valued in Pakistan; and water extracts, from soaking buffelgrass for 48 and 72 hours, prevented germination of both buffelgrass and *Chrysopogon*. Due to these results, Hussain et al. (2010) suggest allelopathy may not only result in decreases in other species density and growth, but may also have inhibitory effects on itself (auto-toxicity). Hussain et al. (2010) found that toxicity of aboveground parts had a greater toxicity than roots. Extracts from buffelgrass did have inhibitory effects on germination and caused decline in biomass of roots and shoots in several tested species. Viability tests on seeds showed that seeds remained viable although were prevented from germination. This study also demonstrates the possibility of inhibitory effects from leachates resulting from rain on litter.

In contrast to the above studies, Cheam (1984) found that buffelgrass had a possible allelopathic effect in established buffelgrass roots, and there was not an inhibitory affect due to shoots. He tested established buffelgrass competition with calotrope (*Calotropis procera*), which is considered an undesirable pasture weed in Australia. He used buffelgrass at different densities and ages and found that the calotrope was drastically suppressed in growth, irrespective of buffelgrass densities. However, when buffelgrass and calotrope were germinated together there was no marked suppression. He also tested germination and growth of calotrope in cleaned soils that previously had grown buffelgrass. There was no inhibition of germination; however, there was an inhibitory effect on the growth of calotrope, but not as much as with established live buffelgrass individuals. It is likely that until inhibitory chemicals are leached out of the soil, there will continue to be an inhibitory effect on other plants. In addition, it is uncertain specifically what parts of the buffelgrass plant contain possible allelopathic chemicals and which parts may contain greater amounts.

Seed Bank Longevity

Several studies provide evidence that buffelgrass seeds can remain viable in the soil seed bank and potentially contain factors that contribute to latent germination. With these factors in mind, buffelgrass could have an extended impact on native soil seed banks even after treatment and removal of established plants. Winkworth (1963) compared germination of stored versus buried seeds over a three and a half year period. Buried seeds were excavated monthly and germination tests were done in soil; however, the number of seeds recovered was not counted. Buried seeds began with a 30-35% germination rate and continued at this level for 8 months before a decline to 12% at the end of year one. Germination dropped to about 10% and maintained at this level for two years. In contrast, stored seed gained in germinability after 8 months to its peak at 18 months with 94% germination. It then decreased rapidly to 64% at month 24 where it did not drop drastically for the remainder of test period.

Parihar and Rai (1985) studied the seed germinability and viability during nine years of collection and storage of grasses under ordinary environmental conditions. Germination tests were conducted under uniform conditions at 32°C. For buffelgrass, the life span in storage was about 48 months with the greatest percent germination occurring at 24 months at 53% and declining to 11% by 48 months.

Hacker (1989) conducted several germination and viability experiments on buffelgrass fascicles and seeds under different treatments over a two year period. An initial experiment was used to determine the dormancy and survival of buffelgrass seed in the field. Ripe fascicles were harvested on 6 occasions from January until June and placed in nylon mesh envelopes and affixed to a bare soil surface. Samples were retrieved and germination and viability tests conducted on 10 occasions over a 13-month period. Germination of seeds within fascicles in the laboratory was less than 2% from all the envelopes retrieved in the first 8 months. For the remaining envelopes there was an increase in germination. For hulled seeds, germination had a higher percentage for older seeds than younger seeds at later retrieval dates. Viability remained relatively high throughout the study, rarely falling below 80%. Hacker (1989) also compared germination of seeds that had been exposed on a bare soil surface for 51 weeks to freshly harvested seed from the same locations. Older seeds had a higher germination in the fascicle and

hulled, than freshly collected fascicle and hulled seed. Seed that had been left on the bare soil surface for an additional 6 to 7 weeks did have a decrease in seed germination within the fascicle and with hulled seed (Hacker 1989).

Hacker and Ratcliff (1989) designed an experiment to determine if any climate-related genetic variation exists in dormancy and dormancy-break characteristics. High temperature and low temperature treatments were prescribed for several varieties of buffelgrass. High temperatures increased germination for all cultivars of buffelgrass used in this study until after week 12, which resulted in a decline in germination due to seed mortality. Low temperature treatments with and without moisture had little or no effect on germination; however with moisture there was an increase in mortality.

Lahiri (1964) presented evidence that the spikelets of buffelgrass contained germination inhibitors and that rain allowed for leaching of germination inhibitors for buffelgrass seeds. Germination was inhibited while grains were still enclosed in spikelet glumes. Lahiri hypothesized that once these inhibitors were leached out, germination would be able to commence. Husked grains had a significant increase in germination. Hacker (1989) also found a higher germination rate for hulled seed. With the elimination of other factors such as osmotic pressure or water absorption by seed, Lahiri deduced that inhibition of germination may result from water-soluble inhibitors present in the spikelets. This may extend buffelgrass seed persistence and cause leached inhibitors to impact other seed germination.

These observations suggest that while buffelgrass seeds can remain viable in soil seed banks, the longevity of buffelgrass seed banks may not exceed that of many native species. This suggests that there may be opportunities for exhausting buffelgrass soil seed reserves through management activities.

Table 1. Experimental studies showing competition between buffelgrass and other species.

Study	Species (growth habitat)	Study location	Outcome
Ball (1964)	<i>Setaria leucopila</i> (grass), <i>Hilaria belangeri</i> (grass), <i>Pappophorum bicolor</i> (grass), <i>Trichachne californica</i> (grass) and <i>Panicum halli</i> (grass) in varying densities and diversity	Texas	Buffelgrass established and spread rapidly in cultivated, seeded areas with some fill by native grass species; in 2-3 years, native grasses became more dominant and buffelgrass began to decline.
Cook and Dolby (1981)	<i>Heteropogon contortus</i> (grass), <i>Aristida</i> spp., <i>Eragrostis</i> spp. (grass), <i>Digitaria</i> spp. (grass), <i>Cymbopogon refractus</i> (grass) and <i>Rhynchelytrum repens</i> (grass) in prepared pastures	Australia	Buffelgrass experienced competition when seeded into untreated native pasture and mown native pasture and competition developed in pastures treated with herbicide prior to buffelgrass seeding.
Stevens & Fehmi (2009a)	<i>Digitaria californica</i> (grass)	Arizona	Buffelgrass reduced aboveground biomass by 69% in competition pots. Neighboring effect by buffelgrass caused a 81% decrease in number of flowering culms. There was no significant effect (only 22% decrease) on aboveground biomass of buffelgrass.
Hussain et al. (1982)	<i>Bothriochloa pertusa</i> (grass), <i>Chrysopogon aucheri</i> (grass), <i>Hyparrhenia rufa</i> (grass), <i>Panicum antidotale</i> (grass), <i>Setaria italic</i> (grass) and <i>Pennisetum americanum</i> (grass)	Pakistan	When planted with other grasses, there was mutual suppression and when buffelgrass was planted with itself resulted in mutual suppression compared to control plants.
McIvor (2003)	<i>Stylosanthes hamata</i> or <i>S. Scabara</i> (forbs)	Australia	When buffelgrass was sown together with one of the <i>Stylosanthes</i> species there was a reduction in seedling survival and biomass per individual; eventually leading to no buffelgrass seedling survival in competition sites.
Pyon et al. (1977)	<i>Trichachne insularis</i> (grass)	Hawaii	The growth of <i>Trichachne</i> was suppressed when grown with buffelgrass compared to controls.

Table 2. Observational studies on buffelgrass competition in ecosystems.

Study	Species (growth habitat)	Study location	Outcome
Bowers (2006) ^a	Native Sonoran species	Sonoran Desert	Buffelgrass reduced species richness and densities.
Sands et al. (2009) ^a	Texas forbs and grasses	Texas	When under the influence of buffelgrass, native forb and grass cover, richness, and diversity decreased; forb stem density decreased; and the cover of other exotic grasses increased.
Clarke et al. (2005) ^a	Native Central Australian vegetation	Australia	Buffelgrass resulted in decline of all native growth forms over time.
Daehler & Carino (1998)	<i>Heteropogon contortus</i> (grass)	Hawaii	Introduction of buffelgrass to <i>Heteropogon</i> habitat resulted in decline of <i>Heteropogon</i> cover and the lowest diversity sites compared to sites with other introduced African grasses.
Daehler & Goergen (2005)	<i>Heteropogon contortus</i> (grass)	Hawaii	In unburned treatments, buffelgrass continued to dominate sites compared to burned treatments where aboveground buffelgrass biomass was removed and <i>Heteropogon</i> grass became dominant species.
Fiarfax & Fensham (2000)	<i>Acacia harpophylla</i> , <i>A. cambagei</i> , and <i>Eucalyptus</i> spp. (trees)	Australia	Study shows exotic pastures established after tree clearance of <i>Acacia harpophylla</i> , <i>A. cambagei</i> and <i>Eucalyptus</i> spp. systems, and buffelgrass was found to be significantly more abundant in Exotic pastures (comprising of 10% or more exotic grasses) than in Uncleared pastures that still contained native tree and shrub species.
Hamilton & Scifres (1982)	<i>Prosopis glandulosa</i> var. <i>glandulosa</i> , <i>Acacia rigidula</i> , <i>Acacia tortuosa</i>	Texas	Even after burns, woody plants re-established and appeared to not be hindered by buffelgrass growth, which declined after moisture-limited years and grazing.
Mayeux & Hamilton (1983)	<i>Isocoma coronopifolia</i> (forb)	Texas	Without fire and soil-applied herbicides in buffelgrass infested areas, <i>Isocoma coronopifolia</i> produced thick stands in three years.
McIvor (1998) ^a	Savanna woodland	Australia	Declines in native species diversity resulted after establishment of buffelgrass pastures

a. Study did not list specific plant species.

PART II. Summary of Revegetation Publications in the Sonoran Desert

Submitted 8 May 2011

We compiled as many Sonoran Desert articles published on revegetation as we are aware of. We included abandoned farmland situations, which may be less relevant to the Saguaro National Park (Park) context, because the total number of Sonoran revegetation articles is limited. In 2008 while preparing a review of desert revegetation research it was intended to include the Sonoran Desert with the Mojave Desert. Because of the sparse Sonoran literature and the shortcomings often present in the few available articles, only the Mojave was included in that review which was published in 2009 (Abella and Newton 2009). The new search for the current Park project uncovered little new material. The 5 available planting and 6 seeding articles in the Sonoran Desert are summarized in the following sections. If new articles are uncovered of which we are not aware, we would want to include them in this summary.

For each article, the location of the study and a summary of the methods, species included, project conclusions, and study limitations are included.

Outplanting articles

1. Bainbridge, D.A., and R.A. Virginia. 1990. Restoration in the Sonoran Desert of California. Restoration and Management Notes 8:3-14.

Denuded highway borrow pit areas, south of Indio, CA, in the western Sonoran Desert, with less disturbed sites dominated by *Larrea tridentata* shrublands including *Cercidium floridum* and other species. Much of the article provides general descriptive information and observations about the sites and undisturbed areas. Some data on the survival of *C. floridum* outplants are provided in Fig. 2, showing that after about a year $\geq 80\%$ of the trees survived with buried clay pot, capsule, or deep pipe irrigation, whereas 'conventional basin irrigation' (which was not well described) resulted in 0% survival. The paper also noted that seeding *C. floridum* was not successful, but the context of the seeding was not well described.

2. Bainbridge, D.A. 1994. Tree shelters improve establishment on dry sites. Tree Planters' Notes 45:13-16.

Denuded site along a highway near the Salton Sea and in Anza-Borrego Desert State Park, both in California. At the first site, 10 *Prosopis glandulosa* were enclosed by each of three types of protective shelters. After an unclear time period, survival ranged from 0% in rigid plastic-mesh protectors to 70% in TUBEX tree shelters. At the second site, survival of *Fouquieria splendens* was around 90% with tree shelters and 10% without. *Ambrosia dumosa* survival was about 75% with shelters and 45% without. *Atriplex canescens* had no plants alive without shelter compared to 45% with shelter. *Larrea tridentata* had similar survival with and without shelter of about 60%. A major shortcoming of this article is that it is not clearly reported how many months or years after planting these survival data correspond to.

3. Bainbridge, D.A., J. Tiszler, R. MacAller, and M.F. Allen. 2001. Irrigation and mulch effects on desert shrub transplant establishment. *Native Plants Journal* 2:25-29.

Western Sonoran Desert in the Imperial Valley east of San Diego, at an abandoned borrow pit with surrounding vegetation dominated by *Larrea tridentata* flats with occasional *Prosopis glandulosa*. A total of 144 *P. glandulosa* (each ca. 20 cm tall) were planted and all enclosed with tree shelters in November 1995. Three different mulch treatments (pine bark chips, vertical corn sprigs, and none) and three different irrigation treatments (deep pipe, buried clay pots, and hand watering) were tested. Note that all of the plants received some irrigation so that survival without irrigation was not tested. Survival was monitored for 3.5 years. Mulch did not affect survival, and the 3.5-year survival rate was 71% for deep pipe, 52% for clay pot, and 23% for hand watering irrigation treatments.

4. Bean, T.M., S.E. Smith, and M.M. Karpiscak. 2004. Intensive revegetation in Arizona's hot desert: the advantages of container stock. *Native Plants Journal* 5:173-180.

Abandoned farmland 80 km southwest of Phoenix, AZ, with adjacent less disturbed sites dominated by *Larrea-Ambrosia-Atriplex* shrubland. The paper describes a seeding and outplanting of 17 native perennial species, though the identities of all 17 species that were tested are not provided. Data are shown in Table 1 for six native shrub species illustrating perceived low establishment through seeding ($\leq 2\%$ of seeds resulting in seedlings after one year) but relatively high survival rates of 60-100% among species after one year for irrigated, 3.8-L greenhouse-grown outplants. It is important to note, however, that the survival rate given applies to the six species that became established; apparently the other 11 species (which were not listed) had lower survival rates. In a separate planting shown in Table 2, 1-year survival for six native shrubs ranged from 69-96% for 3.8-L outplants, which was overall greater than for rose or paper pots (paper pots can be planted with the plant and biodegrade). All plants were irrigated during the study so survival without irrigation cannot be assessed. Based on their study conditions in the two plantings, *Acacia greggii*, *Ambrosia dumosa*, *Larrea tridentata*, *Lycium exsertum*, *Pleuraphis rigida*, *Prosopis velutina*, and *Atriplex canescens*, *A. lentiformis*, and *A. polycarpa* can become established through one year as 3.8-L outplants with irrigation.

5. Cox, J.R., R.D. Madrigal, and G.W. Frasier. 1987. Survival of perennial grass transplants in the Sonoran Desert of the southwestern U.S.A. *Arid Soil Research and Rehabilitation* 1:77-87.

At a site 30 km south of Tucson, AZ, herbicide was used to reduce woody competition and contouring was used to retain on-site rainfall to evaluate the establishment of 9-week-old perennial grass species. Only two of the 14 species tested, *Bouteloua curtipendula* and *B. gracilis*, were native. After 32 months, survival was 18% for *B. curtipendula* and 28% for *B. gracilis*.

Seeding articles

1. Abella, S.R., J.L. Gunn, M.L. Daniels, J.D. Springer, and S.E. Nyoka. 2009. Using a diverse seed mix to establish native plants on a Sonoran Desert Burn. *Native Plants Journal* 10:21-31.

Sonoran uplands, northeast of Cave Creek, AZ. Post-fire seeding using 28 native species, establishment monitored for 3 years which was a dry period. Only about 25% of the species became established, but due to this highly successful subset, the seeding was deemed to have met management objectives. Successful species included: *Senna covesii*, *Aristida purpurea*, *Phacelia crenulata*, *Eschscholzia californica*, *Lesquerella gordonii*, and less consistently *Castilleja exserta*, *Lupinus sparsiflorus*, and *Baileya multiradiata*. *Sphaeralcea ambigua* became established initially then faded. *Larrea tridentata* and many other species either did not establish at all or became minimally established. While a variety of species were tested, genetic sources varied which is not necessarily good for isolating species effects.

2. Banerjee, M.J., V.J. Gerhart, and E.P. Glenn. 2006. Native plant regeneration on abandoned desert farmland: effects of irrigation, soil preparation, and amendments on seedling establishment. *Restoration Ecology* 14:339-348.

Sought to revegetate abandoned farmland currently dominated by weedy annuals near Phoenix, AZ in what was formerly *Larrea tridentata* and mixed species shrubland. In February 2002, 9 native shrub species (see their Table 1), 1 native forb, and 3 native grasses were seeded and their establishment monitored for 18 months. It is important to note that in Table 1 and throughout the paper, *Plantago ovata* is misclassified as an annual grass (it is an annual forb). This is disconcerting because it creates uncertainty about this study's ability to accurately identify species. It was difficult to extract meaningful data from this paper because the entire site was seeded, and given the site preparation treatments (e.g., fertilization, irrigation), we are not able to tell whether the seeding or these other factors influenced seedling establishment. Table 2 provides a list of species (but no quantitative data) that were observed at the site, but again, we cannot tell if the seeding benefited plant establishment. The study concluded that the total density of all native species was less than 1 plant m⁻² and the plots were dominated by exotic annuals. Fig. 4 provides the densities of *Bouteloua aristidoides* and *P. ovata* through time as a function of whether the plot was irrigated or weeded.

3. Jackson, L.L., J.R. McAuliffe, and B.A. Roundy. 1991. Desert restoration: revegetation trials on abandoned farmland in the Sonoran Desert lowlands. *Restoration and Management Notes* 9:71-80.

Revegetation project of abandoned, denuded farmland in *Larrea tridentata* lowlands between Phoenix and Tucson, AZ. Plots were seeded with native perennials (*L. tridentata*, *Lycium* [species not provided], *Atriplex*, and *Prosopis velutina*) and native annuals (*Bouteloua barbata*, *Bouteloua aristidoides*, and *Plantago ovata*) and the exotic, invasive annual *Schismus barbatus*. Few to no useable data were able to be extracted

from this publication. Control plots were not established, so we cannot isolate influences of the seeding on plant establishment. Establishment was only monitored for about 3 months after the January seeding, which did not cover the first summer and is not sufficiently long to assess whether any plants stayed established for any type of meaningful time period. Fig. 5 provides data on plant cover of *Atriplex* but it is not clear if the ‘other’ species represents only the seeded perennials, seeded perennials + seeded annuals (which also would include the exotic *Schismus*), or all of the above + non-seeded volunteers. Nevertheless, the paper does provide a discussion of the potential for mulch and weeding to assist plant establishment and reports an early effort at Sonoran Desert revegetation.

4. Cox, J.R., H.L. Morton, T.N. Johnson, G.L. Jordan, S.C. Martin, and L.C. Fierro. 1982. Vegetation restoration in the Chihuahuan and Sonoran Deserts of North America. U.S. Department of Agriculture, Agricultural Research Service, Reviews and Manuals No. 28. Tucson, AZ.

As we know this paper synthesizes past seeding projects, which often focused on exotic species. We did not go through the large tables to attempt to extract the native species, which is not as straightforward as it may seem given that manipulated cultivars often were used even for the ‘native’ species. It may be worth going through this document, however, to search for native species, with an understanding that methods were rarely well described for the seedings and monitoring in the early seeding projects.

5. Judd, I.B., and L.W. Judd. 1976. Plant survival in the arid Southwest 30 years after seeding. *Journal of Range Management* 29:248-251.

This retrospective study assessed whether species seeded in the mid-1940s were still present 20-30 years later. Two sites (the ‘semidesert shrub’ and ‘chaparral’), which were located on the Tonto National Forest, were either in or near the Sonoran Desert. The paper did not describe how the re-assessment was conducted or how it was determined if the observed plants actually resulted from the seeding and not natural establishment, and only presence/absence was reported (thus having only a single plant on the site of undefined area would result in being evaluated the same as if many plants had become established). These issues, combined with the limited information provided on the original seeding, limits the interpretational utility of the study. Nevertheless, the study at least provides a list of the species that were seeded. One of the conclusions was that the natives *Muhlenbergia porteri* and *Menodra scabra* were still present at one of the seeded sites after at least 20 years.

6. Roundy, B.A., H. Heydari, C. Watson, S.E. Smith, B. Munda, and M. Pater. 2001. Summer establishment of Sonoran Desert species for revegetation of abandoned farmland using line source sprinkler irrigation. *Arid Land Research and Management* 15:23-39.

This experimental seeding was conducted at the Tucson Plant Materials Center to evaluate moisture requirements for candidate species for revegetating abandoned farmland in situations where irrigation was possible. In July 1992 and 1993 prior to the

monsoon, 5 native perennial grass species, 4 native shrubs, 3 native trees, and 1 exotic perennial grass (*Eragrostis lehmanniana*) were seeded on plots that were intensively irrigated to test the effects of distance from a line source sprinkler. Plant emergence was monitored for 2-3 months following seeding. The study provided useful data on moisture requirements and early establishment of the species, which was the goal of the study. A much longer monitoring time period for survival would be needed for relevance to field restoration (e.g., to evaluate whether further irrigations were necessary), but the study does provide information on the potential early water requirements of candidate species. This may be relevant for considering whether to provide seeding projects with supplemental water and what timings and amounts of supplemental water may be useful.

Conclusion

There are not many papers on revegetation using native species in the Sonoran Desert. Moreover, the handful of papers that do exist often are quite limited with how the methods and data are described and reported, in addition to other shortcomings such as testing few species or monitoring outcomes for short time periods (< 1 year).

While conclusions from the existing literature cannot be considered strong, some general conclusions that could be tentatively drawn may include:

(i) Species selection is important, with some species establishing better than others (Abella et al. 2009). Additionally, a given species can perform differently in seeding versus outplanting, illustrated by Bean et al. (2004) and Bainbridge and Virginia (1990) that tested planting versus seeding on the same species. Unfortunately, a definitive list of successful species is not available at this time. However, *Senna covesii* seems to have potential, as the species became established in two studies (Banerjee et al. 2006, Abella et al. 2009). As noted above, however, it is not clear whether *Senna* plants in the Banerjee et al. (2006) resulted from the actual seeding or became established through natural successional processes.

(ii) Establishing some native species through seeding appears feasible even without supplemental irrigation in the Sonoran Desert upland subdivision (Abella et al. 2009), which is the most relevant to Saguaro National Park. Seeding is likely more risky in abandoned farmland contexts at lower elevations where much of the seeding research has been conducted. However, we have a different interpretation of Bean et al.'s (2004) seeding results in abandoned farmland. Survival rates of 1-2% were reported for seeds of some species, which they interpreted as low. In contrast, we believe that is high, as the recommended seeding rates by Bainbridge and Virginia (1990) are 100-500 live seeds m^{-2} . By seeding 100 seeds m^{-2} , a survival rate of 1% would result in 1 plant m^{-2} , which would be dense for the large shrub species Bean et al. (2004) considered. Clearly much work is needed in conducting and interpreting seeding trials.

(iii) Irrigation has shown mixed results in enhancing seeding and planting projects, and with some exceptions, has generally not been effectively evaluated. The potential for variations in effectiveness among different species, different types of irrigation systems, and the amount and timing of water delivered is enormous. The strongest data set on irrigation effects on long-term plant survival in either the Mojave or Sonoran Deserts is being collected by Lindsay Chiquoine

in the Mojave Desert (*in development*). Chiquoine has found that DriWater and hand watering are approximately equal at increasing survival (overall doubling survival compared to no irrigation) for 1+ year for salvaged transplants. Careful thought would be needed to decide the feasibility and utility of irrigation in the Saguaro National Park context.

Most of the critical questions central to planning revegetation projects in the Sonoran have been little evaluated. For example, one of the only studies to evaluate the key factor of species selection (Abella et al. 2009) had to use varying genetic sources for different species. Avoiding having genetics as a potential varying factor in isolating species effects would be desirable. No study has assessed the competitive abilities of native species with key exotic species such as buffelgrass in a restoration context. Ideally, the best candidate native species for restoration would be competitive with both exotic perennials and annuals. It also remains largely unclear which methods of revegetation (planting versus seeding) are most effective for different species, and which treatments (e.g., irrigation) some species may or may not need to become established. Lastly, the functional utility of different candidate species has not been assessed. Some species may have the abilities to become established in early successional environments and then help desirable later successional species to become established either through nurse plant effects or positively influencing general site conditions. Taking advantage of these types of natural processes could greatly reduce the cost of restoration and increase its effectiveness.

In summary, existing literature is valuable for illustrating some of the considerations about revegetation projects but is generally not able to directly address some of the key questions that Saguaro National Park has about revegetating sites disturbed by buffelgrass. However, the existing literature can help new research avoid some of the problems of the older research to maximize information gained. New, original studies are especially needed for screening a variety of native species for their ability to become established in disturbed sites and promote the recovery of indigenous ecosystems containing minimal amounts of exotic species.

PART III. Soil, Vegetation, and Seed Bank of Buffelgrass (*Pennisetum ciliare*)-Invaded Sites

Revised 31 December 2011



Buffelgrass-invaded site



Uninvaded site

Abstract

Understanding ecological differences between areas invaded and not invaded by exotic plants is a major priority for invasive plant science and management. At 14 sites in Saguaro National Park in the Sonoran Desert, we compared the soil, vegetation, and soil seed bank of patches invaded and not invaded by buffelgrass. This perennial is a priority for managers of conservation lands in the United States, Australia, Mexico, and other locations where the species is not native. Soil nutrients, such as $\text{NO}_3\text{-N}$, were approximately 2-fold greater in buffelgrass compared to non-buffelgrass patches. This was similar to the fertile-island effect of native, desert perennial plants reported in the literature. Average native species richness was identical (14 species 100 m^{-2}) between patch types, but native plant cover was 43% lower in buffelgrass patches. While overall native species composition did not differ between patch types, two species of special conservation significance – saguaro and bush muhly – had lower frequency and cover in buffelgrass patches. Unexpectedly, native seed bank densities were larger in buffelgrass compared to non-buffelgrass patches and were 40% denser than buffelgrass seed banks below individual plants of buffelgrass itself. Results suggest that: (i) soil nutrient status should not be unfavorable for native plant colonization at buffelgrass sites if buffelgrass is treated; (ii) at least in the early stages of buffelgrass patch formation (studied patches were ca. 10 years old), native vegetation species were not excluded but rather their cover was reduced; and (iii) the likely time-dependence of buffelgrass impacts indicates that a precautionary approach is to treat buffelgrass in its early invasion stages.

Introduction

A major focus of invasive plant science is understanding characteristics of areas invaded by exotic species and how they differ from non-invaded areas (e.g., Parker et al. 1999; Blank 2008; Olsson et al. 2012). Three key characteristics of ecosystems that could be impacted by exotic plant invasions include the soil, native vegetation, and soil seed bank. For example, some plant invasions can alter soil properties such as N availability, which in turn can induce other ecosystem changes (Parker and Schimel 2010). Altered soils are a legacy of site occupancy by the invasive species that can affect management needs of the site after the species has been removed (Corbin and D'Antonio 2004; Jordan et al. 2011). Some exotic plants also reduce native vegetation, altering habitat values and reducing propagules available for assisting the re-colonization of sites by native vegetation (Brown et al. 2008). Due to a lack of inputs or other mechanisms, some studies have reported that native seed banks become depleted on sites invaded by exotic plants (Cox and Allen 2008; Gioria and Osborne 2009).

Buffelgrass (*Pennisetum ciliare* (L.) Link), a perennial C₄ bunchgrass, is considered a major invasive threat to indigenous ecosystems since its introduction to areas such as Australia and arid lands of southwestern North America outside the species' native range in arid and semi-arid Africa, Asia, and the Middle East (Marshall et al. 2012). This species increases fuel loads and the risk of fire spread, which is a concern to land managers especially in areas such as the Sonoran Desert in North America not considered fire-adapted (Esque et al. 2007; Stevens and Falk 2009).

However, other potential impacts of buffelgrass on indigenous ecosystems in the absence of fire (Olsson et al. 2012), including on soil, vegetation, and seed banks that could have major legacy effects and influence site management after buffelgrass control, are not as well understood. Only one study known to us has examined influences of buffelgrass on soil properties (Ibarra-Flores et al. 1999). That study, conducted in cultivated buffelgrass pastures in Mexico, included the combined effects of pasture cultivation and buffelgrass occupancy and reported variable differences in soil properties between buffelgrass pastures and native rangelands among study areas. It remains unclear if or how buffelgrass might influence soils when invading indigenous ecosystems. By comparing invaded and non-invaded sites, several studies in Australia and the United States suggest that buffelgrass reduces both native species richness and cover in pasture and wildland ecosystems (e.g., Jackson 2005; Sands et al. 2009; McDonald and McPherson 2011; Olsson et al. 2012). As with soils, however, potential influences of buffelgrass on soil seed banks have been little examined. Hand pulling or herbicide can effectively treat buffelgrass, but the literature suggests that reestablishing native vegetation on treated sites can be important to forestall re-invasion (McIvor et al. 2003; Daehler and Goergen 2005; Tjelmeland et al. 2008). Unfortunately, reestablishing native vegetation through natural succession may be a slow process if native vegetation and soil seed banks have been reduced on buffelgrass-invaded sites in arid lands (Abella 2010).

This study was conducted to compare ecological properties of buffelgrass-invaded patches with non-invaded patches on a desert landscape. This type of comparative sampling, widely employed in invasive plant science, can help identify how post-invasion characteristics differ between invaded and non-invaded areas (Blank 2008; Hejda et al. 2009). Quantifying these differences has practical value for understanding characteristics of invaded areas to be managed and for

identifying key features to examine in other research approaches, such as before-after invasion or experimental study designs (Chambers et al. 2007). We assessed three questions:

(1) Do soil properties differ between patches invaded and not invaded by buffelgrass? We anticipated that some soil properties would show greater differences than others and that properties more susceptible to short-term biotic influences (e.g., C and N) would differ more sharply between patches than properties under longer term abiotic control (e.g., soil texture).

(2) Is native vegetation altered in buffelgrass compared to non-buffelgrass patches? We hypothesized that all native plant measures (species richness, diversity, and cover) would be lower in buffelgrass patches, which also would exhibit different species composition compared to non-buffelgrass patches.

(3) Do buffelgrass and non-buffelgrass patches contain different soil seed banks? We expected that buffelgrass seed bank density would be greatest in buffelgrass patches and that native seed density would be greatest in non-buffelgrass patches.

Methods

Study Area

We conducted this study within the 36,960-ha Saguaro National Park (Park), 15 km northwest (Saguaro West, Tucson Mountain District) and 8 km east (Saguaro East, Rincon Mountain District) of Tucson, AZ (Figure 1). The Park lies within the Arizona Upland Subdivision of the Sonoran Desert, containing a scrubland or low woodland physiognomy with a diverse assemblage of shrub-trees, cacti, forbs, and graminoids (Brown 1994). Saguaro cactus (*Carnegiea gigantea* (Engelm.) Britton & Rose) is a characteristic species of this region. The climate in Tucson, AZ (Airport Weather Station, 787 m in elevation, 1930 to 2010 records), includes an average of 29 cm yr⁻¹ of precipitation, an average daily July high temperature of 37°C, and an average daily January low temperature of 4°C (WRCC 2011). Topography is rolling with hills, alluvial fans, and concave drainageways. Soils are primarily derived from granite and classified as Torriorthents and Haplargids (Cochran and Richardson 2003). Livestock grazing is not authorized in the park. The Park has been visited by > 600,000 people yr⁻¹ since 1983, although most visitation is concentrated along park roads and to a lesser extent trails (National Park Service, Public Use Statistics Office, Denver, CO). Buffelgrass was first observed in the study area by park managers in 1989 (records kept by Saguaro National Park, Tucson, AZ).

Data Collection

Using a map provided by the Park (Tucson, AZ) of buffelgrass sites (containing patches covering 25 to 500 m²) within the park, we randomly selected 20 sites for field reconnaissance. After reconnaissance and rejecting sites not containing buffelgrass or not able to be located, we sampled 14 sites (one in the western and 13 in the larger and more extensively invaded eastern district; Figure 1). Based on photographs and observations of managers, the buffelgrass patches we examined were estimated to have been formed by approximately 2000, making them about

10-15 years old at the time of this study (records kept by Saguaro National Park, Tucson, AZ, and P. Grissom, Saguaro National Park, personal communication). Based on the size of patches, this age estimation appears consistent with Olsson et al.'s (2012) chronosequence of buffelgrass patches in a nearby study area. Sites ranged in elevation from 780 to 1150 m, and their locations and other characteristics are summarized in Appendix A. We established a 100-m² circular plot in the center of the buffelgrass patch and in a paired non-buffelgrass patch at each site. Non-buffelgrass patches were selected as near as possible (within 50 to 150 m) and on topography as similar as possible to the buffelgrass patch.

We recorded geography and plant community data and collected soil samples on each plot. From the center of each plot, we recorded geographic location and elevation using a global positioning system, slope gradient using a clinometer, and aspect using a compass and transformed following Beers et al. (1966). We visually categorized the areal cover of each live vascular plant species on each plot following cover classes modified from Peet et al. (1998): 1 = < 0.1% cover, 2 = 0.1 to 1%, 3 = 1 to 2%, 4 = 2 to 5%, 5 = 5 to 10%, 6 = 10 to 25%, 7 = 25 to 50%, 8 = 50 to 75%, 9 = 75 to 95%, and 10 = 95 to 100%. Nomenclature and classification of growth form and native/exotic status follow NRCS (2011). We collected four subsamples plot⁻¹ of the 0 to 5 cm mineral soil (totaling a 400-cm³ sample plot⁻¹) for bulk density analysis from within 10 cm of the crown of the four largest buffelgrass plants in buffelgrass plots and in interspaces $\geq$ 1 m from the nearest perennial plant in non-buffelgrass plots. We collected soil samples for laboratory characterization using the same methods. Vegetation, soil, and seed bank sampling occurred near the peak of the spring growing season from March 21 to April 25, 2011.

We collected samples of the 0 to 5 cm (which could include litter) soil seed bank from interspaces on all plots and from below buffelgrass on all buffelgrass plots, and, when $\geq$ three individuals were present, from below canopies of the native perennials brittlebush (*Encelia farinosa* Gray ex Torr.) and cactus apple (*Opuntia engelmannii* Salm-Dyck ex Engelm.). Samples were collected from three individuals of each of these microsite types per plot, representing the largest perennial individuals and interspaces available on plots. Three subsamples were collected from each individual, equally spaced around the perennial plant 10 cm from its root crown and every 10 cm in a circular pattern in the interspace. Soil was composited for all individuals of a microsite type for each plot to result in a 1200-cm³ seed bank sample per microsite type per plot.

Soil and Seed Bank Analysis

Soil samples were analyzed for bulk density by sieving out coarse fragments > 2 mm in diameter, oven drying the fine fraction at 105°C for 24 hr, and weighing both fractions and determining the volume of coarse fragments by water displacement. The fine fraction was analyzed for texture (hydrometer method following Tan [2005]); pH and electrical conductivity (saturated pastes); CaCO₃ (manometer); organic C and total N and S (dry combustion using an elemental CNS analyzer, with organic C determined by subtraction of inorganic C from total C); available P (Olsen method); NO₃-N (2 M KCl extraction, ion chromatography method); and NH₄-N (2 M KCl extraction, salicylate colorimetric method) following Burt (2004). The samples for the available N analysis were stored in a chilled cooler immediately after collection and extracted by the laboratory within 24 hr.

To assay the readily germinable fraction of seed banks using the emergence method (Bakker et al. 1996), we filled 4-L cylindrical pots two-thirds full with potting soil (1:3:1 mulch:sand:gravel) and placed 360 cm³ of seed bank soil in a layer 2 cm thick on top of the potting soil. Pots were randomly arranged on a bench in a greenhouse with temperatures fluctuating between 21 (nighttime) and 32°C (daytime). Samples were started in May 2011, and over a three-month period, were watered by hand twice per week to moisture capacity. Pots containing only potting soil were also randomly arranged to check for seed contamination (which was not detected during the study). Seedlings were inventoried twice weekly and removed from pots when identified to the finest taxonomic resolution possible. Not all seedlings matured to allow accurate identification, and 59 (14%) of 436 total seedlings were only identified to growth form (forb or graminoid). An unknown forb that consistently died a few days after the cotyledon stage constituted 61% of the total unidentified seedlings. Unknowns were included in seed totals but were not included in species richness and species composition analyses.

Data Analysis

Data were analyzed using several multivariate techniques conducted in the software PC-ORD (version 6; McCune and Mefford 1999) and bivariate and univariate techniques conducted in SAS (version 9.2; SAS Institute 2009). The soil data were ordinated using principal components analysis (cross-products matrix derived from correlation). Each topographic variable, soil measure, and seed bank density (by microsite) was compared between buffelgrass and non-buffelgrass patches using a paired *t* test, which was not corrected for multiple comparisons because each variable in the univariate part of our analysis was considered independent (Cabin and Mitchell 2000). We calculated buffelgrass percent cover and the total cover of native species (exotic species other than buffelgrass were recorded on nine plots and never constituted > 1.5% cover) using the midpoints of cover classes. We compared these variables and vegetation species richness (per 100-m² plot) and Shannon's diversity index (calculated in PC-ORD with an input matrix of 0 to 10 corresponding to cover classes) between patch types with paired *t* tests.

We further compared vegetation species composition between patch types using several techniques. Based on a matrix of cover classes, which qualitatively returned the same conclusions as cover classes converted to percent cover and relative cover class (target species cover class/∑ all species cover classes on each plot), we used non-metric multidimensional scaling (NMS) to ordinate vegetation species composition in PC-ORD's slow and thorough mode (McCune and Mefford 1999). We displayed the ordination as a joint plot with environmental variables and species as vectors to illustrate correlations with ordination axes. We conducted ordinations with and without buffelgrass included in the species matrix. We tested the hypothesis of no difference in species composition (based on relative cover) between buffelgrass and non-buffelgrass patches (also including and excluding buffelgrass from the species matrix) using blocked multi-response permutation procedures (Euclidean distance, no median alignment within blocks because data were paired). We used blocked indicator species analysis in PC-ORD with significance determined through 1000 permutations to identify relationships of individual species with patch types. Indicator species analysis combines the relative frequency (based on the number of sampling units a species occupies) and relative abundance (percent cover in this

study) of a species to produce an indicator value ranging from zero (no indication) to 100 (perfect indication; Dufrêne and Legendre 1997).

Results

Geography and Soil

None of the geographic variables (elevation, slope gradient, and aspect) or soil physical variables (texture, bulk density, and coarse fragments) differed significantly between buffelgrass and non-buffelgrass patches (Table 1). Conversely, the soil chemical properties of electrical conductivity, organic C, total N, $\text{NH}_4\text{-N}$, and $\text{NO}_3\text{-N}$ were significantly and ca. 2-fold greater in buffelgrass patches. In the multivariate principal components analysis, the first principal component accounted for 35% of the variance in the soil data set, the second 15%, and the third 14% (64% overall). The ordination suggested that buffelgrass plots generally grouped in the center and upper right and were positively correlated with chemical variables such as electrical conductivity, N, and organic C (Figure 2).

Vegetation

Some, but not all, vegetation variables differed between patch types (Table 1). Buffelgrass averaged 45% cover in buffelgrass patches and was absent from non-buffelgrass patches. In buffelgrass patches, native plant cover was only 57% of its amount in non-buffelgrass patches. Conversely, native species richness and diversity were identical between patch types. The NMS ordination of multivariate species composition with buffelgrass included displayed a clear separation of patch types (Figure 2). Native species such as saguaro, brittlebush, bush muhly (*Muhlenbergia porteri* Scribn. ex Beal), and slender janusia (*Janusia gracilis* A. Gray) were positively correlated with non-buffelgrass patches, whereas buffelgrass and soil variables such as N and organic C were positively correlated with buffelgrass patches. The separation of patch types disintegrated, however, when buffelgrass was excluded. This also was supported by the blocked multi-response permutation procedures tests, where patch types differed significantly when buffelgrass was included (T -statistic = -9.4, $A = 0.43$, $P < 0.001$) but not when excluded (T -statistic = -0.8, $A = 0.00$, $P = 0.209$).

Of 60 taxa (56 native, 4 exotic) detected on plots (Appendix 2), 4 significantly indicated a patch type based on blocked indicator species analysis. Buffelgrass was a perfect indicator (indicator value [IV] = 100, $P < 0.001$) of buffelgrass patches. Saguaro (IV = 60, $P = 0.029$), brittlebush (72, 0.009), and bush muhly (72, 0.002) indicated non-buffelgrass patches. Brittlebush was present on all 28 plots across patch types, but had 6-fold greater relative cover in non-buffelgrass patches (Appendix A). Excepting saguaro and bush muhly that had sharply greater frequency in non-buffelgrass compared to buffelgrass patches, native species occurred with similar frequency in both patch types. However, native species typically had greater cover in non-buffelgrass patches. Few native species (e.g., velvet mesquite [*Prosopis velutina* Woot.]) exhibited greater frequency and cover in buffelgrass patches and none were significant indicator species.

Seed Bank

High variability in seed densities resulted in only one difference being statistically significant, yet trends emerged of potential biological importance (Table 1). First, buffelgrass seed bank density in the brittlebush microsite was significantly greater in buffelgrass compared to non-buffelgrass patches. Buffelgrass further averaged 645 seeds m⁻² below its own canopy. Second, although not statistically significant, native seed banks were unexpectedly larger in buffelgrass compared to non-buffelgrass patches in all three microsites. Furthermore, the density of native seed banks exceeded that of buffelgrass seed bank density by 40% below buffelgrass itself.

A total of 41 taxa identified to genus or species emerged, along with members of Cactaceae (Appendix 3). Of the 41 taxa, 38 (93%) were native. The only exotic taxa detected were buffelgrass, another perennial grass, Africa lovegrass (*Eragrostis echinochloidea* Stapf), and the annual grasses *Schismus* spp. Of the 38 native taxa, 50% were annual forbs, 11% annual-biennial forbs, 11% annual-perennial forbs, 8% each perennial forbs, annual graminoids, and perennial graminoids, and 5% were shrubs. The most abundant native taxa in the seed bank were, in descending order, sand pygmyweed (*Crassula connata* (Ruiz & Pav.) A. Berger), many flowered monkeyflower (*Mimulus floribundus* Lindl.), mealy goosefoot (*Chenopodium incanum* (S. Watson) A. Heller), toad rush (*Juncus bufonius* L.), green carpetweed (*Mollugo verticillata* L.), California cottonrose (*Logfia californica* (Nutt.) Holub), and Cactaceae. Seed bank species that also were detected in vegetation included desert tobacco (*Nicotiana obtusifolia* M. Martens & Galeotti), bush muhly, brittlebush, slender janusia, and canyon morning-glory (*Ipomoea barbatisepala* A. Gray).

Discussion

Soil

Similarity in soil type and properties such as texture and coarse fragments, in addition to similar geography, between buffelgrass and non-buffelgrass patches supports the idea that differences between patches in properties (e.g., N availability) under biological influence are likely linked to buffelgrass occupancy. Although isolating cause and effect of buffelgrass occupancy would require experimentation, results identify the current characteristics of buffelgrass-invaded sites. These are the characteristics that managers have to manage. Our results have similarities and differences with results of other studies and have important implications for managing sites invaded by buffelgrass.

Our results of greater amounts of soil properties such as N and organic C in buffelgrass patches contrast with work in buffelgrass pastures in Mexico, yet are similar to the ‘fertile island’ effect of native perennial plants. In cultivated, ≥ 10 -year-old Mexican buffelgrass pastures, Ibarra-Flores et al. (1999) found that at semi-arid and moist study areas, soil organic C was reduced by approximately 40% and total N by 25 and 40% compared to native rangelands. Reasons for these contrasting results with our study remain unclear and could be related to the cultivation that was associated with buffelgrass in their study, denser buffelgrass stands under cultivation, low species richness in the cultivated pastures, differences in climate between our study areas, or

pasture management practices (e.g., livestock grazing, which removes plant biomass) unlike the more natural ecological setting of the present study.

We compared buffelgrass patches with interspace soils not under a perennial plant canopy, but based on the published literature, buffelgrass appears to increase soil nutrients similar to native perennial plants. We are aware of six studies in the Sonoran Desert that compared soil chemistry between interspaces and a total of 7 native perennial species including the shrubs triangle bursage (*Ambrosia deltoidea* (Torr.) Payne) and creosote bush (*Larrea tridentata* (Sessé & Moc. ex DC.) Coville; Smith et al. [1987]; Butterfield and Briggs [2009]); the shrub-trees yellow paloverde (*Parkinsonia microphylla* Torr.; Butterfield and Briggs [2009]), honey mesquite (*Prosopis glandulosa* Torr.; Virginia and Jarrell [1983]), and velvet mesquite (Carrillo-Garcia et al. 2000; Schade et al. 2003, 2005); and the perennial grass big galleta (*Pleuraphis rigida* Thurb; Nobel [1989]). This literature portrays some variation among species and nutrients, but overall typically a 2-fold or greater abundance of nutrients such as NO₃-N below native perennials. For instance, Nobel (1989) found that total N at a 5-cm depth was twice as concentrated below big galleta as in interspaces. These influences of the native perennials are remarkably similar to our findings of approximately 2-fold greater concentrations of organic C and N below buffelgrass.

Buffelgrass influences on soils might change with time, underscoring the utility of unraveling the mechanisms by which buffelgrass influences soils. The patches we studied are estimated to have formed by approximately 10 years prior to this study. Thus, based on our study and Ibarra-Flores et al. (1999), buffelgrass may influence soils within 10 years of invasion. This is not uncommon for perennial plants (Scholes and Archer 1997). Perennial plants can form soil fertile islands through many mechanisms, such as trapping dust, harvesting nutrients from interspaces and concentrating them below the canopy via litterfall, root exudates and decomposition, providing protected habitat for other biota (e.g., small mammals) which also can concentrate resources, facilitating recruitment of annual plants that provide rapidly cycling fine biomass, and forming symbiotic relationships with soil microorganisms for some species (McAuliffe 1988).

Vegetation

While buffelgrass appeared to concentrate soil nutrients similar to native perennials, this fertile-island effect apparently did not provide a ‘nurse-plant’ effect that native perennials often provide for other native plants. Nurse effects, which result in the facilitated recruitment of ‘nursling’ seedlings, are well documented in many deserts including the Sonoran (e.g., Halvorson and Patten 1975; McAuliffe 1988; Carrillo-Garcia et al. 2000). If buffelgrass was providing nurse effects, the richness and cover of native plants should have been higher than in interspaces, a finding not observed. While native perennial grasses such as big galleta are key nurse plants, several traits might preclude buffelgrass from being a nurse like native perennials. For instance, the growth form of buffelgrass differs from native grass nurses by being denser with little or no space between the ground and main canopy. It also is possible that buffelgrass could produce allelopathic chemicals that inhibit other plants (Hussain et al. 2010), although many native species produce a variety of chemicals and still serve as nurses (Halvorson and Patten 1975). It also is possible that mature buffelgrass plants are more competitive than many native perennials, which can compete with their nurslings yet still have overall facilitative effects (Holzapfel and Mahall 1999). Some experiments have suggested that buffelgrass is a better competitor than

native Sonoran Desert perennial grasses (Stevens and Falk 2009). While buffelgrass appears to reduce native plants, it remains unclear whether buffelgrass stands have facilitative effects on buffelgrass's own recruitment.

Identical richness and diversity between buffelgrass and non-buffelgrass patches in this study sharply contrasts with previous research that has found that buffelgrass reduces these measures. Six studies, conducted in Australia (Franks 2002; Clarke et al. 2005; Jackson 2005), Texas (Sands et al. 2009), and Arizona (McDonald and McPherson 2011; Olsson et al. 2012), reported a consistent 2-3-fold reduction in species richness for areas most heavily infested with buffelgrass compared to indigenous ecosystems or pastures. In our study, buffelgrass did not exclude native species but rather reduced their cover.

As with buffelgrass influences on soil, time may be important in buffelgrass influences on vegetation (Olsson et al. 2012). In Australia, for example, Clarke et al. (2005) found that when native perennial grass sites were weakened by fire and drought in the early 1980s, buffelgrass came to dominate. In the first 5-10 years of buffelgrass dominance, buffelgrass did not influence richness, but after 1990 to the present, buffelgrass reduced richness by 2-fold. Although cultivated and grazed buffelgrass pastures appear to decline after a period of decades and can become partly colonized by native perennials, buffelgrass declines have not been reported in wildland settings such as our study area (Clarke et al. 2005; Olsson et al. 2012). We hypothesize that buffelgrass in our study area is in an intermediate stage of impacting native plant communities, and the next stage would result in declines in richness as natives are excluded and further cover reductions. Moreover, spatially continuous buffelgrass fuel loads can facilitate fire, which dramatically impacts mature desert plant communities (Esque et al. 2007; McDonald and McPherson 2011).

Buffelgrass influences on native species appeared relatively uniform across species, with two main exceptions. Saguaro cacti had a lower frequency in buffelgrass patches. If this lowered frequency is related to buffelgrass invasion, it is a major concern because in addition to saguaro's prominence in indigenous ecosystems, the species is economically important for tourism and recreational viewsheds. Also working in Sonoran Desert uplands, Olsson et al. (2012) did not observe a significant correlation between cover or density of saguaro and buffelgrass cover, but significantly fewer small (≤ 2 m tall) saguaro occurred where buffelgrass cover exceeded 43%. Careful consideration should be given to the possibility that buffelgrass can compete with saguaro directly or reduce cover of the nurse plants on which saguaro depends (Morales-Romero and Molina-Freaner 2008) even in the absence of fire (Olsson et al. 2012). The second exception was the reduction in the perennial grass bush muhly. This also is a potential concern if directly linked to buffelgrass invasion, as land managers are concerned that perennial grasses have declined from past livestock grazing or climate change and often wish to reestablish native perennial grasses (Abella and Newton 2009).

Seed Bank

Results were inconsistent with the expectation that native seed banks would be sparser in buffelgrass compared to non-buffelgrass patches. In fact, native seed banks were larger in buffelgrass patches in all three microsites and were denser than buffelgrass seed banks below

buffelgrass itself. Understanding underlying mechanisms for these results requires further research, and is especially warranted because the results differ from several studies reporting that native seed banks are depauperate (Cox and Allen 2008; Gioria and Osborne 2009) or at least compositionally altered (Vilà and Gimeno 2007) in areas invaded by exotic plants. Larger native seed banks in buffelgrass patches could result from seed retention prior to buffelgrass invasion and persistence during its occupancy, or post-invasion seed accumulation possibly because of mechanisms such as retention of seed by the buffelgrass vegetation structure. Because native plant cover was lowest in buffelgrass patches, yet native seed banks were greatest, the larger native seed banks have not corresponded with sufficient plant establishment to forestall lowered native plant cover.

Findings also suggest several important considerations for management. First, not knowing the potential persistence ability of the native seeds in buffelgrass patches, a pre-cautionary principle approach would be treating buffelgrass in as early of an invasion stage as possible if post-treatment recruitment potential of the native seed bank for site colonization is to be fully utilized. Second, it would be useful to determine recruitment potential from seed banks post-treatment and if management could stimulate the native seed bank but not buffelgrass germination. For example, a grass-specific, pre-emergent herbicide might be effective (Tjelmeland et al. 2008), because most (79%) of the 38 native taxa detected in the seed bank were forbs. This is potentially problematic for native grasses, however, especially considering that in the vegetation, a native grass (bush muhly) was sharply lower in buffelgrass compared to non-buffelgrass patches. Where practical, however, one strategy might be to use pre-emergent herbicide spot treatments (especially near buffelgrass plants where buffelgrass seed banks were largest) to allow for untreated areas where native grasses could emerge. Moreover, strategically facilitating recruitment of native grasses, or other desired species, through seeding, planting, or other treatments (e.g., establishing nurse plants or structures) might be useful where establishment through natural seed banks is not effective. Third, results also highlight that limitations of the seed bank for facilitating native plant recruitment should be recognized. As is typical across many ecosystems (Bakker et al. 1996), some species important in the vegetation (e.g., *Lycium* spp, yellow paloverde) were not detected in the seed bank. For these species, maintaining vegetation to produce seed or actively establishing these species might be important to facilitate site colonization by native species following buffelgrass treatment. Additionally, consideration should be given to the vegetation that may have existed in buffelgrass patches prior to buffelgrass establishment and what desired conditions are. For instance, if buffelgrass has simply filled in areas formerly relatively open, then maintaining sparse native plant cover might be warranted. On the other hand, if buffelgrass displaced formerly dense native vegetation patches or if competition is desired to potentially limit buffelgrass resurgence (e.g., Bakker and Wilson 2004), reestablishing denser native vegetation patches may be desirable.

Summary and Management Implications

This study provides several considerations for the management of buffelgrass sites related to the potential ecological effects of buffelgrass, the timing of management treatments, and post-treatment site management. The data indicated that soil nutrients (e.g., $\text{NO}_3\text{-N}$) were concentrated in buffelgrass patches, which should actually enhance soil fertility in these patches similar to the fertile-island effects of native perennials. Native plant cover, but not species

richness or diversity, was reduced in buffelgrass patches. Unexpectedly, native seed banks were actually larger in buffelgrass compared to non-buffelgrass patches, but it is unclear how long native seed banks might remain large in buffelgrass patches. These findings suggest that (i) the early treatment of buffelgrass patches while native plant species still persist might promote re-colonization by native vegetation of treated sites; (ii) soil nutrient status should not be unfavorable for native plant re-establishment on post-treatment buffelgrass sites; and (iii) two native species (saguaro and bush muhly) of conservation concern were lower in buffelgrass patches, warranting further research to determine if linked to buffelgrass occupancy.

Treating sites while native species still persist to promote site re-colonization might be especially important given that several studies suggest that buffelgrass has difficulty dominating within established stands of other species (McIvor 2003). If natural colonization does not sufficiently re-vegetate treated sites with native species, active restoration of native species might be important and is feasible in desert ecosystems (e.g., Abella and Newton 2009). Buffelgrass can be reduced or eradicated entirely from patches using herbicide or hand pulling (Rutman and Dickson 2002), but promoting site colonization by native species can be important for constraining resurgence of buffelgrass (Daehler and Goergen 2005). This observation also illustrates the potential utility of future research to try and identify how buffelgrass invaded these sites in the first place (e.g., if native vegetation was somehow weakened) and mechanisms behind the initial ecological effects of the invasion. It is not clear how buffelgrass originally invaded these sites, as invasion processes are not well understood generally and in the case of buffelgrass, could result from weakened native communities, open patches available for colonization, intense propagule pressure, or other factors (Stevens and Falk 2009).

Table 1. Characteristics of buffelgrass and non-buffelgrass patches in Saguaro National Park, Sonoran Desert. Values are mean (coefficient of variation, in %).

	Buffelgrass	Non-buffelgrass	t	P
<u>Geography</u>				
Elevation (m)	1019 (8)	1003 (9)	1.4	0.184
Slope gradient (%)	33 (104)	21 (76)	1.82	0.092
Aspect (transformed)	0.20 (96)	0.28 (135)	0.7	0.496
<u>Vegetation</u>				
Buffelgrass cover (%)	45 (47)	0 (0)	7.99	<0.001
Native cover (%)	16 (46)	28 (76)	3.28	0.006
Species 100 m ⁻²	14 (21)	14 (27)	0.27	0.791
Shannon diversity	2.5 (10)	2.5 (12)	0.22	0.827
<u>Soil (0 to 5 cm)</u>				
Sand (%)	67 (11)	68 (10)	0.7	0.495
Silt (%)	24 (30)	24 (25)	0.05	0.962
Clay (%)	10 (12)	9 (26)	1.71	0.112
CaCO ₃ (%)	2.3 (268)	2.8 (295)	0.91	0.379
pH	7.4 (5)	7.1 (8)	1.79	0.096
EC (uS cm ⁻¹) ^a	757 (50)	328 (57)	4.83	<0.001
Organic C (%)	1.7 (33)	0.9 (49)	4.82	<0.001
Total N (%)	0.16 (28)	0.09 (36)	5.93	<0.001
NH ₄ -N (%)	0.00110 (65)	0.00063 (56)	3.06	0.009
NO ₃ -N (%)	0.00140 (99)	0.00052 (61)	2.63	0.021
P (%)	0.0041 (40)	0.0034 (26)	1.53	0.149
S (%)	0.11 (181)	0.06 (123)	0.85	0.408
Bulk density (g m ⁻²)	0.91 (9)	0.98 (12)	1.99	0.068
Fragments (% wt.)	34 (14)	34 (18)	0.12	0.903
Fragments (% vol.)	22 (32)	22 (23)	0.01	0.990
<u>Buffelgrass seed bank^b</u>				
Buffelgrass (seeds m ⁻²)	645 (164)	—	—	—
Interspace (seeds m ⁻²)	10 (374)	30 (374)	0.62	0.547
Brittlebush (seeds m ⁻²)	222 (129)	0 (0)	2.45	0.037
Cactus apple (seeds m ⁻²)	232 (245)	0 (0)	1.00	0.374
<u>Native seed bank^b</u>				
Buffelgrass (seeds m ⁻²)	904 (221)	—	—	—
Interspace (seeds m ⁻²)	616 (144)	278 (100)	1.44	0.173
Brittlebush (seeds m ⁻²)	1015 (153)	427 (186)	1.74	0.115
Cactus apple (seeds m ⁻²)	649 (111)	185 (140)	1.76	0.153

^aElectrical conductivity.

^bSeed densities are provided separately for buffelgrass and native species according to sampling microsite, consisting of below buffelgrass, interspaces between perennial plants, or below the native perennials brittlebush (*Encelia farinosa*) or cactus apple (*Opuntia engelmannii*). The buffelgrass microsite was not present in non-buffelgrass patches.

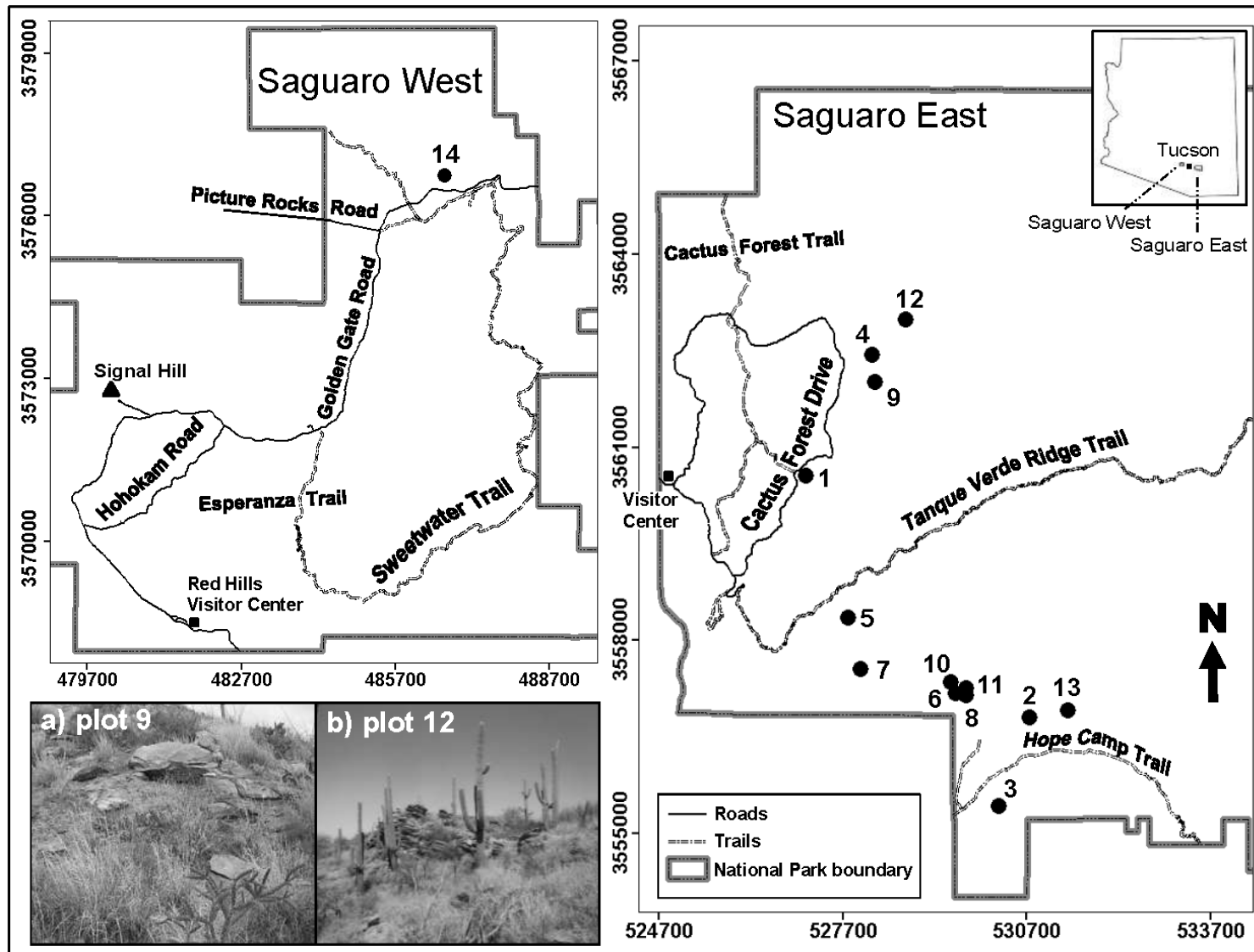


Figure 1. Location of study sites in Saguaro National Park, Sonoran Desert. Site numbers correspond to descriptions in Appendix A.

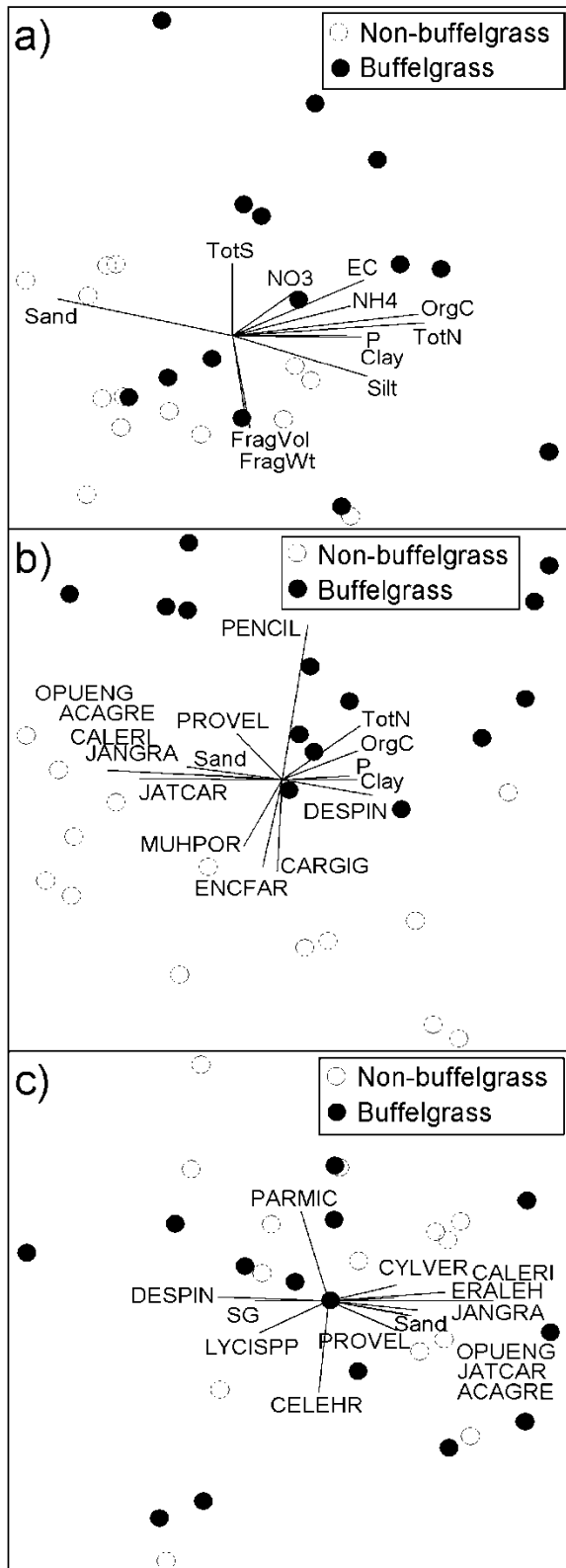


Figure 2. Ordination of (a) soil properties, (b) vegetation including buffelgrass, and (c) vegetation excluding buffelgrass in buffelgrass and non-buffelgrass patches of Saguaro National Park, Sonoran Desert. Vectors display correlations ($|r| \geq 0.50$) of variables with ordination axes. Abbreviations (a): EC, electrical conductivity; FragVol, coarse fragments by volume; FragWt, coarse fragments by weight; OrgC, organic C. Abbreviations (b): ACAGRE, *Acacia greggii*; CALERI, *Calliandra eriophylla*; CARGIG, *Carnegiea gigantea*; DESPIN, *Descurainia pinnata*; ENCFAR, *Encelia farinosa*; JANGRA, *Janusia gracilis*; JATCAR, *Jatropha cardiophylla*; MUHPOR, *Muhlenbergia porteri*; OPUENG, *Opuntia engelmannii*; PENCIL, *Pennisetum ciliare*; PROVEL, *Prosopis velutina*. Abbreviations (c): CELHR, *Celtis ehrenbergiana*; CYLVER, *Cylindropuntia versicolor*; ERALEH, *Eragrostis lehmanniana*; LYCISPP, *Lycium* spp; PARMIC, *Parkinsonia microphylla*; SG, slope gradient.

PART IV. Passive Colonization Following Buffelgrass Treatment, and Summary of Outplanting Effectiveness for Revegetation at Saguaro National Park

Contents

This report summarizes data provided by Saguaro National Park (Park) on (i) passive colonization along transects following buffelgrass treatment and (ii) outplanting effectiveness for establishing native species along the Cactus Forest Drive.

Passive Colonization

The Park collected pre-treatment data on plant counts and sizes (length/width dimensions used to calculate plant area) along permanent transects in 2005 prior to buffelgrass treatment and in 2009 after buffelgrass treatment (Backer and Foster 2007). Prior to treatment, transects contained only 34 native plant individuals compared to 645 buffelgrass individuals (Table 1). By 2009, however, the percentage of native individuals increased 12-fold from only 5% before treatment to 60% after treatment. *Encelia farinosa* (ENCFAR; brittlebush) comprised 84% of the native individuals. The only other species represented by more than 5 individuals was *Abutilon incanum* (ABUINC; pelotazo). Buffelgrass declined from 645 to 187 individuals after treatment.

An important finding related to the area occupied by plants was that buffelgrass was drastically reduced from a volume of 38 m³ to 0.7 m³ after treatment. Brittlebush comprised the greatest volume of native plant colonization, as it did for density.

Results suggest that treating buffelgrass achieved a greater reduction (based on before-after monitoring) in the volume occupied by buffelgrass than it did the density of buffelgrass, although there was still a 3-fold reduction in buffelgrass density. The diversity of native plants passively colonizing the transects was low – brittlebush comprised 84% of the colonizing native individuals. Brittlebush is a common colonizer of disturbed areas in southwestern deserts, but several other important colonizers, such as *Ambrosia* and *Sphaeralcea* spp. (Abella 2010), were not represented in the colonizing flora of the transects. Among many possible reasons for this paucity of colonization, insufficient time for colonization, alteration of sites by buffelgrass occupancy or treatment, suboptimal climatic conditions, or inherently poor site conditions for colonization might have limited colonization diversity.

Outplanting Effectiveness

Habitat in national parks is periodically disturbed for road maintenance, and few revegetation protocols of known financial cost exist for this disturbance, especially in deserts where extreme environments constrain natural revegetation. In the Park, we monitored survival of 1,554 outplanted individuals of 33 native perennial species for revegetating a 2006 re-construction project of the park's Cactus Forest Drive. Outplants were caged to deter vertebrate herbivory and provided with supplemental water in the hot, dry part of summer. Overall plant survival was high – 86% (1,340 of 1,554 outplants) – one year after planting. Survival was generally consistent across species, with survival > 50% for 32 of 33 (96%) species (Table 2). Fifteen species exhibited ≥90% survival and 24 exhibited ≥80% survival. Survival of two tree species

(*Parkinsonia microphylla* and *Prosopis velutina*), monitored for two years, declined little or not at all from the first to the second year and was 55% and 67% at two years.

The project met management goals of reestablishing a 1:3 lost: restored ratio of tree density required for habitat restoration of an endangered owl species and of reestablishing a range of native species for aesthetic and vegetation structural restoration. Budget estimates indicated a cost per plant of approximately \$55 from grow-out in a nursery through plant maintenance in the field. This cost also included supporting activities of site preparation, exotic plant control, and effectiveness monitoring. The monitoring data, combined with longer term observations, suggest that the National Park Service's revegetation strategy effectively established a range of native plant growth forms and met habitat restoration targets.

Table 1. Transect data summarized for pre-treatment (2005) and post-treatment (2009), illustrating increase in native species.

Species	Number of individuals per transect				2005 Total						2009 Total
	2005 LBC 1	LBC 2	Split Plot UBC	UBC 1 Whole			2009 LBC 1	LBC 2	Split Plot UBC	UBC 1 Whole	
ABUINC			1		1		12	3	3		18
ACACON	1				1		1				1
ARISPP									1		1
CALERI	5			2	7		2			2	4
CARGIG	1			1	2		1			1	2
CHAMS SPP									1		1
CYLBIG	2	2		1	5		2	1	1	1	5
DYSSODIA										1	1
ENCFAR		1	6	1	8		29	156	19	38	242
JANGRA	2	1			3		2	1			3
LYCIUM SP		1			1						
MAM SP				3	3						
MAMGRA								1			1
MAMSP										2	2
MENSCA										1	1
PARMIC										1	1
PENCIL	182	119	125	219	645		110	63	11	3	187
PROVEL		1		2	3			1		1	2
PROVEL **										1	1
TRICAL										1	1
UNKFRB								1			1
Total	193	125	132	229	679		159	227	36	53	475
Total minus PENCIL	11	6	7	10	34		49	164	25	50	288

Area occupied (sum of cm³ from plant dimensions, then converted to m³)

						2.243	0.162			
ABUINC	0	0	0.000152	0	0.000152	6	8	0.48202	0	2.888418
	3.146				3.146316					
ACACON	3	0	0	0	3	4.284	0	0	0	4.284
ARISPP	0	0	0	0	0	0	0	0.000294	0	0.000294
	0.761					0.346				
CALERI	1	0	0	0.001926	0.763056	9	0	0	0.000621	0.347517
CARGIG	0	0	0	0	0	0	0	0	0	0
CHAMS SPP	0	0	0	0	0	0	0	0.0012	0	0.0012
					0.909517	0.761	0.162			
CYLBIG	0.712	0.18	0	0.01785	4	6	4	0.000384	0	0.924384
DYSSODIA	0	0	0	0	0	0	0	0	0.001904	0.001904
		0.16				0.345	3.649	5.85691512		10.99385
ENCFAR	0	7	0.998325	0.001288	1.166563	8	8	5	1.1413375	5
	0.047				0.167409	0.345	0.433			
JANGRA	3	0.12	0	0	5	2	4	0	0	0.778648
		0.04								
LYCIUM SP	0	1	0	0	0.0414	0	0	0	0	0
MAM SP	0	0	0	0.000297	0.000297	0	0	0	0	0
MAMGRA	0	0	0	0	0	0	8E-05	0	0	0.00008
MAMSP	0	0	0	0	0	0	0	0	0.00024	0.00024
MENSCA	0	0	0	0	0	0	0	0	0.01944	0.01944
PARMIC	0	0	0	0	0	0	0	0	0.00342	0.00342
	11.52	9.78			37.95853	0.290	0.274			0.679275
PENCIL	7	3	7.634399	9.013925	8	2	4	0.10889775	0.005746	3
		0.07					1.156			
PROVEL	0	5	0	6.573	6.648072	0	2	0	7.488	8.6442
PROVEL**	0	0	0	0	0	0	0	0	6.2016	6.2016
TRICAL	0	0	0	0	0	0	0	0	0.601392	0.601392
							0.000			
UNKFRB	0	0	0	0	0	0	3	0	0	0.00033
	16.19	10.3			50.80132	8.617	5.839	6.44971087		36.37019
Total	4	7	8.632876	15.608286	2	3	5	5	15.4637005	7
Total minus	4.666	0.58			12.84278		5.565	6.34081312		35.69092
PENCIL	7	3	0.998477	6.594361	3	8.327	1	5	15.4579545	2

Table 2. Survival of native plant species along roadsides of Saguaro National Park, Arizona, one and two years after outplanting for tree species and one year after outplanting for other species

Species	No. planted	Survival (%)
Grass		
<i>Aristida purpurea</i>	34	94
<i>Bothriochloa barbinodis</i>	48	85
<i>Bouteloua repens</i>	77	92
<i>Digitaria californica</i>	29	100
<i>Heteropogon contortus</i>	43	98
<i>Muhlenbergia porteri</i>	32	97
<i>Setaria macrostachya</i>	31	90
Forb		
<i>Baileya multiradiata</i>	2	50
<i>Dalea pringlei</i>	16	75
<i>Isocoma tenuisecta</i>	112	86
<i>Menodora scabra</i>	44	75
<i>Nicotiana obtusifolia</i>	4	75
<i>Psilostrophe cooperi</i>	37	89
<i>Senna covesii</i>	30	60
<i>Sphaeralcea ambigua</i>	9	100
<i>Zinnia acerosa</i>	193	96
Shrub		
<i>Calliandra eriophylla</i>	26	88
<i>Dalea pulchra</i>	16	50
<i>Encelia farinosa</i>	94	93
<i>Ephedra trifurca</i>	13	15
<i>Ericameria laricifolia</i>	9	89
<i>Fouquieria splendens</i>	80	89
<i>Jatropha cardiophylla</i>	1	100
<i>Larrea tridentata</i>	85	80
<i>Simmondsia chinensis</i>	50	78
<i>Trixis californica</i>	49	90
Shrub-tree		
<i>Acacia constricta</i>	56	86
<i>Acacia greggii</i>	46	100
<i>Celtis ehrenbergiana</i>	30	93
<i>Gossypium thurberi</i>	31	94
Tree		
<i>Parkinsonia florida</i>	1	100 (100) ^a
<i>Parkinsonia microphylla</i>	123	62 (55)
<i>Prosopis velutina</i>	136	67 (67)

^aPercent survival after two years is provided in parentheses after the first-year survival.

Part V. Soil, Vegetation, and Seed Bank of a Sonoran Desert Ecosystem along an Exotic Plant (*Pennisetum ciliare*) Treatment Gradient

Submitted 31 December 2012

Abstract Ecological conditions following removal of exotic plants are a key part of comprehensive environmental management strategies to combat exotic plant invasions. The perennial buffelgrass (*Pennisetum ciliare*) is viewed as a priority exotic species for management in conservation lands of Australia, Mexico, North America, and other locales where the species alters indigenous disturbance regimes and displaces native biota. In Saguaro National Park of the North American Sonoran Desert, we assessed soil, vegetation, and seed banks on seven buffelgrass treatment types: five different frequencies of buffelgrass herbicide plus hand removal treatments (ranging from 5 years of annual treatment to a single year of treatment), untreated sites, and non-invaded sites, with 3 replicates of each of the 7 treatment types. The 22 measured soil properties (e.g., total N) differed little among sites. Regarding vegetation, buffelgrass cover was low ($\leq 1\%$ median cover), or absent, across all treated sites but was high (10-70%) in untreated sites. Native vegetation cover, diversity, and composition were indistinguishable across sites. Species composition was dominated by native species ($> 93\%$ relative cover) across all sites except untreated sites. Native soil seed bank density did not differ across sites, and of 41 species detected, 38 (93%) were native and 12 (29%; e.g., *Aristida purpurea*) were also in aboveground vegetation. Results suggest that: 1) buffelgrass cover was minimal across treated sites; 2) aside from high buffelgrass cover in untreated sites, ecological conditions were largely indistinguishable across sites; 3) soil seed banks harbored some species that were frequent in the aboveground vegetation; and 4) native species dominated post-treatment vegetation composition, and removing buffelgrass did not result in replacement by other exotic species.

Introduction

Understanding the condition of ecosystems following treatment of exotic plants is a key part of comprehensive exotic species control on conservation and managed lands (Corbin and D'Antonio 2012). Relative to similar, but non-invaded areas, post-treatment ecological condition can be conceived as contingent upon three main factors: impact of the exotic species to the ecosystem during the species' residence, legacy effects of the species persisting after the species is removed, and effect of the treatment itself (Zavaleta et al. 2001; Hejda et al. 2009). Exotic plants can impact ecosystems in numerous ways, such as competitively reducing native species, altering soil properties, and changing disturbance regimes (Levine et al. 2003; Wolfe and Klironomos 2005). These impacts do not necessarily dissipate upon removal of the species, with soil and seed bank modifications accrued during the species' occupancy often forming legacies persisting even after the species is treated (Ehrenfeld 2003; Parker and Schmel 2010; Schneider and Allen 2012). Exotic plant treatments themselves can have known or unintended non-target impacts, such as herbicide effects on native species or soil disturbance accompanying manually removing exotic plants (Sheley and Denny 2006; Flory and Clay 2009). Together, species impacts, legacy effects, and treatment influences can affect post-treatment condition of ecosystems relative to non-invaded areas (Jordan et al. 2011; Owen et al. 2011).

Post-treatment ecological condition is important for evaluating treatment effectiveness, if ecological restoration is needed to facilitate recovery of native ecosystems, and if maintenance treatments are necessary to keep exotic plant abundance low. It is often uncertain if simply removing an invader results in native ecosystem recovery (Corbin and D'Antonio 2012). Following removal of exotic *Tamarix* spp. in southwestern USA riparian areas, for example, Harms and Hiebert (2006) reported that native plant cover overall doubled on removal sites, but recovery varied among ecosystems and was not related to time-since-treatment even 11 years after treatment. In a repeat-removal experiment of four exotic perennials in a deciduous forest, Vidra et al. (2007) demonstrated that post-treatment species composition was contingent upon the number of times that the exotic species were removed through time. These authors also used a seed bank assay to help explain that minimal recovery of native species richness and cover might have related to sparse indigenous soil seed banks. This differed from conclusions of Reynolds and Cooper (2011) in exotic-dominated riparian areas, where soil seed banks contained more native species than occurred in the extant vegetation. Another important consideration in post-treatment site condition is assessing if the treated exotic species is simply replaced by other (potentially even more damaging) exotic species (Ransom et al. 2012). These observations suggest the importance not only of evaluating post-treatment condition of the target exotic species, but also the condition of other ecosystem components such as the soil, native plant community, other exotics, and seed bank to help inform post-treatment site management.

Buffelgrass (*Pennisetum ciliare*) is a prime example of an exotic species for which understanding post-treatment ecological condition is important for environmental management because the species infests large areas where it is not native, can dramatically alter indigenous ecosystems, and is proposed for treatments across large areas (Marshall et al. 2012). Native to arid and semi-arid Africa, Asia, and the Middle East, buffelgrass has been intentionally and unintentionally introduced to such areas as arid regions of Australia and southwestern North America (Stevens and Falk 2009). The species is highly invasive in these regions, competes with

native plants, and increases fuel loads to create fire hazards in previously fuel-limited ecosystems considered poorly adapted to fire (Esque et al. 2007; Olsson et al. 2012a). Some studies have reported on the ecological characteristics of sites inhabited by buffelgrass, which might have important implications for post-treatment site condition. Compared to non-invaded sites, buffelgrass sites have exhibited lower native plant cover (e.g., Daehler and Goergen 2005; Marshall et al. 2012); usually (e.g., Clarke et al. 2005; McDonald and McPherson 2011; Olsson et al. 2012b), but not always (Abella et al. 2012), reduced overall native species richness; and extremely high fuel loads for arid lands that can exceed 2400 kg ha⁻¹ and represent a major fire hazard (Esque et al. 2007; McDonald and McPherson 2011). Soil properties in buffelgrass patches are less well understood but appeared to be similar in magnitude for organic C, total N, and available N as below native perennial plants compared to interspaces between perennials in a Sonoran Desert study (Abella et al. 2012). Also in that study, native soil seed banks were not reduced in buffelgrass patches, but not all species in the seed bank were likely to establish as plants at the sites (Abella et al. 2012).

Fortunately for management, buffelgrass is susceptible to uprooting and herbicide treatments which have constrained its abundance in large infestations and completely eradicated small (a few to tens of hectares) patches. In Organ Pipe Cactus National Monument of the Sonoran Desert, for example, Rutman and Dickson (2002) reported that using hand tools in patches with up to 44,000 buffelgrass individuals ha⁻¹ at 17 sites, managers and citizen volunteers had achieved complete or near completion eradication after 1-3 years of treatments. Dixon et al. (2002) reported that different combinations of herbicide type, timing of application, and number of repeated treatments could essentially eradicate buffelgrass from their 25-ha site in western Australia. Their study, et al. (e.g., Daehler and Goergen 2005; Lyons et al. 2013), however, have asserted the importance of assessing post-treatment native vegetation and evaluating if active restoration can accelerate recovery and forestall buffelgrass reinvasion or invasion by other exotic species.

Here, we examined ecological condition following a range of combined manual and herbicide treatments aimed at reducing buffelgrass. Our specific objective was to assess soil properties, plant communities, and soil seed banks on sites annually treated for buffelgrass up to 5 years in a row and on single-year treatments up to 4 years old. The study occurred in an applied environmental management context of treatments implemented by the U.S. National Park Service, which, like other conservation organizations, is struggling to maintain indigenous ecosystems in the face of increasing biological invasions (Allen et al. 2009).

Methods

Study Area and Buffelgrass Description

We performed this study within the 37,006-ha Rincon Mountain District of Saguaro National Park (Park), 8 km east of Tucson, Arizona, in the southwestern USA (Fig. 1). The Park is within the northeastern Sonoran Desert's Arizona Upland Subdivision, which occupies higher elevations, receives more precipitation, and contains greater vegetation structural diversity than Sonoran Desert lowlands (Bowers and McLaughlin 1987). Climate, recorded by the Tucson Airport Weather Station (787 m in elevation, 1930 to 2011 records), is arid/semi-arid with

averages of 29 cm yr⁻¹ of precipitation, 37°C daily July high temperature, and 4°C daily January low temperature (Western Regional Climate Center, Reno, Nevada). The Park's topography consists of rolling hills, alluvial fans, and concave drainageways. Soils are primarily derived from granite and classified as Torriorthents and Haplargids (Cochran and Richardson 2003). Characterized by a scrubland or low woodland physiognomy, vegetation consists of a diverse assemblage of shrub-trees, forbs, graminoids, and cacti, including saguaro (*Carnegiea gigantea*), a columnar cactus diagnostic for the Upland Subdivision (Bowers and McLaughlin 1987). Animal inhabitants include a variety of small mammals (e.g., shrews, coyotes, fox, mice, rats, and rabbits), amphibians and reptiles (e.g., toads, tortoises, lizards, snakes), and birds (e.g., hawks, owls, vireos, warblers, and sparrows). Livestock grazing (primarily of cattle) occurred prior to 1976 but was not authorized thereafter. Since 1983, the park has been visited by > 600,000 people annually, with most visitors concentrated along park roads and to a lesser extent trails (National Park Service, Public Use Statistics Office, Denver, Colorado).

Buffelgrass is apparently well adapted to its new environment of the Sonoran Desert, including Saguaro National Park, and has several traits that likely facilitate its success (Olsson et al. 2012a). Buffelgrass uses a C₄ photosynthetic pathway and can have two growth periods (spring and late summer following summer monsoonal rains) in the Sonoran Desert (Ward et al. 2006). The species is a perennial bunchgrass but differs from the architecture of the Sonoran's native bunchgrasses by exhibiting denser foliage which also is closer to the ground and has more biomass plant⁻¹ (Marshall et al. 2012). Like many exotic plants, buffelgrass can readily usurp soil resources and experimentally has been shown to vigorously compete with native plants (Daehler and Goergen 2005; Stevens and Falk 2009). Buffelgrass propagules are dispersed by wind and adhesion to animals, with seeds exhibiting high germinability (Stevens and Falk 2009). Soil seed bank longevity and dynamics are not well known, but density of germinable buffelgrass seed averaged 645 seeds m⁻² in 0-5-cm deep soil banks below buffelgrass plants in 2011 within the study area (Abella et al. 2012). This density was only 259 seeds m⁻² less than the total density of all native species germinable seeds.

Managers first observed buffelgrass within the Park in 1989 (Perry Grissom, personal communication). Buffelgrass subsequently was observed to expand its distribution through establishment of new patches and enlargement and coalescence of existing patches (Olsson et al. 2012a). The species has invaded a variety of landforms and soils, even in the absence of fire (Olsson et al. 2012b), and occupies interior areas of the park several km from the nearest road or trail based on geospatial data provided by the Park (Tucson, Arizona). By the early 2000s, buffelgrass had become noticeably more abundant in the Park (with patches beginning to attain sizes of 0.1 ha to > 1 ha). This spurred more extensive treatments in an attempt to follow a major principle of weed management by initiating treatments in the relatively early stages of invasion.

Site Selection

Using a map of buffelgrass treatment polygons within the park provided by the National Park Service (Tucson, Arizona), we randomly selected three polygons for sampling in each of the following available treatment types:

- 1) 2007-2011 (5 years) annual buffelgrass treatment
- 2) 2009-2011 (3 years) annual buffelgrass treatment
- 3) 2010-2011 (2 years) annual buffelgrass treatment
- 4) 2008 single year (4-year-old) buffelgrass treatment
- 5) 2011 single year (1-year-old) buffelgrass treatment
- 6) Control, buffelgrass but no treatment
- 7) Control, no buffelgrass and no treatment

The Park Service treated buffelgrass in the treated polygons in winter and summer within a year for the number of years (1 to 5) listed above. A combination of manual and herbicide treatment was used, with the goal of removing or killing all buffelgrass individuals present. The manual treatment consisted of uprooting whole buffelgrass plants using hand tools including digging bars, geopicks and picnatics. Plant material was placed on site in piles of $\leq 4 \text{ m}^2$ preferably on top of sparsely or unvegetated rocky areas. Herbicides that contain the active ingredient glyphosate effectively kills buffelgrass (e.g., Dixon et al. 2002; Daehler and Goergen 2005; Tjelmeland et al. 2008). The Park used a 3% glyphosate solution to kill buffelgrass during its period of active growth. The Razor PRO (Nufarms America Inc., Burr Ridge, Illinois), KleenUp (Bonide Inc., Oriskany, New York), and Roundup PRO (Monsanto Corp., St. Louis, Missouri) post-emergence formulations were used and included a water conditioner (e.g., $[\text{NH}_4]_2\text{SO}_4$) and indicator dye to mark application locations. Individual plants were sprayed from a single nozzle using a backpack sprayer with a manual pump. Decisions regarding whether to use a manual or herbicide treatment on particular plants depended on the size of the infestation (larger infestations were typically treated with herbicide, whereas both herbicide and manual treatments were done on smaller infestations), number of plants to be treated (e.g., for a few plants, often it was faster to simply manually remove them), and time of year. The manual and herbicide combination used by the managers provided a realistic, practical setting in which to evaluate post-treatment ecological conditions, because managers view manual and herbicide as complementary treatments and employ both at the current patch scale of buffelgrass invasion in the park (Woods et al. 2012).

Treatment polygons we sampled ranged in size from 0.03-5 ha and represented buffelgrass patches that were ca. 5-10 years old when treatments were initiated, based on records kept by SAGU. Patches contained ≥ 100 buffelgrass individuals and exhibited areal cover of buffelgrass ranging from 18-88% prior to treatment. We identified sites for the two types of controls (untreated buffelgrass and non-invaded sites) by randomly selecting three of 13 sites of each type established during a previous study of untreated buffelgrass patches and non-invaded sites (Abella et al. 2012). Treated and untreated sites were interspersed and exhibited similar topography, 0-5 cm soil texture, and soil taxonomy (Fig. 1, Appendix D).

Plot Sampling

In May 2012, we established and sampled a circular (5.28 m radius), 0.01-ha sampling plot randomly located within each of the 21 polygons. Within each plot, we categorized total areal cover of vascular plants and the areal cover of each vascular plant species (including senesced annuals) rooted in each plot using the following cover classes: 1 = trace (assigned 0.1% cover), 2 = 0.1 to 1%, 3 = 1 to 2%, 4 = 2 to 5%, 5 = 5 to 10%, 6 = 10 to 25%, 7 = 25 to 50%, 8 = 50 to 75%, 9 = 75 to 95%, and 10 = 95 to 100% (Peet et al. 1998). Plants not able to be readily identified in the field were collected, pressed, and keyed to the finest taxonomic resolution possible. Nomenclature, growth form (e.g., forb, graminoid), and North American native/exotic status follow NRCS (2012). At the center of each plot, we recorded location and elevation using a global positioning system, slope gradient using a clinometer, and aspect using a compass.

We collected soil analytical, bulk density, and seed bank samples from below the three largest individuals of brittlebush (*Encelia farinosa*, a native perennial shrub) and in the three largest interspaces (open areas usually ca. 1 m² between perennial plants) on each plot. We chose the below-brittlebush and interspace sampling microsites because they were present on every plot. On untreated buffelgrass plots, we also sampled below buffelgrass canopies. We sampled across these microsites because desert soil and vegetation properties can sharply vary between interspaces and below perennial plant canopies (Butterfield et al. 2010). Samples were of the 0-5 cm upper mineral soil for soil analysis and bulk density and of the upper 0-5 cm soil (which could include O horizons containing litter) for the seed bank. We collected three subsamples (each 230 cm³) equally spaced midway between the main stem and canopy drip line below brittlebush, equally spaced within a 1-m² area for interspaces, and equally spaced 10 cm from the root crown below buffelgrass on untreated buffelgrass plots. Subsamples (9 per microsite type per plot) for each of the respective microsites were composited on a plot basis to result in one sample per microsite per plot for each analysis.

Soil Analysis

The < 2-mm fraction of soil samples was analyzed by the Oklahoma State University Soil, Water, and Forage Analytical Laboratory (Stillwater, Oklahoma). Samples were analyzed for texture (hydrometer method); pH, electrical conductivity, sodium absorption ratio, exchangeable sodium percentage, and total soluble salts (1:1 soil:water); extractable Fe, Zn, Cu, and B (diethylene triamine pentaacetic acid [DTPA]-sorbitol extractant, inductively coupled plasma [ICP]); elemental concentrations of Na, Ca, Mg, and K (ICP); and organic C and total N (Leco C/N analyzer). We measured coarse fragment content and bulk density for the bulk density samples by sieving out coarse fragments > 2 mm in diameter, oven drying the fine fraction at 105°C for 24 h, weighing both fractions, and estimating volume of coarse fragments by water displacement. Bulk density was calculated based on the full sample volume including volume of coarse fragments (Throop et al. 2012). We converted nutrient concentrations to volumetric contents using bulk density, but because bulk density did not differ significantly among microsites or treatments (Appendix D), we report concentrations.

Seed Bank Assay

We assayed seed bank composition using the emergence method to measure readily germinable seed density (Bakker et al. 1996). Within a week of sample collection, we filled 4-L, 16-cm diameter cylindrical pots two-thirds full with potting soil (1:3:1 mulch:sand:gravel). On top of this potting soil, we placed 360 cm³ of seed bank soil (extracted from a thoroughly mixed plot sample) in a layer 2 cm thick. We randomly arranged pots on a bench in a greenhouse, without supplemental lighting, and with temperatures fluctuating between 21 (nighttime) and 32°C (daytime). We also randomly arranged pots containing only potting soil to check for greenhouse seed contamination, which was not detected. During the four-month period that samples resided in the greenhouse, we watered samples daily to moisture capacity, counted seedlings every two weeks, and removed seedlings upon identification to the finest feasible taxonomic level following NRCS (2012). At 4 and 8 weeks we applied 1000ppm solution gibberellic acid to each pot. Of the 734 total seedlings that emerged, 727 (99%) were identified to species. We retained in the final data set for analysis 3 seedlings only identified to the *Acacia* genus but we deleted 3 seedlings identified only to Poaceae and 1 seedling identified only to Asteraceae. As is customary in seed bank research (Bakker et al. 1996), we converted seedling counts to seeds m⁻² corresponding to a 0-5 cm depth.

Data Analysis

We analyzed each soil variable in a two-factor, mixed model analysis of variance consisting of treatment (7 levels corresponding to the 7 treatment types), sampling microsite (interspace or below brittlebush) nested within treatment, and the interaction of treatment and microsite using PROC MIXED in SAS 9.2 software (SAS Institute 2009). The univariate vegetation variables were based on ordinal (cover) or count (species richness) data, so we compared medians of buffelgrass cover, the sum of species cover (based on summing cover of species, excluding buffelgrass, within a plot, which returned the same statistical conclusion as the whole plot-cover estimate), species plot⁻¹ (richness, excluding buffelgrass), and Shannon's diversity index among treatments using Kruskal-Wallis tests (PROC NPAR1WAY, SAS Institute 2009). When a Kruskal-Wallis test was significant, we used Tukey's test to separate treatments. We calculated Shannon's diversity index using relative cover (cover of species_i/Σ cover of all species, excluding buffelgrass, on a plot) in the software PC-ORD (McCune and Mefford 1999). We used the multivariate, non-parametric technique multi-response permutation procedures (Sørensen distance, n/sum[n] default group weighting) to compare species composition (relative cover, excluding buffelgrass) among treatments using PC-ORD. A corresponding pairwise matrix of Sørensen similarities between treatments also was calculated in PC-ORD. For the seed bank data (which were count data), we compared native seeds m⁻² of species also found in the vegetation, total native seeds m⁻², and species richness (per 360-cm³ sample) in a general linear mixed model including treatment and microsite (interspace or below brittlebush) and their interaction, with microsite nested within treatment. The model assumed a Poisson distribution, consistent with the count data, and was implemented using PROC GLIMMIX in SAS 9.2 software (SAS Institute, 2009). We also calculated descriptive statistics for all seed bank measures, including for buffelgrass density and density of other exotic species (both of which were too sparse to analyze inferentially), and buffelgrass seed density below its own canopy in untreated buffelgrass plots.

Results

Soil

None of the 22 soil variables displayed a treatment $\times$ microsite interaction (Fig. 2). Almost all of the variables displayed no significant relationship to treatment type. The only two exceptions were: Fe, which exhibited most consistently low values in the 2010-2011 buffelgrass treatment but had no other consistent pattern across the treatment gradient; and sand, which was slightly higher (5-10%) in uninvaded sites compared to the 5 treatment types and did not differ significantly from untreated buffelgrass. However, microsite (interspace or below brittlebush) as a main effect significantly influenced 13 variables. Means of these 13 variables were greater below brittlebush compared to interspaces except for volumetric content of coarse fragments, which was slightly greater in interspace soils. Soil properties below buffelgrass canopies in untreated buffelgrass plots were generally more similar to those below brittlebush than to interspaces.

Vegetation

Across all 21 plots, 120 taxa were recorded comprised of 113 (94%) native and 7 exotic taxa. The 13 most frequently occurring native species were: the shrub brittlebush (present on 21 plots); the shrub fairyduster (*Calliandra eriophylla*), annual forb *Lepidium* spp., and annual forb California cottonrose (*Logfia californica*; all on 18 plots); the perennial graminoid *Eragrostis* spp. and cactus apple (*Opuntia engelmannii*) both on 17 plots; the annual forb American wild carrot (*Daucus pusillus*) and annual grass sixweeks fescue (*Vulpia octoflora*) both on 16 plots; and the annual-perennial grass purple threeawn (*Aristida purpurea*), annual forb miniature woollystar (*Eriastrum diffusum*), shrub sangre de cristo (*Jatropha cardiophylla*), Graham's cactus (*Mammillaria grahamii*), and annual forb curvenut combseed (*Pectocarya recurvata*) occupying 14 plots. The exotic taxa included buffelgrass (present on 14 plots); the annual grass *Avena* spp. (1 plot), red brome (*Bromus rubens*; 3 plots), and *Schismus* spp. (11 plots); the annual forb London rocket (*Sisymbrium irio*; 5 plots); and the annual-biennial forbs Maltese star-thistle (*Centaurea melitensis*; 4 plots) and redstem stork's bill (*Erodium cicutarium*; 1 plot). By growth form and life span, the 120 taxa consisted of 23% shrubs; 22% perennial forbs; 20% annual forbs; 6% cacti; 5% each annual-perennial forbs, annual graminoids, and perennial graminoids; 4% each annual-biennial forbs and trees; 3% ferns, 2% annual-perennial graminoids; and 1% biennial-perennial forbs.

Buffelgrass cover was $\leq 1\%$ on 14 of the 15 treated plots and was only 3% on the remaining plot (Fig. 3). In contrast, buffelgrass cover ranged from 10-70% on untreated buffelgrass plots. Native plant cover, richness, and diversity were statistically indistinguishable across treatment types.

Plant community composition (excluding buffelgrass) did not differ significantly across the treatment gradient (multi-response permutation procedures, A-statistic = 0.01, $P = 0.30$). Similarity of species composition of sites within treatments was low (below 39%) and was not greater than similarity of sites among treatments (Table 1). Aside from untreated buffelgrass,

which exhibited 63% relative cover of buffelgrass, treatments were dominated by native species, averaging 93-100% relative cover of natives (Fig. 4, top left graph). Combined relative cover of all 6 exotic species other than buffelgrass was low, averaging only 0-2.5% across sites.

Seed bank

Forty-one species were detected in the 45 seed bank samples across all treatment/microsite combinations and consisted of 38 (93%) native and only 3 (7%) exotic species (Appendix D). The seven most frequently occurring native species were sand pygmyweed (*Crassula connata*; 19 of 45 samples), brittlebush (15 samples), California cottonrose (13 samples), needle grama (*Bouteloua aristidoides*; 11 samples), Wright's cudweed (*Pseudognaphalium canescens*; 9 samples), sixweeks fescue (9 samples), and violet snapdragon (*Sairocarpus nuttallianus*; 8 samples). By growth form and life span, the 38 native species were distributed as: 39% annual forbs; 16% annual-perennial forbs; 11% annual grasses; 8% perennial grasses; 5% each annual-biennial forbs, annual-perennial grasses, and perennial forbs; and 3% each biennial forbs, cacti, shrubs, and trees. Thirteen (34%) native seed bank species also occurred in vegetation of one or more plots. The three exotic species were buffelgrass (6 samples), the perennial African lovegrass (*Eragrostis echinochloidea*, 2 samples), and the annual hairy crabgrass (*Digitaria sanguinalis*, 1 sample, and not detected in vegetation of any plot).

A treatment $\times$ microsite interaction occurred for both native seed bank density of species also in vegetation ($F = 692$, $P < 0.01$) and total native seed bank density ($F = 996$, $P < 0.01$). In both cases, these interactions resulted from two treatments that exhibited seed densities in interspaces similar to those below brittlebush, whereas the rest of treatment types had greater seed bank densities below brittlebush (Fig. 4, right graph, mean densities at tops of bars). Treatment was never a significant main effect ($P > 0.31$). Richness averaged 3.2 species/360 cm³ sample in interspaces among treatments and 4.5 species below brittlebush but was not significantly affected (lowest $P = 0.08$ for microsite) by any factor.

Seed bank species composition was dominated by the natives sand pygmyweed (annual forb), jump-up (*Mecardonia procumbens*; annual-perennial forb), and Wright's cudweed (annual-perennial forb), none of which were detected in vegetation, but also by some native species that did occur in vegetation, such as brittlebush, sixweeks fescue, California cottonrose, needle grama, purple threeawn, and American wild carrot (Fig. 4, bottom left graph). Buffelgrass was not detected in interspace soil and was sparse, but present, in samples sporadically across the 7 site types below brittlebush and below its own canopy on untreated plots (Fig. 4, right graphs). The two other exotic species (African lovegrass and hairy crabgrass) were infrequent and sparse across treatments and microsites.

Discussion

A main conclusion from this study was that following buffelgrass treatment, the major difference between treated and untreated areas was that buffelgrass cover was minimal or absent in treated areas compared to untreated buffelgrass plots. Post-treatment soil, native vegetation, and soil seed banks were largely indistinguishable between treated areas and areas not invaded by

buffelgrass. Moreover, treated sites did not simply exhibit replacement of buffelgrass by other exotic plants, as all treated plots were dominated by native species.

Some factors warrant consideration when placing our results in context with those of other studies. Several studies have noted the importance of post-treatment weather in regulating vegetation transitions following buffelgrass treatment. Based on the nearby Tucson, Arizona, Airport Weather Station, our study generally occurred during a period of below-average precipitation (Western Regional Climate Center, Reno, Nevada). In 2006, the year prior to the 2007 initiation of the first treatments we examined, precipitation was 104% of the long-term (1930-2011) average of 29 cm yr⁻¹, but precipitation was below average in 2007 (86% of average), 2008 (76%), 2009 (50%), and 2010 (98%). Precipitation in 2011 was 108% of average, but the January through April precipitation in 2012 prior to our May 2012 sampling was only 26% of the 7-cm average total for those months. Although in the Sonoran Desert buffelgrass germination and seedling survival are favored by wet summers and warm winters, Olsson et al. (2012a) found that climatic conditions for buffelgrass germination were met nearly every year in their study of buffelgrass distribution since 1988. Moreover, buffelgrass spread rates were nearly constant (with infested area doubling on average every 6 years) and exhibited only weak or non-significant correlations with climate. While buffelgrass establishment during our study may or may not have been influenced by weather, the possibility that dry conditions during the treatment period influenced establishment of other species should not be dismissed. Another factor providing important context to our study is the potential for allelopathic effects of buffelgrass. Hussain et al. (2010) summarized allelopathic influences of buffelgrass in Pakistan and elsewhere, noting that extracts from foliage and roots have reduced germination and growth of other species but that in natural settings, it is difficult to separate effects of allelopathy and competition and to identify importance of allelopathic chemicals in natural soils. The possible importance of buffelgrass allelopathy is unclear for desert soils such as those of the Sonoran, and apparently allelopathy was not sufficiently active to forestall plant community measures in treated areas from being indistinguishable from those of non-invaded areas. Another important consideration is that livestock grazing was not present during our study.

Previous studies of post-treatment buffelgrass community dynamics afford a range of treatment strategies and ecosystems for comparison. On a 25-ha Australian island, Dixon et al. (2002) found that with the exception of native grasses, herbicides employed (Roundup Biactive and Verdict) that killed buffelgrass had no measureable adverse effects on native vegetation. In Hawaiian grasslands, Daehler and Goergen (2005) found that burning (which was part of the evolutionary environment of the indigenous ecosystem) to temporarily reduce buffelgrass, combined with seeding native Hawaiian Pili grass (*Heteropogon contortus*), resulted in 81% relative cover of Pili grass and low buffelgrass cover. Burning combined with hand pulling or herbicide treatment of buffelgrass also significantly reduced buffelgrass while increasing native species, and exotics other than buffelgrass were sparse when irrigation was not provided. In Texas grasslands of the southern USA, Tjelmeland et al. (2008) found that effects of a variety of herbicide treatments on buffelgrass and native vegetation were subtle within two years after treatment, yet buffelgrass cover did decline and cover of natives increased. In a previous Sonoran Desert study, Woods et al. (2012) reported that combined herbicide and manual removal of buffelgrass nearly eradicated buffelgrass from treated sites within a few years. All sites were dominated by native shrubs such as brittlebush.

Collectively, these previous studies combined with our results suggest several potential principles regarding efficacy of buffelgrass treatments: 1) buffelgrass can be reduced or even locally eradicated by various treatments (e.g., different herbicide protocols, manual pulling, strategic burning in certain ecosystems); 2) except in certain cases like some native flora (e.g., perennial grasses) being susceptible to the same herbicide used to kill buffelgrass, native plants are not reduced by buffelgrass treatments, and in some instances, increase without other management or with management such as fire depending on the ecosystem; 3) dominance by other exotic species simply replacing buffelgrass after treatment has not been reported to date, and Daehler and Goergen (2005) found that when other exotics surged following buffelgrass removal, they rapidly dissipated when supplemental irrigation was terminated; and 4) natives appear highly susceptible to competition from buffelgrass, but buffelgrass also appears susceptible to competition from established stands of natives in some ecosystems such as Hawaiian grasslands where native perennial grasses dominated following buffelgrass removal (Daehler and Goergen 2005). This fourth point is additionally supported by agronomic studies that had the goal of establishing buffelgrass for purported pasture benefits, where several studies found that buffelgrass had difficulty establishing within pastures of other established species (e.g., McIvor 2003).

A key management question following buffelgrass removal is whether active revegetation is desirable to accelerate native community recovery and potentially provide competition to constrain buffelgrass resurgence, or whether natural transitions in native communities meet management objectives. Because native seed sources had been eliminated, Daehler and Goergen (2005) found that seeding the native Hawaiian Pili grass was key to its establishment following buffelgrass treatment. Other studies attempting revegetation following buffelgrass removal have reported mixed success. Dixon et al. (2002) outplanted three species of greenhouse-grown native shrubs without any further treatment (no supplemental water or grazing protection) and found that efficacy appeared to hinge upon rainfall immediately after planting with near total failure in dry conditions. Woods et al. (2012) reported that none of the 72 individuals of outplanted slender grama (*Bouteloua repens*) and brittlebush survived (no supplemental water or grazing protection was provided), and seeding six species of native grasses and shrubs resulted in minimal establishment during their dry, two-year study period. These authors concluded that buffelgrass did not resurge following treatment and that management efforts might be best utilized by treating buffelgrass in other areas rather than attempting to manipulate natural colonization of native species.

Our results, combined with those of Woods et al. (2012), suggest that simply removing buffelgrass can result in post-treatment ecological conditions largely indistinguishable from those of non-invaded areas in the current context of relatively early buffelgrass invasion and relatively small patch sizes at these Sonoran Desert sites. Plant succession following severe soil disturbance (e.g., bulldozing) can require centuries for colonizing vegetation to resemble that of undisturbed areas in the Sonoran Desert (Abella 2010). However, soil disturbance associated with our buffelgrass treatments was minimal. Moreover, native shrub cover was not reduced at the current stage of buffelgrass patch formation (Abella et al. 2012). The protected, nutrient-enriched areas ('fertile islands') below canopies of native shrubs are critical microsites for plant recruitment, and when these shrubs are removed, the pace of facilitation-based succession can be

extremely slow (Butterfield et al. 2010). A key finding of our study was that the pattern of fertile-island formation below native shrubs was largely indistinguishable in treated and non-invaded areas, suggesting that environmental conditions for plant recruitment were similar across site types.

While soil seed banks often display weak correlations with extant vegetation (e.g., Bakker et al. 1996), our results suggest that seed banks can supply propagules to facilitate recruitment of some important species in extant vegetation (Appendix D). Brittlebush, for example, was a dominant species both in the seed bank and extant vegetation and may not appreciably benefit from active revegetation effort in this situation (Woods et al. 2012). The finding that treatment as a main effect did not significantly influence soil seed bank density also suggests that active revegetation may not be required as part of post-treatment management strategies. It further provides evidence that other exotics were sparse in both the post-treatment vegetation and seed bank.

Conclusion

The data suggest that treatments implemented by the National Park Service effectively reduced buffelgrass – and the potential for risk of buffelgrass-fueled wildfire and longer term negative impacts of buffelgrass – while resulting in post-treatment ecological conditions largely indistinguishable from those of areas not invaded by buffelgrass. While the potential for non-target and unintended consequences of exotic species removal warrants consideration when initiating exotic species removal projects (Zavaleta et al. 2001), no negative consequences of removing buffelgrass were evident based on our analysis of native vegetation, soil, and seed banks. Results support continuation of treatments by the National Park Service to reduce exotic plants and meet park management goals of maintaining ecological communities dominated by native species.

Table 1 Sørensen similarities of plant community composition of plots within treatments (diagonal, bold font) and among treatments (off-diagonals) for the exotic perennial buffelgrass in Saguaro National Park, Sonoran Desert. Values are mean $\pm$ SD (%)

Treatment ^a	1	2	3	4	5	6	7
1. BG 07-11	28$\pm$11						
2. BG 09-11	22 $\pm$ 11	37$\pm$3					
3. BG 10-11	29 $\pm$ 7	32 $\pm$ 10	21$\pm$0				
4. BG 08	24 $\pm$ 9	38 $\pm$ 7	33 $\pm$ 12	37$\pm$11			
5. BG 11	25 $\pm$ 8	28 $\pm$ 12	34 $\pm$ 12	34 $\pm$ 14	31$\pm$20		
6. BG no tmt	21 $\pm$ 6	35 $\pm$ 12	29 $\pm$ 4	38 $\pm$ 10	29 $\pm$ 9	31$\pm$11	
7. No BG	21 $\pm$ 6	34 $\pm$ 9	31 $\pm$ 10	41 $\pm$ 12	32 $\pm$ 11	39 $\pm$ 12	39$\pm$12

^a BG = buffelgrass, with the numbers following describing the year(s) in which BG was treated. For example, BG 07-11 indicates that BG was treated each year for 5 years between 2007 and 2011, and BG 08 indicates that BG was treated during only one year (in 2008). The BG no tmt indicates BG occupied sites but was not treated, and the No BG indicates non-invaded sites.

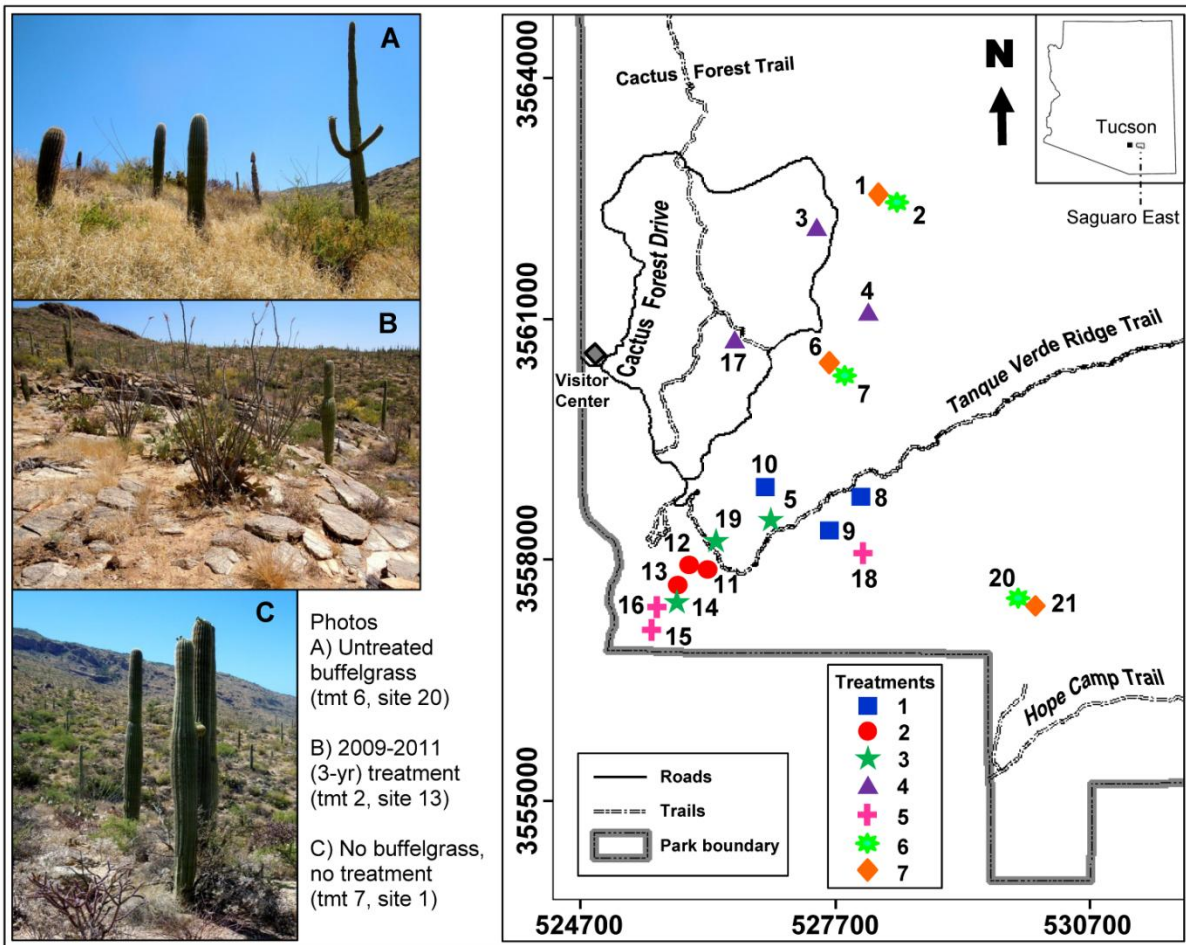


Fig. 1 Location of study plots, classified by buffelgrass treatment type, within eastern (Rincon Mountain District) Saguaro National Park, Sonoran Desert. Geographic coordinates are Universal Transverse Mercator (zone 12, m), North American Datum 1983. Plots are numbered according to plot descriptions in Appendix D. Treatment numbers correspond with: 1) 2007-2011 (5 years) annual buffelgrass treatment, 2) 2009-2011 (3 years) annual buffelgrass treatment, 3) 2010-2011 (2 years) annual buffelgrass treatment, 4) 2008 single year (4-year-old) buffelgrass treatment, 5) 2011 single year (1-year-old) buffelgrass treatment, 6) control, buffelgrass but no treatment, and 7) control, no buffelgrass and no treatment.

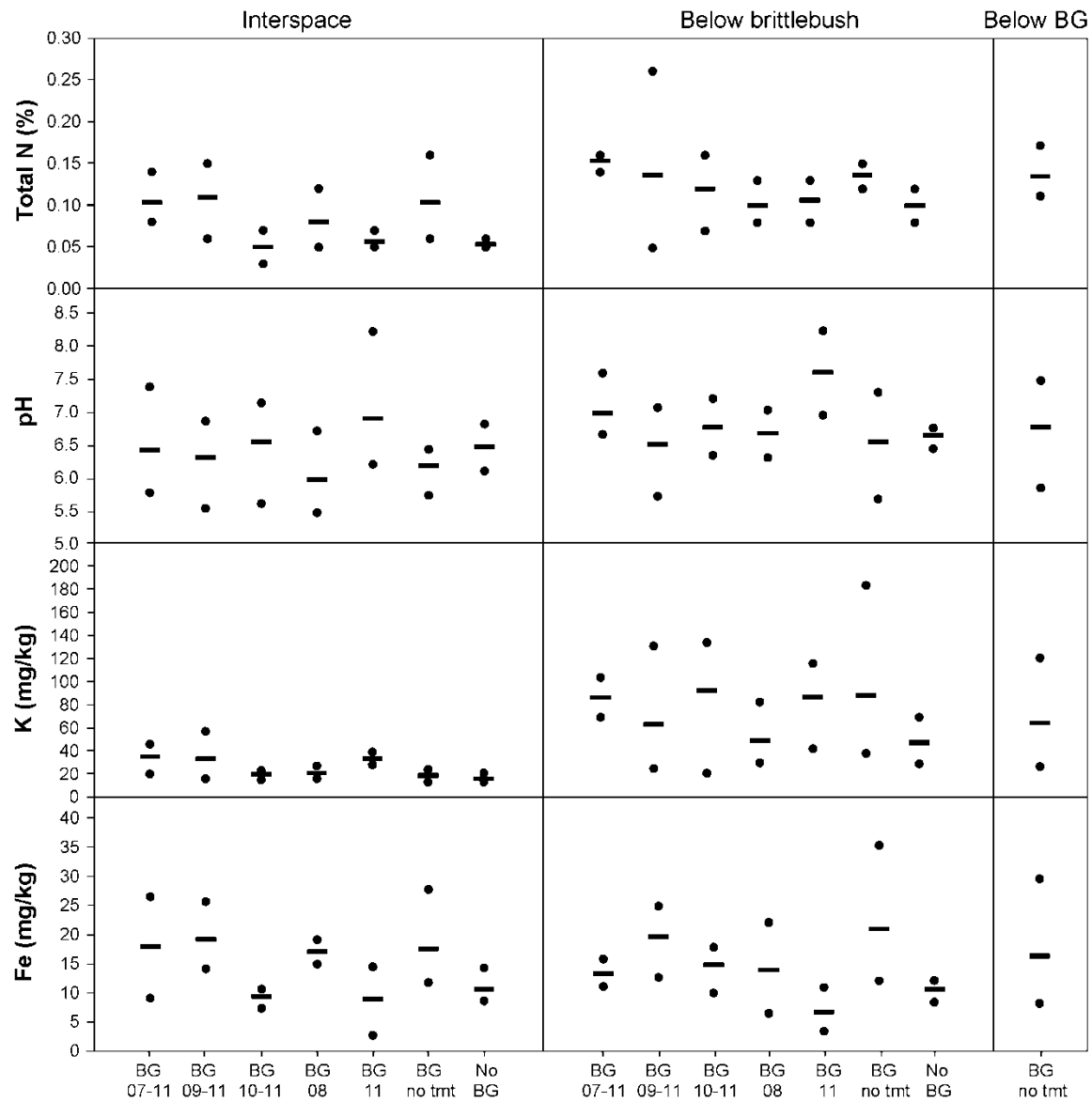


Fig. 2 Soil properties (0-5 cm mineral soil) by microsite and among treatments along a buffelgrass treatment gradient in Saguaro National Park, Sonoran Desert. The below-buffelgrass microsite existed only for untreated buffelgrass plots. Horizontal lines represent means and circles represent minimum and maximum values. For treatment abbreviations along the x axis: BG = buffelgrass, with the numbers following describing the year(s) in which BG was treated. For example, BG 07-11 indicates that BG was treated each year for 5 years between 2007 and 2011, and BG 08 indicates that BG was treated during only one year (in 2008). The BG no tmt indicates BG occupied sites but was not treated, and the No BG indicates non-invaded sites.

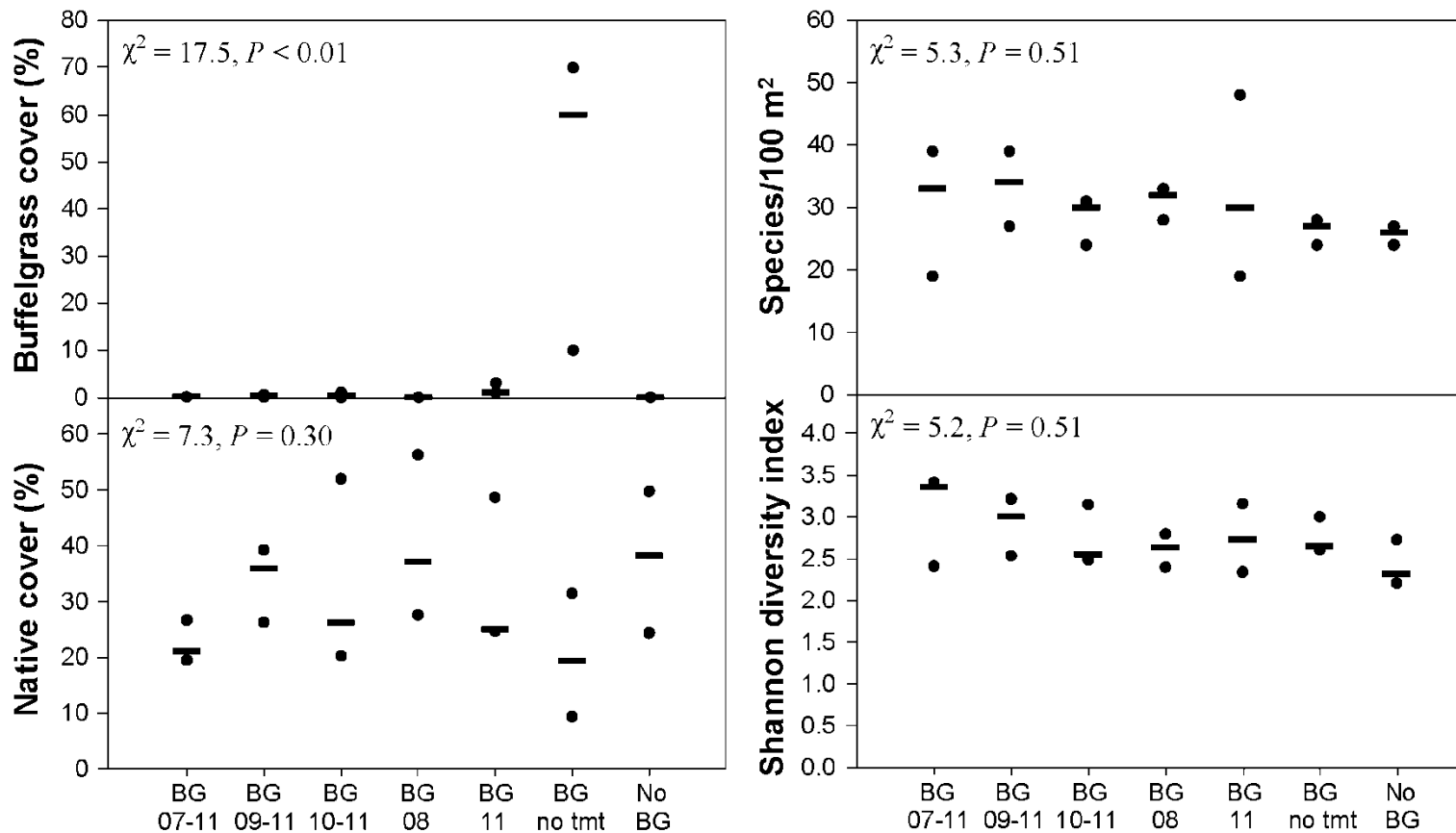


Fig. 3 Vegetation characteristics along a buffelgrass treatment gradient in Saguaro National Park, Sonoran Desert. Horizontal lines represent medians and circles represent minimum and maximum values. Results of Kruskal-Wallis tests comparing medians across treatments are provided for each response variable. For treatment abbreviations along the x axis: BG = buffelgrass, with the numbers following describing the year(s) in which BG was treated. For example, BG 07-11 indicates that BG was treated each year for 5 years between 2007 and 2011, and BG 08 indicates that BG was treated during only one year (in 2008). The BG no tmt indicates BG occupied sites but was not treated, and the No BG indicates non-invaded sites.

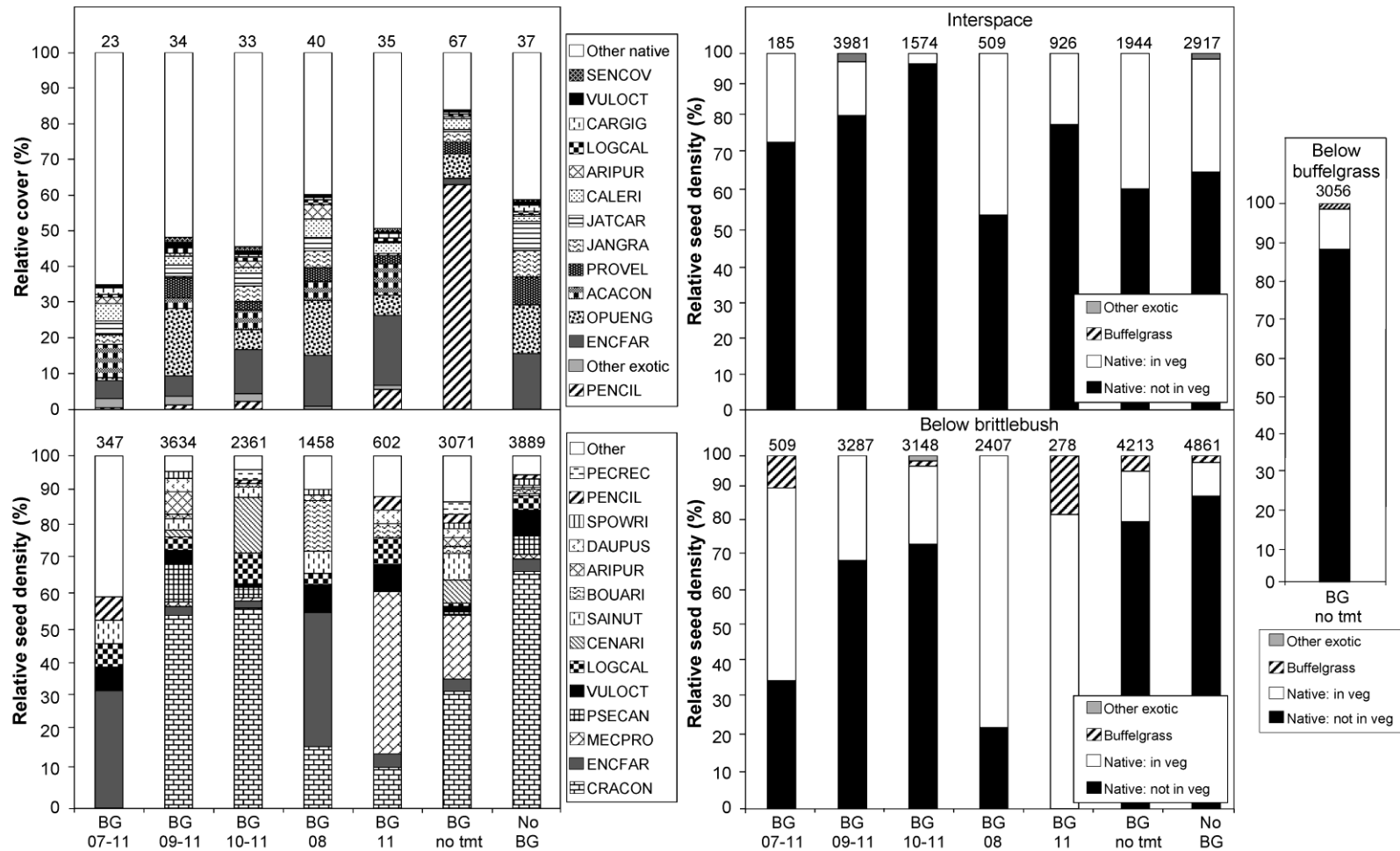


Fig. 4 Comparison of relative cover of the most dominant species in vegetation with relative seed density of the most abundant species in the 0-5 cm soil seed bank along a buffelgrass treatment gradient in Saguaro National Park, Sonoran Desert. Top-left graph: vegetation. Bottom-left graph: seed bank composition averaged across interspace and below-brittlebush microsites. Right graphs: seed bank composition, by microsite, with native species classified as to occurrence in vegetation. For treatment abbreviations along

the x axis: BG = buffelgrass, with the numbers following describing the year(s) in which BG was treated. For example, BG 07-11 indicates that BG was treated each year for 5 years between 2007 and 2011, and BG 08 indicates that BG was treated during only one year (in 2008). The BG no tmt indicates BG occupied sites but was not treated, and the No BG indicates non-invaded sites. Numbers at the top of bars represent mean cover (%; top-left graph) or mean seeds m⁻² (other graphs). Species, from top to bottom, are abbreviated as: SENCOV = *Senna covesii*, VULOCT = *Vulpia octoflora*, CARGIG = *Carnegiea gigantea*, LOGCAL = *Logfia californica*, ARIPUR = *Aristida purpurea*, CALERI = *Calliandra eriophylla*, JATCAR = *Jatropha cardiophylla*, JANGRA = *Janusia gracilis*, PROVEL = *Prosopis velutina*, ACACON = *Acacia constricta*, OPUENG = *Opuntia engelmannii*, ENCFAR = *Encelia farinosa*, PENCIL = *Pennisetum ciliare*, PECREC = *Pectocarya recurvata*, SPOWRI = *Sporobolus wrightii*, DAUPUS = *Daucus pusillus*, BOUARI = *Bouteloua aristidoides*, SAINUT = *Sairocarpus nuttallianus*, CENARI = *Centaurium arizonicum*, PSECAN = *Pseudognaphalium canescens*, MECPRO = *Mecardonia procumbens*, and CRACON = *Crassula connata*.

Part VI. Characterizing soil seed banks in invaded and treated buffelgrass stands in the Sonoran Desert

Abstract Soil seed bank investigations assist with guiding restoration practices for recovery of disturbed and invaded ecosystems by quantifying the ability for passive recovery of a community after removal of exotic species and to provide a means for evaluating invasive plant treatment success. To quantify the potential for native vegetation recovery after manual and herbicide treatment of the invasive, exotic buffelgrass, and to assess the extent to treatment of buffelgrass we collected 0- to 5-cm soil seed bank samples from the same microsites across plots from five different frequencies of buffelgrass herbicide plus manual removal treatments (ranging from 5 years of annual treatment to a single year of treatment), untreated sites, and non-invaded sites, with three replicate sites for each of the seven treatments. We applied both emergence and extraction methods for assessing seed bank samples to identify which method most represents the landscape species composition. We observed that species composition detected with extraction was more representative of landscape vegetation and resulted in greater densities and species richness. Treatments did not significantly impact soil seed bank density or richness, which may suggest that once buffelgrass is removed the above-ground vegetation may recover to similar composition as uninvaded sites. At a site and microsite level, total native densities and species richness detected by the two methods were relatively strongly correlated to each other; however methods followed diverging trends between important vegetation groups and species that dominate the landscape. Results also reveal similar conclusions for effectiveness of buffelgrass treatment; however extraction suggests that buffelgrass and other exotic species seed are still pervasive at treated sites and continued monitoring may be necessary to detect reinvasion during optimal years. Our results suggest that differences in seed detectability influence management approaches for removing and detecting exotic species and can influence future land management and restoration decisions.

Introduction

Seed bank assessments are important for understanding site ecology and assist with identifying conservation priorities (e.g., species that support wildlife; rare or exotic species) for land managers (Schneider and Allen 2012). These assessments facilitate elucidating key ecological processes that can guide land management objectives by providing site history (e.g., evidence of past disturbance), estimating how an ecosystem will respond during unfavorable conditions (e.g., population persistence) or after disturbances and reestablish during favorable conditions (Pake and Venable 1996), providing insight on regeneration potential after disturbance or potential vegetation reestablishment in ecological restoration (Richardson et al. 2012), estimating treatment effectiveness on non-native vegetation (Forcella 1992), and estimating potential genetic diversity which may be required to buffer a system for global change (Damschen et al. 2012). However, different assessment methods may result in contrasting results (Brown 1992; Forcella 1992; Ishikawa-Goto and Tsuyuzaki 2004; Bernhardt et al. 2008) leading to conflicting management recommendations. Application and utility of different approaches is debatable (e.g. Brown 1992). Ideal methods would detect all viable seed species accurately, would be easy to implement and provide a representation of the above-ground vegetation, either in its current or potential future state. Choosing an appropriate method is particularly a concern when relying on seed banks assessments to assist with future restoration decisions and treatments. Different seed bank techniques may be preferable depending upon the habitat, seed community and the diversity of germination requirements and seed dormancy.

Two main methods for elucidating soil seed banks are seedling emergence and seed extraction (Thompson et al. 1997; Baskin and Baskin 1998). Seedling emergence method includes spreading a thin layer of a soil sample over sterilized medium in pots or flats in a greenhouse or similar environments from which the sample was acquired, and as seedlings emerge individuals are identified and tallied as an estimate of viable seed providing an indicator of readily germinable seed. Advantages to this method include detecting viable individuals, greater ability to identify species, and avoiding sifting through soils and a non-detection bias due to seed size, shape, or color that can occur during extraction (Roberts 1981). However, not all seeds may germinate under the experimental conditions and may require several months to allow as many seeds as possible to emerge, which can underestimate seed density and richness due to dormancy or specific environmental requirements (Brown 1992; Bernhardt et al. 2008; Wright & Clark 2009). Also, species may emerge also which would not normally occur in the above-ground vegetation or are isolated to specific areas within the landscape (Abella et al. 2013a) due to more appropriate artificial conditions. Additionally, a space or facility and resources (e.g., water, gibberellic acid) are required. Extraction requires separating seeds from soil media by sifting and/or flotation, isolating and identifying seed (Roberts 1981; Brown 1992). Extraction provides better estimates of total seed densities and may detect species that would not emerge under artificial conditions. However, there are several disadvantages with extraction. Seeds require identification, which can be labor-intensive and challenging, and seed detection is not uniform across species (e.g., small-seeded species are difficult and challenging to identify, especially ‘weathered’ seeds). Very small seeds are difficult to detect and separate from soil particles. Also, determining viability of seeds may be difficult due to germination requirements and length of time for processing and can result in overestimating the viable seed bank (Baskin & Baskin

1998). For both methods, it is possible to identify species that are not represented in the above-ground vegetation, requiring comparisons of detected species with above-ground vegetation.

Performance of seed bank characterization can also differ depending on habitat. For example, Brown (1992) observed greater extracted seed densities and species richness in forest seed bank samples compared to seedling emergence. Poiani and Johnson (1998) also detected greater seed densities with extraction but detected similar species richness between both methods in samples from prairie wetlands. Seed bank methods are not well established in deserts. Several studies in the Mojave and Sonoran Deserts of North American Southwest have applied extraction (e.g. Nelson and Chew 1977; Pake and Venable 1996; Guo et al. 1998). More recent studies have applied the emergence method (Abella et al. 2009; DeFalco et al. 2009; Esque et al. 2010; Schneider and Allen 2012). To the authors' knowledge only one study has compared the two methods in southwest US deserts to determine if one method had advantages in desert habitats or if the methods may be predictive of each other. Abella et al. (2013a) found that method comparison depended upon the scale of analysis for species richness, and combining data from both methods provided the strongest correlation with above-ground vegetation in a Mojave Desert system. It is unclear which detection method will provide the more representative results of existing vegetation. What we do know is that only a fraction of the viable seed normally germinate under a nature precipitation regime, and that species have a range of dormancy and germination requirements. Additionally, there are limited examples of applying assessment methods to assess differences along gradients, which may have a significant impact on future land management decisions.

Due to reliance and applicability of different seed bank assessment methods further research is required to elucidate which methods will provide the best representation the existing or desired vegetation conditions and if methods will result in concurrent or conflicting conclusions.

The goals of this study were:

- (1) To assess and identify the extent of herbicide and manual treatment required to reduce or exclude the exotic perennial grass buffelgrass (*Pennisetum ciliare* (L.) Link) from the soil seed bank within buffelgrass sites along a treatment gradient with two seed bank assessment methods;
- (2) To identify site potential for natural recovery post-buffelgrass treatment with two seed bank assessment methods; and
- (3) To compare and contrast seed bank assessment method results and observe if results lead to different conclusions or determine if methods are correlated to each other.

We hypothesize that longer treatments will have reduced buffelgrass seed and correlate with reduced buffelgrass cover and time since treatment or years of treatment. Additionally, we hypothesize that with longer treatment times native seed bank densities will recover to conditions similar to uninfested patches, and that the treatment gradient will correlate with native seed bank recovery. We also hypothesize that extraction will detect higher seed densities, although richness will not greatly differ with emergence or with above-ground vegetation. Extraction will likely overestimate viable seed densities, and emergence will likely detect species unlikely to normally germinate in a field setting due to environmental restrictions, but density will correlate between the two methods.

Methods

This study was performed within the 37,006 ha Rincon Mountain District of Saguaro National Park (Park), 8 km east of Tucson, Arizona, in the southwestern USA (Fig. 1). The park is within the Arizona Upland Subdivision of the Sonoran Desert Region, which occurs at higher elevations, receives more precipitation, and contains greater vegetation structural diversity than Sonoran Desert lowlands (Bowers and McLaughlin 1987). The climate (recorded by the Tucson Airport Weather Station; 787 m in elevation, 1930 to 2011 records) is arid/semi-arid with averages of 29 cm yr⁻¹ of precipitation, 37°C daily July high temperature, and 4°C daily January low temperature (Western Regional Climate Center, Reno, Nevada).

The Rincon Mountain District's topography consists of rolling hills, alluvial fans, and concave drainageways. Soils are primarily derived from granite and classified as Torriorthents and Haplargids (Cochran and Richardson 2003). Vegetation is characterized by scrubland or low woodland physiognomy, and consists of a diverse assemblage of shrub-trees, forbs, graminoids, and cacti, including saguaro (*Carnegiea gigantea*), a columnar cactus diagnostic for the Upland Subdivision (Bowers and McLaughlin 1987). We obtained vegetation data in a previous study at these sites (Abella et al. 2013b; Part V of this report). These data were collected in 2012 (March-April) on the same plots as seed bank samples were collected in the present study. The data consist of aerial cover of each plant species rooted in each plot (Abella et al. 2013b). Livestock grazing (primarily by cattle) occurred prior to 1976 but was not authorized thereafter. Since 1983, the park has been visited by > 600,000 people annually. Most visitors concentrate along park roads and to a lesser extent trails (National Park Service, Public Use Statistics Office, Denver, Colorado).

Site Selection

Using information provided by the Park (Tucson, Arizona), we identified buffelgrass treatment polygons within the park and randomly selected three polygons for sampling in each of the following available treatment types:

- 1) 2007-2011 (5 years) annual buffelgrass treatment (BG 07-11)
- 2) 2009-2011 (3 years) annual buffelgrass treatment (BG 09-11)
- 3) 2010-2011 (2 years) annual buffelgrass treatment (BG 10-11)
- 4) 2008 single year (4-year-old) buffelgrass treatment (BG 08)
- 5) 2011 single year (1-year-old) buffelgrass treatment (BG 11)
- 6) Control, buffelgrass but no treatment (BG no tmt)
- 7) Control, no buffelgrass and no treatment (No BG)

The National Park Service treated buffelgrass in these polygons in winter and summer within a year for the number of years (1 to 5) above for each treatment type. A combination of manual and herbicide treatment was used, with the goal of killing all buffelgrass individuals apparent during the treatment period (Abella et al. 2013b). The manual treatment consisted of uprooting whole buffelgrass plants using hand tools including digging bars, geopicks and picmatics. Plant material was placed on site in piles of ≤ 4 m² preferably on top of sparsely or unvegetated rocky areas. Herbicide that contains the active ingredient glyphosate effectively kills buffelgrass (e.g.,

Dixon and others 2002; Daehler and Goergen 2005; Tjelmeland and others 2008). Park Service personnel used a 3% glyphosate solution to kill buffelgrass during its period of active growth. The Razor PRO (Nufarms America Inc., Burr Ridge, Illinois), KleenUp (Bonide Inc., Oriskany, New York), and Roundup PRO (Monsanto Corp., St. Louis, Missouri) post-emergence formulations were used and included a water conditioner (e.g., $[\text{NH}_4]_2\text{SO}_4$) and indicator dye to mark application locations. Individual plants were sprayed from a single nozzle using a backpack sprayer with a manual pump. Decisions regarding whether to use a manual or herbicide treatment on particular plants depended on the size of the infestation (larger infestations were typically treated with herbicide, whereas both herbicide and manual treatments were done on smaller infestations), number of plants to be treated (e.g., for a few plants, often it was faster to simply manually remove them), and how many personnel on site were certified to apply herbicide. The manual and herbicide combination used by the managers provided a realistic, practical setting in which to evaluate post-treatment ecological conditions, because managers view manual and herbicide as complementary treatments and employ both at the current patch scale of buffelgrass invasion in the park (Woods et al. 2012).

Treatment polygons we sampled ranged in size from 0.03-5 ha and represented buffelgrass patches that were ca. 5-10 years old when treatments were initiated, based on records kept by the Park (Tucson, Arizona). Patches contained ≥ 100 buffelgrass individuals and exhibited areal cover of buffelgrass ranging from 18-88% prior to treatment. We identified sites for the two types of controls (untreated buffelgrass and non-invaded sites) by randomly selecting three of 13 sites of each type established during a previous study of untreated buffelgrass patches and non-invaded sites (Abella et al. 2012). Treated and untreated sites were interspersed and exhibited similar topography, 0-5 cm soil texture, and soil taxonomy (see Abella et al. 2013b).

Plot Sampling

We established a circular (5.28 m radius), 0.01-ha sampling plot randomly located within each of the 21 polygons. At the center of each plot, we recorded location and elevation using a global positioning system, slope gradient using a clinometer, and aspect using a compass.

We collected soil seed bank samples from below the three largest individuals of brittlebush (*Encelia farinosa*, a native perennial shrub) and in the three largest interspaces (open areas usually ca. 1 m² between perennial plants) on each plot in April and May 2012. We chose the below-brittlebush and interspace sampling microsites because they were present on every plot. On untreated buffelgrass plots, we also sampled below buffelgrass canopies. We sampled across these microsites because desert soil and vegetation properties can sharply vary between interspaces and below perennial plant canopies (Butterfield et al. 2010). Three samples were acquired per microsite (each 240 cm³) at 0-5 cm depth which included the upper mineral soil and any overlying debris. Samples under brittlebush or buffelgrass were collected equally spaced 10 cm from the root crown below. Subsamples (6-9 per microsite type per plot) for each of the respective microsites were composited on a plot basis to result in one sample per microsite per plot for each analysis.

Seed Bank Assays

We assayed seed bank composition using the emergence method to measure readily germinable seed density (Bakker et al. 1996). Samples were stored dry and in an environmental control room (4°C) until all samples were collected. We filled 4-L, 16-cm diameter cylindrical pots two-thirds full with potting soil (1:3:1 mulch:sand:gravel). On top of this potting soil, we placed 360-cm³ of seed bank soil (extracted from a thoroughly mixed plot sample) in a layer 2 cm thick. We randomly arranged pots on a bench in a greenhouse, without supplemental lighting, and with temperatures fluctuating between 21°C (nighttime) and 32°C (daytime). We also randomly arranged pots containing only potting soil to check for greenhouse seed contamination, which was not detected during the study period. During the four-month period that samples resided in the greenhouse, we watered samples daily to moisture capacity, counted seedlings every two weeks, and removed seedlings upon identification to the finest feasible taxonomic level following NRCS (2012). At 4 and 8 weeks we applied 1000ppm solution gibberellic acid to each pot. Of the 734 total seedlings that emerged, 727 (99%) were identified to species. We retained in the final data set for analysis 3 seedlings only identified to the *Acacia* genus but we deleted 3 seedlings identified only to Poaceae and 1 seedling identified only to Asteraceae. As is customary in seed bank research (Bakker et al. 1996), we converted seedling counts to seeds m⁻² corresponding to a 0-5 cm depth.

With the remaining 360-cm³ of seed bank soil sample from each microsite, we applied a modified extraction technique using flotation (e.g. Gross 1990; Pake and Venable 1996; Bernhardt et al. 2008). Samples were sifted with progressively finer sieves (Thompson et al. 1997) prior to flotation with the fines material (<2 mm) reserved without flotation. Each level of sieved material greater than 2mm was placed in a beaker, water added, and the suspension filtered through a stainless steel sieve (the smallest sieve had openings 0.18 mm in diameter). Samples were rinsed until water ran clear. Wetted samples were oven dried at 35°C for 12 to 24 hours or until samples were dry. Seeds were visually separated from other organic material under microscopes with $\geq 10 \times$ magnification. We identified extracted seeds to the finest taxonomic level possible using seeds identified in the field or greenhouse on live plants, local flora records (e.g. Bowers and MacLaughlin 1987) and botanical references (Jepson, Arizona Flora, SEINet). Seeds were visually assessed for viability. Not all seeds are amenable to tetrazolium testing for viability due to size, dormancy state or other factors (Pake and Venable 1996). We did not assay viability and report seed densities and species richness based on all recovered seeds, which may overestimate viable seed bank density and is further discussed in the Discussion section. Of the 32,354 total seeds that were extracted, 27,315 (84%) were identified to species, 4,150 (13%) were identified to genus, and 517 (1.6%) were identified to family. We converted seeds to seeds m⁻² corresponding to a 0-5 cm depth.

Data Analysis

Abella et al. (2013b) previously analyzed emergence data and focused on total seed and native seed densities and richness. We compared total native and non-native seeds m⁻² and species richness (per 360-cm³ sample) overall for the two seed bank assessment methods within and between treatment and microsites. We also calculated at the plot level, seed densities and richness of species which were also observed within plots to compare in-vegetation or not-in-

vegetation densities and richness within and between microsites, treatments, and seed bank assessment method. We additionally grouped vegetation by duration and growth habit to identify differences between methods, if any, for detecting different vegetation groups, and to elucidate the differences between methods for detecting in-vegetation taxa. Data were analyzed using a mixed model analysis of variance as a partially hierarchical design containing the fixed effects of sampling microsite (interspace or below brittlebush; tested over the interaction between microsite and site), treatment (7 levels corresponding to the 7 treatment types, 3 plots per treatment; tested over the interaction between treatment and microsite), seed bank assessment method (emergence and extraction, separately or together tested over the residual), vegetation (in or not in vegetation plot⁻¹) and the interaction between factors (tested over the residual term) using PROC MIXED in SAS 9.2 software (SAS Institute 2009). Random effects include site, soil sample and their interactions with microsite, method, and treatment. Data were rank transformed prior to analysis if there were significant zero values. Additionally, linear regression and Pearson correlations were performed in Microsoft Excel (2008) to identify if native (total or vegetation groups as duration $\times$ growth habit) or in-vegetation (total or vegetation groups) estimated seeds m⁻² and species richness (per 360-cm³ sample) or their proportions correlate with treatments or can be used as predictors for between methods within microsites, and if buffelgrass seed densities are correlated with time since initial treatment length or number of years of treatment. We graphically displayed species composition (relative seed density) among methods within microsites and within methods between microsites with non-metric multidimensional scaling ordination using “slow and thorough” autopilot setting and Sørensen distance in PC-ORD 5.1 (McCune and Mefford 1999).

Results

Seed density

Total native seed bank density did not significantly differ across the buffelgrass treatment gradient for either the extraction or emergence method and did not differ between treatments within microsite and method (Table 1). Extraction detected significantly greater native seed densities by orders of magnitude within interspace and below brittlebush microsites across treatments (Table 1; Fig. 2). Microsite also affected seed density estimates for both methods with greater seed densities in below brittlebush microsites across treatments (Fig. 2), although this was only marginally significant for emergence (Table 1). For both methods shrub seeds, particularly brittlebush, tended to predominate under brittlebush across sites, and annual forb seeds tended to be greater in interspace microsites. Overall emergence seed densities averaged 4 seeds/360-cm³ sample in interspaces and 4 seeds/360-cm³ sample in below brittlebush, and extracted seed densities averaged 59 seeds/360-cm³ sample in interspace and 89 seeds/360-cm³ sample in below brittlebush microsites. There was considerable variation across microsite samples within methods (see Appendix F for list of species seed densities m⁻² in treatments microsites⁻¹).

At a site level total native densities of both methods were strongly positively correlated ($r = 0.56$). At a microsite level between methods, interspace native densities were also strongly positively correlated ($r = 0.86$), while below brittlebush microsites densities were only weakly correlated ($r = 0.28$). Relationships between vegetation group densities and time since treatment

or number of years of treatment varied between microsites and methods, although for most groups there were few significant differences between treatments (Appendix F). General trends from correlations show relationships between densities and time since treatment or number of years of treatment are not consistent between methods and in some vegetation groups, result in opposite conclusions. For example with emergence shrub densities in interspaces were strongly negatively correlated with both time since treatment and number of years of treatment, but were strongly positively correlated with both time since treatment and number of years of treatment in interspaces with extraction. Also, annual forb densities, which were a significant component of both seed banks, were weakly negatively correlated with time since treatment and number of years of treatment using emergence, but were moderately positively correlated with time since treatment and weakly correlated with years of treatment using extraction.

Extraction also detected much greater exotic seed densities (Fig. 3). For buffelgrass seed densities at a site level, methods were strongly correlated ($r = 0.44$). There was a strong negative relationship with buffelgrass densities between treatments with time since treatment ($r = -0.79$ - -0.59) and number of years of treatment ($r = -0.56$ - -0.40). This trend was stronger in below brittlebush microsites and with emergence, although buffelgrass seed densities only significantly differed between treatments in extraction microsites ($F_{1,14}=5.251$, $P=0.038$; Fig. 3). Buffelgrass seed densities detected with emergence did not differ significantly across treatments within microsites, but did differ between microsites ($F_{1,14}=4.76$, $P=0.047$). Emergence did not detect buffelgrass seeds in interspace microsites. Out of 45 microsite samples emergence only detected buffelgrass in 6 samples, 5 of which were below brittlebush microsites and one was a below buffelgrass microsite. One sample containing buffelgrass was in a No BG site. Extraction detected buffelgrass in 33 samples and in all microsite types per treatment, with significantly greater densities detected in below brittlebush microsites. Interspace BG no tmt densities only marginally differed ($F_{6,14}=2.849$, $P=0.051$) with other treatments, and below brittlebush BG no tmt densities significantly differed ($F_{6,14}=3.69$, $P=0.021$) with other treatments (Fig. 3). Other exotics were also detected but in fewer microsites and densities significantly differed between microsites within methods, between methods within microsites, and between treatments within both interspace and below brittlebush microsites within both methods (Fig. 3).

Species richness

Significant differences occurred for seed bank richness between methods. Extraction detected significantly higher richness than emergence across sites and at a microsite level (Table 1; Fig. 4), particularly annual forbs in interspaces and shrubs under brittlebush. Average richness for emergence was 3.2 taxa/360-cm³ sample in interspaces among treatments and 4.5 taxa/360-cm³ sample in below brittlebush. Extracted richness averaged 17.5 taxa/360-cm³ sample in interspaces among treatments and 17 taxa/360-cm³ sample in below brittlebush, and microsites were only marginally significantly different (Table 1). Within methods and microsites, there were no significant total richness differences between treatments. At a microsite level across sites for emergence below brittlebush microsites detected marginally higher richness than interspaces. For extraction below brittlebush microsites detected significantly more taxa across sites compared to interspaces. Relationship between methods show across sites, methods were strongly correlated ($r = 0.55$), and at a microsite level for both microsites methods were strongly correlated (interspaces, $r = 0.61$; below brittlebush $r = 0.55$). Relationships between treatments

with microsites and methods between richness of different vegetation groups and time since initial treatment and number of years since treatment varied (Appendix F). Below brittlebush microsites in either method showed shrub richness increase with time since treatment, while interspace microsite results contrast with emergence indicating a strong negative response in shrub seed densities with time since treatment and years of treatment and extraction indicating a strong positive relationship with time since treatment and years of treatment and extraction. Also, within both methods and microsites, annual forbs appear to decrease in species richness with increasing years of treatment.

Species composition

A total of 127 taxa were detected through both extraction and emergence. Eighty-six taxa were detected by extraction, with 54 (63%) identified to species, 11 (13%) identified only to genus, and 21 (24%) taxa unidentified, although distinguishable as different species from the identified seeds and not similar to the emergence taxa list. Of the identified extracted taxa, 60 (92%) were native and 5 (6%) were exotic species. Only 41 taxa were detected by emergence and all species were identified (see Appendix F for full species list). Emergence detected 38 (93%) native and 3 (7%) exotic species. Some species, such as those in the genera *Opuntia* and *Cylindropuntia*, have seeds that are difficult to distinguish potentially underestimating the total number of species extracted. During emergence, only *Opuntia engelmannii* was identified amongst the emerged cactus. Both methods detected mostly annual forbs (23 taxa, 56% of total taxa for emergence; 34 taxa, 52% of total taxa for extraction). Extraction also identified more perennial taxa than emergence (Table 2).

Common species were detected by both methods (Table 2; Appendix F). Twenty-five taxa were detected in-common, and 15 of these were also detected within vegetation plots. Extraction detected 39 taxa not detected by emergence, compared to 16 taxa unique to emergence. Different exotic species were also detected between the two methods (Appendix F). Similarity of species composition within sites and microsites varied between 33% (interspace) and 53% below brittlebush between methods. Ordinations further reveal differences between method species composition within microsites (Fig. 5). There was little overlap between interspace microsites within both methods, although there is a distinct separation between emergence and extraction indicating that species composition differed between assessment methods. Additionally microsites within treatment groups tended to only loosely cluster with treatment type. For below brittlebush microsites, species composition detected with extraction did not differ as significantly as did emergence. There was also a distinction between loosely clustered emergence brittlebush microsites and the more tightly clustered extraction brittlebush microsites indicating emergence microsites were dissimilar to each other and to extraction.

Seed bank:vegetation relationships

Extraction tended to result in a greater proportion of seeds detected from species that occurred in above-ground vegetation (mean in-vegetation proportion $\pm$ S.D., $57 \pm 17\%$) across treatments compared to species that did not occur in the above-ground vegetation, while emergence resulted in a lower proportion ($34 \pm 23\%$) across treatments (Fig. 6). This trend existed at the microsite level for most vegetation groups. Proportions of extracted seeds detected from species occurring

in vegetation across sites were $57 \pm 19\%$ in interspace and $70 \pm 20\%$ in below brittlebush microsites and for seedling emergence were $26 \pm 26\%$ in interspaces and $35 \pm 28\%$ in below brittlebush microsites. Proportions of total native species also in vegetation estimated with emergence and extraction were not highly correlated ($r = 0.35$) at a site level and species composition of in-vegetation taxa differed between methods (Appendix F). At a microsite level, methods were poorly correlated ($r = 0.10-0.20$).

Within both methods there were no significant differences between treatments of in-vegetation densities of native vegetation groups (duration $\times$ growth habit), but there were significant differences in buffelgrass and other exotic, mainly *Eragrostis* spp, seed densities between treatments (Fig. 6). There were several significant differences between seed bank assessment methods within vegetation groups (in-vegetation or not-in-vegetation) and microsites (Appendix F), with extraction in both microsites contained significantly greater densities of species also in the vegetation. Extraction also detected greater seed densities of exotic species observed in vegetation plots (Fig. 6), including buffelgrass, compared to emergence. Extraction was more likely to detect the presence of exotics within microsites when exotics were present in the vegetation. For buffelgrass detected in below brittlebush microsites, extraction and emergence densities were highly correlated ($r = 0.94$). Buffelgrass seed was also detected with extraction at sites that did not have above-ground buffelgrass evidence (Appendix F). Additionally, extraction detected greater proportions of other exotic seed densities in several treatments, and all of these treatments had significantly lower buffelgrass seed densities compared to BG no tmt.

Taxa richness detected between methods significantly differed (Fig. 7). Extraction tended to detect a higher number of in-vegetation species compared to emergence (Fig. 7), and across vegetation groups (Appendix F). Emergence had a greater proportion of taxa not observed in vegetation plots in both microsites compared to extraction (Fig. 7), particularly annual forb species which made up the bulk of species detected with emergence (Appendix F). Of species observed in vegetation plots, overall richness detected with extraction or emergence did not significantly differ between buffelgrass treatments (Fig. 7). Additionally, the proportion of species observed and not observed in vegetation plots did not significantly differ between microsites within each method, except for one instance. Below brittlebush microsites using emergence tended to detect higher species richness of shrubs compared to within interspace microsites (Fig. 7). With extraction, a greater diversity of exotic species was also detected, including *Eragrostis* spp which are known exotics to occur in the Park's units. Both *E. curvula* and *E. echinochloa* were observed within the Park in vegetation plots.

Discussion

Native seed bank and seed bank assessment methods

One of the goals of this study was to identify site potential for natural recovery post-buffelgrass treatment, although it was hypothesized that results may depend on seed bank assessment method. We observed that extraction resulted in greater densities and total species richness for all natives and for natives also observed in vegetation. Additionally, at a site and microsite level, the two methods are relatively strongly correlated to each other and may be used to develop a model to reconcile the differences between the two methods generally. At a treatment level, total

native densities in BG no tmt sites were not significantly different from other treatments with either method. This is consistent with Abella et al. (2012) which observed using an emergence assay that buffelgrass infested patches had equal to or higher native densities than uninfested patches, and with Woods et al. (2012) which observed that removing buffelgrass can result in post-treatment ecological conditions largely indistinguishable from uninvaded patches. Other studies have observed in areas invaded by exotic plants that native seed banks are depauperate (Cox and Allen 2008; Gioria and Osborne 2009), compositionally altered (Vilà and Gimeno 2007), or have a reduction in richness (Jackson 2004; Daehler and Carino 1998).

At the vegetation group level between treatments, emergence did not detect a majority of species which were observed in vegetation. Emergence and extraction followed diverging trends between important vegetation groups, such as annual forbs which constitute the majority of seed density and richness in interspaces and shrubs which constitute the majority of seed density and richness in below brittlebush microsites, and which constitute a majority of the vegetation cover across sites and seed bank in uninvaded sites. Method relationships and species composition differences indicate a divergence between the two methods for estimating the native seed bank and recovery of species consistent with uninvaded sites. The differences in native species composition and in-vegetation richness detected in the seed bank between methods indicate a difference in species detection between methods. Extraction was more representative of vegetation compared to emergence and results indicate that buffelgrass presence and treatment do not negatively impact site potential for recovery and after treatment there is a high potential for native species composition recovery at treatment sites. Emergence result suggest an alteration in the seed bank from that in the above-ground vegetation and a reduction in important species in the seed bank, which may impact future native species composition and richness.

Both seed bank methods provide information on which species may be undetected by a particular method due to a range of difficulties including size threshold for collection and germination requirements. Many annuals have small seeds that are difficult to detect in extraction (Thompson et al. 1993). Several of our smaller seed species were detected by both methods, but did not have a strong presence in the spring vegetation sampling. For example, green carpetweed (*Mollugo verticillata* L.) and sleepy silene (*Silene antirrhina* (L.)) were observed in both seed bank assessment methods but did not constitute a dominant portion of the vegetation. For other species detected with emergence and had the smallest seeds, such as *Mimulus* spp., these were not detected with extraction even with our modified method. For the large seeded species such as brittlebush and cactus, we detected seeds using both methods, although for emergence, the estimated seed m^{-2} was low even in sites that had high cover. We also detected significantly fewer shrub species with emergence, which may be a result of seed dormancy.

Additionally, not testing viability limits our estimation of the extraction seed bank. Due to the length of time required for extraction per sample, it was not practical to test for viability or germinability of extracted seed. Extraction samples were processed over several months, would have been processed during different time periods and time scales, and seeds have a range of germination requirements that would have to be applied (Megill et al. 2011). Not all seeds are amenable to tetrazolium testing for viability due to their small size, dormancy stage, or other factors (Pake and Venable 1996). Germination of recently collected seed or seed stored in a laboratory setting is likely different to seeds residing in soil seed banks (Baskin and Baskin

1998). Seed banks provide an idea of the potential species which may emerge in the field. In our study, extraction appears to have the greater predictive power, although also potentially over estimating the native seed present.

Buffelgrass treatment effectiveness

Seed bank assessments along with above-ground vegetation surveys and soil assessments provide evidence to suggest that treatments can successfully reduce buffelgrass without a large negative impact on the potential for native revegetation once buffelgrass is removed (Abella et al. 2013b). Previously reported in Abella et al. (2013b), vegetation data suggested effective removal of above-ground buffelgrass from treatment sites. We observed with both methods that with increasing number of years of treatment, there was decrease in buffelgrass seed accumulation at sites. However, in this study the two seed bank assessment methods differ in the extent of effective treatment. Emergence lacked identifiable trends, although results suggest low buffelgrass seed densities in the soil seed bank within treatments. However, this may be partly due to the lack of detection with the emergence method. Extraction detected buffelgrass in a majority of microsites, including treated and No BG sites that did not have buffelgrass evidence in vegetation plots in spring 2012. Extraction results suggest some treatments along the gradient have been effective at reducing the buffelgrass seed bank, but there are still high buffelgrass densities present. Sampling at this time would capture the seed accumulation from current and previous growing seasons, which may have been more productive. Additionally, treated patches were in close proximity to each other, and seed may have been sources from other sites. It is likely that not all extracted seed are viable due to length of residence in soils or due to effective herbicide treatment during vegetative production of seed. However without testing viability these data are inconclusive.

Native recovery

In the previous evaluation of vegetation present along the buffelgrass treatment gradient, Abella et al. (2013b) was observed that vegetation has not filled in interspaces formerly invaded by buffelgrass and increased N was observed in buffelgrass treated areas with the potential effect of providing similar locations as islands of fertility. Vegetation and soil seed bank data elucidates the importance of early colonizers, such as brittlebush, to provide the vegetative structure for accumulation of native seeds. Brittlebush appeared to be impacted by the presence of buffelgrass and/or treatment of buffelgrass in the vegetation, although seed bank assessments show no significant impact on seed densities across treatments. Brittlebush vegetative cover was incrementally lower with increased years of buffelgrass treatment, which may be a legacy effect from buffelgrass or an unintended effect of treatment. It is possible that buffelgrass produces allelopathic chemicals that inhibit other plants from establishing (Hussain et al. 2010), although many native species produce a variety of chemicals and still serve as nurses (Halvorson and Patten 1975). Large native seed banks along the buffelgrass treatment gradient could result from retention of native seeds prior to invasion and persistence during buffelgrass occupancy, post-invasion seed retention due to buffelgrass vegetative structure and persistence of seed during treatment (as observed in Abella et al. 2012), or colonization or increased productivity of natives during and after buffelgrass treatment which were not observed during our survey season. In this case, the seed bank assessments suggest that brittlebush, either existing or newly established,

may provide conditions for native seed accumulation in the seed bank even at low cover. Although we did not test the competitiveness of buffelgrass against other native species like brittlebush, there is evidence in other studies (Sands et al. 2009; Clarke et al. 2005; and Daehler and Carino 1998) that buffelgrass does have a competitive advantage.

Further investigation may be required to gain a greater perspective on the effectiveness of buffelgrass removal and revegetation by native species over the long term. Since we only sampled in the spring after winter rains we are missing a critical time period for examining the potential of natives to outcompete, prevent or suppress buffelgrass reinvasion during its growing season in late summer in the Sonoran Desert. We also were not able to capture above-ground emerging vegetation during this time period. We found evidence of late summer species in the seed bank. Sonoran Desert buffelgrass germination and seedling survival are favored by wet summers and warm winters. Estimating species' contributions to the seed bank per growing season per year and observing above-ground emerging vegetation can provide both seasonal and yearly variations in the soil seed bank and residual effects of seasonal and yearly fluctuations to establishing above-ground vegetation. For example, during the buffelgrass treatment years, post-treatment weather varied. Based on the nearby Tucson, Arizona, Airport Weather Station, our study generally occurred during a period of below-average precipitation (Western Regional Climate Center, Reno, Nevada). In 2006, the year prior to the initial 2007 treatments we examined, precipitation was 104% of the long-term (1930-2011) average of 29 cm yr⁻¹, but precipitation was below average in 2007 (86% of average), 2008 (76%), 2009 (50%), and 2010 (98%). Precipitation in 2011 was 108% of average, but the January through April precipitation in 2012 prior to our May 2012 sampling was only 26% of the 7-cm average total for those months, which likely had an impact on the 2012 seed bank contributions of both native and exotic species. Olsson and others (2012) found that climatic conditions for buffelgrass germination were met nearly every year in their study of buffelgrass distribution since 1988 even without optimal conditions. While buffelgrass establishment during our study period may or may not have been influenced by weather, the possibility that dry conditions during the treatment period influenced establishment of other species should not be dismissed.

Conclusion

The results of this study suggest that differences in detection between seedling emergence and seed extraction result in different conclusions and have land management implications. The two seed bank methods are correlated at a site level, but do not consistently correlate at a treatment level within microsites. Additionally, emergence and extraction detected different taxa revealing important considerations when selecting seed bank methods to use in assessments. For example, an important purpose of a seed bank assay could be to detect exotic species during non-optimal years or species that are short-lived or may not be evident in vegetation for several years.

Table 1. Statistical results for the influence of method (seedling emergence and seed extraction), microsite (interspace and below brittlebush), and treatments of buffelgrass along a gradient (5 treatments and a positive and negative control) on native species richness and seed density m⁻² estimated from soil seed bank samples from plots located in eastern (Rincon Mountain District) Saguaro National Park, Sonoran Desert, USA. Significance at alpha >0.05 in bold; alpha >0.10 in italics.

	Species Richness			Seed Density		
	<i>df</i>	<i>F</i>	<i>P</i>	<i>df</i>	<i>F</i>	<i>P</i>
Between Methods						
Extraction>Emergence	1,28	462.12	<0.001	1,28	547.47	<0.001
Interspace (Extraction>Emergence)	1,14	301.76	<0.001	1,14	323.65	<0.001
Below Brittlebush (Extraction>Emergence)	1,14	173.24	<0.001	1,14	186.14	<0.001
Between Microsites within Method						
	1,14	4.55	<i>0.051</i>	1,14	3.95	<i>0.067</i>
Below Brittlebush>Interspace (Emergence)						
Below Brittlebush>Interspace (Extraction)	1,14	7.13	0.018	1,14	0.26	0.619
Between Treatments within Method						
Extraction	6,14	0.92	0.510	6,14	0.10	0.995
Interspace	6,14	0.58	0.739	6,14	0.28	0.935
Below Brittlebush	6,14	0.94	0.498	6,14	0.21	0.968
Emergence	6,14	1.26	0.337	6,14	1.09	0.417
Interspace	6,14	0.83	0.567	6,14	0.97	0.478
Below Brittlebush	6,14	1.92	0.148	6,14	1.26	0.337

Table 2. Total number of species detected and number of species identified within two seed bank assessment methods (seedling emergence and seed extraction) that were observed within the above-ground vegetation from plots located in eastern (Rincon Mountain District) Saguaro National Park, Sonoran Desert; plants grouped by growth habit and duration. Number in parentheses indicates the number of exotic species included in total. # Shrubs include cactus and species classified as trees. * Some species, such as species in Cactaceae, have similar seeds and were not distinguished using extraction method*Some species, such as species in in the family Cactaceae, have similar seeds and were not distinguishable using the extraction method.

Plant Category	Emergence		Extraction		Species in both methods	Total species detected	Total detected & in vegetation
	Total Species	Occurred in Vegetation	Total Species	Occurred in Vegetation			
Annual Forb	23	6	34 (1)	15 (1)	15	42 (1)	6
Annual Grass	5	2	5 (1)	4 (1)	2	7 (1)	2
Perennial Forb	3	2	11	5	2	12	2
Perennial Grass	7 (2)	1	8 (3)	3	4 (2)	11 (3)	3(2)
Shrub [#]	3	3	7	7	2	>8*	2

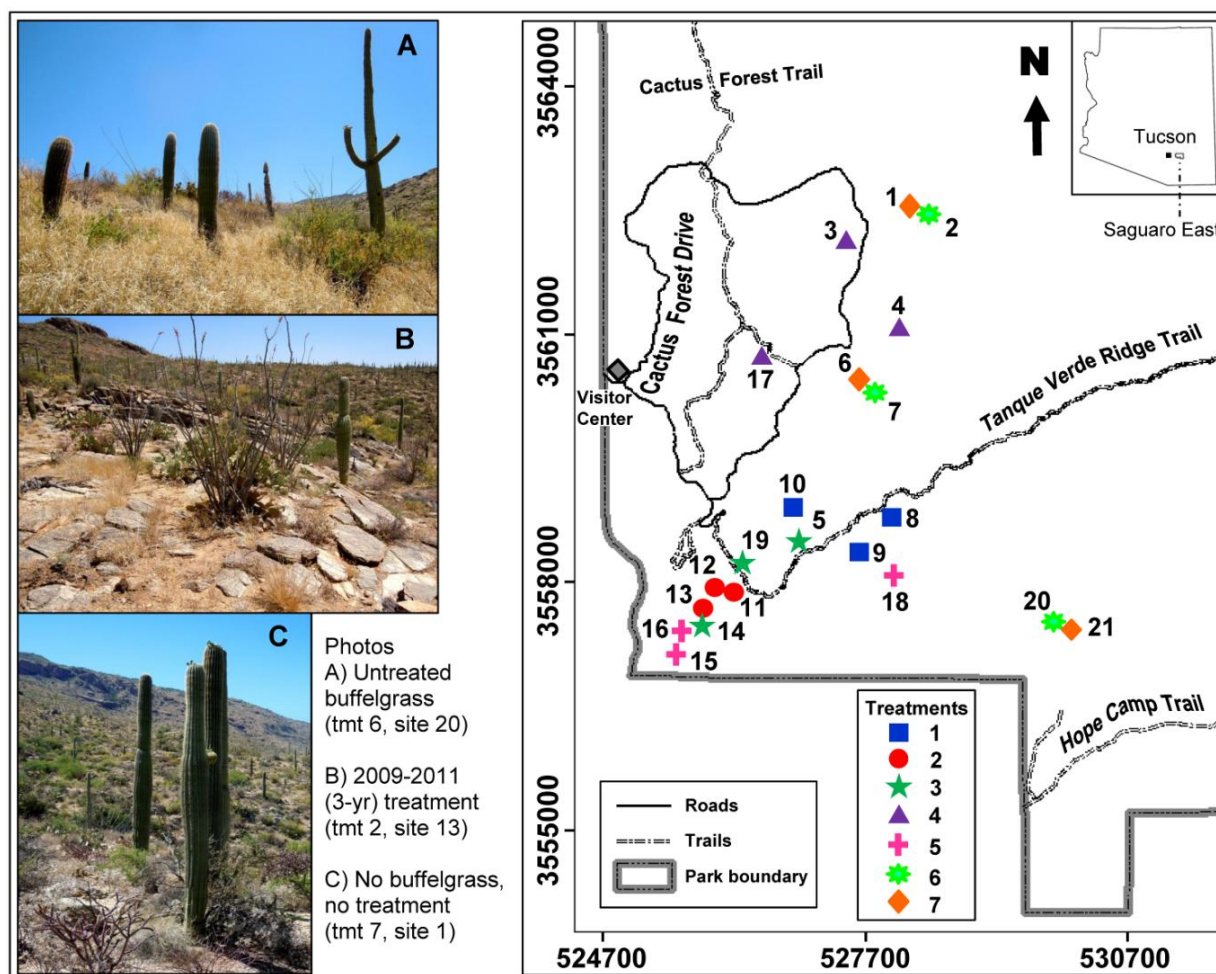


Fig. 1 Location of study plots, classified by buffelgrass treatment type, within eastern (Rincon Mountain District) Saguaro National Park, Sonoran Desert. Geographic coordinates are Universal Transverse Mercator (zone 12, m), North American Datum 1983. Treatment numbers correspond with: 1) 2007-2011 (5 years) annual buffelgrass treatment, 2) 2009-2011 (3 years) annual buffelgrass treatment, 3) 2010-2011 (2 years) annual buffelgrass treatment, 4) 2008 single year (4-year-old) buffelgrass treatment, 5) 2011 single year (1-year-old) buffelgrass treatment, 6) control, buffelgrass but no treatment, and 7) control, no buffelgrass and no treatment.

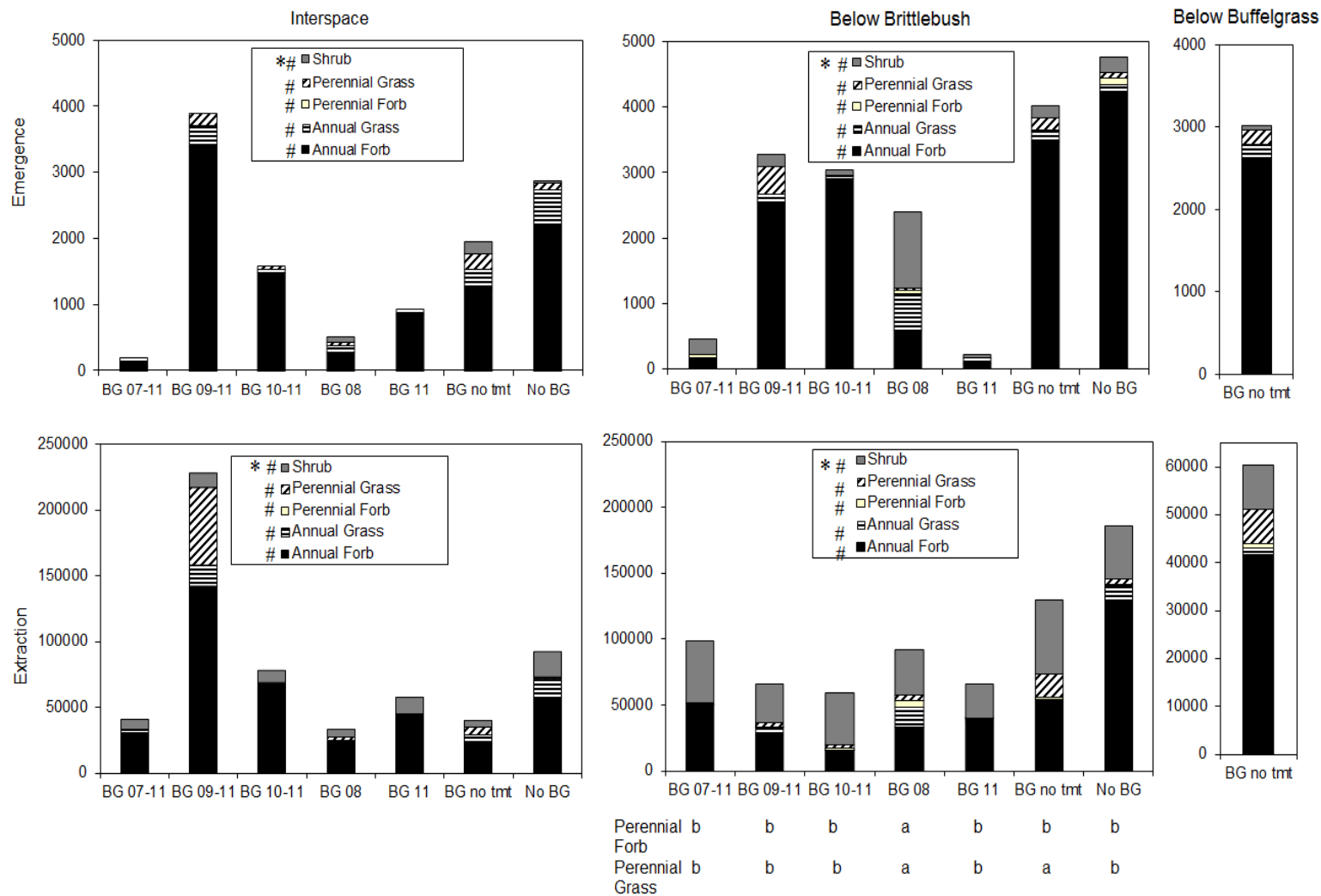


Fig. 2. Native seed densities m^{-2} for two seed bank assessment methods from three microsites in 0-5 cm soil seed bank along a buffelgrass treatment gradient in Saugaro National Park, Sonoran Desert. Treatment abbreviations along x axis: BG = buffelgrass, with the numbers following describing the year(s) in which BG was treated. # Indicates significant differences between seed bank assessment method within microsite significant differences. * Indicates significant differences between microsites within seed bank assessment method. Letters groups denote significant differences between groups.

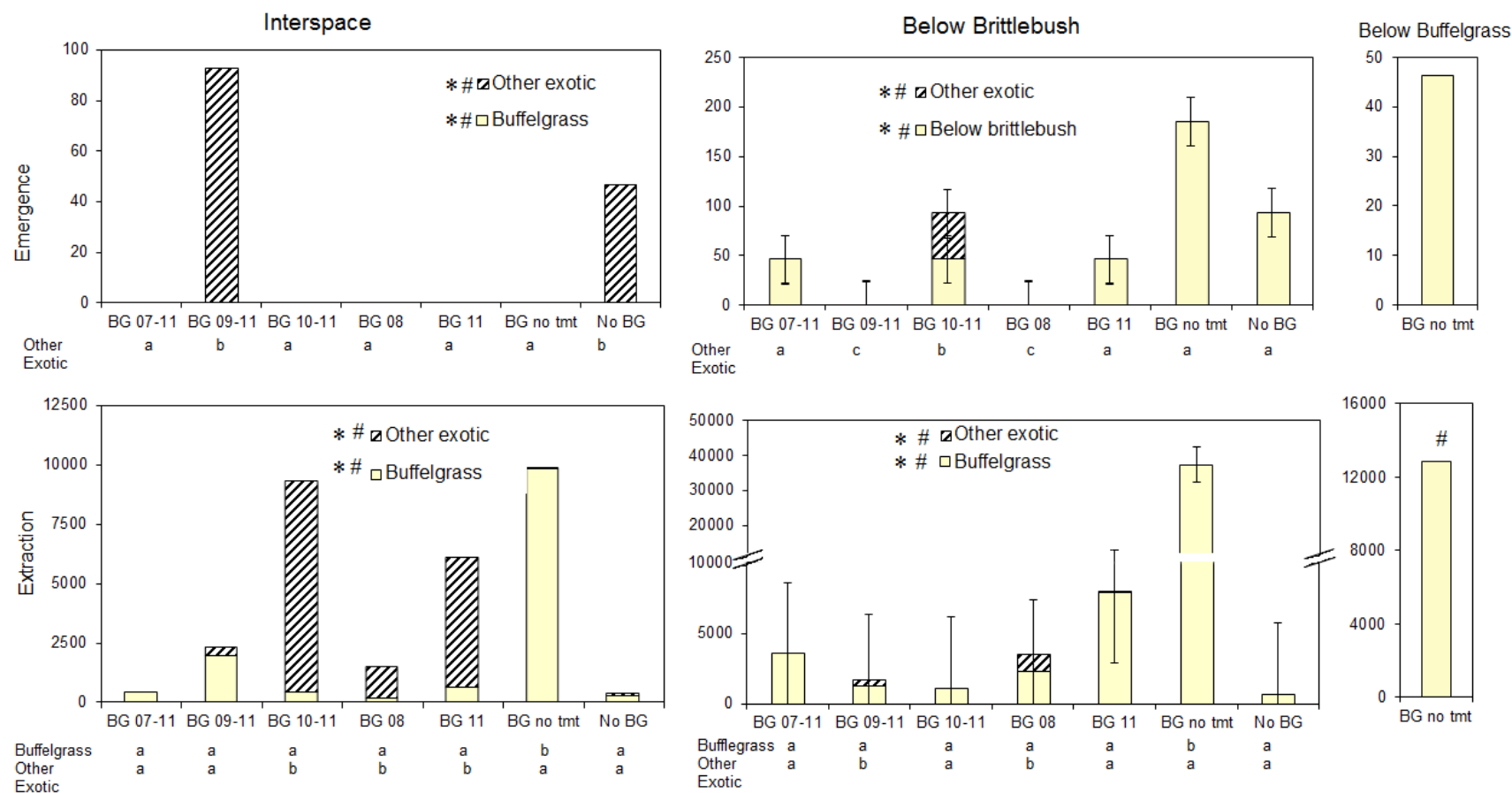


Fig. 3. Exotic seed densities m^{-2} for two seed bank assessment methods from three microsites in 0-5 cm soil seed bank along a buffelgrass treatment gradient in Saugaro National Park, Sonoran Desert. Treatment abbreviations along x axis: BG = buffelgrass, with the numbers following describing the year(s) in which BG was treated. # Indicates significant differences between seed bank assessment method within microsite significant differences. * Indicates significant differences between microsites within seed bank assessment method. Letters denote differences between treatments. Letters groups denote significant differences between groups.

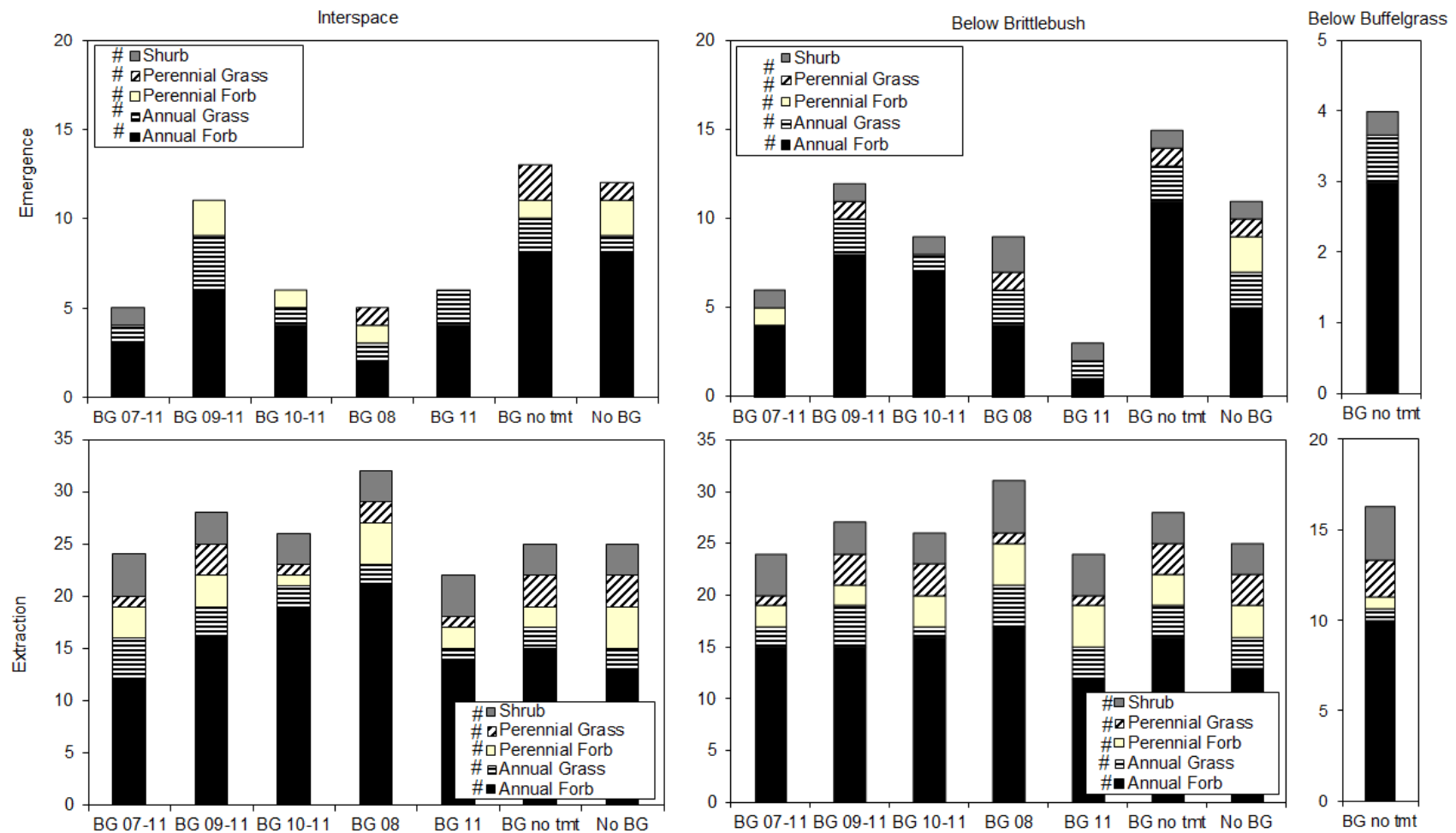


Fig. 4 Species richness for two seed bank assessment methods from three microsites in 0-5 cm soil seed bank along a buffelgrass treatment gradient in Saugaro National Park, Sonoran Desert. Treatment abbreviations along x axis: BG = buffelgrass, with the numbers following describing the year(s) in which BG was treated. # Indicates significant differences between seed bank assessment method within microsite significant differences.

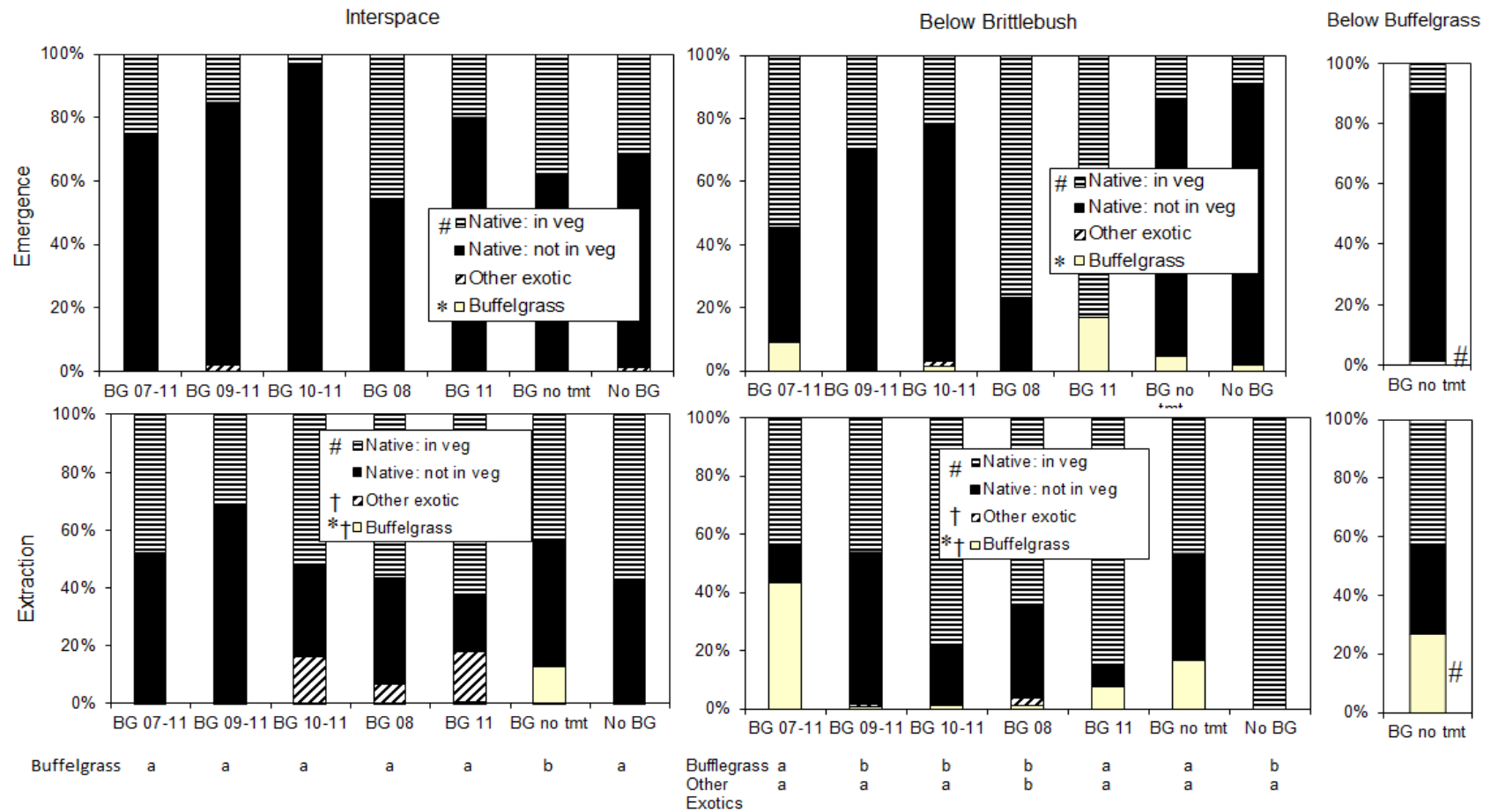


Fig. 6 Relativized seed densities of native and exotic species observed in vegetation for microsites examined with two seed bank assessment methods along a buffelgrass treatment gradient in Saugaro National Park, Sonoran Desert. Treatment abbreviations along x axis: BG = buffelgrass, with the numbers following describing the year(s) in which BG was treated. # Indicates significant differences between seed bank assessment method within microsite and vegetation group (in-vegetation or not-in-vegetation). * Indicates significant differences between microsites within seed bank assessment method and within vegetation group (in-vegetation or not-in-vegetation). † Indicates significant differences between species detected within above-ground vegetation and species not detected within above-ground vegetation within microsites and within seed bank assessment method. Letters groups denote significant differences between groups.

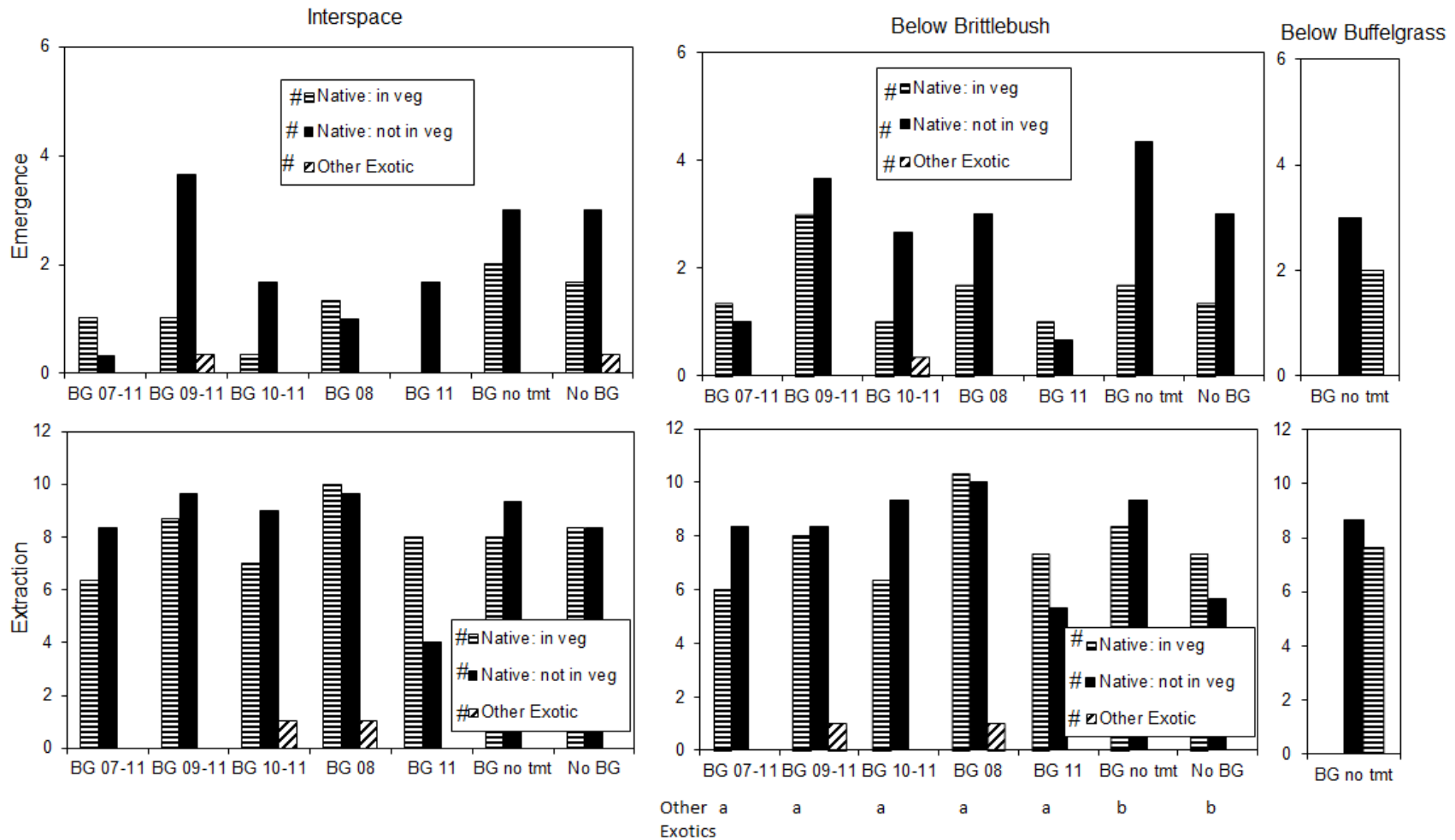


Fig. 7 Species richness of native and exotic species observed in vegetation for microsites examined with two seed bank assessment methods along a buffelgrass treatment gradient in Saugaro National Park, Sonoran Desert. Treatment abbreviations along x axis: BG = buffelgrass, with the numbers following describing the year(s) in which BG was treated. # Indicates significant differences between seed bank assessment method within microsite and vegetation group (in-vegetation or not-in-vegetation). * Indicates significant differences between microsites within seed bank assessment method and within vegetation group (in-vegetation or not-in-vegetation). Letters groups denote significant differences between groups.

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APPENDIX A

Supplemental material for PART III.

Table A1. Description of study sites in Saguaro National Park, Sonoran Desert.

ID ^a	UTMx ^b	UTMy ^b	Elev. (m)	SG (°) ^c	Aspect (°)	PM ^d	Soil subgroup(s)
1BG	527112	3560559	962	2	233	G	Lithic Torriorthents/ Lithic Haplargids
2BG	530761	3556795	1062	32	215	G	Lithic Torriorthents
3BG	530249	3555423	981	20	160	M/L	Typic Calciorthids
4BG	528184	3562428	929	9	245	G	Lithic Torriorthents
5BG	527802	3558358	1147	35	178	G	Lithic Torriorthents
6BG	529467	3557343	1025	8	128	G	Lithic Torriorthents
7BG	527994	3557556	1034	22	196	G	Lithic Torriorthents
8BG	529557	3557174	1012	5	236	G	Lithic Torriorthents
9BG	528241	3562019	972	14	243	I/G	Lithic Torriorthents/ Ustic Torriorthents
10BG	529722	3557140	1017	11	133	G	Lithic Torriorthents
11BG	529730	3557255	1048	13	185	G	Lithic Torriorthents
12BG	528733	3562988	978	9	222	I/G	Lithic Torriorthents/ Ustic Torriorthents
13BG	531382	3556911	1098	21	195	I/G	Lithic Torriorthents/ Ustic Torriorthents
14BG	486675	357673	780	15	190	I/M/G	Typic Haplargids/ Lithic Torriorthents
1NBG	527166	3560545	961	3	184	G/I	Lithic Torriorthents/ Lithic Haplargids
2NBG	530720	3556814	1059	40	215	G	Lithic Torriorthents
3NBG	530300	3555477	990	32	196	M/L	Typic Calciorthids
4NBG	528208	3562400	932	15	252	G	Lithic Torriorthents
5NBG	527771	3558353	1150	50	168	G	Lithic Torriorthents
6NBG	529547	3557335	1013	6	206	G	Lithic Torriorthents
7NBG	527933	3557733	1044	30	192	G	Lithic Torriorthents
8NBG	529552	3557150	1011	4	265	G	Lithic Torriorthents
9NBG	528673	3561257	1127	13	270	I/G	Lithic Torriorthents/ Ustic Torriorthents
10NBG	529740	3557163	1019	21	163	G	Lithic Torriorthents
11NBG	529687	3557275	1055	9	235	G	Lithic Torriorthents
12NBG	528864	3562986	989	29	212	I/G	Lithic Torriorthents/ Ustic Torriorthents
13NBG	531516	3556911	1091	21	160	I/G	Lithic Torriorthents/ Ustic Torriorthents
14NBG	486704	3576801	826	45	215	I/M/G	Typic Haplargids/ Lithic Torriorthents

^aSite identification number (corresponding to Figure 1), with BG = buffelgrass patch and NBG = non-buffelgrass patch.

^bUniversal Transverse Mercator coordinates (m), North American Datum 1983.

^cSG = slope gradient.

^dSoil parent material: G = granite, I = igneous rock, L = limestone, and M = metamorphic (Cochran and Richardson 2003).

Table A2. Species recorded in vegetation of buffelgrass and non-buffelgrass patches of Saguaro National Park, Sonoran Desert.

	Frequency (%) ^a		Relative Cover (%)	
	BG ^b	NBG ^b	BG	NBG
Annual graminoid				
<i>Bouteloua aristidoides</i>	14	21	0.3	0.1
<i>Panicum hirticaule</i>	7	29	0.0	0.9
Perennial graminoid				
<i>Aristida purpurea</i>	14	14	0.2	0.4
<i>Bothriochloa barbinodis</i>	7	0	0.0	0.0
<i>Eragrostis echinochloidea</i> * ^c	7	0	0.0	0.0
<i>Eragrostis lehmanniana</i> *	14	21	0.1	0.2
<i>Muhlenbergia porteri</i>	21	79	0.2	3.5
<i>Pennisetum ciliare</i> *	100	0	72.3	0.0
<i>Poa pratensis</i> *	0	14	0.0	0.5
<i>Tridens muticus</i>	0	7	0.0	0.1
Fern				
<i>Astrolepis sinuata</i>	7	21	0.0	0.1
<i>Pentagramma triangularis</i>	36	29	0.2	0.3
Annual forb				
<i>Eriastrum diffusum</i>	0	7	0.0	0.2
<i>Ipomoea barbatisepala</i>	7	21	0.1	0.3
Annual-perennial forb				
<i>Descurainia pinnata</i>	43	36	0.5	1.4
<i>Nicotiana obtusifolia</i>	7	0	0.1	0.0
Perennial forb				
<i>Chamaesyce melanadenia</i>	14	7	0.1	0.2
<i>Dichelostemma capitatum</i>	14	0	0.1	0.0
<i>Evolvulus arizonicus</i>	7	14	0.1	0.3
<i>Janusia gracilis</i>	79	71	1.8	4.1
<i>Lomatium nevadense</i>	7	7	0.1	0.0
<i>Psilostrophe cooperi</i>	0	7	0.0	0.4
<i>Senna covesii</i>	0	7	0.0	0.1
<i>Sphaeralcea laxa</i>	7	0	0.0	0.0
<i>Thymophylla pentachaeta</i>	7	0	0.1	0.0
<i>Tidestromia oblongifolia</i>	0	7	0.0	0.4
Shrub				
<i>Abutilon</i> spp.	43	29	0.3	0.6
<i>Aloysia wrightii</i>	7	0	0.0	0.0
<i>Ambrosia ambrosioides</i>	14	14	0.1	2.2
<i>Ayenia filiformis</i>	7	7	0.1	0.0
<i>Brickellia coulteri</i>	7	14	0.1	0.4
<i>Calliandra eriophylla</i>	57	57	0.6	1.8
<i>Celtis ehrenbergiana</i>	21	14	0.5	2.2
<i>Coursetia glandulosa</i>	21	7	1.0	2.2
<i>Encelia farinosa</i>	100	100	4.4	24.7
<i>Eriogonum fasciculatum</i>	0	7	0.0	0.1
<i>Fouquieria splendens</i>	57	71	2.0	6.5
<i>Haplophyton crooksii</i>	29	29	0.4	0.5
<i>Hibiscus denudatus</i>	7	7	0.1	0.3
<i>Hyptis emoryi</i>	7	7	0.2	0.1
<i>Jatropha cardiophylla</i>	71	71	1.0	7.4
<i>Larrea tridentata</i>	14	0	1.0	0.0

<i>Lycium</i> spp.	79	71	1.7	7.6
<i>Lysiloma watsonii</i>	7	7	0.1	0.2
<i>Porophyllum gracile</i>	0	7	0.0	0.1
<i>Tecoma stans</i>	7	0	0.5	0.0
<i>Trixis californica</i>	14	7	0.1	0.1
Shrub-tree				
<i>Acacia constricta</i>	0	7	0.0	0.4
<i>Acacia greggii</i>	29	29	0.1	1.4
<i>Parkinsonia microphylla</i>	64	57	2.9	11.2
<i>Prosopis velutina</i>	43	21	1.8	1.9
Cactus				
<i>Carnegiea gigantea</i>	43	79	0.3	2.8
<i>Cylindropuntia bigelovii</i>	14	14	0.1	0.2
<i>Cylindropuntia fulgida</i>	0	7	0.0	0.1
<i>Cylindropuntia leptocaulis</i>	7	0	0.1	0.0
<i>Cylindropuntia versicolor</i>	50	57	0.4	1.4
<i>Ferocactus wislizeni</i>	29	43	0.2	0.8
<i>Mammillaria grahamii</i>	64	64	0.3	0.6
<i>Mammillaria heyderi</i>	7	0	0.0	0.0
<i>Opuntia engelmannii</i>	64	64	2.7	8.2

^aOut of 14, 100-m² plots for each patch type.

^bBG, buffelgrass patch; NBG, non-buffelgrass patch.

^cAsterisks denote exotic species.

Table A3. Percent frequency by patch type (buffelgrass or non-buffelgrass) and microsite for 41 taxa identified to genus or species along with Cactaceae detected in soil seed bank samples in Saguaro National Park, Sonoran Desert.

	Buffelgrass				Non-buffelgrass		
	BG ^b	IN	BB	CA	IN	BB	CA
Annual graminoid							
<i>Bouteloua aristidoides</i>	7	0	0	0	0	0	11
<i>Juncus bufonius</i>	7	7	10	17	7	0	0
<i>Schismus</i> spp.* ^a	0	0	0	0	0	7	0
<i>Vulpia octoflora</i>	0	0	20	0	0	0	0
Perennial graminoid							
<i>Digitaria californica</i>	0	0	10	0	0	0	0
<i>Eragrostis echinochloidea</i> *	0	0	0	0	0	0	11
<i>Muhlenbergia porteri</i>	0	21	0	0	0	0	11
<i>Pennisetum ciliare</i> *	86	7	50	17	7	0	0
<i>Sporobolus wrightii</i>	0	7	0	0	0	0	11
Annual forb							
<i>Camissonia chamaenerioides</i>	0	0	0	0	0	7	0
<i>Chenopodium incanum</i>	7	0	10	0	0	0	0
<i>Chenopodium</i> spp.	0	7	10	0	0	0	0
<i>Crassula connata</i>	7	43	10	33	29	7	11
<i>Cryptantha nevadensis</i>	0	0	0	0	0	7	0
<i>Cryptantha</i> spp.	0	7	0	0	0	0	0
<i>Daucus pusillus</i>	7	0	10	0	0	0	0
<i>Eucrypta micrantha</i>	0	0	0	0	0	7	0
<i>Ipomoea barbatisepala</i>	7	0	0	0	0	0	0
<i>Logfia californica</i>	7	14	0	17	14	7	0
<i>Mimulus floribundus</i>	7	0	10	17	0	0	0
<i>Mollugo verticillata</i>	0	0	10	0	7	7	11
<i>Nemacladus glanduliferus</i>	0	7	0	0	7	0	0
<i>Parthenice mollis</i>	7	0	10	0	0	0	0
<i>Pectocarya recurvata</i>	0	0	0	0	7	0	11
<i>Perityle emoryi</i>	7	7	0	0	0	0	0
<i>Pterostegia drymarioides</i>	0	0	10	0	0	0	0
<i>Silene antirrhina</i>	7	7	0	0	0	7	0
<i>Stemodia durantifolia</i>	0	0	0	0	7	0	0
Annual-biennial forb							
<i>Centaurium arizonicum</i>	0	7	10	0	0	0	0
<i>Pseudognaphalium stramineum</i>	0	7	0	0	0	0	0
<i>Sairocarpus nuttallianus</i>	7	0	10	17	0	7	0
<i>Streptanthus carinatus</i>	7	0	0	0	0	7	0
Annual-perennial forb							
<i>Lepidium virginicum</i>	7	7	10	0	0	7	0
<i>Mecardonia procumbens</i>	0	0	10	17	0	0	0
<i>Mimulus guttatus</i>	7	7	0	0	0	0	0
<i>Nicotiana obtusifolia</i>	14	0	10	0	0	0	0
Perennial forb							
<i>Astragalus arizonicus</i>	0	0	0	0	0	7	0
<i>Janusia gracilis</i>	0	0	0	0	0	7	0
<i>Sisyrinchium</i> spp.	0	7	0	0	0	0	0
Shrub							
<i>Baccharis sarathroides</i>	0	0	0	17	0	0	0
<i>Encelia farinosa</i>	0	0	0	0	0	7	22
Cactus							

Cactaceae	7	0	10	0	7	7	0
Sample size (n)	14	14	10	6	14	14	9

^aAsterisks denote exotic species.

^bMicrosite abbreviations: BG, buffelgrass (*Pennisetum ciliare*); IN, interspace; BB, brittlebush (*Encelia farinosa*); CA, cactus apple (*Opuntia engelmannii*). The buffelgrass microsite was not present in non-buffelgrass patches.

Supplemental Notes A1.

1. A main acknowledged limitation of the study is that we do not know specifically how old the buffelgrass patches are. Determining this might be helpful to place the results in context. On the other hand, the characteristics that were quantified represent the current condition of the sites, which is what is relevant to formulating contemporary management strategies.
2. Another limitation is that vegetation was done only once. This would likely especially affect annuals, but as Olsson et al. (2012) noted, perennial plants such as brittlebush also can wink in and out of buffelgrass patches as well. Ideally, these, and other, sites would be monitored temporally to evaluate if or how results might change. Soil properties likely will be less sensitive to temporal variation, as soil C for example does not normally change drastically seasonally. However, soil seed banks could vary seasonally. We don't have a great way to evaluate how seasonality might influence comparisons of native species richness and diversity in the literature. Really in almost all studies, ideally a greater temporal frequency of sampling would occur, but this is obviously frequently limited by funding, etc.
3. The emergence method for characterizing the seed bank was employed in this study. This method quantifies the readily germinable fraction of the seed bank. Some seeds with specialized germination requirements may not have been detected. Directly extracting seeds from the soil (e.g., by sifting and picking out) is laborious but can detect seeds with deep dormancy that may not be detectable via the emergence method. However, extraction also can 'miss' seeds, such as small seeds or 'weathered' seeds difficult to see, and then determining viability/germinability also is often problematic as it is for emergence. Only viable seeds are part of the seed bank and of interest for quantifying plant regeneration potential. Thus, both methods have advantages and disadvantages. The emergence method detected over 41 taxa at the 14 sites during a single sampling, which we consider to be quite a few species based on comparing the results to other studies. Emergence therefore did detect a lot of taxa (including some that may not have been detected via extraction), but it should be acknowledged that additional viable seeds may be present in the samples but were not detected.
4. We obviously should not necessarily expect a 1:1 correspondence of the seed bank with what might colonize the sites even if buffelgrass is removed. Some of the wetland plants in the seed bank, for example, may have blown in or been otherwise transported in from elsewhere. Their seed may never be able to germinate or result in established plants at these sites. We found seed banks dominated by cattail in the middle of the desert in Lake Mead National Recreation Area! These seeds likely blew in long distances from Lake Mead. Many wetland plants are, in fact, wind dispersed with small seeds.
5. The seed bank data presented here for the microsites in buffelgrass and non-buffelgrass patches could be extrapolated to the site-scale with some additional information, but are not able to be extrapolated in the current form. To extrapolate to the plot scale (100 m²), information on the area (or areal percent cover) occupied by each microsite is needed, which could be obtained by estimating area on the plot or by counting the number of each microsite and multiplying by their average area. In the current form, even if a given microsite had a much larger seed density than other microsites, it does not necessarily contribute much to site-level seed banks unless the

microsite covers substantial area. Quantifying site-level seed bank potential at these sites, and then evaluating what species actually do establish in the field (e.g., some of the wetland plants may not be adapted to the sites; on the other hand, species not detected in the seed bank may also colonize) would be valuable.

6. The possibility of allelopathic effects or some other type of unmeasured soil modification by buffelgrass should not be dismissed, as was pointed out in the report. A way to test for this could be simply to bring in soil from buffelgrass areas into the greenhouse, alleviate all other limitations (water, light, etc), and see how native plants grow on soil from buffelgrass areas compared to soil from native plant areas. That would not necessarily specifically isolate allelopathy but would help determine to what extent the buffelgrass soils would support native plants, with the idea being of course that if native plants can establish on the soils, apparently allelopathy is not limiting. Ideally this also would be coupled with field experimentation.

7. A little cheat sheet for the soil properties in Table 1:

Texture (sand, silt, clay): affects soil water-holding capacity, among other things (e.g., different sized soil particles can also affect soil seed banks by trapping different sized seeds). In our case here, we would not expect that buffelgrass would influence texture, at least within the time scale of current invasion. Thus, we would hope that texture would be as similar as possible between buffelgrass invaded and non-invaded areas to help isolate possible effects of buffelgrass on the ecosystem. Texture did not differ between patch types, so this assumption was supported.

Calcium carbonate: can affect pH, among other things. Similar considerations to above in that buffelgrass should not affect calcium carbonate, and the lack of a difference between patch types supports an assumption that overall site characteristics of the patchy types were generally similar.

pH: levels deviating far from neutral can cause problems for plant growth. Greater availability of bases increases pH. There was no significant difference in pH between patch types, and the range of averages (7.1-7.4) should be fine for most plant growth.

Electrical conductivity: quantifies ability of soil water to carry an electric current, providing an indirect measure of salt content. This is correlated with texture, organic matter, and soil chemistry. Likely because there was greater organic matter (indicated by greater organic C), conductivity was greater in buffelgrass patches.

N measures: the total N pool (which includes all N – the mineral forms and N that is bound up in various organic compounds and unavailable to plants) and the available forms (nitrate and ammonium) all were greater below buffelgrass. The fact that all of them were greater results in a strong conclusion, as this effect is likely persistent throughout the year.

P and S: important nutrients to plant growth; neither differed between patch types.

Bulk density: measures the density of the fine fraction (< 2 mm in diameter, i.e. the sand, silt, clay fraction) of soil. If the soil is compacted, bulk density increases. Organic matter, by being

of low density, decreases bulk density. Rocky soils also have low bulk density, because so much of the soil volume consists of rocks and not the fine soil fraction. This reduces nutrient content because there is simply less soil to contain nutrients. In our case, bulk density was slightly lower (though not significantly statistically) in buffelgrass patches, likely again because of the greater organic matter below buffelgrass. However, bulk density was not likely different enough to have any appreciable effect on plant growth.

Fragments: the content by weight and volume of coarse fragments larger than 2 mm in diameter (e.g., pebbles, stones). Maybe buffelgrass invades areas that tend to have high concentrations of rocks on the soil surface (or maybe this relationship is not consistent or not cause-effect, appears worthy of future investigation), but the fragments by weight and volume in the soil were identical between patch types.

APPENDIX B

Manuscript developed from Report 3, PART III of this report. (Attached)

Abella SR, Chiquoine LP, Backer DM. 2012. Ecological characteristics of sites invaded by buffelgrass (*Pennisetum ciliare*). *Invasive Plant Science and Management*, 5(4):443-453.

Three Online Resource Supplements
Appendices 1-3

Ecological Characteristics of Sites Invaded by Buffelgrass (*Pennisetum ciliare*)

Scott R. Abella, Lindsay P. Chiquoine, and Dana M. Backer*

Understanding the ecological characteristics of areas invaded and not invaded by exotic plants is a priority for invasive plant science and management. Buffelgrass is an invasive perennial species that managers view as a major threat to indigenous ecosystems of conservation lands in Australia, Mexico, the United States, and other locations where the species is not native. At 14 sites in Saguaro National Park in the Arizona Uplands of the Sonoran Desert, we compared the soil, vegetation, and soil seed bank of patches invaded and not invaded by buffelgrass. Abiotic variables, such as slope aspect and soil texture, did not differ between buffelgrass patches and patches without buffelgrass. In contrast, variables under primarily biotic control differed between patch types. Soil nutrients, such as organic C and $\text{NO}_3\text{-N}$, were approximately twofold greater in buffelgrass compared with nonbuffelgrass patches. Average native species richness was identical (14 species 100 m^{-2}) between patch types, but native plant cover was 43% lower in buffelgrass patches. Unexpectedly, native seed-bank densities did not differ significantly between patch types and were 40% greater than buffelgrass seed density below buffelgrass canopies. Results suggest that (1) soil nutrient status should not be unfavorable for native plant colonization at buffelgrass sites if buffelgrass is treated; (2) at least in the early stages of buffelgrass patch formation (studied patches were about 10 yr old), native vegetation species were not excluded, but rather, their cover was reduced; and (3) native soil seed banks were not reduced in buffelgrass patches.

Nomenclature: Buffelgrass, *Pennisetum ciliare* (L.) Link.

Key words: *Cenchrus ciliaris* L., diversity, fertile island, invasibility, native species richness, seed bank, soil, species composition.

A major focus of invasive plant science is understanding characteristics of areas invaded by exotic species and how they differ from noninvaded areas (e.g., Blank 2008; Olsson et al. 2012; Parker et al. 1999). Three key characteristics of ecosystems that could be affected by exotic plant invasions include soil, native vegetation, and soil seed bank. For example, some plant invasions can alter soil properties, such as N availability, which, in turn, can induce other ecosystem changes (Parker and Schimel 2010). Altered soils are a legacy of site occupancy by invasive species that can affect the management needs of the site, even after the species is removed (Corbin and D'Antonio 2004; Jordan et al. 2011). Some exotic plants

also reduce native vegetation, altering habitat functions and decreasing propagules available for recolonization of sites by native vegetation (Brown et al. 2008). Consequently, native soil seed banks can become depleted on sites invaded by exotic plants (Cox and Allen 2008; Gioria and Osborne 2009).

Buffelgrass [*Pennisetum ciliare* (L.) Link], a perennial C_4 bunchgrass, is considered a major invasive threat to arid regions of Australia and southwestern North America, which are outside the species' native range of arid and semiarid Africa, Asia, and the Middle East (Marshall et al. 2012). Increased fuel loads and wildfire hazard are recognized consequences of buffelgrass invasion (Esque et al. 2007; Stevens and Falk 2009). However, less immediately observable components of ecosystems, such as soil, vegetation, and soil seed banks, could also be influenced by buffelgrass and could have legacy effects that influence site management during and after buffelgrass treatment (Lyons et al. 2013; Marshall et al. 2012; Olsson et al. 2012).

Potential influences of buffelgrass on soil, vegetation, and seed banks have received variable attention in the literature. For example, only one study known to us has focused on potential effects of buffelgrass on soils (Ibarra-Flores et al. 1999). That study found that differences in soil

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Management Implications

Buffelgrass is a priority invasive, exotic species for managers of conservation lands in Australia, Mexico, and the United States because it can alter fire regimes and reduce native biodiversity. We compared ecological characteristics (soil, vegetation, and seed bank) of patches invaded and not invaded by buffelgrass at 14 sites in Saguaro National Park in the Arizona Upland Subdivision of the Sonoran Desert. Abiotic variables (e.g., aspect, soil texture) did not differ between patch types, whereas properties under biological control (e.g., soil organic C) differed between patch types. Soil nutrients, such as $\text{NO}_3\text{-N}$ and organic C, were about twice as concentrated in buffelgrass compared with patches without buffelgrass. Given that the nutrient-rich soils below native, perennial plants are key locations for native plant recruitment and nutrient concentrations below buffelgrass were similar to those below native perennials reported in the literature, results suggest that soil nutrient status in buffelgrass patches should not be unfavorable for native plant recruitment. Native plant species richness and diversity were identical on average between patch types, but native cover was less by about one-half in buffelgrass patches. Unexpectedly, native-soil seed banks were not reduced in buffelgrass patches.

Understanding cause–effect mechanisms of buffelgrass invasion, temporal changes in the characteristics of buffelgrass-invaded sites, and responses of these characteristics to buffelgrass treatment are important research needs. If buffelgrass invasion is the principal driver of the observed reduced cover of native plants in patches invaded by buffelgrass, treatment of buffelgrass in its early stages of invasion might be important, before the exclusion of native species. To summarize, compared with nonbuffelgrass patches, buffelgrass patches exhibited higher soil nutrients, identical native plant species richness and diversity, lower native plant cover, and similar native species soil seed bank densities.

properties between buffelgrass pastures and native range-lands in Mexico varied among study areas and could have resulted from the combined influences of pasture management and buffelgrass itself (Ibarra-Flores et al. 1999). It remains uncertain whether or how buffelgrass might influence soils when invading indigenous ecosystems. By comparing invaded and noninvaded sites, several studies in Australia and the United States suggest that buffelgrass reduces both native plant-species richness and cover in pasture and wildland ecosystems (Clarke et al. 2005; Jackson 2005; McDonald and McPherson 2011; Olsson et al. 2012; Sands et al. 2009). Potential influences of buffelgrass on soil seed banks, however, are poorly understood. Hand-pulling or herbicides can effectively treat buffelgrass, but the literature suggests that reestablishing native vegetation on treated sites can be important to forestall reinvasion (Daehler and Goergen 2005; McIvor et al. 2003; Tjelmeland et al. 2008). Unfortunately, reestablishing native vegetation through natural succession may be a slow process if native vegetation and soil seed banks have been reduced on buffelgrass-invaded sites in arid lands (Abella 2010).

This study was conducted to compare ecological characteristics of buffelgrass-invaded patches with non-invaded patches on a desert landscape. This type of comparative sampling, widely employed in invasive plant science, can help identify how postinvasion characteristics differ between invaded and noninvaded areas to assist with the development of management strategies (Blank 2008; Hejda et al. 2009). We assessed the following three questions:

- (1) Do soil properties differ between patches invaded and not invaded by buffelgrass? We anticipated that some soil properties would show greater differences than others and that properties more susceptible to short-term biotic influences (e.g., C and N) would differ more sharply between patches than would properties under longer-term abiotic control (e.g., soil texture).
- (2) Is native vegetation altered in buffelgrass patches compared with patches without buffelgrass? We hypothesized that all native plant measures (species richness, diversity, and cover) would be lower in buffelgrass patches and that buffelgrass and nonbuffelgrass patches would exhibit different plant-community composition.
- (3) Do buffelgrass patches and patches without buffelgrass contain different soil seed banks? We expected that buffelgrass seed-bank density would be greatest in buffelgrass patches and that native seed density would be greatest in nonbuffelgrass patches.

Materials and Methods

Study Area. We conducted this study within the 36,960-ha (91,328-ac) Saguaro National Park, 15 km (9 mi) northwest (Saguaro West, Tucson Mountain District) and 8 km east (Saguaro East, Rincon Mountain District) of Tucson, AZ (Figure 1). The park lies within the Arizona Upland Subdivision of the Sonoran Desert (Brown 1994). This subdivision occupies higher elevations, receives more precipitation, and contains greater structural diversity in its vegetation than do the Sonoran Desert lowlands. Vegetation has a scrubland or low-woodland physiognomy, with a diverse assemblage of shrub–trees, forbs, graminoids, and cacti, including saguaro [*Carnegiea gigantea* (Engelm.) Britton & Rose], a columnar cactus diagnostic for the region (Brown 1994). The climate in Tucson, AZ (Airport Weather Station, 787 m [2,581 ft] in elevation, 1930 to 2010 records) is arid/semiarid. It exhibits an average of 29 cm yr^{-1} (11 in yr^{-1}) of precipitation, an average daily July high temperature of 37°C (99°F), and an average daily January low temperature of 4°C (WRCC 2011). Topography consists of rolling hills, alluvial fans, and concave drainages. Soils are primarily derived from granite and classified as Torriorthents and Haplargids (Cochran and Richardson 2003). Livestock grazing has not been

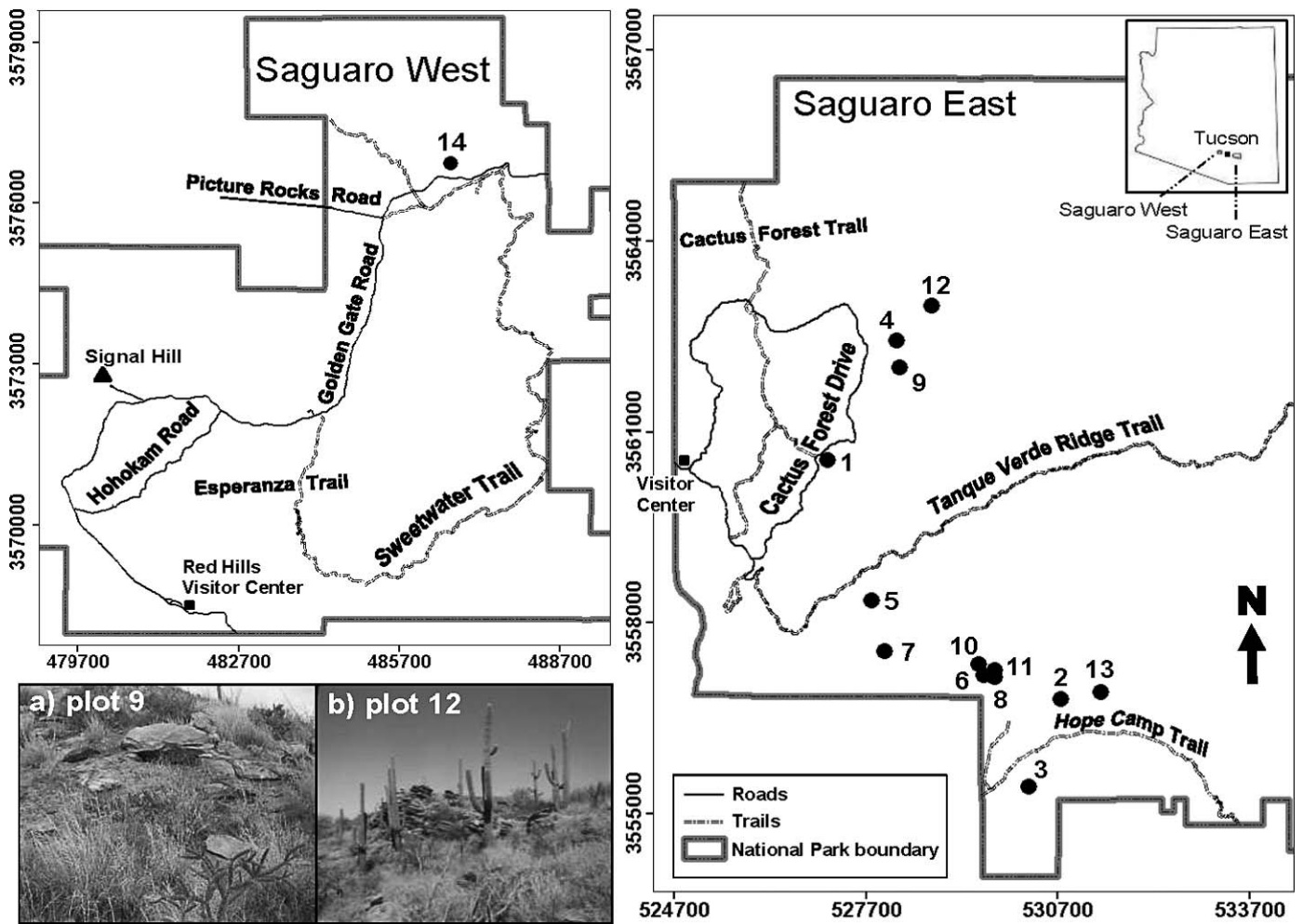


Figure 1. Location of the study area in Saguaro National Park units west and east of Tucson, AZ (inset, top right), and study sites with site numbers corresponding to descriptions in Appendix 1. Photos by L. P. Chiquoine, 2011.

authorized in the park since 1976. The park has been visited by $> 600,000$ people yr^{-1} since 1983, although most visitation is concentrated along park roads and, to a lesser extent, trails (National Park Service, Public Use Statistics Office, Denver, CO).

Buffelgrass (nonrhizomatous variety) was first observed in the study area by park managers in 1989 (records kept by Saguaro National Park, Tucson, AZ). It has since expanded to a variety of soils, even in the absence of fire (P. Grissom, personal communication). This concurs with Olsson et al. (2012), who examined buffelgrass distribution in another part of the Arizona Upland Subdivision. Only 2 of our 14 buffelgrass study sites have had any recorded fires since record keeping began in 1937 (P. Grissom, personal communication). Sites 4 and 9 (Figure 1) were within the boundaries of the 465-ha 1994 Mother's Day Fire, and site 9 was also within the 2,621-ha 1999 Box Canyon Fire.

Data Collection. Using a map provided by the National Park Service (Tucson, AZ) of buffelgrass sites within the

park, we randomly selected 20 sites for field reconnaissance. We rejected sites that did not contain buffelgrass or were not able to be visited and, ultimately, sampled 14 sites (1 in the western district and 13 in the larger and more-extensively invaded eastern district; Figure 1). The sizes of the buffelgrass patch at study sites ranged from approximately 0.2 to 9 ha. Based on photographs and observations of managers, the buffelgrass patches we examined were estimated to have been formed by approximately 2000 and were not older than about 10 to 15 yr in 2011 at the time of this study (records kept by Saguaro National Park, Tucson, AZ; P. Grissom, personal communication). Based on the sizes of sampled patches, this age estimation appears consistent with the Olsson et al. (2012) chronosequence of buffelgrass patches in a nearby study area. Sites ranged in elevation from 780 to 1,150 m, and their locations and other characteristics are summarized in Appendix 1. We established a 100-m^2 ($1,076\text{ ft}^2$) circular plot in the center of the buffelgrass patch and in a paired nonbuffelgrass patch at each site. Nonbuffelgrass patches were selected as

near as possible (within 50 to 150 m) and on topography as similar as possible to the buffelgrass patch.

We recorded geography and plant community data and collected soil samples from each plot. From the center of each plot, we recorded geographic location and elevation using a global positioning system, slope gradient using a clinometer, and aspect using a compass. Aspect was transformed to a linear scale ranging from 0 (southwest, driest) to 2 (northeast, moistest; Beers et al. 1966). We visually categorized the areal cover of each live, vascular plant species on each plot following cover classes modified from Peet et al. (1998): 1 = < 0.1% cover, 2 = 0.1 to 1%, 3 = 1 to 2%, 4 = 2 to 5%, 5 = 5 to 10%, 6 = 10 to 25%, 7 = 25 to 50%, 8 = 50 to 75%, 9 = 75 to 95%, and 10 = 95 to 100%. Classification of growth form and native/exotic status followed Natural Resources Conservation Service (2011). We collected four subsamples per plot of the 0 to 5-cm mineral soil (totaling a 400-cm³ [24-in³] sample plot⁻¹) for bulk-density analysis from within 10 cm of the crown of the four largest buffelgrass plants in buffelgrass plots and in interspaces $\geq$ 1 m from the nearest perennial plant in nonbuffelgrass plots. We collected soil samples for laboratory characterization using the same methods at the same locations. We sampled the 0–5 cm depth to provide a consistent depth across sites while remaining within typical depths of A horizons at the sites (Cochran and Richardson 2003). Vegetation, soil, and seed-bank sampling occurred near the peak of the spring growing season from March 21, 2011, to April 25, 2011. Buffelgrass can grow both in spring and after late-summer monsoon rains, so our sampling time is a balance of a buffelgrass growth period and the active growing season of spring native plants.

We collected samples of the 0 to 5-cm (which could include litter) soil seed bank from the following microsites: (1) in the interspaces on all plots; (2) below canopy of buffelgrass on all buffelgrass plots; (3) below canopy of the native, perennial brittlebush (*Encelia farinosa* Gray ex Torr.) on all plots where $\geq$ 3 individuals were present; and (4) below canopy of the native, perennial cactus apple (*Opuntia engelmannii* Salm-Dyck ex Engelm.) on all plots where $\geq$ 3 individuals were present.

We chose the two native, perennial species because they were among the most-common native, perennial plants across patch types. Samples were collected from three individuals of each of the microsite types per plot, representing the largest perennial individuals and interspaces available on plots. Three subsamples were collected from each individual, equally spaced around the perennial plant 10 cm from its root crown and every 10 cm in a circular pattern in the interspace. Soil was composited for all individuals of a microsite type for each plot to total an 1,800-cm³ seed-bank sample per microsite type per plot.

Soil and Seed-Bank Analysis. Soil samples were analyzed for bulk density by sieving out coarse fragments > 2 mm

(0.08 in) in diameter, oven drying the fine fraction at 105 C for 24 h, and weighing both fractions and determining the volume of coarse fragments by water displacement. The fine fraction was analyzed by the Environmental Soil Analysis Laboratory (University of Nevada, Las Vegas, NV) following Tan (2005) for texture (hydrometer method) and following Burt (2004) for pH and electrical conductivity (saturated paste); CaCO₃ (manometer); organic C and total N and S (dry combustion using an elemental CNS analyzer, with organic C determined by subtraction of inorganic C from total C); available P (Olsen method); NO₃-N (2-M KCl extraction, ion chromatography method); and NH₄-N (2-M KCl extraction, salicylate colorimetric method). The samples for the available N measures were stored in a chilled cooler after collection and extracted by the laboratory within 48 h.

To assay the readily germinable fraction of seed banks using the emergence method (Bakker et al. 1996), we filled 4-L (1-gal) cylindrical pots two-thirds full with potting soil (1 : 3 : 1 mulch : sand : gravel) and placed 360 cm³ of seed-bank soil in a layer 2 cm thick on top of the potting soil. Pots were randomly arranged on a bench in a greenhouse with temperatures fluctuating between 21 (nighttime) and 32 C (daytime). Samples were started in May 2011, and over a 3-mo period, were watered by hand twice per week to moisture capacity. Pots containing only potting soil were randomly arranged as seed-contamination checks. Seedlings were inventoried twice weekly and removed from pots when identified to the finest taxonomic resolution possible. Not all seedlings matured to allow accurate identification, and 59 (14%) of 436 total seedlings were only identified to growth form (forb or graminoid). An unknown forb that consistently died a few days after the cotyledon stage constituted 61% of the total unidentified seedlings. Unknowns were included in seed totals but were not included in species richness and species composition analyses.

Data Analysis. Data were analyzed using several multivariate techniques conducted in the software PC-ORD (version 6; McCune and Mefford 1999) and bivariate and univariate techniques conducted in SAS (version 9.2; SAS Institute 2009). The soil data were ordinated using principal components analysis (cross-products matrix derived from correlation). We calculated buffelgrass percentage cover and the total cover of native species (exotic species other than buffelgrass were recorded on nine plots and never constituted > 1.5% cover) using the midpoints of cover classes. We computed vegetation species richness (per 100-m² plot) and Shannon's diversity index (calculated in PC-ORD with an input matrix of 0 to 10 corresponding to cover classes). Each topographic, soil, and vegetation variable, along with seed-bank density (by microsite), was compared between buffelgrass and non-

buffelgrass patches using a paired t test. P values for these tests were not Bonferroni corrected because each variable in the univariate part of our analysis was considered independent (Cabin and Mitchell 2000).

We further compared vegetation species composition between patch types using several techniques. Based on a matrix of cover classes, which qualitatively returned the same conclusions as cover classes converted to percentage cover and relative cover class (target species cover class/sum of all species cover classes on each plot), we used nonmetric multidimensional scaling to ordinate vegetation species composition in PC-ORD's slow and thorough mode (McCune and Mefford 1999). We displayed the ordination as a joint plot with environmental variables and species as vectors to illustrate correlations with ordination axes. We conducted ordinations with and without buffelgrass included in the species matrix. We tested the hypothesis of no difference in species composition (based on relative cover) between buffelgrass and nonbuffelgrass patches (also including and excluding buffelgrass from the species matrix) using blocked, multiresponse permutation procedures (Euclidean distance, no median alignment within blocks because data were paired). We used blocked indicator species analysis in PC-ORD with significance determined through 1,000 permutations to identify relationships of individual species with patch types. Indicator species analysis combines the relative frequency (based on the number of sampling units a species occupies) and relative abundance (percentage cover in this study) of a species to produce an indicator value ranging from zero (no indication) to 100 (perfect indication; Dufrêne and Legendre 1997).

Results

Geography and Soil. In the principal components analysis of soil properties, the first principal component accounted for 35% of the variance in the soil data set, the second 15%, and the third 14% (64% overall). Variables exhibiting the highest loadings on the first two components included total N (loading = 0.86), organic C (0.84), and sand (−0.82) for component 1; and coarse fragments by weight (−0.61), volume (−0.57), and total S (0.54) for component 2. Buffelgrass and nonbuffelgrass plots separated in the principal components ordination, with buffelgrass plots positively correlated with chemical variables, such as electrical conductivity, N, and organic C (Figure 2a). In the paired t tests of individual variables, none of the geographic (elevation, slope gradient, and aspect) or soil physical variables (texture, bulk density, and coarse fragments) differed significantly between buffelgrass and nonbuffelgrass patches (Table 1). Conversely, the soil chemical properties of electrical conductivity, organic C, total N, $\text{NH}_4\text{-N}$, and $\text{NO}_3\text{-N}$ were significantly and approximately twofold greater in buffelgrass patches.

Vegetation. Some, but not all, vegetation variables differed between patch types (Table 1). Buffelgrass averaged 45% cover in buffelgrass patches and was absent from nonbuffelgrass patches. In buffelgrass patches, native plant cover was only 57% of its amount in nonbuffelgrass patches. Conversely, native-plant species richness and diversity were identical between patch types. The ordination of multivariate species composition, with buffelgrass included, displayed a clear separation of patch types (Figure 2b). Native species such as saguaro, brittlebush, bush muhly (*Muhlenbergia porteri* Scribn. ex Beal), and slender janusia (*Janusia gracilis* A. Gray) were positively correlated with nonbuffelgrass patches, whereas buffelgrass and soil variables, such as N and organic C, were positively correlated with buffelgrass patches. The separation of patch types disintegrated when buffelgrass was excluded (Figure 2c). This was also supported by the blocked, multiresponse-permutation procedures tests: patch types differed significantly when buffelgrass was included (T statistic = −9.4, A = 0.43, P < 0.001), but not when excluded (T statistic = −0.8, A = 0.00, P = 0.209).

We recorded a total of 60 plant species, consisting of 35% shrubs, 17% perennial forbs, 15% cacti, 13% perennial graminoids, 7% shrub–trees, and 3% each annual graminoids, ferns, annual forbs, and annual–perennial forbs (Appendix 2). Ninety-three percent of the species were native, and 7% (4 species) were exotic. Based on blocked indicator species analysis, four species significantly indicated a patch type. Buffelgrass was a perfect indicator (indicator value [IV] = 100, P < 0.001) of buffelgrass patches. Saguaro (IV = 60, P = 0.029), brittlebush (IV = 72, P = 0.009), and bush muhly (IV = 72, P = 0.002) indicated nonbuffelgrass patches. Brittlebush was present on all 28 plots across patch types, but had sixfold greater relative cover in nonbuffelgrass patches (Appendix 2). Excepting saguaro and bush muhly that had sharply greater frequencies in the nonbuffelgrass patches compared with buffelgrass patches and a few species (e.g., velvet mesquite [*Prosopis velutina* Woot.]) more frequent in buffelgrass patches, native species occurred with similar frequency in both patch types. However, native species typically had greater relative cover in nonbuffelgrass patches.

Seed Bank. A total of 41 taxa identified to genus or species, along with members of Cactaceae, emerged from seed-bank samples (Appendix 3). Of the 41 taxa, 38 (93%) were native. The only exotic taxa detected were buffelgrass, African lovegrass (*Eragrostis echinoclloidea* Stapf), and the annual Mediterranean grasses (*Schismus* spp.). Of the 38 native taxa, 50% were annual forbs; 11% annual–biennial forbs; 11% annual–perennial forbs; 8% each perennial forbs, annual graminoids, and perennial graminoids; and 5% were shrubs. The most abundant native taxa in the seed

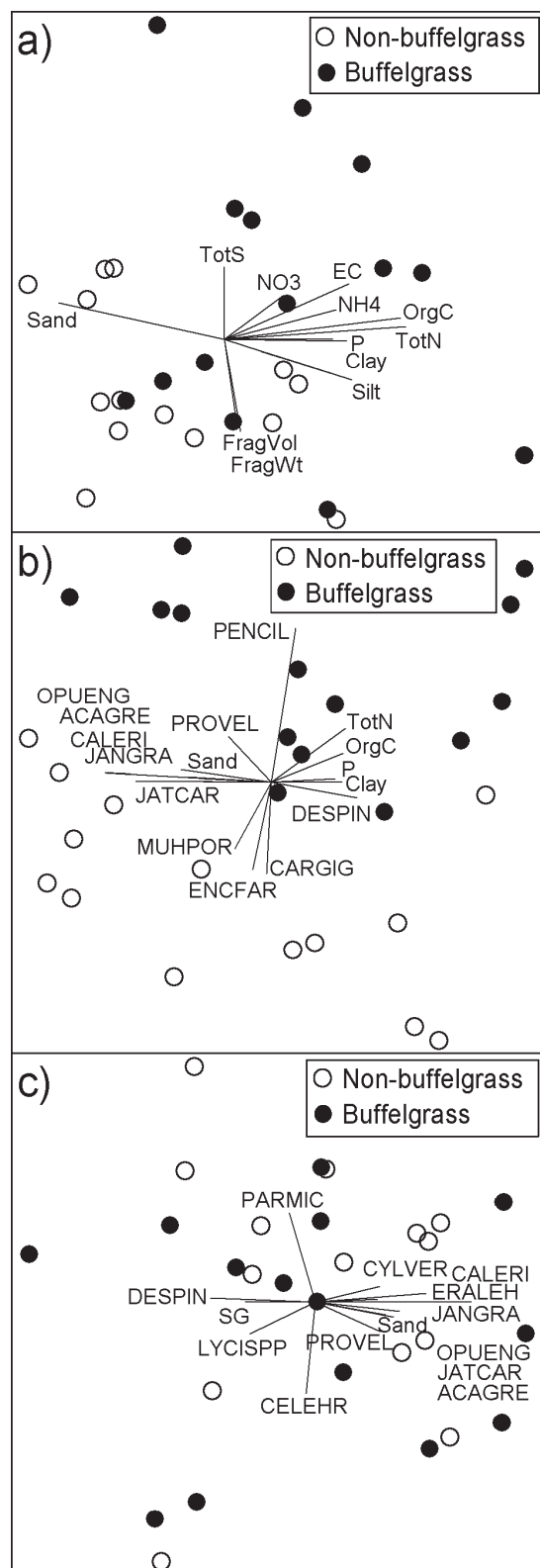


Figure 2. Ordination of (a) soil properties; (b) vegetation, including buffelgrass; and (c) vegetation, excluding buffelgrass, in buffelgrass and nonbuffelgrass patches of Saguaro National Park,

bank were, in descending order: sand pygmyweed [*Crassula connata* (Ruiz & Pavón) Berger], manyflowered monkey-flower [*Mimulus floribundus* Lindl.], mealy goosefoot [*Chenopodium incanum* (S. Wats.) Heller], toad rush [*Juncus bufonius* L.], carpetweed [*Mollugo verticillata* L.], California cottonrose [*Logfia californica* (Nutt.) Holub], and Cactaceae. Seed-bank species that also were detected in vegetation included the perennials desert tobacco (*Nicotiana obtusifolia* Martens & Galeotti var. *obtusifolia*), bush muhly, brittlebush, and slender janusia and the annual forb canyon morningglory (*Ipomoea barbatisepala* A. Gray).

Buffelgrass seed bank density averaged over 600 seeds m^{-2} below its own canopy and more than 200 seeds m^{-2} below native perennial species within buffelgrass patches, whereas buffelgrass seed banks were sparse or absent across microsites within nonbuffelgrass patches (Table 1). Native seed banks did not differ significantly between buffelgrass and non-buffelgrass patches for any microsite. Native seed density was 40% greater than buffelgrass seed density below buffelgrass canopies.

Discussion

Soil. Similarity in soil type and abiotic properties, such as texture and coarse fragments, in addition to similar geography, between buffelgrass and nonbuffelgrass patches supports the idea that differences between patches in properties (e.g., N availability) under biological influence are likely linked to buffelgrass occupancy. Moreover, buffelgrass is likely capable of invading the nonbuffelgrass sites but has not yet done so because of insufficient propagule pressure or other factors (Olsson et al. 2012).

←

Sonoran Desert. Vectors display correlations ($|r| \geq 0.50$) of variables with ordination axes. Abbreviations (a): EC, electrical conductivity; FragVol, coarse fragments by volume; FragWt, coarse fragments by weight; OrgC, organic C. Abbreviations (b): ACAGRE, catclaw acacia, *Acacia greggii* Gray; CALERI, fairy duster, *Calliandra eriophylla* Benth.; CARGIG, saguaro, *Carnegiea gigantea*; DESPIN, pinnate tansymustard, *Descurainia pinnata* (Walt.) Britt.; ENCFAR, brittlebush, *Encelia farinosa* Gray ex Torr.; JANGRA, slender janusia, *Janusia gracilis* Gray; JATCAR, sangre de cristo, *Jatropha cardiophylla* (Torr) Müll. Arg.; MUHPOR, bush muhly, *Muhlenbergia porteri* Scribn. ex Beal; OPUENG, cactus apple, *Opuntia engelmannii* Salm-Dyck ex Engelm.; PENCIL, buffelgrass, *Pennisetum ciliare* (L.) Link; PROVEL, velvet mesquite, *Prosopis velutina* Woot. Abbreviations (c): CELEHR, spiny hackberry, *Celtis ehrenbergiana* (Klotzsch) Liebm.; CYLVER, staghorn cholla, *Cylindropuntia versicolor* (Engelm. ex J.M. Coul.) F.M. Knuth; ERALEH, Lehmann lovegrass, *Eragrostis lehmanniana* Nees.; LYCISPP, desert-thorn, *Lycium* spp.; PARMIC, yellow paloverde, *Parkinsonia microphylla* Torr.; SG, slope gradient.

Table 1. Characteristics of buffelgrass and nonbuffelgrass patches in Saguaro National Park, Sonoran Desert, Arizona.

Characteristic	Buffelgrass	Nonbuffelgrass	$ t ^a$	P
	Mean (CV ^b %)			
Geography				
Elevation (m)	1,019 (8)	1,003 (9)	1.40	0.184
Slope gradient (%)	33 (104)	21 (76)	1.82	0.092
Aspect (transformed)	0.20 (96)	0.28 (135)	0.70	0.496
Vegetation				
Buffelgrass cover (%)	45 (47)	0 (0)	7.99	< 0.001
Native cover (%)	16 (46)	28 (76)	3.28	0.006
No. species 100 m ⁻²	14 (21)	14 (27)	0.27	0.791
Shannon diversity	2.5 (10)	2.5 (12)	0.22	0.827
Soil (0 to 5 cm)				
Sand (%)	67 (11)	68 (10)	0.70	0.495
Silt (%)	24 (30)	24 (25)	0.05	0.962
Clay (%)	10 (12)	9 (26)	1.71	0.112
CaCO ₃ (%)	2.3 (268)	2.8 (295)	0.91	0.379
pH	7.4 (5)	7.1 (8)	1.79	0.096
EC (μS cm ⁻¹) ^b	757 (50)	328 (57)	4.83	< 0.001
Organic C (%)	1.7 (33)	0.9 (49)	4.82	< 0.001
Total N (%)	0.16 (28)	0.09 (36)	5.93	< 0.001
NH ₄ -N (%)	0.00110 (65)	0.00063 (56)	3.06	0.009
NO ₃ -N (%)	0.00140 (99)	0.00052 (61)	2.63	0.021
P (%)	0.0041 (40)	0.0034 (26)	1.53	0.149
S (%)	0.11 (181)	0.06 (123)	0.85	0.408
Bulk density (g cm ⁻³)	0.91 (9)	0.98 (12)	1.99	0.068
Fragments (% wt.)	34 (14)	34 (18)	0.12	0.903
Fragments (% vol.)	22 (32)	22 (23)	0.01	0.990
Buffelgrass seed bank ^c				
Buffelgrass (seeds m ⁻²)	645 (164)	—	—	—
Interspace (seeds m ⁻²)	10 (374)	30 (374)	0.62	0.547
Brittlebush (seeds m ⁻²)	222 (129)	0 (0)	2.45	0.037
Cactus apple (seeds m ⁻²)	232 (245)	0 (0)	1.00	0.374
Native seed bank ^c				
Buffelgrass (seeds m ⁻²)	904 (221)	—	—	—
Interspace (seeds m ⁻²)	616 (144)	278 (100)	1.44	0.173
Brittlebush (seeds m ⁻²)	1015 (153)	427 (186)	1.74	0.115
Cactus apple (seeds m ⁻²)	649 (111)	185 (140)	1.76	0.153

^a Statistical results from a paired *t* test comparing patch types, with statistics in bold noting differences significant at *P* < 0.05.

^b Abbreviations: CV, coefficient of variation; EC, electrical conductivity.

^c Values below the “buffelgrass seed bank” heading are buffelgrass seed densities according to sampling microsite (e.g., below the canopy of buffelgrass or in interspaces between perennial plants), and values below the “native seed bank” heading are native species seed densities. The buffelgrass microsite was not present within nonbuffelgrass patches.

Although isolating cause and effect of buffelgrass occupancy would require experimentation, our results identify the current characteristics of buffelgrass-invaded sites.

Our results of elevated amounts of soil nutrients, such as N and organic C, below buffelgrass canopies are similar in magnitude to results commonly found in deserts that soil

nutrient concentrations are greater below native perennial plants relative to interspaces (Butterfield and Briggs 2009). For example, soil NO₃-N is often about twice as concentrated below native perennial plants in the Sonoran Desert (Butterfield and Briggs 2009). This is similar to the approximately twofold greater N concentration we found

below buffelgrass compared with interspaces in nonbuffelgrass patches. Soil nutrients can be greater below perennial plants through many mechanisms, such as through the perennial plant trapping dust; harvesting nutrients from interspaces and concentrating them below the canopy via litterfall; exuding root material; providing protected habitat for other biota (e.g., small mammals), which also can concentrate resources; facilitating recruitment of annual plants that provide rapidly cycling, fine biomass; and forming symbiotic relationships with soil microorganisms (McAuliffe 1988). Buffelgrass influences on soils might be time-dependent, underscoring the importance of unraveling the mechanisms by which buffelgrass potentially influences soils. As buffelgrass patches age, for example, the process of litter accumulation might affect soils and vegetation. Esque et al. (2007) found that within our study area, total biomass of buffelgrass can exceed $2,500 \text{ kg ha}^{-1}$ ($2,233 \text{ lb ac}^{-1}$), an extremely large amount of grass biomass relative to uninvaded areas.

Vegetation. Although buffelgrass appeared to concentrate soil nutrients similar to native perennials, it did not provide “nurse-plant” benefits that native perennials often provide for other plants. Nurse effects, which result in the facilitated recruitment of “nursling” seedlings, are well documented in many deserts, including the Sonoran (e.g., Carrillo-Garcia et al. 2000; Halvorson and Patten 1975; McAuliffe 1988). If buffelgrass was providing nurse effects, the richness and cover of native plants should have been higher than in interspaces, a finding not observed. Although some native, perennial grasses are key nurse plants, several traits might preclude buffelgrass from being a nurse. For instance, the growth form of buffelgrass differs from native grass nurses by being denser, with little or no space between the ground and main canopy. It also is possible that buffelgrass could produce allelopathic chemicals that inhibit other plants (Hussain et al. 2010), although many native species produce a variety of chemicals and still serve as nurses (Halvorson and Patten 1975). Moreover, it is possible that mature buffelgrass plants are more competitive than are many native, perennial plants, which can compete with their nurslings yet still have overall facilitative effects (Rodríguez-Buritica and Miriti 2009). Although buffelgrass appears to reduce native plant cover, it remains unclear whether buffelgrass stands have facilitative effects on buffelgrass’s own recruitment.

Identical richness and diversity between buffelgrass and nonbuffelgrass patches in this study sharply contrasts with previous research that has found that buffelgrass reduces these measures. Six studies, conducted in Australia (Clarke et al. 2005; Franks 2002; Jackson 2005), Texas (Sands et al. 2009), and Arizona (McDonald and McPherson 2011; Olsson et al. 2012), reported a consistent twofold to

threefold reduction in species richness for areas most heavily infested with buffelgrass compared with indigenous ecosystems or pastures. It should be noted that livestock grazing is not authorized in our study area but has been a factor in other studies. As with buffelgrass influences on soil, time may also be important in buffelgrass influences on vegetation (Olsson et al. 2012). In Australia, for example, Clarke et al. (2005) found that when native, perennial grass sites were weakened by fire and drought in the early 1980s, buffelgrass came to dominate. In the first 10 yr of buffelgrass dominance, buffelgrass did not influence richness, but after 1990 to the present, buffelgrass reduced richness by twofold. Although cultivated and grazed buffelgrass pastures appear to senesce after a period of decades and can become partly colonized by native perennials, buffelgrass senescence has not been reported, to our knowledge, in wildland settings, such as our study area (Clarke et al. 2005; Olsson et al. 2012). We hypothesize that buffelgrass in our study area is in an intermediate stage of affecting native plant communities after 10 yr of infestation, and the next stage would result in declines in richness as natives are excluded. Moreover, heavy buffelgrass fuel loads can facilitate fires, which eliminate mature desert plant communities (Esque et al. 2007; McDonald and McPherson 2011).

Buffelgrass correlations to individual native species appeared relatively uniform across species, with two main exceptions: saguaro and the perennial grass bush muhly, which exhibited lower frequency in buffelgrass patches. It cannot be determined by this study whether these species had lower frequency at these sites before buffelgrass invasion or if the species were reduced by buffelgrass. Also in Sonoran Desert uplands, Olsson et al. (2012) did not observe a significant correlation between buffelgrass cover and cover or density of saguaro, but significantly fewer small ($\leq 2 \text{ m}$ tall) saguaro occurred where buffelgrass cover exceeded 43%. Careful consideration should be given to the possibility that buffelgrass can compete with saguaro directly or reduce cover of the nurse plants on which saguaro depends for recruitment (Morales-Romero and Molina-Freaner 2008). Based on findings of Stevens and Fehmi (2009), who found experimentally that buffelgrass directly outcompeted the native, perennial grass Arizona cottontop [*Digitaria californica* (Benth.) Henr.], it is possible that the lowered frequency of bush muhly we found was related to competitive reduction by buffelgrass.

Seed Bank. Results were inconsistent with the expectation that native seed banks would be sparser in buffelgrass compared with nonbuffelgrass patches. Native seed-bank density did not differ significantly between buffelgrass and nonbuffelgrass patches and was greater than buffelgrass seed-bank density below buffelgrass itself. Understanding the underlying mechanisms for these results requires

further research, which is especially warranted because the results differ from several studies reporting that native seed banks are depauperate (Cox and Allen 2008; Gioria and Osborne 2009) or at least compositionally altered (Vilà and Gimeno 2007) in areas invaded by exotic plants. Native seed banks in buffelgrass patches could result from seed retention before buffelgrass invasion and persistence during its occupancy, or postinvasion seed accumulation possibly because of mechanisms such as retention of seed by the buffelgrass vegetation structure. However, native seed banks have not corresponded with sufficient plant establishment to forestall the lowered native plant cover observed in buffelgrass patches. This could partly result from the seed bank containing some species (e.g., desert-broom [*Baccharis sarothroides* A. Gray]) not observed in aboveground vegetation.

Managing Buffelgrass Sites. Results suggest several considerations for managing unburned, buffelgrass-invaded sites. First, not knowing how long native plant species can persist within buffelgrass patches, a precautionary approach would be treating buffelgrass as early as possible when patches remain small. In addition to limiting buffelgrass patch expansion and fuel continuity, early treatment might also reduce dispersal distances required by native species to colonize treated buffelgrass patches. Second, it would be useful to determine recruitment potential from seed banks posttreatment and if management could stimulate native seed but not buffelgrass germination (Lyons et al. 2013). For example, a grass-specific herbicide might be effective (Tjelmeland et al. 2008) because most (79%) of the 38 native taxa detected in the seed bank were forbs. This is potentially problematic for native grasses, however, especially considering that in the vegetation, a native grass (bush muhly) was reduced in buffelgrass compared with nonbuffelgrass patches. Where practical, however, one strategy might be to use PRE herbicide spot treatments (especially near buffelgrass plants where buffelgrass seed banks were largest) to allow for untreated areas where native grasses could emerge or to focus treatment in years with few native emergents. Moreover, strategically facilitating recruitment of native grasses or other desired species through seeding, planting, or other treatments (e.g., establishing nurse plants or structures) might be useful where establishment through natural seed banks is not effective (Abella and Newton 2009). Third, results also highlight that limitations of the seed bank for facilitating native plant recruitment should be recognized. As is typical across many ecosystems (Bakker et al. 1996), some species important in the vegetation (e.g., desert-thorn [*Lycium* spp.] and yellow paloverde [*Parkinsonia microphylla* Torr.]) were not detected in the seed bank and likely are rare in seed banks or have germination requirements not met in the greenhouse.

Fourth, consideration could be given to the vegetation that may have existed in buffelgrass patches before buffelgrass establishment and what desired conditions are for them. For instance, if buffelgrass has simply filled in areas formerly relatively open, then maintaining sparse native plant cover might be warranted. On the other hand, if buffelgrass displaced formerly dense, native vegetation patches or if competition is desired to potentially limit buffelgrass resurgence (e.g., Bakker and Wilson 2004), reestablishing denser, native vegetation patches may be desirable. Fifth, the structural legacy of buffelgrass plants and litter is an important consideration. If buffelgrass is killed by herbicide, removing the large amount of accumulated dead biomass (Esque et al. 2007) is not often logistically feasible for managers (P. Grissom, personal communication). Potential influences of dead buffelgrass material on native seed bank retention and germination are unknown and warrant further research to better understand posttreatment site dynamics. Dead plant material often can be piled on site after buffelgrass is treated by uprooting plants using hand tools, which can successfully reduce buffelgrass (Rutman and Dickson 2002). In summary, results suggest that sites invaded by buffelgrass exhibit similar abiotic features (e.g., soil texture), plant diversity, and native soil seed-bank density as compared to sites without buffelgrass; reduced native plant cover; and greater soil electrical conductivity, organic C, and N below buffelgrass than in interspaces between perennial plants.

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Appendix 1. Description of study sites in Saguaro National Park, Sonoran Desert.

ID ^a	UTMx ^b	UTMy ^b	Elev. (m)	SG (°) ^c	Aspect (°)	PM ^d	Soil subgroup(s)
1BG	527112	3560559	962	2	233	G	Lithic Torriorthents/Lithic Haplargids
2BG	530761	3556795	1062	32	215	G	Lithic Torriorthents
3BG	530249	3555423	981	20	160	M/L	Typic Calciorthids
4BG	528184	3562428	929	9	245	G	Lithic Torriorthents
5BG	527802	3558358	1147	35	178	G	Lithic Torriorthents
6BG	529467	3557343	1025	8	128	G	Lithic Torriorthents
7BG	527994	3557556	1034	22	196	G	Lithic Torriorthents
8BG	529557	3557174	1012	5	236	G	Lithic Torriorthents
9BG	528241	3562019	972	14	243	I/G	Lithic Torriorthents/Ustic Torriorthents
10BG	529722	3557140	1017	11	133	G	Lithic Torriorthents
11BG	529730	3557255	1048	13	185	G	Lithic Torriorthents
12BG	528733	3562988	978	9	222	I/G	Lithic Torriorthents/Ustic Torriorthents
13BG	531382	3556911	1098	21	195	I/G	Lithic Torriorthents/Ustic Torriorthents
14BG	486675	357673	780	15	190	I/M/G	Typic Haplargids/Lithic Torriorthents
1NBG	527166	3560545	961	3	184	G/I	Lithic Torriorthents/Lithic Haplargids
2NBG	530720	3556814	1059	40	215	G	Lithic Torriorthents
3NBG	530300	3555477	990	32	196	M/L	Typic Calciorthids
4NBG	528208	3562400	932	15	252	G	Lithic Torriorthents
5NBG	527771	3558353	1150	50	168	G	Lithic Torriorthents

6NBG	529547	3557335	1013	6	206	G	Lithic Torriorthents
7NBG	527933	3557733	1044	30	192	G	Lithic Torriorthents
8NBG	529552	3557150	1011	4	265	G	Lithic Torriorthents
9NBG	528673	3561257	1127	13	270	I/G	Lithic Torriorthents/Ustic Torriorthents
10NBG	529740	3557163	1019	21	163	G	Lithic Torriorthents
11NBG	529687	3557275	1055	9	235	G	Lithic Torriorthents
12NBG	528864	3562986	989	29	212	I/G	Lithic Torriorthents/Ustic Torriorthents
13NBG	531516	3556911	1091	21	160	I/G	Lithic Torriorthents/Ustic Torriorthents
14NBG	486704	3576801	826	45	215	I/M/G	Typic Haplargids/Lithic Torriorthents

^aSite identification number (corresponding to Figure 1), with BG = buffelgrass patch and NBG = non-buffelgrass patch.

^bUniversal Transverse Mercator coordinates (m), North American Datum 1983.

^cSG = slope gradient.

^dSoil parent material: G = granite, I = igneous rock, L = limestone, and M = metamorphic (Cochran and Richardson 2003).

Appendix 2. Species recorded in vegetation of buffelgrass and non-buffelgrass patches of Saguaro National Park, Sonoran Desert.

	Frequency (%) ^a		Relative Cover (%)	
	BG ^b	NBG ^b	BG	NBG
Annual graminoid				
<i>Bouteloua aristidoides</i>	14	21	0.3	0.1
<i>Panicum hirticaule</i>	7	29	0.0	0.9
Perennial graminoid				
<i>Aristida purpurea</i>	14	14	0.2	0.4
<i>Bothriochloa barbinodis</i>	7	0	0.0	0.0
<i>Eragrostis echinochloidea</i> * ^c	7	0	0.0	0.0
<i>Eragrostis lehmanniana</i> *	14	21	0.1	0.2
<i>Muhlenbergia porteri</i>	21	79	0.2	3.5
<i>Pennisetum ciliare</i> *	100	0	72.3	0.0
<i>Poa pratensis</i> *	0	14	0.0	0.5
<i>Tridens muticus</i>	0	7	0.0	0.1
Fern				
<i>Astrolepis sinuata</i>	7	21	0.0	0.1
<i>Pentagramma triangularis</i>	36	29	0.2	0.3
Annual forb				
<i>Eriastrum diffusum</i>	0	7	0.0	0.2
<i>Ipomoea barbatisepala</i>	7	21	0.1	0.3
Annual-perennial forb				
<i>Descurainia pinnata</i>	43	36	0.5	1.4
<i>Nicotiana obtusifolia</i>	7	0	0.1	0.0
Perennial forb				
<i>Chamaesyce melanadenia</i>	14	7	0.1	0.2
<i>Dichelostemma capitatum</i>	14	0	0.1	0.0
<i>Evolvulus arizonicus</i>	7	14	0.1	0.3
<i>Janusia gracilis</i>	79	71	1.8	4.1
<i>Lomatium nevadense</i>	7	7	0.1	0.0
<i>Psilostrophe cooperi</i>	0	7	0.0	0.4
<i>Senna covesii</i>	0	7	0.0	0.1
<i>Sphaeralcea laxa</i>	7	0	0.0	0.0
<i>Thymophylla pentachaeta</i>	7	0	0.1	0.0
<i>Tidestromia oblongifolia</i>	0	7	0.0	0.4
Shrub				
<i>Abutilon</i> spp.	43	29	0.3	0.6
<i>Aloysia wrightii</i>	7	0	0.0	0.0
<i>Ambrosia ambrosioides</i>	14	14	0.1	2.2

<i>Ayenia filiformis</i>	7	7	0.1	0.0
<i>Brickellia coulteri</i>	7	14	0.1	0.4
<i>Calliandra eriophylla</i>	57	57	0.6	1.8
<i>Celtis ehrenbergiana</i>	21	14	0.5	2.2
<i>Coursetia glandulosa</i>	21	7	1.0	2.2
<i>Encelia farinosa</i>	100	100	4.4	24.7
<i>Eriogonum fasciculatum</i>	0	7	0.0	0.1
<i>Fouquieria splendens</i>	57	71	2.0	6.5
<i>Haplophyton crooksii</i>	29	29	0.4	0.5
<i>Hibiscus denudatus</i>	7	7	0.1	0.3
<i>Hyptis emoryi</i>	7	7	0.2	0.1
<i>Jatropha cardiophylla</i>	71	71	1.0	7.4
<i>Larrea tridentata</i>	14	0	1.0	0.0
<i>Lycium</i> spp.	79	71	1.7	7.6
<i>Lysiloma watsonii</i>	7	7	0.1	0.2
<i>Porophyllum gracile</i>	0	7	0.0	0.1
<i>Tecoma stans</i>	7	0	0.5	0.0
<i>Trixis californica</i>	14	7	0.1	0.1
Shrub-tree				
<i>Acacia constricta</i>	0	7	0.0	0.4
<i>Acacia greggii</i>	29	29	0.1	1.4
<i>Parkinsonia microphylla</i>	64	57	2.9	11.2
<i>Prosopis velutina</i>	43	21	1.8	1.9
Cactus				
<i>Carnegiea gigantea</i>	43	79	0.3	2.8
<i>Cylindropuntia bigelovii</i>	14	14	0.1	0.2
<i>Cylindropuntia fulgida</i>	0	7	0.0	0.1
<i>Cylindropuntia leptocaulis</i>	7	0	0.1	0.0
<i>Cylindropuntia versicolor</i>	50	57	0.4	1.4
<i>Ferocactus wislizeni</i>	29	43	0.2	0.8
<i>Mammillaria grahamii</i>	64	64	0.3	0.6
<i>Mammillaria heyderi</i>	7	0	0.0	0.0
<i>Opuntia engelmannii</i>	64	64	2.7	8.2

^aOut of 14, 100-m² plots for each patch type.

^bBG, buffelgrass patch; NBG, non-buffelgrass patch.

^cAsterisks denote exotic species.

Appendix 3. Percent frequency by patch type (buffelgrass or non-buffelgrass) and microsite for 41 taxa identified to genus or species along with Cactaceae detected in soil seed bank samples in Saguaro National Park, Sonoran Desert.

	Buffelgrass				Non-buffelgrass		
	BG ^b	IN	BB	CA	IN	BB	CA
Annual graminoid							
<i>Bouteloua aristidoides</i>	7	0	0	0	0	0	11
<i>Juncus bufonius</i>	7	7	10	17	7	0	0
<i>Schismus</i> spp.* ^a	0	0	0	0	0	7	0
<i>Vulpia octoflora</i>	0	0	20	0	0	0	0
Perennial graminoid							
<i>Digitaria californica</i>	0	0	10	0	0	0	0
<i>Eragrostis echinocloidea</i> *	0	0	0	0	0	0	11
<i>Muhlenbergia porteri</i>	0	21	0	0	0	0	11
<i>Pennisetum ciliare</i> *	86	7	50	17	7	0	0
<i>Sporobolus wrightii</i>	0	7	0	0	0	0	11
Annual forb							
<i>Camissonia chamaenerioides</i>	0	0	0	0	0	7	0
<i>Chenopodium incanum</i>	7	0	10	0	0	0	0
<i>Chenopodium</i> spp.	0	7	10	0	0	0	0
<i>Crassula connata</i>	7	43	10	33	29	7	11
<i>Cryptantha nevadensis</i>	0	0	0	0	0	7	0
<i>Cryptantha</i> spp.	0	7	0	0	0	0	0
<i>Daucus pusillus</i>	7	0	10	0	0	0	0
<i>Eucrypta micrantha</i>	0	0	0	0	0	7	0
<i>Ipomoea barbatisepala</i>	7	0	0	0	0	0	0
<i>Logfia californica</i>	7	14	0	17	14	7	0
<i>Mimulus floribundus</i>	7	0	10	17	0	0	0
<i>Mollugo verticillata</i>	0	0	10	0	7	7	11
<i>Nemacladus glanduliferus</i>	0	7	0	0	7	0	0
<i>Parthenice mollis</i>	7	0	10	0	0	0	0
<i>Pectocarya recurvata</i>	0	0	0	0	7	0	11
<i>Perityle emoryi</i>	7	7	0	0	0	0	0
<i>Pterostegia drymarioides</i>	0	0	10	0	0	0	0
<i>Silene antirrhina</i>	7	7	0	0	0	7	0
<i>Stemodia durantifolia</i>	0	0	0	0	7	0	0
Annual-biennial forb							
<i>Centaurium arizonicum</i>	0	7	10	0	0	0	0
<i>Pseudognaphalium stramineum</i>	0	7	0	0	0	0	0
<i>Sairocarpus nuttallianus</i>	7	0	10	17	0	7	0

<i>Streptanthus carinatus</i>	7	0	0	0	0	7	0
Annual-perennial forb							
<i>Lepidium virginicum</i>	7	7	10	0	0	7	0
<i>Mecardonia procumbens</i>	0	0	10	17	0	0	0
<i>Mimulus guttatus</i>	7	7	0	0	0	0	0
<i>Nicotiana obtusifolia</i>	14	0	10	0	0	0	0
Perennial forb							
<i>Astragalus arizonicus</i>	0	0	0	0	0	7	0
<i>Janusia gracilis</i>	0	0	0	0	0	7	0
<i>Sisyrinchium</i> spp.	0	7	0	0	0	0	0
Shrub							
<i>Baccharis sarothroides</i>	0	0	0	17	0	0	0
<i>Encelia farinosa</i>	0	0	0	0	0	7	22
Cactus							
Cactaceae	7	0	10	0	7	7	0
Sample size (n)	14	14	10	6	14	14	9

^aAsterisks denote exotic species.

^bMicrosite abbreviations: BG, buffelgrass (*Pennisetum ciliare*); IN, interspace; BB, brittlebush (*Encelia farinosa*); CA, cactus apple (*Opuntia engelmannii*). The buffelgrass microsite was not present in non-buffelgrass patches.

APPENDIX C

Manuscript developed from Report 4, PART IV of this report. (Attached)

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Revegetating Disturbance in National Parks: Reestablishing Native Plants in Saguaro National Park, Sonoran Desert

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ABSTRACT: Habitat in national parks is periodically disturbed for road maintenance, and few revegetation protocols of known financial cost exist for this disturbance, especially in deserts where extreme environments constrain natural revegetation. In Saguaro National Park of the Arizona Upland Subdivision of the Sonoran Desert, we monitored survival of 1,554 outplanted individuals of 33 native perennial species for revegetating a 2006 re-construction project of the park's Cactus Forest Drive. Outplants were caged to deter vertebrate herbivory and provided with supplemental water in the hot, dry part of summer. Overall plant survival was high – 86% (1,340 of 1,554 outplants) – one year after planting. Survival was generally consistent across species, with survival > 50% for 32 of 33 (96%) species. Survival of two tree species (*Parkinsonia microphylla* and *Prosopis velutina*), monitored for two years, declined little or not at all from the first to the second year and was 55% and 67% at two years. The project met

management goals of reestablishing a 1:3 lost: restored ratio of tree density required for habitat restoration of an endangered owl species and of reestablishing a range of native species for aesthetic and vegetation structural restoration. Budget estimates indicated a cost per plant of approximately \$55 from grow-out in a nursery through plant maintenance in the field. This cost also included supporting activities of site preparation, exotic plant control, and effectiveness monitoring. The monitoring data, combined with longer term observations, suggest that the National Park Service's revegetation strategy effectively established a range of native plant growth forms and met habitat restoration targets.

Index terms: ecological restoration, outplanting, revegetation, road

INTRODUCTION

Effective protocols of known financial cost are often needed for revegetating planned and unplanned disturbances. In U.S. national parks, for example, roads need to be modified (e.g., widened or re-routed) for environmental concerns (e.g., improving water runoff management) or traffic safety (Peterson et al. 2004). These planned projects frequently require that post-construction disturbances are revegetated to curtail negative off-site impacts to surrounding natural areas, reestablish aesthetics, and promote habitat recovery (Tyser et al. 1998, Paschke et al. 2000). Reliable revegetation protocols are also important for supporting decisions about attempting revegetation of unplanned disturbances. Managers can make decisions based on considerations such as how effective active revegetation is compared to natural recovery and the resources and financial expenditures needed to achieve the revegetation (Bean et al. 2004).

Developing effective techniques for revegetation is especially challenging in arid lands, where low and variable precipitation, extreme temperatures, granivory, and herbivory limit both natural and active reestablishment of plant populations (Bainbridge 2007). In the Sonoran Desert of the American Southwest, for example, revegetation efforts reported in the literature have displayed mixed effectiveness. For revegetating highway borrow pits, Bainbridge and Virginia (1990) found that one-year survival of nursery-grown *Parkinsonia florida* (Benth. ex A. Gray) S. Watson (blue paloverde) outplants was 80% with active irrigation, whereas seeding did not successfully establish this species. On derelict farmland, Bean et al. (2004) reported that one-year survival exceeded 60% for outplants (all plants were irrigated) that had been greenhouse-grown in 3.8-L containers of some species such as *Ambrosia dumosa* (Gray) Payne (burrobush), *Larrea tridentata* (Sessé & Moc. ex DC.) Coville (creosote bush), *Pleuraphis rigida* Thurb (big galleta), and *Atriplex canescens* (Pursh) Nutt. (fourwing saltbush). On the other hand, Cox et al. (1987) found that survival of outplanted *Bouteloua curtipendula* (Michx.) Torr. (sideoats grama) and *Bouteloua gracilis* (Willd. ex Kunth) Lag. ex Griffiths (blue grama) was low after 2.5 years at only 18 and 28%. These and other studies indicate that revegetation effectiveness can sharply vary depending on method (seeding versus planting), species, and treatment (e.g., irrigation or cages to provide herbivory protection) used for revegetation (Roundy et al. 2001, Bean et al. 2004, Abella and Newton 2009). No well-established protocols exist for revegetating planned or unplanned disturbances in deserts, and financial cost projections for accomplishing revegetation are rare.

We monitored plant survival to assess outplanting effectiveness for revegetating disturbed roadsides in Saguaro National Park, Sonoran Desert. We also estimated a budget to quantify the resources and finances required to accomplish the revegetation.

METHODS

Study Area

We conducted this study within the 37,006-ha Rincon Mountain District of Saguaro National Park, beginning 1 km east of the city boundary of Tucson, Arizona (Fig. 1). The park lies within the Arizona Upland Subdivision of the Sonoran Desert, characterized by the columnar cactus saguaro (*Carnegiea gigantea* (Engelm.) Britton & Rose), and containing a scrubland or low woodland physiognomy with shrub-trees, cacti, forbs, and graminoids (Brown 1994). Climate consists of an average of 29 cm yr⁻¹ of precipitation, average daily July high temperature of 37°C, and an average daily January low temperature of 4°C (Tucson Airport Weather Station, 787 m elevation, 1930-2011 records; WRCC [2012]). Rolling hills, alluvial fans, and concave drainageways are the principal topographic features. Soils are primarily derived from granite and classified as Torriorthents and Haplargids (Cochran and Richardson 2003). Livestock grazing has not been authorized in the park since 1976, but native herbivores such as *Lepus californicus* (black-tailed jackrabbit) and *Sylvilagus audubonii* (desert cottontail) are present. The park receives over 600,000 anthropogenic visitors annually, including about 30,000 cars, 23,000 bicyclists, and 6,000 walkers on the park's main road, Cactus Forest Drive (National Park Service, Public Use Statistics Office, Denver, Colorado).

The specific study area was a 3.2-ha area corridor along the 13-km Cactus Forest Drive on the western side of the Rincon Mountain District (Fig. 1). This road was scheduled for reconstruction as part of periodic road maintenance activities conducted by the Federal Highway Administration in national park units (Tyser et al. 1998, Petersen et al. 2004). Construction activities were performed in summer 2006 and consisted of milling existing layers of chip seal to create a road base and adding a 5-cm thick layer of asphalt to create a new road surface. Additionally, approximately 100 informal roadside pullouts were to be closed and restored, some existing pullouts paved with designated parking spaces, and roadside natural history exhibits installed at nine pullouts.

The road project affected habitat for *Glaucidium brasilianum cactorum* (cactus ferruginous pygmy-owl), which was listed as an endangered species at the time (Fish and Wildlife Service 2011). As a result, the project Biological Assessment/Biological Opinion, approved by the U.S. Fish and Wildlife Service, required replacing destroyed trees for habitat restoration at a ratio of 3 trees for every tree destroyed. A total of 38 trees of *Parkinsonia microphylla* Torr. (yellow paloverde) and *Prosopis velutina* Woot. (velvet mesquite) were removed by the project, so ≥ 114 restored trees were needed to survive for > 2 years for habitat restoration targets.

Plant Grow Out

Beginning two years before construction, park staff collected seed from the two tree species and other native perennial species growing along the roadside to be reconstructed (Table 1). Seeds were cleaned and refrigerated until grow out in a nursery. In April 2006, seed was sown in pots, and re-seeded as necessary to produce a seedling in each pot. Plants were grown in an outdoor

nursery under shade cloth (open to rainfall) at the Natural Resources Conservation Service's Plant Materials Center (Tucson, Arizona). To encourage deep roots, which can be important for successful establishment of desert plants (Bainbridge 2007), 'tall' pots were used for propagation. The taller-statured tree species (*Parkinsonia*, *Prosopis*, and *Acacia*) were grown in 33-cm tall pots that were 8 cm × 8 cm at the top and 10 cm × 10 cm at the bottom. The bottom consisted of a removable 0.5-cm mesh size hardware cloth panel that allowed full drainage, and when removed at the time of planting, allowed the plants and potting soil to slide into the planting hole. The other species were grown in pots of the same dimensions except that they were 23 cm tall. Pots were either plastic or paper, and because survival was high across outplants, pot types are not differentiated. The potting soil mixture consisted of 10 parts sand : 15 perlite : 30 potting soil (Sunshine Professional Growing Mix, Sun Gro Horticulture, Inc., Bellevue, Washington). Pots were regularly watered to soil moisture capacity during the 8-month growth period. Plants were moved to a shade cloth-covered holding area at the park in January 2007 where they were watered periodically and kept until outplanting during 6 weeks of revegetation activities.

Revegetation Procedure

Outplanting occurred in January-February 2007 at 104 locations – roadside berms and decommissioned vehicle pullouts – along Cactus Forest Drive (Fig. 1). Planting on soft soils was done by digging holes with a shovel and allowing the entire contents (potting soil and plant) of pots to empty out of pots into the holes. On hard-packed soils, holes were dug using a one-person auger or with a Poinjar rock drill. Planting holes were saturated with water prior to planting and were re-saturated once the plant was in place. The species mixture and density planted at each of

the 104 locations were prescribed based on the species composition of adjacent undisturbed land, balanced with the available species of propagated plants. Tree species were placed at all of the larger sites and were planted at least 4 m from the edge of the road to eliminate the need for future pruning. In all, 1,554 propagated plants of 33 species were outplanted on 3.2 ha, corresponding to a density of 645 plants/ha. After planting, small depressions ('saucers') were excavated to a depth ca. 5 cm and ca. 25 cm beyond the root ball to catch and retain moisture around each outplant (Bainbridge 2007). Cages 0.7 m tall and 0.5 m in diameter and made of chicken wire (3-cm openings) were installed around each outplant, other than *Fouquieria splendens* Engelm. (ocotillo), to deter vertebrate herbivory. Vertical mulch, consisting of an *Opuntia* spp. pad or an approximately 5-cm diameter branch, was placed inside each cage to provide shade and microclimate amelioration.

Other associated activities with the revegetation included additional 'vertical mulching' and salvaging and replanting 3,000 *Mammillaria* spp. cacti and other cactus species across locations. Vertical mulch consisted of dead plant material collected on site: tree limbs, *Fouquieria splendens* pieces, *Opuntia* pads and stems, and other material that was 'planted' in the ground. Vertical mulch can provide several functions by mimicking the surrounding desert (which has standing dead plant debris) to camouflage the restoration site, creating shade, providing wind breaks, and serving as a visual barrier that may reduce the possibility of anthropogenic disturbance (Bainbridge 2007).

Plant and Site Maintenance

Maintenance activities during the first two years after planting included watering plants, removing exotic plants, and removing herbivory cages at the end of the study two years after planting. Water was delivered using 20, 19-L water containers in the back of a pickup truck, and each outplant was hand watered from a 19-L container. Each outplant was watered six times during the hot, dry period of the summer (May-July) for each of the first two years after planting, with 3 L delivered to each outplant during each watering. The entire Cactus Forest Road was walked during October 2007 to map and treat exotic plants at the revegetated sites and within 1 m of the road. Fourteen species were removed through hand pulling, with the major species being *Eragrostis lehmanniana* Nees (Lehmann lovegrass).

Monitoring and Analysis

All outplants were inventoried in January 2008 to quantify one-year survival and trees were also inventoried in January 2009 to quantify two-year survival. While longer term monitoring is ideal, not all of the forbs have long life spans (some live < 5 years); thus, park managers chose to invest the resources into monitoring the longer lived trees for the additional year. Moreover, the goal of the revegetation project was to quickly provide plant cover in < 2 years to these disturbed sites, so short-term monitoring was designed to quantify whether that objective was met. A rule of thumb for outplanting in deserts is that achieving a target of $\geq 50\%$ survival is considered good (Abella and Newton 2009). An additional target for the project was to have ≥ 114 surviving trees to mitigate habitat loss for *Glaucidium brasilianum cactorum* by construction activities. We calculated the proportion surviving for each outplanted species.

To quantify resources and finances required for the project, we included each stage of the revegetation starting with plant propagation through monitoring. We compiled costs for the plant grow out in the nursery, preparing sites and planting in the field, maintenance watering (e.g., fuel and water costs), and control of exotic plants. We also calculated the amount of water, time, and km driven required to perform maintenance watering after planting.

RESULTS

Effectiveness of Revegetation

All of the 33 species except *Ephedra trifurca* Torr. ex S. Watson (longleaf jointfir) met the target of $\geq 50\%$ survival after one year (Table 1). Moreover, survival was generally consistent among species, with 15 of the species exhibiting $\geq 90\%$ survival and 24 of the species exhibiting $\geq 80\%$ survival. Overall survival was 86% (1,340 of 1,554 total outplants). Survival decreased little or not at all from one to two years for the trees monitored for two years. While quantitative data were not collected after the second year, longer term photographic documentation to six years after treatment (January 2013) suggested continued visual blending of the revegetated areas with their undisturbed surroundings (Fig. 2).

Resources Required

The approximate estimated cost for the revegetation project totaled \$85,870 (Table 2). This translated to approximately \$55/plant that was outplanted and also included the supporting activities of general site preparation (e.g., contouring planting sites using hand tools), installation of vertical mulch, treatments to control exotic plants, and effectiveness monitoring.

DISCUSSION

Considering the high plant survival, exceeding required tree replacement ratios for habitat restoration, and the fact that the project can be viewed by approximately 600,000 human visitors/year, managers believed the project successfully met goals. The project exceeded the targets of $\geq 50\%$ survival and ≥ 114 trees surviving for owl habitat mitigation. Park managers considered the project to have accomplished the goal of rapid revegetation of the disturbed roadside. Moreover, the project is among the most effective revegetation projects in the Sonoran Desert reported to date and resulted in the greatest number of established species compared to any planting or seeding study. For example, Abella et al. (2009) included 28 species in their seed mix, with 14 species established by one year after seeding and only five species occupying $\geq 50\%$ of 10-m² plots three years after seeding. Other seeding studies in the Sonoran Desert have reported no (Bainbridge and Virginia 1990, Woods et al. 2012) or minimal plant establishment (Bean et al. 2004), or have noted limited establishment based on retrospectively measuring plant community composition of seeded sites (Judd and Judd 1976, Jackson et al. 1991, Banerjee et al. 2006). The next most species-rich outplanting study in the Sonoran Desert, Bean et al. (2004), reported that at least 6 species of shrubs and grasses exhibited $\geq 69\%$ one-year survival on derelict farmland. Outplants in their study were grown in 3.8-L pots and were also irrigated, and the study site was much drier (19 cm/year average rainfall) than our site (29 cm/year average rainfall). In reviewing other outplanting studies, *Parkinsonia florida*, *Prosopis glandulosa* Torr. (honey mesquite), *Fouquieria splendens*, *Ambrosia dumosa*, *Atriplex canescens*, and *Larrea tridentata* constituted some species of our study that also were successfully established in other studies (Bainbridge and Virginia 1990, Bainbridge 1994, Bainbridge et al. 2001).

Our results of reasonably consistent survival across species differ from other studies that have found species-specific outplant survival (Abella and Newton 2009). We suspect that intensive care of plants in the nursery and caging and irrigation might have tempered variation among species in our study, but other possibilities cannot be dismissed.

While monitoring was conducted only for first-year survival of all outplants and for first- and second-year survival for trees, we found that survival declined little ($< 5\%$) from the first to the second year for the trees. These results supported those of Abella et al.'s (2012) outplanting of 10 species (including forbs, grasses, and shrubs) in the Mojave Desert, where survival declined $< 10\%$ from the first year to the third year.

Several factors are important to consider when evaluating if the revegetation technique reported here would be effective elsewhere. Precipitation in 2006, the year before outplanting, was 30 cm, near (104%) the long-term average (WRCC 2012). Precipitation in 2007 (25 cm, 86% of average) and 2008 (22 cm, 76% of average), the first two years survival was monitored, was less than average. While precipitation following outplanting was below average, average precipitation is still greater at 29 cm/yr in the study area (typical of Sonoran Desert Uplands) than in many other North American desert areas that have < 20 cm/yr of precipitation (Brown 1994). Monsen et al. (2004) suggested that revegetation through seeding is difficult to achieve when precipitation averages < 20 cm but did not provide lower limits for outplants, which are more frequently irrigated. The roadside environment also could have influenced results. On one hand, roadsides can accumulate moisture because of runoff from the road (Brooks and Lair

2009). On the other hand, exotic plants can be more troublesome along roadsides, though not always (Craig et al. 2010). Exotic plants were treated in this project.

It is typical for costs per plant to be in the range of tens of dollars for desert revegetation projects because a series of steps ranging from seed collection through grow out and maintenance in the field are required to provide field outplants (Bainbridge 2007). The project costs reported here further include several supporting activities such as exotic plant control and documenting effectiveness of the project. Several actions were performed to efficiently use the project budget, such as conducting monitoring and assessment activities during the course of other activities (e.g., exotic plant control). Use of volunteers or youth conservation corps can also help reduce costs on these types of projects, while engaging a range of people, and were used in other aspects (e.g., salvaging plants) of the overall road project.

Many of the resources required for revegetation projects such as this one are fixed (e.g., plant grow out). The major areas where managers might have flexibility for reducing resource inputs likely are grazing protection and irrigation (Table 2). Research in the Mojave and Sonoran Deserts suggests that influences of grazing protection on outplant survival are species- and site-specific, likely a function of palatability of the outplant species and intensity of herbivory (Bainbridge 1994). Grazing protection was provided to all outplants in our project, and future research that assesses which most require protection might help reduce the number of cages installed and removed. Effectiveness of irrigation also has been situational specific in southwestern deserts (Abella and Newton 2009). This is likely a function of drought tolerance of the species, precipitation during the project, and interactions of water with other factors (e.g.,

herbivory). Additional research, such as Roundy et al.'s (2001) study, which assessed moisture requirements for early survival of a range of native species, might help irrigation be focused on those species most requiring it. Moreover, drought-tolerant species that least require irrigation could be favored in projects where extensive irrigation is not feasible (Newton 2001). General ecological literature might provide some expectations as to the most drought-tolerant species (Smith et al. 1997), which need testing for revegetation to potentially develop species suitability.

While the data revealed that revegetation targets were met, further work is needed to understand what functional benefits might accrue from revegetation. Monitoring beyond establishment of the revegetation individuals themselves is rare, with Grantz et al.'s (1998) study for how revegetation reduced fugitive dust in the Mojave Desert being one of the few in southwestern deserts. Monitoring whether the outplants themselves produce seed to facilitate recruitment of their own populations, or whether revegetation facilitates recruitment of other species, could be informative for designing revegetation treatments that maximize benefits. A limitation of outplanting, for instance, is that often it is not feasible to revegetate large areas. However, if establishing revegetated 'islands' can initiate or speed succession, the area positively influenced by outplanting would be much greater than suggested by just the planted area (Reever Morghan et al. 2005).

This study reports a protocol effective for meeting revegetation targets even in relatively dry years in a desert ecosystem. Considerable investment in plant materials development, planting effort, and maintenance were required to achieve this success. Future work could explore ways to reduce costs and identify potential functional benefits of revegetation.

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Table 1. Survival of native plant species along roadsides of Saguaro National Park, Arizona, one and two years after outplanting for tree species and one year after outplanting for other species.

Species	No. planted	Survival (%)
Grass		
<i>Aristida purpurea</i>	34	94
<i>Bothriochloa barbinodis</i>	48	85
<i>Bouteloua repens</i>	77	92
<i>Digitaria californica</i>	29	100
<i>Heteropogon contortus</i>	43	98
<i>Muhlenbergia porteri</i>	32	97
<i>Setaria macrostachya</i>	31	90
Forb		
<i>Baileya multiradiata</i>	2	50
<i>Dalea pringlei</i>	16	75
<i>Isocoma tenuisecta</i>	112	86
<i>Menodora scabra</i>	44	75
<i>Nicotiana obtusifolia</i>	4	75
<i>Psilostrophe cooperi</i>	37	89
<i>Senna covesii</i>	30	60
<i>Sphaeralcea ambigua</i>	9	100
<i>Zinnia acerosa</i>	193	96
Shrub		
<i>Calliandra eriophylla</i>	26	88
<i>Dalea pulchra</i>	16	50
<i>Encelia farinosa</i>	94	93
<i>Ephedra trifurca</i>	13	15
<i>Ericameria laricifolia</i>	9	89
<i>Fouquieria splendens</i>	80	89
<i>Jatropha cardiophylla</i>	1	100
<i>Larrea tridentata</i>	85	80
<i>Simmondsia chinensis</i>	50	78
<i>Trixis californica</i>	49	90
Shrub-tree		
<i>Acacia constricta</i>	56	86
<i>Acacia greggii</i>	46	100
<i>Celtis ehrenbergiana</i>	30	93
<i>Gossypium thurberi</i>	31	94
Tree		
<i>Parkinsonia florida</i>	1	100 (100) ^a

<i>Parkinsonia microphylla</i>	123	62 (55)
<i>Prosopis velutina</i>	136	67 (67)

^aPercent survival after two years is provided in parentheses after the first-year survival.

Table 2. Summary of estimated financial cost, resources required, and labor for a revegetation project along roadsides of Saguaro National Park, Arizona.

Item	Cost (\$)	Description
Nursery grow out ^a	4,600	Propagate 1,554 outplants
Revegetation ^b	76,300	Prepare sites, vertical mulch, install plants and cages
Maintenance watering ^c		
Water	43	53,753 L of water at \$0.0008/L
Fuel	274	1891 Km driven (24 Km/3.8 L fuel at \$3.50/3.8 L)
Labor	3,875	(310 hrs at \$12.50/hr)
Weeding		
Fuel	28	193 Km driven (24 Km/3.8 L fuel at \$3.50/3.8 L)
Labor	750	(60 hrs at \$12.50/hr)

^aSeed-collection costs are not included. Seed collection was done by Saguaro National Park staff when working at sites prior to implementation of the project. The nursery grow out was done at the Natural Resources Conservation Service's Plant Materials Center (Tucson, Arizona) and included supplies (e.g., potting soil), watering, and performing plant care.

^bRevegetation activities were performed by contract and included laying out sites, collecting and installing vertical mulch, acquiring and constructing cages, installing the 1,554 outplants, performing the initial watering, conducting initial exotic plant control treatments, and general site care until the project entered the maintenance phase.

^cQuantity of water used was recorded for each trip. City of Tucson 2012 commercial potable water rates were used. Approximately 3 L of water was provided to each outplant on each visit, with 133 round-trips on the full 13-Km Cactus Forest Drive and 22 round-trips on the two-way traffic portion of the drive (8 Km each round trip). Labor included hourly salary. For efficiency, monitoring of plant survival and photo documentation were performed during maintenance site visits.

Fig. 1. Location of revegetation sites (triangles) along Cactus Forest Drive of the Rincon Mountain District (RMD) of Saguaro National Park, Arizona. The inset map displays the location of the RMD and the Cactus Forest Drive in the western part of the RMD. Sites numbered as 82 and 84 in the main figure correspond with photos in Fig. 2.

Fig. 2. Repeat photographs of revegetation sites in Saguaro National Park, Arizona. The left panel shows site 82 and the right panel site 84 corresponding to Fig. 1. Site 82: a) before restoration in January 2007, and after restoration in b) January 2007, c) September 2007, d) January 2009, and e) January 2013. Site 84: f) before restoration in January 2007, and after restoration in g) January 2007, h) September 2007, i) January 2009, and j) January 2013. Photos by K.L. O'Brien except for January 2007 by Kate Smith Connor.

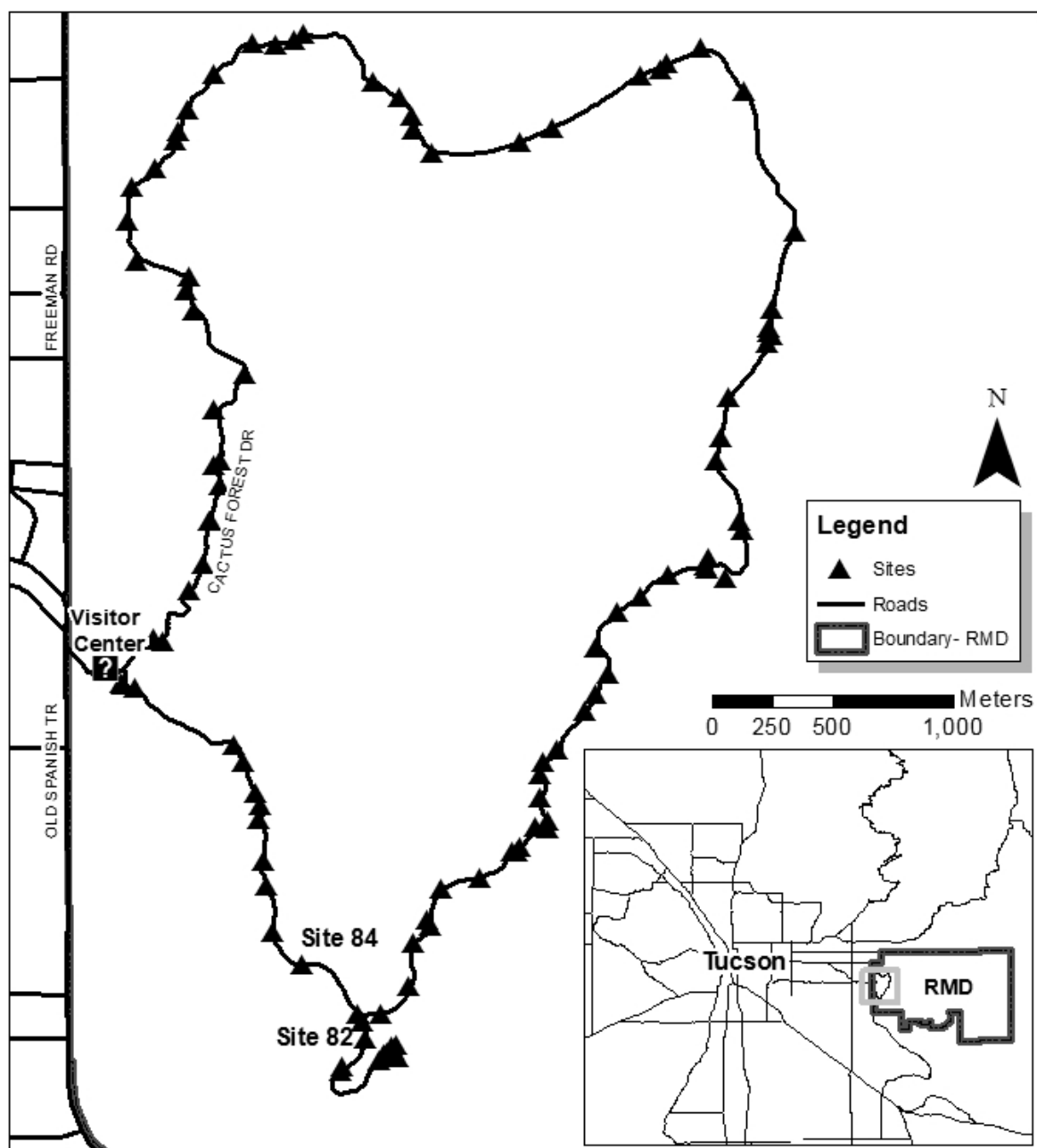


Fig. 1

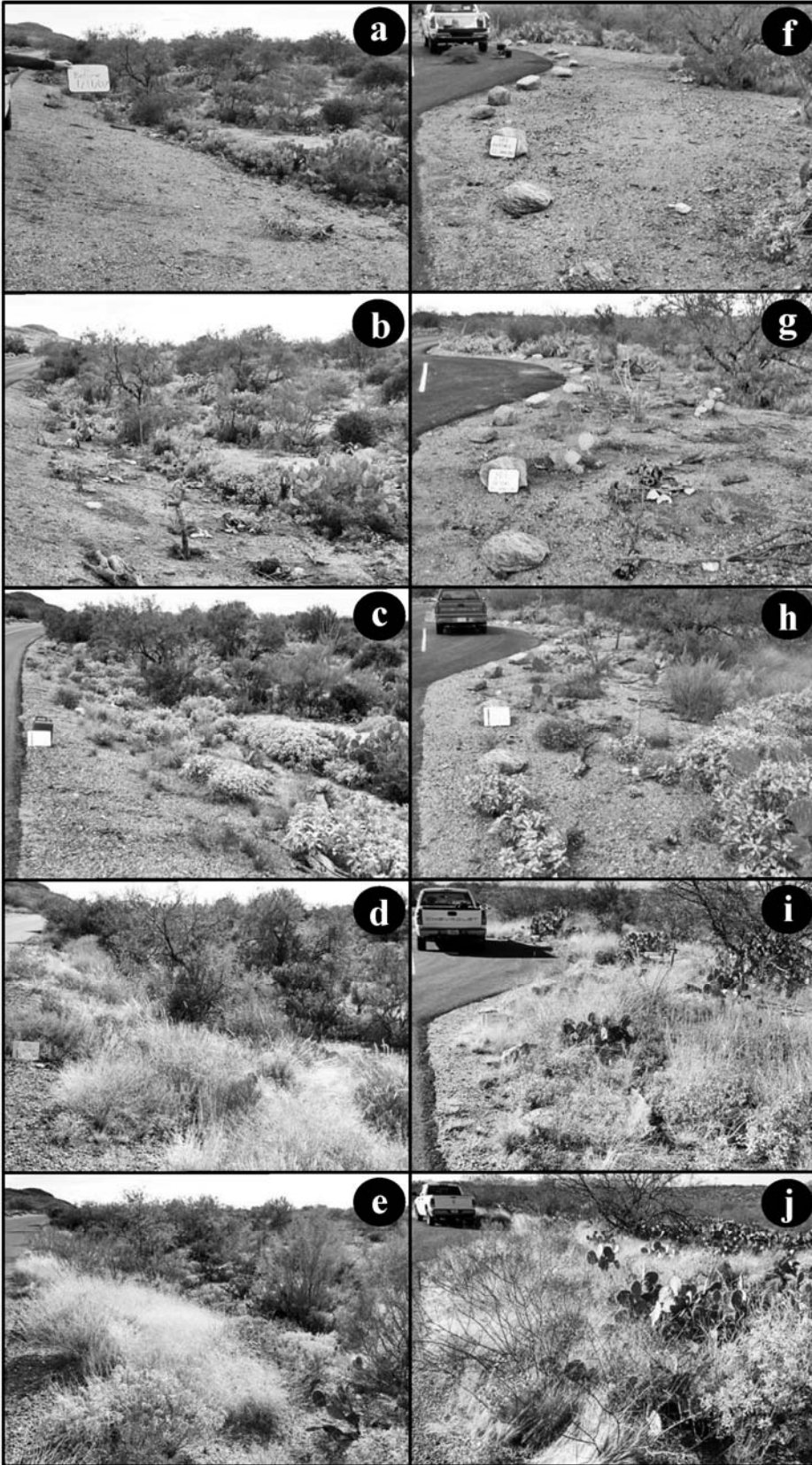


Fig. 2

APPENDIX D

Supplemental information for Part V

Table D1. Characteristics of plots in 2012 used to assess post-treatment ecological condition along a buffelgrass treatment gradient in Saguaro National Park, Sonoran Desert

Treatment ^a	Plot ID ^b	UTMx ^c (m)	UTMy ^c (m)	Elevation (m)	Slope gradient (degrees)	Aspect (degrees)	Buffelgrass cover (%)	Plant taxa Richness ₂ 100 m ⁻²	Soil parent material ^d	Soil subgroup(s)
7	1	528184	3562428	929	9	245	0	26	G	Lithic Torriorthents
6	2	528208	3562400	932	15	252	60	24	G	Lithic Torriorthents
4	3	527429	3562189	929	10	203	0	28	G	Lithic Torriorthents
4	4	527723	3560986	997	10	220	0	33	G/I	Lithic UsticTorriorthents/ UsticTorriorthents
3	5	526421	3558388	1008	13	180	0.5	24	G	Lithic Torriorthents
7	6	527112	3560559	962	2	233	0	27	G	Lithic Torriorthents/ Lithic Haplargids
6	7	527166	3560545	961	3	184	10	27	G/I	Lithic Torriorthents/ Lithic Haplargids
1	8	527150	3558613	1172	15	210	0.1	39	G/I	Lithic UsticTorriorthents/ UsticTorriorthents
1	9	526920	3558040	1091	22	170	0.1	19	G/I	Lithic UsticTorriorthents/ UsticTorriorthents
1	10	526412	3558704	997	27	292	0.1	33	G/I	Lithic UsticTorriorthents/ UsticTorriorthents
2	11	525781	3557937	938	14	290	0.1	39	G	Lithic Torriorthents
2	12	525732	3557951	937	6	170	0.5	27	G	Lithic Torriorthents
2	13	525687	3557871	932	9	200	0.5	34	G	Lithic Torriorthents
3	14	525687	3557825	923	10	254	1	31	G	Lithic Torriorthents
5	15	525516	3557675	922	10	80	1	48	G	Lithic Torriorthents
5	16	525532	3557802	935	24	180	1	30	G	Lithic Torriorthents/ Lithic Haplargids
4	17	526555	3560851	929	11	300	0	32	G/I	TypicHaplocalcids/ TypicHaplargids
5	18	527135	3557849	1002	29	168	3	19	G	Lithic Torriorthents
3	19	526161	3558090	1000	10	210	0	30	G	Lithic Torriorthents
6	20	529687	3557275	1055	9	235	70	28	G	Lithic Torriorthents
7	21	529730	3557255	1048	13	185	0	24	G	Lithic Torriorthents

^a1) 2007-2011 (5 years) annual buffelgrass treatment; 2) 2009-2011 (3 years) annual buffelgrass treatment; 3) 2010-2011 (2 years) annual buffelgrass treatment; 4) 2008 single year (4-year-old) buffelgrass treatment; 5) 2011 single year (1-year-old) buffelgrass treatment; 6) Control, buffelgrassbut no treatment; 7) Control, no buffelgrassand no treatment

^bIdentification number corresponding to Fig. 1 ^cUniversal Transverse Mercator coordinates, North American Datum 1983 dG = Granite, I = Igneous (Cochran and Richardson 2003)

Table D2a. Physical and chemical properties of 0-5 cm soil in sampling interspace microsites along a buffelgrass treatment gradient (treatments labeled 1-7) in Saguaro National Park, Sonoran Desert

	Interspace						
	1 ^a	2	3	4	5	6	7
Physical							
Sand (%)	65 (61-69)	66 (65-68)	70 (68-74)	68 (66-73)	71 (69-73)	72 (69-74)	75 (69-84)
Silt (%)	23 (19-25)	23 (21-25)	21 (19-24)	19 (19-20)	20 (19-20)	19 (16-20)	18 (12-23)
Clay (%)	13 (13-14)	10 (9-14)	9 (6-13)	13 (9-15)	9 (8-11)	9 (6-11)	7 (4-9)
CF (% wt.)	41 (37-46)	36 (35-36)	43 (25-56)	41 (35-50)	46 (42-54)	39 (35-42)	38 (30-43)
CF (% vol.)	26 (23-29)	20 (18-23)	29 (16-38)	25 (21-32)	29 (22-38)	24 (22-29)	23 (20-26)
BD (g/cm ³)	0.9 (0.8-1.0)	0.9 (0.8-0.9)	0.9 (0.7-1.2)	0.9 (0.8-1.0)	0.8 (0.8-0.9)	0.9 (0.9-1.0)	1.0 (0.8-1.2)
Chemistry							
pH	6.4 (5.8-7.4)	6.3 (5.5-6.9)	6.5 (5.6-7.1)	6 (5.5-6.7)	6.9 (6.2-8.2)	6.2 (5.7-6.4)	6.5 (6.1-6.8)
EC (umhos/cm)	770 (461-1227)	786 (347-1623)	510 (338-702)	699 (383-1320)	464 (382-588)	423 (241-738)	272 (214-335)
SAR	0.5 (0.2-1)	0.5 (0.3-0.7)	2.1 (0.3-5.2)	0.5 (0.3-0.8)	0.4 (0.2-0.5)	1.5 (0.3-3.8)	0.5 (0.4-0.6)
EPP	10 (9-12)	9 (8-11)	9 (7-10)	8 (7-8)	12 (10-14)	9 (7-11)	9 (7-12)
PAR	0.7 (0.6-0.9)	0.7 (0.5-0.8)	0.6 (0.4-0.7)	0.5 (0.4-0.5)	0.9 (0.7-1.2)	0.6 (0.4-0.8)	0.6 (0.4-1)
TSS	508 (304-810)	519 (229-1071)	337 (223-463)	461 (253-871)	306 (252-388)	279 (159-487)	180 (141-221)

^a Treatment numbers correspond with: 1) 2007-2011 (5 years) annual buffelgrass treatment, 2) 2009-2011 (3 years) annual buffelgrass treatment, 3) 2010-2011 (2 years) annual buffelgrass treatment, 4) 2008 single year (4-year-old) buffelgrass treatment, 5) 2011 single year (1-year-old) buffelgrass treatment, 6) control, buffelgrass but no treatment, and 7) control, no buffelgrass and no treatment

^b Treatment (T), Microsite (M), * $P < 0.05$, ** $P < 0.01$

Table D2b. Physical and chemical properties of 0-5 cm soil in sampling below brittlebush microsites along a buffelgrass treatment gradient (treatments labeled 1-7) in Saguaro National Park, Sonoran Desert

	Below brittlebush						
	1	2	3	4	5	6	7
Physical							
Sand (%)	63 (61-66)	66 (64-69)	68 (66-71)	69 (68-71)	67(64-71)	70 (66-74)	73 (73-74)
Silt (%)	24 (23-26)	23 (21-25)	22 (18-25)	20 (18-21)	23(21-25)	20 (19-23)	20 (19-20)
Clay (%)	13 (11-14)	11 (9-15)	10 (9-11)	11 (9-14)	11(8-14)	10 (8-11)	8 (6-9)
CF (% wt.)	47 (39-55)	34 (30-36)	36 (32-40)	33 (26-44)	45(38-50)	34 (29-40)	33 (23-38)
CF (% vol.)	29 (20-36)	20 (18-21)	23 (20-26)	20 (14-28)	26(24-27)	18 (15-19)	17 (15-20)
BD (g/cm ³)	0.8 (0.7-0.8)	0.9 (0.8-1.1)	0.9 (0.9-1.0)	0.9 (0.9-1.1)	0.8 (0.7-0.9)	0.9 (0.8-1.0)	1.0 (0.8-1.2)
Chemistry							
pH	7.0 (6.7-7.6)	6.5 (5.7-7.1)	6.8 (6.4-7.2)	6.7 (6.3-7.1)	7.6(7-8.3)	6.6 (5.7-7.3)	6.7 (6.5-6.8)
EC (umhos/cm)	1238 (1005-1557)	1094 (374-2202)	1135 (963-1332)	652 (612-726)	1023(572-1305)	887 (528-1428)	612 (435-888)
SAR	0.3 (0.2-0.3)	0.4 (0.4-0.4)	0.3 (0.2-0.5)	0.3 (0.1-0.5)	0.4(0.1-1)	0.4 (0.3-0.7)	0.3 (0.3-0.4)
EPP	15 (14-18)	15 (10-23)	16 (7-21)	13 (9-20)	16(13-19)	16 (12-25)	13 (11-15)
PAR	1.4 (1.2-1.7)	1.4 (0.7-2.6)	1.5 (0.4-2.1)	1.1 (0.6-2)	1.5(1.1-1.9)	1.6 (0.9-2.9)	1.1 (0.9-1.3)
TSS	817 (663-1028)	722 (247-1453)	749 (636-879)	430 (404-479)	675(377-861)	585 (348-942)	404 (287-586)

^a Treatment numbers correspond with: 1) 2007-2011 (5 years) annual buffelgrass treatment, 2) 2009-2011 (3 years) annual buffelgrass treatment, 3) 2010-2011 (2 years) annual buffelgrass treatment, 4) 2008 single year (4-year-old) buffelgrass treatment, 5) 2011 single year (1-year-old) buffelgrass treatment, 6) control, buffelgrass but no treatment, and 7) control, no buffelgrass and no treatment

^b Treatment (T), Microsite (M), * $P < 0.05$, ** $P < 0.01$

Table D2c. Physical and chemical properties of 0-5 cm soil in sampling below buffelgrass microsites along a buffelgrass treatment gradient (treatments labeled 1-7) in Saguaro National Park, Sonoran Desert

	Below BG			
	6	T × M	T ^b	M ^b
Physical				
Sand (%)	69 (66-74)	0.4	4.3*	2.9
Silt (%)	21 (19-23)	0.3	2.8	3.2
Clay (%)	10 (8-11)	1.3	1.7	1.4
CF (% wt.)	34 (27-40)	1	1.4	3.3
CF (% vol.)	19 (16-23)	1	1.5	7.7*
BD (g/cm ³)	0.9 (0.7-1.0)	0.6	0.9	0.5
Chemistry				
pH	6.8 (5.9-7.5)	0.3	1	8.3*
EC (umhos/cm)	782 (531-1176)	0.7	0.8	15.7**
SAR	0.4 (0.4-0.5)	0.8	0.8	3.2
EPP	14 (8-20)	0.1	0.4	20.7**
PAR	1.2 (0.5-2)	0.1	0.3	18.5**
TSS	516 (350-776)	0.7	0.8	15.7**

^a Treatment numbers correspond with: 1) 2007-2011 (5 years) annual buffelgrass treatment, 2) 2009-2011 (3 years) annual buffelgrass treatment, 3) 2010-2011 (2 years) annual buffelgrass treatment, 4) 2008 single year (4-year-old) buffelgrass treatment, 5) 2011 single year (1-year-old) buffelgrass treatment, 6) control, buffelgrass but no treatment, and 7) control, no buffelgrass and no treatment

^b Treatment (T), Microsite (M), * $P < 0.05$, ** $P < 0.01$

Table D3a.. Macro and micronutrient properties of 0-5 cm soil in sampling interspace microsites along a buffelgrass treatment gradient (treatments labeled 1-7) in Saguaro National Park, Sonoran Desert

	Interspace						
	1 ^a	2	3	4	5	6	7
Macronutrients							
Organic C (%)	1.1 (0.9-1.6)	1.2 (0.7-1.6)	0.6 (0.4-0.6)	0.9 (0.5-1.4)	0.8 (0.7-1.2)	1.1 (0.7-1.6)	0.6 (0.5-0.7)
Total N (%)	0.10 (0.08-0.14)	0.11 (0.06-0.15)	0.05 (0.03-0.07)	0.08 (0.05-0.12)	0.06 (0.05-0.07)	0.1 (0.06-0.16)	0.05 (0.05-0.06)
K (mg/kg)	35 (20-46)	33 (16-57)	20 (15-23)	21 (16-27)	33 (28-39)	19 (13-24)	16 (13-21)
Ca (mg/kg)	58 (24-112)	67 (21-159)	22 (19-27)	47 (26-87)	31 (20-51)	17 (12-23)	16 (9-23)
Mg (mg/kg)	9 (5-15)	11 (4-23)	5 (4-6)	9 (5-16)	4 (3-4)	4 (2-7)	3 (2-4)
Micronutrients							
B (mg/kg)	0.38 (0.17-0.73)	0.28 (0.06-0.5)	0.18 (0.07-0.25)	0.25 (0.11-0.51)	0.33 (0.12-0.72)	0.17 (0.13-0.21)	0.15 (0.12-0.18)
Cu (mg/kg)	3.2 (3.1-3.2)	3.1 (2.3-3.8)	2 (1.9-2.1)	5.4 (2-10.4)	2.4 (1.6-3.1)	3.9 (2.7-5.9)	2.5 (1.9-3)
Fe (mg/kg)	18 (9-26)	19 (14-26)	9 (7-11)	17 (15-19)	9 (3-14)	18 (12-28)	11 (9-14)
Na (mg/kg)	13 (8-21)	13 (10-15)	38 (6-94)	17 (8-31)	8 (7-9)	31 (6-81)	8 (7-9)
Zn (mg/kg)	2.7 (1.5-4.1)	1.9 (0.9-3.1)	1 (0.8-1.2)	1.6 (1.5-1.7)	1.3 (0.8-1.6)	1.9 (1.6-2.4)	1.7 (1.3-2.4)

^a Treatment numbers correspond with: 1) 2007-2011 (5 years) annual buffelgrass treatment, 2) 2009-2011 (3 years) annual buffelgrass treatment, 3) 2010-2011 (2 years) annual buffelgrass treatment, 4) 2008 single year (4-year-old) buffelgrass treatment, 5) 2011 single year (1-year-old) buffelgrass treatment, 6) control, buffelgrass but no treatment, and 7) control, no buffelgrass and no treatment

^b Treatment (T), Microsite (M), * $P < 0.05$, ** $P < 0.01$

Table D3b. Macro and micronutrient properties of 0-5 cm soil in sampling below brittlebush microsites along a buffelgrass treatment gradient (treatments labeled 1-7) in Saguaro National Park, Sonoran Desert

	Below brittlebush						
	1	2	3	4	5	6	7
Macronutrients							
Organic C (%)	1.7 (1.6-1.8)	1.6 (0.6-2.9)	1.5 (0.9-1.9)	1.1 (0.9-1.4)	1.6(1.1-2.4)	1.6 (1.4-1.9)	1.1 (0.8-1.4)
Total N (%)	0.15 (0.14-0.16)	0.14 (0.05-0.26)	0.12 (0.07-0.16)	0.1 (0.08-0.13)	0.11(0.08-0.13)	0.14 (0.12-0.15)	0.1 (0.08-0.12)
K (mg/kg)	88 (71-105)	65 (27-132)	94 (23-135)	51 (32-84)	88(44-117)	89 (40-184)	49 (31-71)
Ca (mg/kg)	88 (74-114)	32 (20-56)	77 (72-83)	44 (32-51)	72(32-98)	52 (40-73)	40 (24-63)
Mg (mg/kg)	14 (11-18)	15 (5-30)	16 (12-19)	9 (8-10)	12 (6-19)	13 (7-20)	8 (6-12)
Micronutrients							
B (mg/kg)	0.73 (0.64-0.85)	0.49 (0.19-1.01)	0.59 (0.25-0.97)	0.49(0.28-0.69)	0.86 (0.43-1.61)	0.44 (0.32-0.58)	0.48 (0.26-0.71)
Cu (mg/kg)	3.1 (2.4-4.1)	2.7 (2.4-2.9)	2.6 (2.1-2.9)	4.1(2.7-6.3)	2.3 (1.8-2.7)	4.4 (2-7.2)	2.3 (2-2.6)
Fe (mg/kg)	13 (11-16)	20 (13-25)	15 (10-18)	14(7-22)	7 (3-11)	21 (12-35)	11 (8-12)
Na (mg/kg)	11 (9-12)	11 (7-14)	12 (9-17)	8(4-15)	12 (5-24)	13 (9-19)	9 (6-10)
Zn (mg/kg)	3.9 (2.3-6.5)	1.7 (1.3-2.1)	2.2 (1.3-2.9)	2.3(2.1-2.6)	1.8 (0.9-2.3)	2.5 (2.2-2.8)	2.4 (1.8-2.8)

^a Treatment numbers correspond with: 1) 2007-2011 (5 years) annual buffelgrass treatment, 2) 2009-2011 (3 years) annual buffelgrass treatment, 3) 2010-2011 (2 years) annual buffelgrass treatment, 4) 2008 single year (4-year-old) buffelgrass treatment, 5) 2011 single year (1-year-old) buffelgrass treatment, 6) control, buffelgrass but no treatment, and 7) control, no buffelgrass and no treatment

^b Treatment (T), Microsite (M), * $P < 0.05$, ** $P < 0.01$

Table D3c. Macro and micronutrient properties of 0-5 cm soil in sampling below buffelgrass microsites along a buffelgrass treatment gradient (treatments labeled 1-7) in Saguaro National Park, Sonoran Desert

	Below BG			
	6	T × M	T ^b	M ^b
Macronutrients				
Organic C (%)	1.5 (1.2-1.7)	0.5	0.8	19.2**
Total N (%)	0.13 (0.11-0.17)	0.3	1.5	12.8**
K (mg/kg)	63 (26-119)	0.5	0.5	25.5**
Ca (mg/kg)	48 (36-65)	1.5	1.3	4.9*
Mg (mg/kg)	12 (7-16)	1.2	0.7	23.8**
Micronutrients				
B (mg/kg)	0.37 (0.2-0.48)	0.6	0.6	41.4**
Cu (mg/kg)	3.3 (1.9-4.3)	0.9	1.3	0.4
Fe (mg/kg)	16 (8-29)	0.5	3.0*	0
Na (mg/kg)	13 (9-15)	0.6	0.7	1.8
Zn (mg/kg)	2 (1.6-2.6)	1	1.8	15.5**

^a Treatment numbers correspond with: 1) 2007-2011 (5 years) annual buffelgrass treatment, 2) 2009-2011 (3 years) annual buffelgrass treatment, 3) 2010-2011 (2 years) annual buffelgrass treatment, 4) 2008 single year (4-year-old) buffelgrass treatment, 5) 2011 single year (1-year-old) buffelgrass treatment, 6) control, buffelgrass but no treatment, and 7) control, no buffelgrass and no treatment

^b Treatment (T), Microsite (M), * $P < 0.05$, ** $P < 0.01$

Table D4. Average emerged seeds/m² (0-5 cm depth) in soil seed banks by treatment and microsite along a buffelgrass (BG) treatment gradient in Saguaro National Park, Sonoran Desert

Species ^a	Interspace							Below brittlebush						BG	
	1 ^b	2	3	4	5	6	7	1	2	3	4	5	6	7	6
Acacia spp. (T)	0	0	0	93	0	0	0	0	0	0	46	0	0	0	0
<i>Agrostis elliotiana</i> (aG)	0	46	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Agrostis scabra</i> (pG)	0	0	0	0	0	231	0	0	0	0	0	0	0	0	0
<i>Amsinckia tessellata</i> (aF)	0	0	0	0	0	0	0	0	0	0	0	0	46	0	0
Aristida purpurea (a-pG)	0	93	0	46	0	0	46	0	370	0	0	0	139	0	93
<i>Astragalus nuttallianus</i> (a-pF)	0	0	0	0	0	0	0	0	0	0	46	0	0	0	0
Bouteloua aristidoides (aG)	0	0	0	93	46	0	0	0	93	46	324	0	139	93	46
<i>Camissonia chamaenerioides</i> (aF)	0	0	0	0	0	0	0	0	0	0	0	0	46	0	0
<i>Carex athrostachya</i> (pG)	0	0	0	0	46	0	0	0	0	0	0	0	0	0	0
<i>Centaurium arizonicum</i> (a-bF)	0	139	648	0	0	0	0	0	0	93	0	0	370	0	231
<i>Chenopodium incanum</i> (aF)	0	0	0	0	0	46	0	0	46	0	0	0	46	46	0
<i>Crassula connata</i> (aF)	0	2546	648	231	139	463	1528	0	1435	2037	278	0	1759	3704	833
<i>Cryptantha decipiens</i> (aF)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	46
Cryptantha nevadensis (aF)	0	0	0	0	0	46	0	0	0	0	0	0	0	0	0
Daucus pusillus (aF)	0	185	0	0	46	139	46	0	93	0	0	0	0	0	93
<i>Digitaria sanguinalis</i> (aG)*	0	93	0	0	0	0	0	0	0	0	0	0	0	0	0
Encelia farinosa (S)	0	0	0	0	0	139	46	231	185	93	1111	46	185	231	0
<i>Eragrostis echinochloidea</i> (pG)*	0	0	0	0	0	0	46	0	0	46	0	0	0	0	0
Eriastrum diffusum (aF)	0	0	0	0	93	0	0	0	0	0	0	0	0	0	0
<i>Erigeron divergens</i> (bF)	0	0	0	0	0	0	46	46	46	0	0	0	0	0	0
Janusia gracilis (pF)	0	0	0	0	0	0	0	0	0	0	0	0	0	46	0
<i>Juncus bufonius</i> (aG)	0	46	0	0	0	139	0	0	0	0	0	0	46	46	139
<i>Leptochloa panicea</i> (a-pG)	0	0	46	0	0	0	0	0	0	0	0	0	0	0	0
<i>Lepidium virginicum</i> (a-pF)	46	0	0	46	0	0	0	46	46	46	0	0	0	46	0
<i>Logfia arizonica</i> (aF)	46	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Logfia californica (aF)	0	93	0	0	0	46	231	46	185	417	93	93	46	93	0
<i>Mecardonia procumbens</i> (a-pF)	0	93	0	0	556	278	93	0	0	46	0	0	509	0	880
<i>Mimulus floribundus</i> (aF)	0	0	46	0	0	0	0	0	0	0	0	0	0	0	0
<i>Mimulus guttatus</i> (a-pF)	0	0	0	0	0	46	93	0	0	0	0	0	0	0	0
<i>Mimetanthe pilosa</i> (aF)	0	0	0	0	0	0	0	0	0	0	0	0	93	0	0
<i>Mollugo verticillata</i> (aF)	46	0	0	0	0	0	0	0	0	0	0	0	0	0	46
Nicotiana obtusifolia (a-pF)	0	0	0	0	0	0	0	0	0	0	46	0	0	0	0
Opuntia engelmannii (C)	0	0	0	0	0	46	0	0	0	0	0	0	0	0	46
Pectocarya recurvata (aF)	0	0	0	0	0	185	0	0	0	139	0	0	93	0	46
Pennisetum ciliare (pG)*	0	0	0	0	0	0	0	46	0	46	0	46	185	93	46
<i>Pseudognaphalium canescens</i> (a-pF)	0	324	139	0	0	0	93	0	463	0	0	0	93	324	0
<i>Pterostegia drymarioides</i> (aF)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	93
<i>Sairocarpus nuttallianus</i> (a-bF)	0	0	0	0	0	0	46	46	231	139	185	0	370	0	324
<i>Senecio parryi</i> (pF)	0	0	0	0	0	0	0	46	0	0	0	0	0	46	0
<i>Sporobolus wrightii</i> (pG)	0	93	0	0	0	0	46	0	46	0	46	0	46	93	93
Vulpia octoflora (aG)	46	231	46	0	0	139	556	0	46	0	231	93	0	0	0

^a Species in bold also occurred in vegetation of one or more plots. Asterisks signify exotic. Life spans and growth forms are provided in parentheses: a = annual, b = biennial, p = perennial; C = cactus, F = forb, G = graminoid, S = shrub, and T = tree. For *Eragrostis echinocloidea*, the species may also have occurred in vegetation, but vegetation was only able to be identified to *Eragrostis* spp.

^b Treatment numbers correspond with: 1) 2007-2011 (5 years) annual buffelgrass treatment, 2) 2009-2011 (3 years) annual buffelgrass treatment, 3) 2010-2011 (2 years) annual buffelgrass treatment, 4) 2008 single year (4-year-old) buffelgrass treatment, 5) 2011 single year (1-year-old) buffelgrass treatment, 6) control, buffelgrass but no treatment, and 7) control, no buffelgrass and no treatment

APPENDIX E

Manuscript developed from Report 5, PART V of this report. (Attached)

Abella SR, Chiquoine LP, Backer DM. 2013. Soil, vegetation and seed bank of a Sonoran Desert Ecosystem along an exotic plant (*Pennisetum ciliare*) treatment gradient. *Environmental Management*, **52**, 946-957.

Soil, Vegetation, and Seed Bank of a Sonoran Desert Ecosystem Along an Exotic Plant (*Pennisetum ciliare*) Treatment Gradient

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Abstract Ecological conditions following removal of exotic plants are a key part of comprehensive environmental management strategies to combat exotic plant invasions. We examined ecological conditions following removal of the management-priority buffelgrass (*Pennisetum ciliare*) in Saguaro National Park of the North American Sonoran Desert. We assessed soil, vegetation, and soil seed banks on seven buffelgrass site types: five different frequencies of buffelgrass herbicide plus hand removal treatments (ranging from 5 years of annual treatment to a single year of treatment), untreated sites, and non-invaded sites, with three replicates for each of the seven site types. The 22 measured soil properties (e.g., pH) differed little among sites. Regarding vegetation, buffelgrass cover was low (≤ 1 % median cover), or absent, across all treated sites but was high (10–70 %) in untreated sites. Native vegetation cover, diversity, and composition were indistinguishable across site types. Species composition was dominated by native species (>93 % relative cover) across all sites

except untreated buffelgrass sites. Most (38 species, 93 %) of the 41 species detected in soil seed banks were native, and native seed density did not differ significantly across sites. Results suggest that: (1) buffelgrass cover was minimal across treated sites; (2) aside from high buffelgrass cover in untreated sites, ecological conditions were largely indistinguishable across sites; (3) soil seed banks harbored ≥ 12 species that were frequent in the aboveground vegetation; and (4) native species dominated post-treatment vegetation composition, and removing buffelgrass did not result in replacement by other exotic species.

Keywords Buffelgrass · Ecological condition · Native species · Recovery · Saguaro National Park · Treatment effectiveness

Introduction

Understanding condition of ecosystems following treatment of exotic plants is a key part of comprehensive exotic species control on conservation and managed lands (Corbin and D’Antonio 2012). Relative to similar, but non-invaded areas, post-treatment ecological condition can be conceived as contingent upon three main factors: impact of the exotic species to the ecosystem during the species’ residence, legacy effects of the species persisting after the species is removed, and effect of the treatment itself (Zavaleta and others 2001; Hejda and others 2009). Exotic plants can impact ecosystems in numerous ways, such as competitively reducing native species, altering soil properties, and changing disturbance regimes (Levine and others 2003; Wolfe and Klironomos 2005). These impacts do not necessarily dissipate upon removal of the species, with soil and seed bank modifications accrued during the

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species' occupancy often creating legacies persisting even after the species is treated (Ehrenfeld 2003; Parker and Schmel 2010; Schneider and Allen 2012). Exotic plant treatments themselves can have known or unintended non-target impacts, such as herbicide effects on native species or soil disturbance accompanying manually removing exotic plants (Sheley and Denny 2006; Flory and Clay 2009). Together, species impacts, legacy effects, and treatment influences can affect post-treatment condition of ecosystems relative to non-invaded areas (Jordan and others 2011; Owen and others 2011).

Understanding post-treatment ecological condition is important for evaluating treatment effectiveness, if ecological restoration is needed to facilitate recovery of native ecosystems, and if maintenance treatments could help keep exotic plant abundance low. It is often uncertain whether simply removing an invader results in native ecosystem recovery (Corbin and D'Antonio 2012). Following removal of exotic *Tamarix* spp. in southwestern USA riparian areas, for example, Harms and Hiebert (2006) reported that native plant cover overall doubled on removal sites, but recovery varied among ecosystems and was not related to time-since-treatment even 11 years after treatment. In a repeat-removal experiment of four exotic perennials in a deciduous forest, Vidra and others (2007) demonstrated that post-treatment species composition hinged upon the number of times that the exotics were removed through time. These authors also used a seed bank assay to help explain that minimal recovery of native species richness and cover might have related to sparse indigenous soil seed banks. This differed from conclusions of Reynolds and Cooper (2011) in exotic-dominated riparian areas, where soil seed banks contained more native species than occurred in the extant vegetation. Another important consideration in post-treatment site condition is assessing if the treated exotic species is simply replaced by other (potentially even more damaging) exotic species (Ransom and others 2012). These observations suggest the importance not only of evaluating post-treatment condition of the target exotic species, but also the condition of other ecosystem components such as the soil, native plant community, other exotics, and seed bank to help inform post-treatment site management.

Buffelgrass (*Pennisetum ciliare*) is a prime example of an exotic species for which understanding post-treatment ecological condition is important for environmental management because the species is invasive where it is not native, can dramatically alter indigenous ecosystems, and is proposed for treatments across large areas (Marshall and others 2012). Native to arid and semi-arid Africa, Asia, and the Middle East, buffelgrass has been intentionally and unintentionally introduced to such areas as arid regions of Australia and southwestern North America (Stevens and Falk 2009). The species is highly invasive in these regions,

competes with native plants, and increases fuel loads to create fire hazards in previously fuel-limited ecosystems considered poorly adapted to fire (Esque and others 2007; Olsson and others 2012a). Some studies have reported on the ecological characteristics of sites inhabited by buffelgrass, which might have important implications for post-treatment site condition. Compared to non-invaded sites, buffelgrass sites have exhibited lower native plant cover (e.g., Daehler and Goergen 2005; Marshall and others 2012); reduced species richness in most cases (e.g., Clarke and others 2005; McDonald and McPherson 2011; Olsson and others 2012b); comparable native richness in rare cases (Abella and others 2012); and extremely high fuel loads for arid lands that can exceed 2,400 kg/ha and represent a major fire hazard (Esque and others 2007; McDonald and McPherson 2011). Soil properties in buffelgrass patches are less well understood but appeared to be similar in magnitude for organic C, total, and available as below native perennial plants compared to interspaces between perennials in a Sonoran Desert study (Abella and others 2012). Also in that study, native soil seed banks were not reduced in buffelgrass patches, but not all species in the seed bank were likely capable of establishing plants at the sites (Abella and others 2012).

Fortunately for management, buffelgrass is susceptible to uprooting and herbicide treatments which have constrained its abundance in large infestations and completely eradicated small (a few to tens of hectares) patches. In Organ Pipe Cactus National Monument of the Sonoran Desert, for example, Rutman and Dickson (2002) reported that managers and citizen volunteers had achieved complete or near complete eradication after 1–3 years of treatments in patches with up to 44,000/ha buffelgrass individuals using hand tools at 17 sites. Dixon and others (2002) found that different combinations of herbicide type, timing, and repeated treatments nearly eradicated buffelgrass from their 25 ha site in western Australia. Their study, and others (e.g., Daehler and Goergen 2005; Lyons and others 2013), however, have asserted the importance of assessing post-treatment native vegetation and evaluating if active restoration can accelerate recovery, forestall buffelgrass reinvasion, and limit other exotic species.

Here, we examined ecological condition following a range of combined manual and herbicide treatments aimed at reducing buffelgrass. Our specific objectives were to assess soil properties, plant communities, and soil seed banks on sites annually treated for buffelgrass up to 5 years in a row and on single-year treatments up to 4 years old. The study occurred in an applied environmental management context of treatments implemented by the U.S. National Park Service, which, like other conservation organizations, is struggling to maintain indigenous ecosystems in the face of increasing biological invasions (Allen and others 2009).

Methods

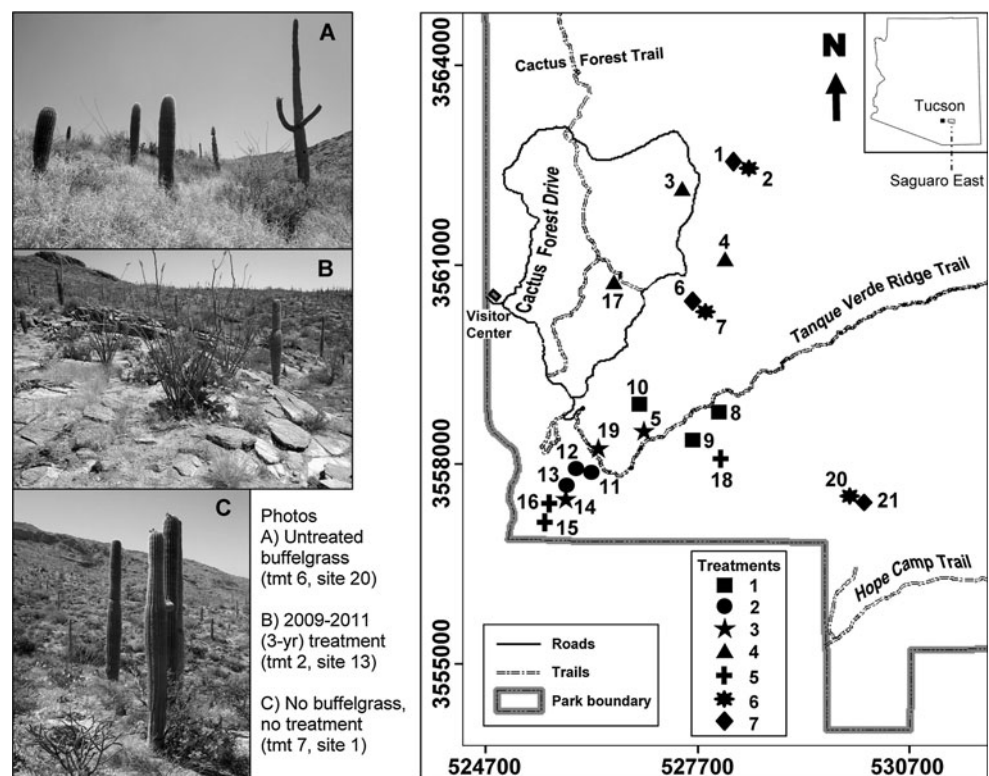
Study Area and Buffelgrass Description

We performed this study within the 37,006 ha Rincon Mountain District of Saguaro National Park, 8 km east of Tucson, Arizona, in the southwestern USA (Fig. 1). The park is within the northeastern Sonoran Desert's Arizona Upland Subdivision, which occupies higher elevations, receives more precipitation, and contains greater vegetation structural diversity than Sonoran Desert lowlands (Bowers and McLaughlin 1987). Climate, recorded by the Tucson Airport Weather Station (787 m in elevation, 1930–2011 records), is arid/semi-arid with averages of 29 cm/yr of precipitation, 37 °C daily July high temperature, and 4 °C daily January low temperature (Western Regional Climate Center, Reno, Nevada). The park's topography consists of rolling hills, alluvial fans, and concave drainageways. Soils are primarily derived from granite and classified as Torriorthents and Haplargids (Cochran and Richardson 2003). Characterized by a scrubland or low woodland physiognomy, vegetation consists of a diverse assemblage of shrub-trees, forbs, graminoids, and cacti, including saguaro (*Carnegiea gigantea*), a columnar cactus diagnostic for the Upland Subdivision (Bowers and McLaughlin 1987). Animal inhabitants include many small mammals (e.g., shrews, coyotes, fox, mice, rats, and rabbits), amphibians and reptiles (e.g., toads, tortoises, lizards, snakes), and birds (e.g.,

hawks, owls, vireos, warblers, and sparrows). Livestock grazing (primarily of cattle) occurred prior to 1976 but was not authorized thereafter. Since 1983, the park has been visited by >600,000 people annually, with most visitors concentrated along park roads and to a lesser extent trails (National Park Service, Public Use Statistics Office, Denver, CO).

Buffelgrass is apparently well adapted to its new environment of the Sonoran Desert, including Saguaro National Park, and has several traits that likely facilitate its success (Olsson and others 2012a). Buffelgrass uses a C₄ photosynthetic pathway and can have two growth periods in the Sonoran Desert: spring following winter rains and late summer after monsoonal rains (Ward and others 2006). The species is a perennial bunchgrass but differs from the architecture of the Sonoran's native bunchgrasses by exhibiting denser foliage, which is also closer to the ground and has more biomass/plant (Marshall and others 2012). Like many exotic plants, buffelgrass can readily usurp soil resources and experimentally has been shown to vigorously compete with native plants (Daehler and Goergen 2005; Stevens and Falk 2009). Buffelgrass propagules are dispersed by wind and adhesion to animals, with seeds exhibiting high germinability (Stevens and Falk 2009). Soil seed bank longevity and dynamics are not well known, but density of germinable buffelgrass seed averaged 645 seeds/m² in 0–5 cm deep soil banks below buffelgrass plants in 2011 within the study area (Abella and others 2012). This

Fig. 1 Location of study plots, classified by buffelgrass treatment type, within eastern (Rincon Mountain District) Saguaro National Park, Sonoran Desert. Geographic coordinates are Universal Transverse Mercator (zone 12, m), North American Datum 1983. Plots are numbered according to plot descriptions in Online Resource 1. Treatment numbers correspond with: (1) 2007–2011 (5 years) annual buffelgrass treatment, (2) 2009–2011 (3 years) annual buffelgrass treatment, (3) 2010–2011 (2 years) annual buffelgrass treatment, (4) 2008 single year (4-year-old) buffelgrass treatment, (5) 2011 single year (1-year-old) buffelgrass treatment, (6) control, buffelgrass but no treatment, and (7) control, no buffelgrass and no treatment



density was only 259 seeds/m² less than the total density of all native species germinable seeds.

Park managers first observed buffelgrass within Saguaro National Park in 1989 (Perry Grissom, personal communication). Buffelgrass subsequently expanded its distribution through establishment of new patches and enlargement and coalescence of existing patches (Olsson and others 2012a). The species has invaded many landforms and soils, even in the absence of fire (Olsson and others 2012b), and occupies interior areas of the park several km from the nearest road or trail (Woods and others 2012). By the early 2000s, buffelgrass had become noticeably more abundant in the park (with patches beginning to attain sizes of 0.1 ha to >1 ha). This spurred more extensive treatments in an attempt to follow a major principle of weed management by initiating treatments in the relatively early stages of invasion (Simberloff and others 2013).

Site Selection

Using a map of buffelgrass treatment polygons within the park provided by the National Park Service (Tucson, AZ), we randomly selected three polygons for sampling in each of the following available site types:

- (1) 2007–2011 (5 years) annual buffelgrass treatment
- (2) 2009–2011 (3 years) annual buffelgrass treatment
- (3) 2010–2011 (2 years) annual buffelgrass treatment
- (4) 2008 single year (4-year-old) buffelgrass treatment
- (5) 2011 single year (1-year-old) buffelgrass treatment
- (6) Control, buffelgrass but no treatment
- (7) Control, no buffelgrass and no treatment

We identified sites for the two types of controls (untreated buffelgrass and non-invaded sites) by randomly selecting three of 13 sites of each type established during a previous study of untreated buffelgrass patches and non-invaded sites (Abella and others 2012). Treated and untreated sites were interspersed and exhibited similar topography, 0–5 cm soil texture, and soil taxonomy (Fig. 1, Online Resource 1). Most sites do not have a history of fire since 1937 when recording of fires began in the park (Saguaro National Park, Tucson, AZ).

Treated polygons we sampled ranged in size from 0.03 to 5 ha and represented buffelgrass patches that were ca. 5–10 years old when treatments were initiated, based on records kept by Saguaro National Park (Tucson, AZ). Patches contained ≥ 100 buffelgrass individuals and exhibited areal cover of buffelgrass ranging from 18 to 88 % before treatment. The National Park Service treated buffelgrass in the treated polygons in winter and summer within a year for the number of years (1–5) listed above for each treatment type. A combination of manual and herbicide treatment was used, with the goal of killing all buffelgrass individuals

present. The manual treatment consisted of uprooting whole buffelgrass plants using hand tools including digging bars, geopicks, and picmatics. Plant material was placed on site in piles of ≤ 4 m² preferably on top of sparsely or unvegetated rocky areas. Herbicide that contains the active ingredient glyphosate effectively kills buffelgrass (e.g., Dixon and others 2002; Daehler and Goergen 2005; Tjelmeland and others 2008). Saguaro National Park used a 3 % glyphosate solution to kill buffelgrass during its period of active growth. The Razor PRO (Nufarms America Inc., Burr Ridge, IL), KleenUp (Bonide Inc., Oriskany, NY), and Roundup PRO (Monsanto Corp., St. Louis, MO) post-emergence formulations were used and included a water conditioner (e.g., [NH₄]₂SO₄) and indicator dye to mark application locations. Individual plants were sprayed from a single nozzle using a backpack sprayer with a manual pump. Decisions regarding whether to use a manual or herbicide treatment on particular plants depended on the size of the infestation (larger infestations were typically treated with herbicide, whereas both herbicide and manual treatments were done on smaller infestations), number of plants to be treated (e.g., for a few plants, often it was faster to simply manually remove them), and time of year. The manual and herbicide combination used by the managers provided a realistic, practical setting in which to evaluate post-treatment ecological conditions, because managers view manual and herbicide as complementary treatments and employ both at the current patch scale of buffelgrass invasion in the park (Woods and others 2012).

Plot Sampling

In May 2012, we established and sampled a circular (5.28 m radius), 0.01 ha plot randomly located within each of the 21 polygons. Within each plot, we categorized total areal cover of vascular plants and the areal cover of each vascular plant species (including senesced annuals) rooted in each plot using the following cover classes: 1 = trace (assigned 0.1 % cover), 2 = 0.1–1 %, 3 = 1–2 %, 4 = 2–5 %, 5 = 5–10 %, 6 = 10–25 %, 7 = 25–50 %, 8 = 50–75 %, 9 = 75–95 %, and 10 = 95–100 % (Peet and others 1998). Plants not able to be readily identified in the field were collected, pressed, and keyed to the finest taxonomic resolution possible. Nomenclature, growth form (e.g., forb, graminoid), and North American native/exotic status follow NRCS (2012). At the center of each plot, we recorded location and elevation using a global positioning system, slope gradient using a clinometer, and aspect using a compass.

We collected soil analytical, bulk density, and seed bank samples from below the three largest individuals of brittlebush (*Encelia farinosa*, a native shrub) and in the three largest interspaces (open areas usually ca. 1 m² between

perennial plants) on each plot. We chose the below-brittlebush and interspace microsites because they were present on every plot. On untreated buffelgrass plots, we also sampled below buffelgrass canopies. We sampled across these microsites because desert soil and vegetation properties can sharply vary between interspaces and below perennial plant canopies (Butterfield and others 2010). Samples were of the 0–5 cm upper mineral soil for soil analysis and bulk density and of the upper 0–5 cm soil (which could include O horizons) for the seed bank. The 0–5 cm depth was chosen based on Guo and others (1998), who found that this depth contained 97 % of viable seeds in desert soil seed banks. We collected three subsamples (each 230 cm³) equally spaced midway between the main stem and canopy drip line below brittlebush, equally spaced within a 1 m² area for interspaces, and equally spaced 10 cm from the root crown below buffelgrass on untreated buffelgrass plots. Subsamples (9 per microsite type per plot) for each of the respective microsites were composited by plot to result in one sample per microsite per plot for each analysis.

Soil Analysis

The <2 mm fraction of soil samples was analyzed by the Oklahoma State University Soil, Water, and Forage Analytical Laboratory (Stillwater, OK). Samples were analyzed for texture (hydrometer method); pH, electrical conductivity, sodium absorption ratio, exchangeable sodium percentage, and total soluble salts (all 1:1 soil:water); extractable Fe, Zn, Cu, and B (diethylene triamine pentaacetic acid [DTPA]-sorbitol extractant, inductively coupled plasma [ICP]); elemental concentrations of Na, Ca, Mg, and K (ICP); and organic C and total N (Leco C/N analyzer). We analyzed for total N because it is a relatively stable nutrient pool among seasons and was correlated with plant available N in previous research in the study area (Abella and others 2012). We measured coarse fragment content and bulk density for the bulk density samples by sieving out coarse fragments >2 mm in diameter, oven drying the fine fraction at 105 °C for 24 h, weighing both fractions, and estimating volume of coarse fragments by water displacement. Bulk density was calculated based on the full sample volume including volume of coarse fragments (Throop and others 2012). We converted nutrient concentrations to volumetric contents using bulk density, but because bulk density did not differ significantly among microsites or treatments (Online Resource 2), we report concentrations.

Seed Bank Assay

We assayed seed bank composition using the emergence method to measure readily germinable seed density (Bakker and others 1996). Within a week of sample collection,

we filled 4 L, 16-cm diameter cylindrical pots two-thirds full with potting soil (1:3:1 mulch:sand:gravel). On top of this potting soil, we placed 360 cm³ of seed bank soil (extracted from a thoroughly mixed plot sample) in a layer 2 cm thick. We randomly arranged pots on a bench in a greenhouse, without supplemental lighting, and with temperatures fluctuating between 21 (nighttime) and 32 °C (daytime). We also randomly arranged pots containing only potting soil to check for greenhouse seed contamination, which was not detected. During the 4-month period that samples resided in the greenhouse, we watered samples daily to moisture capacity, counted seedlings every 2 weeks, and removed seedlings upon identification to the finest taxonomic level possible following NRCS [Natural Resources Conservation Service] (2012). Of the 734 total seedlings that emerged, 727 (99 %) were identified to species. We retained in the final data set for analysis three seedlings only identified to the *Acacia* genus but we deleted three seedlings identified only to Poaceae and one seedling identified only to Asteraceae. As is customary in seed bank research (Bakker and others 1996), we converted seedling counts to seeds/m² corresponding to a 0–5 cm depth.

Data Analysis

We analyzed each soil variable in a two-factor, mixed model analysis of variance consisting of treatment (7 levels corresponding to the 7 site types), sampling microsite (interspace or below brittlebush) nested within treatment, and the interaction of treatment and microsite using PROC MIXED in SAS 9.2 software (SAS Institute 2009). The univariate vegetation variables were based on ordinal (cover) or count (species richness) data, so we compared medians of buffelgrass cover, the sum of species cover (based on summing cover of species, excluding buffelgrass, within a plot, which returned the same statistical conclusion as the whole plot-cover estimate), species/plot (richness, excluding buffelgrass), and Shannon's diversity index among treatments using Kruskal–Wallis tests (PROC NPAR1WAY, SAS Institute 2009). When a Kruskal–Wallis test was significant, we used Tukey's test to separate treatments. We calculated Shannon's diversity index using relative cover (cover of species/ $\sum$ cover of all species, excluding buffelgrass, on a plot) in the software PC-ORD (McCune and Mefford 1999). We used the multivariate, non-parametric technique multi-response permutation procedures (Sørensen distance, n/sum[n] default group weighting) to compare species composition (relative cover, excluding buffelgrass) among treatments using PC-ORD. A corresponding pairwise matrix of Sørensen similarities between treatments also was calculated in PC-ORD. We graphically displayed species composition (relative cover,

excluding buffelgrass) among treatments with non-metric multidimensional scaling ordination using PC-ORDs “slow and thorough” autopilot setting (McCune and Mefford 1999). As a secondary matrix to evaluate correlations with species composition, we input all soil variables (below brittlebush and in interspaces) and displayed variables with an $r^2 \geq 0.25$ as vectors with lengths proportional to their correlation with compositional patterns in the ordination.

For the seed bank data (which were count data), we compared native seeds/m² of species also found in the vegetation, total native seeds/m², and species richness (per 360 cm³ sample) in a general linear mixed model including treatment and microsite (interspace or below brittlebush) and their interaction, with microsite nested within treatment. The model assumed a Poisson distribution, consistent with the count data, and was implemented using PROC GLIMMIX in SAS 9.2 software (SAS Institute 2009). We also calculated descriptive statistics for all seed bank measures, including for buffelgrass density and density of other exotic species (which were too sparse to analyze inferentially), and buffelgrass seed density below its own canopy in untreated buffelgrass plots.

Results

Soil

None of the 22 soil variables displayed a treatment $\times$ microsite interaction (Online Resource 2, Fig. 2). Almost all of the variables displayed no significant relationship to site type. The only two exceptions were: Fe, which exhibited most consistently low values in the 2010–2011 buffelgrass treatment but had no other consistent pattern across the treatment gradient; and sand, which was slightly higher (5–10 %) in uninvaded sites compared to the five treatment types and did not differ significantly from untreated buffelgrass. However, microsite (interspace or below brittlebush) as a main effect significantly influenced 13 variables. Means of these 13 variables were greater below brittlebush compared to interspaces except for volumetric content of coarse fragments, which was slightly greater in interspace soils, indicating enrichment of fine materials and soil nutrients beneath brittlebush canopies (i.e., “fertile islands”). Soil properties below buffelgrass canopies in untreated buffelgrass plots were generally more similar to those below brittlebush than to interspaces.

Vegetation

Across all 21 plots, 120 taxa were recorded, comprised of 113 (94 %) native and 7 (6 %) exotic taxa. The 13 most frequently occurring native species were: the shrub brittlebush (present

on 21 plots); the shrub fairyduster (*Calliandra eriophylla*), annual forb *Lepidium* spp., and annual forb California cottonrose (*Logfia californica*; all on 18 plots); the perennial graminoid *Eragrostis* spp. and cactus apple (*Opuntia engelmannii*; both on 17 plots); the annual forb American wild carrot (*Daucus pusillus*) and annual grass 6 weeks fescue (*Vulpia octoflora*; both on 16 plots); and the annual-perennial grass purple threeawn (*Aristida purpurea*), annual forb miniature woollystar (*Eriastrum diffusum*), shrub sangre de cristo (*Jatropha cardiophylla*), Graham’s cactus (*Mammillaria grahamii*), and annual forb curvenut combseed (*Pectocarya recurvata*; all on 14 plots). The exotic taxa included buffelgrass (present on 14 plots); the annual grasses *Avena* spp. (1 plot), red brome (*Bromus rubens*; 3 plots), and *Schismus* spp. (11 plots); the annual forb London rocket (*Sisymbrium irio*; 5 plots); and the annual-biennial forbs Maltese star-thistle (*Centaurea melitensis*; 4 plots) and redstem stork’s bill (*Erodium cicutarium*; 1 plot). By growth form and life span, the 120 taxa consisted of 23 % shrubs; 22 % perennial forbs; 20 % annual forbs; 6 % cacti; 5 % each annual-perennial forbs, annual graminoids, and perennial graminoids; 4 % each annual-biennial forbs and trees; 3 % ferns, 2 % annual-perennial graminoids; and 1 % biennial-perennial forbs.

Buffelgrass cover was ≤ 1 % on 14 of the 15 treated plots and was only 3 % on the remaining plot (Fig. 3). In contrast, buffelgrass cover ranged from 10 to 70 % on untreated buffelgrass plots. Native plant cover, richness, and diversity were statistically indistinguishable across the treatment gradient.

Plant community composition (excluding buffelgrass) did not differ significantly across the treatment gradient (multi-response permutation procedures, A -statistic = 0.01, $P = 0.30$). Similarity of species composition of sites within treatments was low (below 39 %) and was not greater than similarity of sites among treatments (Table 1). Reinforcing this result, an ordination was weakly structured (stress value = 23), and two dimensions cumulatively represented 54 % of the variance of the original distance matrix (Fig. 4). Aside from untreated buffelgrass, which exhibited 63 % relative cover of buffelgrass, all site types were dominated (93–100 % relative cover) by native species (Fig. 5, top left graph). Combined relative cover of all six exotic species other than buffelgrass was low, averaging only 0–2.5 % across sites.

Seed Bank

Forty-one species were detected in the 45 seed bank samples across all treatment/microsite combinations and consisted of 38 (93 %) native and only 3 (7 %) exotic species (Online Resource 3). The seven most frequently occurring native species were sand pygmyweed (*Crassula connata*;

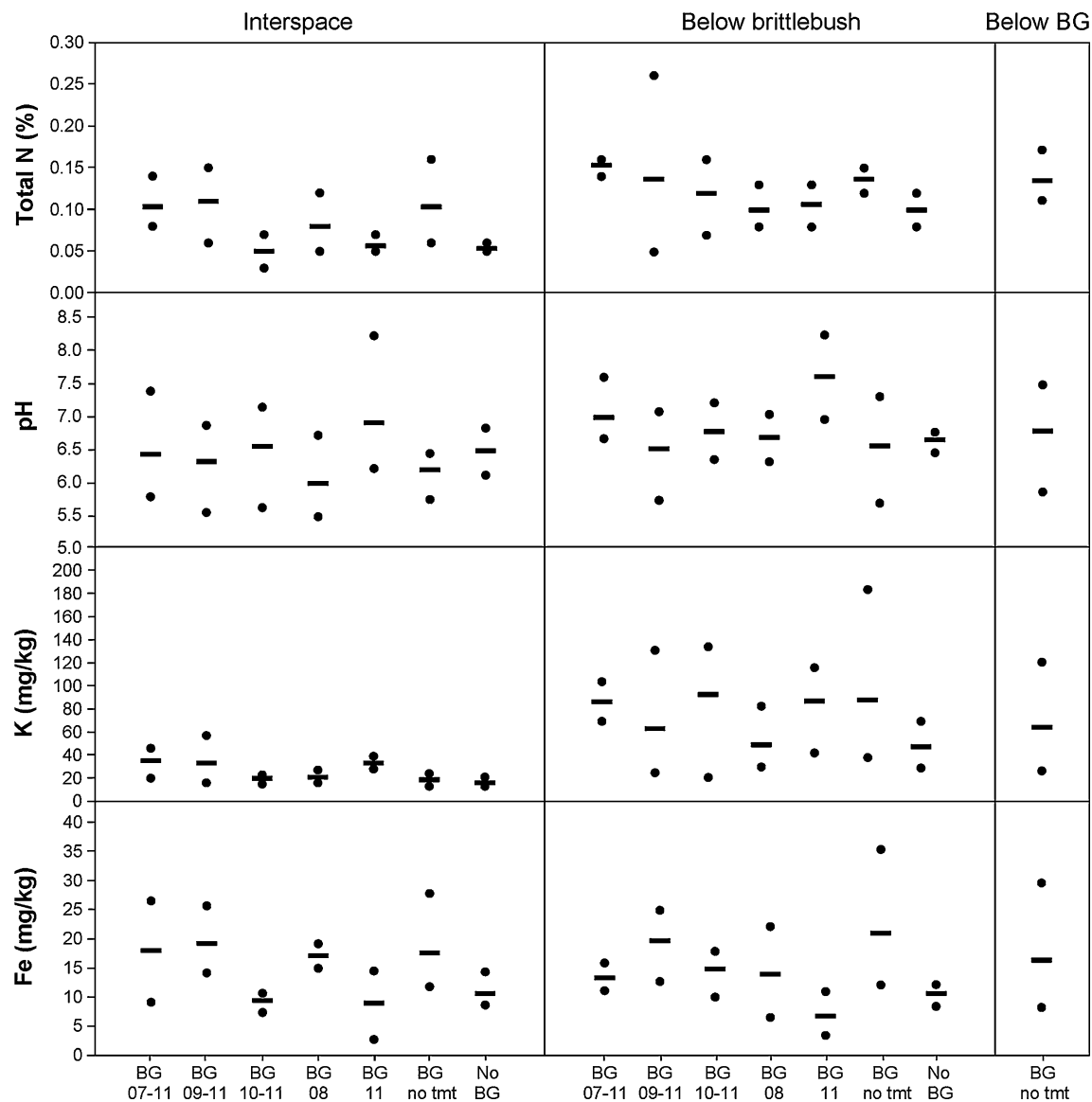


Fig. 2 Soil properties (0–5 cm mineral soil) by microsite and among treatments along a buffelgrass treatment gradient in Saguaro National Park, Sonoran Desert. The below-buffelgrass microsite existed only for untreated buffelgrass plots. Horizontal lines represent means and circles represent minimum and maximum values. For treatment abbreviations along the x axis: BG buffelgrass, with the numbers

following describing the year(s) in which BG was treated. For example, BG 07-11 indicates that BG was treated each year for 5 years between 2007 and 2011, and BG 08 indicates that BG was treated during only 1 year (in 2008). The BG no tmt indicates BG occupied sites but was not treated, and the No BG indicates non-invaded sites

19 of 45 samples), brittlebush (15 samples), California cottonrose (13 samples), needle grama (*Bouteloua aristoides*; 11 samples), Wright's cudweed (*Pseudognaphalium canescens*; 9 samples), 6 weeks fescue (9 samples), and violet snapdragon (*Sairocarpus nuttallianus*; 8 samples). By growth form and life span, the 38 native species were distributed as: 39 % annual forbs; 16 % annual-perennial forbs; 11 % annual grasses; 8 % perennial grasses; 5 % each annual-biennial forbs, annual-perennial grasses, and perennial forbs; and 3 % each biennial forbs, cacti, shrubs, and trees. Thirteen (34 %) native species in the seed bank

also occurred in vegetation of one or more plots. The three exotic species were buffelgrass (6 samples), the perennial African lovegrass (*Eragrostis echinocloidea*, 2 samples), and the annual hairy crabgrass (*Digitaria sanguinalis*, 1 sample, and not detected in vegetation of any plot).

A treatment $\times$ microsite interaction occurred for both native seed bank density of species also in vegetation ($F = 692$, $P < 0.01$) and total native seed bank density ($F = 996$, $P < 0.01$). In both cases, these interactions resulted from two site types that exhibited seed densities in interspaces similar to those below brittlebush, whereas the

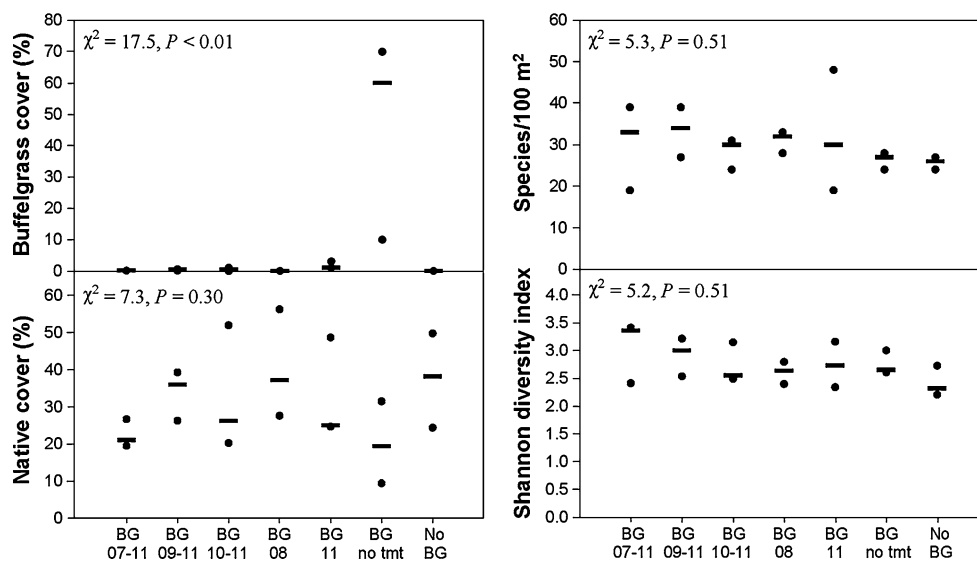


Fig. 3 Vegetation characteristics along a buffelgrass treatment gradient in Saguaro National Park, Sonoran Desert. *Horizontal lines* represent medians and *circles* represent minimum and maximum values. Results of Kruskal–Wallis tests comparing medians across treatments are provided for each response variable. For treatment abbreviations along the *x* axis: *BG* buffelgrass, with the numbers

following describing the year(s) in which BG was treated. For example, *BG 07-11* indicates that BG was treated each year for 5 years between 2007 and 2011, and *BG 08* indicates that BG was treated during only 1 year (in 2008). The *BG no tmt* indicates BG occupied sites but was not treated, and the *No BG* indicates non-invaded sites

Table 1 Sørensen similarities of plant community composition of plots within treatments (*diagonal, bold font*) and among treatments (off-diagonals) for the exotic perennial buffelgrass in Saguaro National Park, Sonoran Desert

Treatment ^a	1	2	3	4	5	6	7
1. BG 07-11	28 ± 11						
2. BG 09-11	22 ± 11	37 ± 3					
3. BG 10-11	29 ± 7	32 ± 10	21 ± 0				
4. BG 08	24 ± 9	38 ± 7	33 ± 12	37 ± 11			
5. BG 11	25 ± 8	28 ± 12	34 ± 12	34 ± 14	31 ± 20		
6. BG no tmt	21 ± 6	35 ± 12	29 ± 4	38 ± 10	29 ± 9	31 ± 11	
7. No BG	21 ± 6	34 ± 9	31 ± 10	41 ± 12	32 ± 11	39 ± 12	39 ± 12

Values are mean ± SD (%)

^a *BG* buffelgrass, with the numbers following describing the year(s) in which BG was treated. For example, *BG 07-11* indicates that BG was treated each year for 5 years between 2007 and 2011, and *BG 08* indicates that BG was treated during only 1 year (in 2008). The *BG no tmt* indicates BG occupied sites but was not treated, and the *No BG* indicates non-invaded sites

rest of sites had greater seed bank densities below brittlebush (Fig. 5, right graph, mean densities at tops of bars). Treatment was never a significant main effect ($P > 0.31$). Richness averaged 3.2 species/360 cm³ sample in interspaces among treatments and 4.5 species/360 cm³ sample below brittlebush but was not significantly affected (lowest $P = 0.08$ for microsite) by any factor.

Seed bank species composition was dominated by the natives sand pygmyweed (annual forb), jump-up (*Mecardonia procumbens*; annual-perennial forb), and Wright's cudweed (annual-perennial forb), none of which were detected in vegetation, but also by some native species that did occur in vegetation. Species detected in both the seed bank and vegetation included brittlebush, 6 weeks fescue,

California cotton rose, needle grama, purple threeawn, and American wild carrot, among others (Fig. 5, bottom-left graph). Buffelgrass was not detected in interspace soil and was sparse, but present, in samples sporadically across the seven site types below brittlebush and below its own canopy on untreated plots (Fig. 5, right graphs). The two other exotic species (African lovegrass and hairy crabgrass) were infrequent and sparse across treatments and microsites.

Discussion

A main conclusion from this study was that following buffelgrass treatment, the major difference between treated

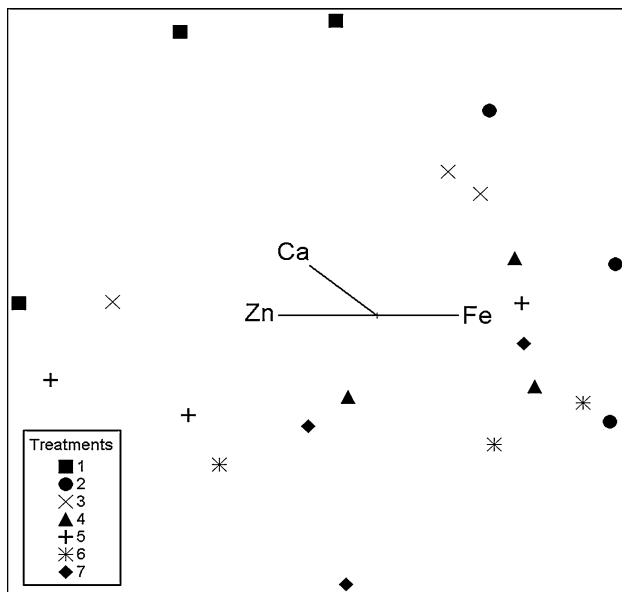


Fig. 4 Ordination of plant species composition (excluding buffelgrass) along a buffelgrass treatment gradient in Saguaro National Park, Sonoran Desert. Soil variables (all of which were below brittlebush shrubs) exhibiting $r^2 \geq 0.25$ with species composition are shown as vectors proportional to their correlation with ordination axes. Treatment numbers correspond with: (1) 2007–2011 (5 years) annual buffelgrass treatment, (2) 2009–2011 (3 years) annual buffelgrass treatment, (3) 2010–2011 (2 years) annual buffelgrass treatment, (4) 2008 single year (4-year-old) buffelgrass treatment, (5) 2011 single year (1-year-old) buffelgrass treatment, (6) control, buffelgrass but no treatment, and (7) control, no buffelgrass and no treatment

and untreated areas was that buffelgrass cover was minimal or absent in treated areas compared to untreated buffelgrass. Post-treatment soil, native vegetation, and soil seed banks were largely indistinguishable between treated areas and areas not invaded by buffelgrass. Moreover, treated sites did not simply exhibit replacement of buffelgrass by other exotic plants, as all treated plots were dominated by native species.

Some factors warrant consideration when placing our results in context with those of other studies. Several studies have noted the importance of post-treatment weather in regulating vegetation transitions following buffelgrass treatment. Based on the nearby Tucson, Arizona, Airport Weather Station, our study generally occurred during a period of below-average precipitation (Western Regional Climate Center, Reno, NV). In 2006, the year before the 2007 initiation of the first treatments we examined, precipitation was 104 % of the long-term (1930–2011) average of 29 cm/year, but precipitation was below average in 2007 (86 % of average), 2008 (76 %), 2009 (50 %), and 2010 (98 %). Precipitation in 2011 was 108 % of average, but the January–April precipitation in 2012 prior to our May 2012 sampling was only 26 % of the 7 cm average total for those months. Although in the

Sonoran Desert buffelgrass germination and seedling survival are favored by wet summers and warm winters, Olsson and others (2012a) found that climatic conditions for buffelgrass germination were met almost every year in their study of buffelgrass distribution since 1988. Moreover, buffelgrass spread rates were nearly constant (with infested area doubling on average every 6 years) and exhibited only weak or non-significant correlations with climate. While buffelgrass establishment during our study may or may not have been influenced by weather, the possibility that dry conditions during the treatment period influenced establishment of other species should not be dismissed. Another factor providing important context to our study is the potential for allelopathic effects of buffelgrass. Hussain and others (2010) summarized allelopathic influences of buffelgrass in Pakistan and elsewhere, noting that extracts from foliage and roots have reduced germination and growth of other species in laboratory experiments. In natural settings, however, it is difficult to separate effects of allelopathy and competition and to identify importance of allelopathic chemicals in natural soils (Hussain and others 2010). The possible importance of buffelgrass allelopathy is unclear for desert soils such as those of the Sonoran, and apparently allelopathy was not sufficiently active to forestall plant community measures in treated areas from being indistinguishable from those of non-invaded areas.

Previous studies of post-treatment buffelgrass community dynamics afford a range of treatment strategies and ecosystems for comparison. On a 25 ha Australian island, Dixon and others (2002) found that with the exception of native grasses, the herbicides employed (Roundup Biactive and Verdict) that killed buffelgrass had no measureable adverse effects on native vegetation. In Hawaiian grasslands, Daehler and Goergen (2005) found that burning (which was part of the evolutionary environment of the indigenous ecosystem) to temporarily reduce buffelgrass, combined with seeding native Hawaiian Pili grass (*Heteropogon contortus*), resulted in 81 % relative cover of Pili grass and low buffelgrass cover. Burning combined with hand pulling or herbicide treatment of buffelgrass also significantly reduced buffelgrass while increasing native species, and exotics other than buffelgrass were sparse when irrigation was not provided. In Texas grasslands of the southern USA, Tjelmeland and others (2008) found that effects of several herbicide treatments on buffelgrass and native vegetation were subtle within 2 years after treatment, yet buffelgrass cover did decline and cover of natives increased. In a previous Sonoran Desert study, Woods and others (2012) reported that combined herbicide and manual removal of buffelgrass nearly eradicated buffelgrass from treated sites within a few years. All sites were dominated by native shrubs such as brittlebush.

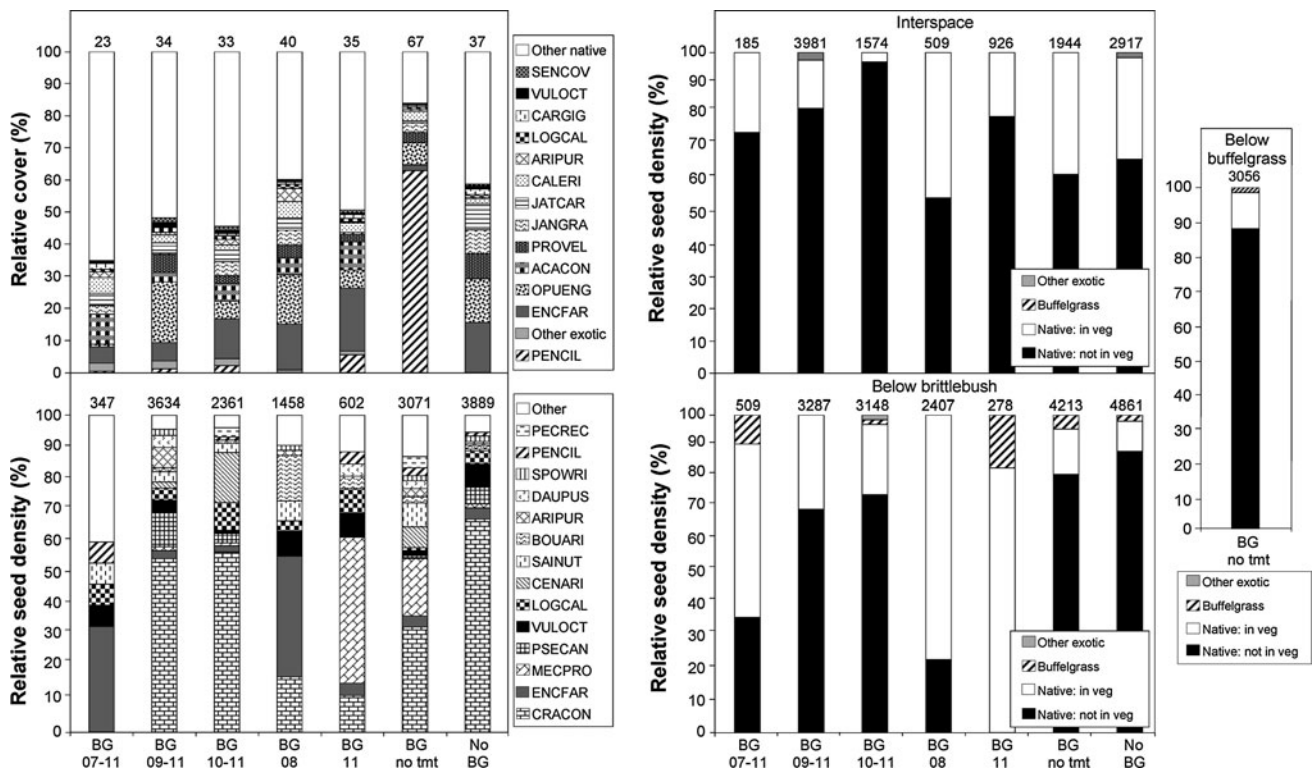


Fig. 5 Comparison of relative cover of the most dominant species in vegetation with relative seed density of the most abundant species in the 0–5 cm soil seed bank along a buffelgrass treatment gradient in Saguaro National Park, Sonoran Desert. *Top-left graph*: vegetation. *Bottom-left graph*: seed bank composition averaged across interspace and below-brittlebush microsites. *Right graphs*: seed bank composition, by microsite, with native species classified as to occurrence in vegetation. For treatment abbreviations along the x axis: BG buffelgrass, with the numbers following describing the year(s) in which BG was treated. For example, BG 07–11 indicates that BG was treated each year for 5 years between 2007 and 2011, and BG 08 indicates that BG was treated during only 1 year (in 2008). The BG no tmt indicates BG occupied sites but was not treated, and the No BG

indicates non-invaded sites. Numbers at the top of bars represent mean cover (%; top-left graph) or mean seeds/m² (other graphs). Species, from top to bottom, are abbreviated as: SENCOV *Senna covesii*, VULOCT *Vulpia octoflora*, CARGIG *Carnegiea gigantea*, LOGCAL *Logfia californica*, ARIPUR *Aristida purpurea*, CALERI *Calliandra eriophylla*, JATCAR *Jatropha cardiophylla*, JANGRA *Janusia gracilis*, PROVEL *Prosopis velutina*, ACACON *Acacia constricta*, OPUENG *Opuntia engelmannii*, ENCFAR *Encelia farinosa*, PENCIL *Pennisetum ciliare*, PECREC *Pectocarya recurvata*, SPOWRI *Sporobolus wrightii*, DAUPUS *Daucus pusillus*, BOUARI *Bouteloua aristidoides*, SAINUT *Sairocarpus nuttallianus*, CENARI *Centaurium arizonicum*, PSECAN *Pseudognaphalium canescens*, MECPRO *Mecardonia procumbens*, and CRACON *Crassula connata*

Collectively, these previous studies combined with our results suggest several potential principles regarding efficacy of buffelgrass treatments: (1) buffelgrass can be reduced or even locally eradicated by various treatments (e.g., different herbicide protocols, manual pulling, strategic burning in certain ecosystems); (2) with the exception of certain cases where native species are susceptible to the same herbicide used to kill buffelgrass, native plants are not reduced by buffelgrass treatments, and in some instances, increase without subsequent management or with management such as fire depending on the ecosystem; (3) dominance by other exotic species simply replacing buffelgrass after treatment has not been reported to date, and Daehler and Goergen (2005) found that when other exotics surged following buffelgrass removal, they rapidly dissipated when supplemental irrigation was terminated; and (4) natives appear highly susceptible to competition

from buffelgrass, but buffelgrass also appears susceptible to competition from established stands of natives in some ecosystems such as Hawaiian grasslands where native perennial grasses dominated following buffelgrass removal (Daehler and Goergen 2005). This fourth point is additionally supported by agronomic studies that sought to cultivate buffelgrass for purported pasture benefits and reported difficulty establishing buffelgrass within existing pastures of other species (e.g., McIvor 2003).

A key management question following buffelgrass removal is whether active revegetation is desirable to accelerate native community recovery and potentially provide competition to constrain buffelgrass resurgence, or whether natural transitions in native communities meet management objectives. Because native seed sources had been eliminated, Daehler and Goergen (2005) found that seeding the native Hawaiian Pili grass was key to its

establishment following buffelgrass treatment. Other studies attempting revegetation following buffelgrass removal have reported mixed success. Dixon and others (2002) outplanted three species of greenhouse-grown native shrubs without any further treatment (no supplemental water or grazing protection) and found that efficacy depended upon rainfall immediately after planting with near total failure in dry conditions. Woods and others (2012) reported that none of the 72 individuals of outplanted slender grama (*Bouteloua repens*) and brittlebush survived (no supplemental water or grazing protection was provided), and seeding six species of native grasses and shrubs resulted in minimal establishment during their dry, 2-year study period. These authors concluded that buffelgrass did not resurge following treatment and that management efforts might be best utilized by treating buffelgrass in other areas rather than attempting to manipulate natural colonization by native species on treated sites.

Our results, combined with those of Woods and others (2012), suggest that simply removing buffelgrass can result in post-treatment ecological conditions largely indistinguishable from those of non-invaded areas in the current context of relatively early buffelgrass invasion and relatively small patch sizes at these Sonoran Desert sites. Olsson and others (2012b) suggested that impacts of buffelgrass to native plant communities intensify as buffelgrass patches age, providing further incentive to treat buffelgrass patches as early in their establishment as possible. Another consideration is that plant succession following severe soil disturbance can require centuries for colonizing vegetation to resemble that of undisturbed areas in the Sonoran Desert (Abella 2010). However, soil disturbance associated with our buffelgrass treatments would not be considered severe. Moreover, native shrub cover was not reduced at the current stage of buffelgrass patch formation (Abella and others 2012). The protected, nutrient-enriched areas (“fertile islands”) below canopies of native shrubs are critical microsites for plant recruitment, and when these shrubs are removed, the pace of facilitation-based succession can be extremely slow (Butterfield and others 2010). A key finding of our study was that the pattern of fertile-island formation below native shrubs was largely indistinguishable in treated and non-invaded areas, suggesting that environmental conditions for plant recruitment were similar across site types.

While soil seed banks often display weak correlations with extant vegetation (e.g., Bakker and others 1996), our results suggest that seed banks can supply propagules to facilitate recruitment of some important species in extant vegetation (Online Resource 3). Brittlebush, for example, was dominant both in the seed bank and extant vegetation and may not appreciably benefit from active revegetation

effort in this situation (Woods and others 2012). The finding that treatment as a main effect did not significantly influence soil seed bank density also suggests that active revegetation may not be required as part of post-treatment management strategies. It further provides evidence that other exotics were sparse in both the post-treatment vegetation and seed bank.

Conclusion

Results suggest that treatments implemented by the National Park Service effectively reduced buffelgrass—and the potential for risk of buffelgrass-fueled wildfire and longer term negative impacts—while resulting in post-treatment ecological conditions largely indistinguishable from those of areas not invaded by buffelgrass. While potential for non-target and unintended consequences of exotic species removal warrants consideration when initiating exotic species removal projects (Zavaleta and others 2001), no negative consequences of removing buffelgrass manually or with spot herbicide were evident based on our analysis of native vegetation, soil, and seed banks. Results support continuation of treatments by the National Park Service to reduce exotic plants and meet park management goals of maintaining ecological communities dominated by native species.

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Online Resource 1 Characteristics of plots in 2012 used to assess post-treatment ecological condition along a buffelgrass treatment gradient in Saguaro National Park, Sonoran Desert

Treatment ^a	Plot ID ^b	UTMx ^c (m)	UTMy ^c (m)	Elevation (m)	Slope gradient (degrees)	Aspect (degrees)	Buffelgrass cover (%)	Plant taxa richness/100 m ²	Soil parent material ^d	Soil subgroup(s)
7	1	528184	3562428	929	9	245	0	26	G	Lithic Torriorthents
6	2	528208	3562400	932	15	252	60	24	G	Lithic Torriorthents
4	3	527429	3562189	929	10	203	0	28	G	Lithic Torriorthents
4	4	527723	3560986	997	10	220	0	33	G/I	Lithic UsticTorriorthents/UsticTorriorthents
3	5	526421	3558388	1008	13	180	0.5	24	G	Lithic Torriorthents
7	6	527112	3560559	962	2	233	0	27	G	Lithic Torriorthents/Lithic Haplargids
6	7	527166	3560545	961	3	184	10	27	G/I	Lithic Torriorthents/Lithic Haplargids
1	8	527150	3558613	1172	15	210	0.1	39	G/I	Lithic UsticTorriorthents/UsticTorriorthents
1	9	526920	3558040	1091	22	170	0.1	19	G/I	Lithic UsticTorriorthents/UsticTorriorthents
1	10	526412	3558704	997	27	292	0.1	33	G/I	Lithic UsticTorriorthents/UsticTorriorthents
2	11	525781	3557937	938	14	290	0.1	39	G	Lithic Torriorthents
2	12	525732	3557951	937	6	170	0.5	27	G	Lithic Torriorthents
2	13	525687	3557871	932	9	200	0.5	34	G	Lithic Torriorthents
3	14	525687	3557825	923	10	254	1	31	G	Lithic Torriorthents
5	15	525516	3557675	922	10	80	1	48	G	Lithic Torriorthents
5	16	525532	3557802	935	24	180	1	30	G	Lithic Torriorthents/Lithic Haplargids
4	17	526555	3560851	929	11	300	0	32	G/I	TypicHaplocalcids/TypicHaplargids
5	18	527135	3557849	1002	29	168	3	19	G	Lithic Torriorthents
3	19	526161	3558090	1000	10	210	0	30	G	Lithic Torriorthents
6	20	529687	3557275	1055	9	235	70	28	G	Lithic Torriorthents
7	21	529730	3557255	1048	13	185	0	24	G	Lithic Torriorthents

^a1) 2007-2011 (5 years) annual buffelgrass treatment; 2) 2009-2011 (3 years) annual buffelgrass treatment; 3) 2010-2011 (2 years) annual buffelgrass treatment; 4) 2008 single year (4-year-old) buffelgrass treatment; 5) 2011 single year (1-year-old) buffelgrass treatment; 6) Control, buffelgrassbut no treatment; 7) Control, no buffelgrassand no treatment

^bIdentification number corresponding to Fig. 1

^cUniversal Transverse Mercator coordinates, North American Datum 1983

^dG = granite, I = igneous rock (Cochran and Richardson 2003)

Online Resource 2 Properties of 0-5 cm soil in sampling microsites (interspaces between perennial plants and below brittlebush [*Encelia farinosa*] and below buffelgrass [BG, *Pennisetum ciliare*]) along a buffelgrass treatment gradient (treatments labeled 1-7) in Saguaro National Park, Sonoran Desert

	Interspace							Below brittlebush							Below BG			
	1 ^a	2	3	4	5	6	7	1	2	3	4	5	6	7	6	T × M	T ^b	M ^b
Physical																		
Sand (%)	65 (61-69)	66 (65-68)	70 (68-74)	68 (66-73)	71 (69-73)	72 (69-74)	75 (69-84)	63 (61-66)	66 (64-69)	68 (66-71)	69 (68-71)	67(64-71)	70 (66-74)	73 (73-74)	69 (66-74)	0.4	4.3*	2.9
Silt (%)	23 (19-25)	23 (21-25)	21 (19-24)	19 (19-20)	20 (19-20)	19 (16-20)	18 (12-23)	24 (23-26)	23 (21-25)	22 (18-25)	20 (18-21)	23(21-25)	20 (19-23)	20 (19-20)	21 (19-23)	0.3	2.8	3.2
Clay (%)	13 (13-14)	10 (9-14)	9 (6-13)	13 (9-15)	9 (8-11)	9 (6-11)	7 (4-9)	13 (11-14)	11 (9-15)	10 (9-11)	11 (9-14)	11(8-14)	10 (8-11)	8 (6-9)	10 (8-11)	1.3	1.7	1.4
CF (% wt.)	41 (37-46)	36 (35-36)	43 (25-56)	41 (35-50)	46 (42-54)	39 (35-42)	38 (30-43)	47 (39-55)	34 (30-36)	36 (32-40)	33 (26-44)	45(38-50)	34 (29-40)	33 (23-38)	34 (27-40)	1	1.4	3.3
CF (% vol.)	26 (23-29)	20 (18-23)	29 (16-38)	25 (21-32)	29 (22-38)	24 (22-29)	23 (20-26)	29 (20-36)	20 (18-21)	23 (20-26)	20 (14-28)	26(24-27)	18 (15-19)	17 (15-20)	19 (16-23)	1	1.5	7.7*
BD (g/cm³)	0.9 (0.8-1.0)	0.9 (0.8-0.9)	0.9 (0.7-1.2)	0.9 (0.8-1.0)	0.8 (0.8-0.9)	0.9 (0.9-1.0)	1.0 (0.8-1.2)	0.8 (0.7-0.8)	0.9 (0.8-1.1)	0.9 (0.9-1.0)	0.9 (0.9-1.1)	0.8 (0.7-0.9)	0.9 (0.8-1.0)	1.0 (0.8-1.2)	0.9 (0.7-1.0)	0.6	0.9	0.5
Chemistry																		
pH	6.4 (5.8-7.4)	6.3 (5.5-6.9)	6.5 (5.6-7.1)	6 (5.5-6.7)	6.9 (6.2-8.2)	6.2 (5.7-6.4)	6.5 (6.1-6.8)	7.0 (6.7-7.6)	6.5 (5.7-7.1)	6.8 (6.4-7.2)	6.7 (6.3-7.1)	7.6(7-8.3)	6.6 (5.7-7.3)	6.7 (6.5-6.8)	6.8 (5.9-7.5)	0.3	1	8.3*
EC (umhos/cm)	770 (461-1227)	786 (347-1623)	510 (338-702)	699 (383-1320)	464 (382-588)	423 (241-738)	272 (214-335)	1238 (1005-1557)	1094 (374-2202)	1135 (963-1332)	652 (612-726)	1023(572-1305)	887 (528-1428)	612 (435-888)	782 (531-1176)	0.7	0.8	15.7**
SAR	0.5 (0.2-1)	0.5 (0.3-0.7)	2.1 (0.3-5.2)	0.5 (0.3-0.8)	0.4 (0.2-0.5)	1.5 (0.3-3.8)	0.5 (0.4-0.6)	0.3 (0.2-0.3)	0.4 (0.4-0.4)	0.3 (0.2-0.5)	0.3 (0.1-0.5)	0.4(0.1-1)	0.4 (0.3-0.7)	0.3 (0.3-0.4)	0.4 (0.4-0.5)	0.8	0.8	3.2
EPP	10 (9-12)	9 (8-11)	9 (7-10)	8 (7-8)	12 (10-14)	9 (7-11)	9 (7-12)	15 (14-18)	15 (10-23)	16 (7-21)	13 (9-20)	16(13-19)	16 (12-25)	13 (11-15)	14 (8-20)	0.1	0.4	20.7**
PAR	0.7 (0.6-0.9)	0.7 (0.5-0.8)	0.6 (0.4-0.7)	0.5 (0.4-0.5)	0.9 (0.7-1.2)	0.6 (0.4-0.8)	0.6 (0.4-1)	1.4 (1.2-1.7)	1.4 (0.7-2.6)	1.5 (0.4-2.1)	1.1 (0.6-2)	1.5(1.1-1.9)	1.6 (0.9-2.9)	1.1 (0.9-1.3)	1.2 (0.5-2)	0.1	0.3	18.5**
TSS	508 (304-810)	519 (229-1071)	337 (223-463)	461 (253-871)	306 (252-388)	279 (159-487)	180 (141-221)	817 (663-1028)	722 (247-1453)	749 (636-879)	430 (404-479)	675(377-861)	585 (348-942)	404 (287-586)	516 (350-776)	0.7	0.8	15.7**
Macronutrients																		
Organic C (%)	1.1 (0.9-1.6)	1.2 (0.7-1.6)	0.6 (0.4-0.6)	0.9 (0.5-1.4)	0.8 (0.7-1.2)	1.1 (0.7-1.6)	0.6 (0.5-0.7)	1.7 (1.6-1.8)	1.6 (0.6-2.9)	1.5 (0.9-1.9)	1.1 (0.9-1.4)	1.6(1.1-2.4)	1.6 (1.4-1.9)	1.1 (0.8-1.4)	1.5 (1.2-1.7)	0.5	0.8	19.2**
Total N (%)	0.10 (0.08-0.14)	0.11 (0.06-0.15)	0.05 (0.03-0.07)	0.08 (0.05-0.12)	0.06 (0.05-0.07)	0.1 (0.06-0.16)	0.05 (0.05-0.06)	0.15 (0.14-0.16)	0.14 (0.05-0.26)	0.12 (0.07-0.16)	0.1 (0.08-0.13)	0.11(0.08-0.13)	0.14 (0.12-0.15)	0.1 (0.08-0.12)	0.13 (0.11-0.17)	0.3	1.5	12.8**
K (mg/kg)	35 (20-46)	33 (16-57)	20 (15-23)	21 (16-27)	33 (28-39)	19 (13-24)	16 (13-21)	88 (71-105)	65 (27-132)	94 (23-135)	51 (32-84)	88(44-117)	89 (40-184)	49 (31-71)	63 (26-119)	0.5	0.5	25.5**
Ca (mg/kg)	58 (24-112)	67 (21-159)	22 (19-27)	47 (26-87)	31 (20-51)	17 (12-23)	16 (9-23)	88 (74-114)	32 (20-56)	77 (72-83)	44 (32-51)	72(32-98)	52 (40-73)	40 (24-63)	48 (36-65)	1.5	1.3	4.9*
Mg (mg/kg)	9 (5-15)	11 (4-23)	5 (4-6)	9 (5-16)	4 (3-4)	4 (2-7)	3 (2-4)	14 (11-18)	15 (5-30)	16 (12-19)	9 (8-10)	12 (6-19)	13 (7-20)	8 (6-12)	12 (7-16)	1.2	0.7	23.8**
Micronutrients																		
B (mg/kg)	0.38 (0.17-0.73)	0.28 (0.06-0.5)	0.18 (0.07-0.25)	0.25 (0.11-0.51)	0.33 (0.12-0.72)	0.17 (0.13-0.21)	0.15 (0.12-0.18)	0.73 (0.64-0.85)	0.49 (0.19-1.01)	0.59 (0.25-0.97)	0.49(0.28-0.69)	0.86 (0.43-1.61)	0.44 (0.32-0.58)	0.48 (0.26-0.71)	0.37 (0.2-0.48)	0.6	0.6	41.4**
Cu (mg/kg)	3.2 (3.1-3.2)	3.1 (2.3-3.8)	2 (1.9-2.1)	5.4 (2-10.4)	2.4 (1.6-3.1)	3.9 (2.7-5.9)	2.5 (1.9-3)	3.1 (2.4-4.1)	2.7 (2.4-2.9)	2.6 (2.1-2.9)	4.1(2.7-6.3)	2.3 (1.8-2.7)	4.4 (2-7.2)	2.3 (2-2.6)	3.3 (1.9-4.3)	0.9	1.3	0.4
Fe (mg/kg)	18 (9-26)	19 (14-26)	9 (7-11)	17 (15-19)	9 (3-14)	18 (12-28)	11 (9-14)	13 (11-16)	20 (13-25)	15 (10-18)	14(7-22)	7 (3-11)	21 (12-35)	11 (8-12)	16 (8-29)	0.5	3.0*	0
Na (mg/kg)	13 (8-21)	13 (10-15)	38 (6-94)	17 (8-31)	8 (7-9)	31 (6-81)	8 (7-9)	11 (9-12)	11 (7-14)	12 (9-17)	8(4-15)	12 (5-24)	13 (9-19)	9 (6-10)	13 (9-15)	0.6	0.7	1.8
Zn (mg/kg)	2.7 (1.5-4.1)	1.9 (0.9-3.1)	1 (0.8-1.2)	1.6 (1.5-1.7)	1.3 (0.8-1.6)	1.9 (1.6-2.4)	1.7 (1.3-2.4)	3.9 (2.3-6.5)	1.7 (1.3-2.1)	2.2 (1.3-2.9)	2.3(2.1-2.6)	1.8 (0.9-2.3)	2.5 (2.2-2.8)	2.4 (1.8-2.8)	2 (1.6-2.6)	1	1.8	15.5**

^a Treatment numbers correspond with: 1) 2007-2011 (5 years) annual buffelgrass treatment, 2) 2009-2011 (3 years) annual buffelgrass treatment, 3) 2010-2011 (2 years) annual buffelgrass treatment, 4) 2008 single year (4-year-old) buffelgrass treatment, 5) 2011 single year (1-year-old) buffelgrass treatment, 6) control, buffelgrass but no treatment, and 7) control, no buffelgrass and no treatment

^b Treatment (T), Microsite (M), * $P < 0.05$, ** $P < 0.01$

Online Resource 3 Average seeds/m² (0-5 cm depth) in soil seed banks by treatment and microsite along a buffelgrass (BG) treatment gradient in Saguaro National Park, Sonoran Desert

[illegible]

<i>Logfia californica</i> (aF)	0	93	0	0	0	46	231	46	185	417	93	93	46	93	0
<i>Mecardonia procumbens</i> (a-pF)	0	93	0	0	556	278	93	0	0	46	0	0	509	0	880
<i>Mimulus floribundus</i> (aF)	0	0	46	0	0	0	0	0	0	0	0	0	0	0	0
<i>Mimulus guttatus</i> (a-pF)	0	0	0	0	0	46	93	0	0	0	0	0	0	0	0
<i>Mimetanthe pilosa</i> (aF)	0	0	0	0	0	0	0	0	0	0	0	0	93	0	0
<i>Mollugo verticillata</i> (aF)	46	0	0	0	0	0	0	0	0	0	0	0	0	0	46
<i>Nicotiana obtusifolia</i> (a-pF)	0	0	0	0	0	0	0	0	0	0	46	0	0	0	0
<i>Opuntia engelmannii</i> (C)	0	0	0	0	0	46	0	0	0	0	0	0	0	0	46
<i>Pectocarya recurvata</i> (aF)	0	0	0	0	0	185	0	0	0	139	0	0	93	0	46
<i>Pennisetum ciliare</i> (pG)*	0	0	0	0	0	0	0	46	0	46	0	46	185	93	46
<i>Pseudognaphalium canescens</i> (a-pF)	0	324	139	0	0	0	93	0	463	0	0	0	93	324	0
<i>Pterostegia drymarioides</i> (aF)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	93
<i>Sairocarpus nuttallianus</i> (a-bF)	0	0	0	0	0	0	46	46	231	139	185	0	370	0	324
<i>Senecio parryi</i> (pF)	0	0	0	0	0	0	0	46	0	0	0	0	0	46	0
<i>Sporobolus wrightii</i> (pG)	0	93	0	0	0	0	46	0	46	0	46	0	46	93	93
<i>Vulpia octoflora</i> (aG)	46	231	46	0	0	139	556	0	46	0	231	93	0	0	0

^a Species in bold also occurred in vegetation of one or more plots. Asterisks signify exotic. Life spans and growth forms are provided in parentheses: a = annual, b = biennial, p = perennial; C = cactus, F = forb, G = graminoid, S = shrub, and T = tree. For *Eragrostis echinochloidea*, the species may also have occurred in vegetation, but vegetation was only able to be identified to *Eragrostis* spp.

^b Treatment numbers correspond with: 1) 2007-2011 (5 years) annual buffelgrass treatment, 2) 2009-2011 (3 years) annual buffelgrass treatment, 3) 2010-2011 (2 years) annual buffelgrass treatment, 4) 2008 single year (4-year-old) buffelgrass treatment, 5) 2011 single year (1-year-old) buffelgrass treatment, 6) control, buffelgrass but no treatment, and 7) control, no buffelgrass and no treatment

APPENDIX F

Supplemental information for PART VI.

Table F1. Average emergence seeds m⁻² (0-5 cm depth) in soil seed banks by treatment and microsite along a buffelgrass (BG) treatment gradient in Saguaro National Park, Sonoran Desert.

Emergence	Interspace							Below brittlebush							BG
Species ^a	1 ^b	2	3	4	5	6	7	1	2	3	4	5	6	7	6
Acacia spp. (T)	0	0	0	93	0	0	0	0	0	0	46	0	0	0	0
Agrostis elliotiana (aG)	0	46	0	0	0	0	0	0	0	0	0	0	0	0	0
Agrostis scabra (pG)	0	0	0	0	0	231	0	0	0	0	0	0	0	0	0
Amsinckia tessellata (aF)	0	0	0	0	0	0	0	0	0	0	0	0	46	0	0
Aristida purpurea (a-pG)	0	93	0	46	0	0	46	0	370	0	0	0	139	0	93
<i>Astragalus nuttallianus</i> (a-pF)	0	0	0	0	0	0	0	0	0	0	46	0	0	0	0
Bouteloua aristidoides (aG)	0	0	0	93	46	0	0	0	93	46	324	0	139	93	46
<i>Camissonia chamaenerioides</i> (aF)	0	0	0	0	0	0	0	0	0	0	0	0	46	0	0
<i>Carex athrostachya</i> (pG)	0	0	0	0	46	0	0	0	0	0	0	0	0	0	0
<i>Centaurium arizonicum</i> (a-bF)	0	139	648	0	0	0	0	0	0	93	0	0	370	0	231
<i>Chenopodium incanum</i> (aF)	0	0	0	0	0	46	0	0	46	0	0	0	46	46	0
<i>Crassula connata</i> (aF)	0	2546	648	231	139	463	1528	0	1435	2037	278	0	1759	3704	833
<i>Cryptantha decipiens</i> (aF)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	46
Cryptantha nevadensis (aF)	0	0	0	0	0	46	0	0	0	0	0	0	0	0	0
Daucus pusillus (aF)	0	185	0	0	46	139	46	0	93	0	0	0	0	0	93
<i>Digitaria sanguinalis</i> (aG)*	0	93	0	0	0	0	0	0	0	0	0	0	0	0	0
Encelia farinosa (S)	0	0	0	0	0	139	46	231	185	93	1111	46	185	231	0
Eragrostis echinochloidea (pG)*	0	0	0	0	0	0	46	0	0	46	0	0	0	0	0
Eriastrum diffusum (aF)	0	0	0	0	93	0	0	0	0	0	0	0	0	0	0
<i>Erigeron divergens</i> (bF)	0	0	0	0	0	0	46	46	46	0	0	0	0	0	0
Janusia gracilis (pF)	0	0	0	0	0	0	0	0	0	0	0	0	0	46	0
<i>Juncus bufonius</i> (aG)	0	46	0	0	0	139	0	0	0	0	0	0	46	46	139
Lepidium virginicum (a-pF)	46	0	0	46	0	0	0	46	46	46	0	0	0	46	0
<i>Leptochloa panicea</i> (a-pG)	0	0	46	0	0	0	0	0	0	0	0	0	0	0	0
<i>Logfia arizonica</i> (aF)	46	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Logfia californica (aF)	0	93	0	0	0	46	231	46	185	417	93	93	46	93	0
<i>Mecardonia procumbens</i> (a-pF)	0	93	0	0	556	278	93	0	0	46	0	0	509	0	880
<i>Mimetanthe pilosa</i> (aF)	0	0	0	0	0	0	0	0	0	0	0	0	93	0	0
<i>Mimulus floribundus</i> (aF)	0	0	46	0	0	0	0	0	0	0	0	0	0	0	0
<i>Mimulus guttatus</i> (a-pF)	0	0	0	0	0	46	93	0	0	0	0	0	0	0	0

<i>Mollugo verticillata</i> (aF)	46	0	0	0	0	0	0	0	0	0	0	0	0	0	46
<i>Nicotiana obtusifolia</i> (a-pF)	0	0	0	0	0	0	0	0	0	0	46	0	0	0	0
<i>Opuntia engelmannii</i> ©	0	0	0	0	0	46	0	0	0	0	0	0	0	0	46
<i>Pectocarya recurvata</i> (aF)	0	0	0	0	0	185	0	0	0	139	0	0	93	0	46
<i>Pennisetum ciliare</i> (pG)*	0	0	0	0	0	0	0	46	0	46	0	46	185	93	46
<i>Pseudognaphalium canescens</i> (a-pF)	0	324	139	0	0	0	93	0	463	0	0	0	93	324	0
<i>Pterostegia drymarioides</i> (aF)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	93
<i>Sairocarpus nuttallianus</i> (a-bF)	0	0	0	0	0	0	46	46	231	139	185	0	370	0	324
<i>Senecio parryi</i> (pF)	0	0	0	0	0	0	0	46	0	0	0	0	0	46	0
<i>Sporobolus wrightii</i> (pG)	0	93	0	0	0	0	46	0	46	0	46	0	46	93	93
<i>Vulpia octoflora</i> (aG)	46	231	46	0	0	139	556	0	46	0	231	93	0	0	0

^a Species in bold also occurred in vegetation of one or more plots. Asterisks signify exotic. Life spans and growth forms are provided in parentheses: a = annual, b = biennial, p = perennial; C = cactus, F = forb, G = graminoid, S = shrub, and T = tree. For *Eragrostis echinochloidea*, the species may also have occurred in vegetation, but vegetation was only able to be identified to *Eragrostis* spp.

^b Treatment numbers correspond with: 1) 2007-2011 (5 years) annual buffelgrass treatment, 2) 2009-2011 (3 years) annual buffelgrass treatment, 3) 2010-2011 (2 years) annual buffelgrass treatment, 4) 2008 single year (4-year-old) buffelgrass treatment, 5) 2011 single year (1-year-old) buffelgrass treatment, 6) control, buffelgrass but no treatment, and 7) control, no buffelgrass and no treatment.

Table F2. Average extraction seeds m⁻² (0-5 cm depth) in soil seed banks by treatment and microsite along a buffelgrass (BG) treatment gradient in Saguaro National Park, Sonoran Desert.

Extraction	Interspace							Below brittlebush							BG
Species ^a	1 ^b	2	3	4	5	6	7	1	2	3	4	5	6	7	6
<i>Agrostis</i> sp (pG)	139	86389	0	1458	0	347	0	833	3056	764	1528	0	1250	0	0
<i>Allionia incarnata</i> (pF)	139	0	0	0	0	0	0	694	0	0	0	0	0	0	0
<i>Allium geyeri</i> (pF)	0	278	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Amaranthus fimbriatus</i> (aF)	139	278	0	139	0	0	0	0	0	0	0	0	0	0	0
<i>Amsinckia menziesii</i> (aF)	0	15347	1250	278	764	0	0	8472	833	4306	417	139	0	0	0
<i>Amsinckia tessellata</i> (aF)	2083	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Aristida purpurea</i> (a-pG)	0	625	0	347	0	764	139	0	1111	139	5278	139	8681	556	7778
<i>Astragalus</i> sp (a-pF)	2083	625	0	347	0	764	139	0	1111	139	5278	139	8681	556	7778
<i>Boerhavia</i> sp (aF)	0	51667	6944	11042	0	764	3056	2639	7500	278	4861	139	417	1389	5139
<i>Bothriochloa barbinodis</i> (pG)	0	278	0	0	0	139	0	417	0	139	417	0	5833	0	0
<i>Bouteloua aristidoides</i> (aG)	972	27917	347	1296	0	5787	20069	278	5347	139	7593	1042	694	27778	278
<i>Bouteloua barbata</i> (aG)	5000	0	0	0	0	0	0	556	139	0	139	0	139	0	0
<i>Bouteloua curtipedula</i> (pG)	0	972	556	602	0	6736	2222	139	3333	5417	0	0	11806	4722	2153
Cactaceae spp (S)	903	2130	648	4653	0	278	5231	1458	972	1435	278	764	2361	880	4120
<i>Calliandra eriophylla</i> (S)	0	0	0	0	0	0	0	1250	0	0	0	0	0	0	0
<i>Camissonia chamaenerioides</i> (aF)	0	0	0	0	0	0	0	1667	0	0	0	0	0	0	0
<i>Chaenactis</i> sp (aF)	0	0	0	139	0	0	0	0	0	139	1111	0	0	0	0
<i>Chamaesyce polycarpa</i> (aF)	5000	40093	5833	509	2917	1597	2292	40139	3958	3056	324	903	4722	6597	2778
<i>Chamaesyce</i> sp (aF)	278	278	26944	625	0	0	417	972	139	833	3148	347	139	0	1319
<i>Chenopodium incanum</i> (aF)	0	7361	0	833	0	278	0	1944	0	139	0	0	0	278	0
<i>Crassula connata</i> (aF)	0	0	278	0	2639	0	0	0	694	139	0	0	0	0	139
<i>Cryptantha decipiens</i> (aF)	0	0	139	0	0	0	0	0	0	0	0	0	139	0	0
<i>Cryptantha nevadensis</i> (aF)	4213	23704	3102	2153	4861	3704	4444	21042	9306	799	3056	1528	13993	5972	10046
<i>Cryptantha pterocarya</i> (aF)	2083	139	139	278	417	0	0	1343	0	0	417	0	139	0	0
<i>Dalea</i> spp (pF)	0	556	0	0	0	0	0	0	0	0	7917	278	139	0	0
<i>Daucus pusillus</i> (aF)	2778	5046	10741	1667	4861	3889	278	6806	1343	8264	3796	8056	11019	694	13287
<i>Digitaria californica</i> (pG)	208	417	0	0	139	833	833	0	417	278	0	0	3889	5694	764

<i>Elatine brachysperma</i> (aF)	0	0	0	139	0	0	0	0	0	0	0	0	0	0	0
<i>Encelia farinosa</i> (S)	6111	1991	7222	2407	9491	5231	13287	45000	27963	37269	32176	18426	53565	37731	4583
<i>Eragrostis curvula</i> (pG)*	0	0	0	139	0	0	0	0	0	0	694	0	0	0	0
<i>Eragrostis echinochloidea</i> (pG)*	0	0	26736	1667	16389	0	278	0	972	0	1389	139	0	0	0
<i>Eriastrum diffusum</i> (aF)	0	0	556	0	0	5069	8194	0	0	0	139	0	3611	13333	1806
<i>Erigeron divergens</i> (bF)	0	0	0	139	0	0	0	0	0	0	0	0	0	0	0
<i>Erodium cicutarium</i> (aF)*	0	1111	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Janusia gracilis</i> (pF)	139	139	208	556	347	0	417	417	139	347	1111	278	417	347	1319
<i>Lappula occidentalis</i> var. <i>occidentalis</i> (aF)	0	0	0	139	0	0	0	0	139	0	0	278	0	0	0
<i>Larrea tridentata</i> (S)	0	0	0	0	139	0	0	0	0	0	1111	1389	0	0	0
<i>Lepidium</i> spp (aF)	0	0	0	0	0	0	0	0	0	0	0	0	139	0	0
<i>Lepidium virginicum</i> (a-pF)	2292	0	521	833	833	1111	1667	903	903	231	1181	3611	1111	625	2130
<i>Lycium</i> sp (S)	0	0	0	0	556	0	0	0	0	0	3611	0	0	0	0
<i>Malvaceae</i> spp (a-pF)	0	972	0	278	0	0	0	0	139	0	0	0	1250	139	0
<i>Mammillaria</i> spp (C)	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Mollugo verticillata</i> (aF)	278	22500	1250	1944	139	1667	35509	0	208	417	2222	139	2569	#####	2639
<i>Oenothera</i> sp (pF)	0	139	0	0	0	0	0	556	0	0	0	0	0	0	0
<i>Panicum hirticaule</i> (aG)	417	5556	0	0	417	417	0	0	2083	0	1389	972	139	833	0
<i>Parkinsonia florida</i> (S)	139	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Pectocarya heterocarpa</i> (aF)	0	0	0	0	2500	0	0	0	0	0	0	0	0	0	0
<i>Pectocarya platycarpa</i> (aF)	0	7639	417	0	1111	139	0	0	0	0	417	0	0	0	0
<i>Pectocarya recurvata</i> (aF)	24306	19954	4583	4352	3819	1435	9028	2153	6065	463	5833	1736	2037	1481	3148
<i>Pennisetum ciliare</i> (pG)*	417	1944	417	139	625	9815	278	3565	1319	1111	2361	7917	37315	694	38472
<i>Polygonaceae</i> sp (aF)	0	0	139	139	0	0	0	0	0	833	556	0	278	0	2917
<i>Pseudognaphaliumstramineum</i> (a-bF)	0	0	21250	139	0	3056	1042	0	2083	0	1111	0	0	8333	556
<i>Psilostrophe cooperi</i> (pF)	0	0	0	0	0	139	0	0	0	0	0	139	1181	1667	0
<i>Pterostegia drymarioides</i> (aF)	0	0	0	0	139	0	0	2361	0	0	0	0	0	0	0
<i>Sairocarpus nuttallianus</i> (a-bF)	0	0	0	0	0	0	0	0	0	0	0	0	139	0	0
<i>Schismus</i> sp (aG)*	0	0	0	0	0	0	0	0	139	0	0	0	0	0	0
<i>Senna covesii</i> (pF)	0	0	0	139	0	0	0	0	0	0	0	0	0	0	0
<i>Silene antirrhina</i> (aF)	2222	6250	6042	4236	26065	7778	417	3657	2963	4514	6852	27824	20486	972	4444
<i>Silene scouleri</i> (aF)	0	0	139	0	0	833	694	694	0	833	0	0	278	694	417
<i>Spermolepis echinata</i> (aF)	0	7870	1343	463	5278	370	2778	0	139	556	3542	486	1042	3889	1667

<i>Thymophylla pentachaeta</i> (aF)	0	0	0	139	0	0	139	0	139	139	0	0	0	0	0
<i>Thysanocarpus curvipes</i> (aF)	556	1944	417	1111	0	139	0	3472	417	833	556	0	1667	0	139
<i>Trixis californica</i> (pF)	0	0	0	0	0	0	278	0	0	0	0	0	0	417	0
<i>Vulpia octoflora</i> (aG)	972	3194	278	1806	0	0	1435	0	1667	0	6250	509	0	2431	4167
<i>Zinnia acerosa</i> (pF)	0	0	0	3472	1944	0	0	0	0	0	7639	278	0	0	0

^a Species in bold also occurred in vegetation of one or more plots. Asterisks signify exotic. Life spans and growth forms are provided in parentheses: a = annual, b = biennial, p = perennial; C = cactus, F = forb, G = graminoid, S = shrub, and T = tree. For *Eragrostis echinocloidea*, the species may also have occurred in vegetation, but vegetation was only able to be identified to *Eragrostis* spp.

^b Treatment numbers correspond with: 1) 2007-2011 (5 years) annual buffelgrass treatment, 2) 2009-2011 (3 years) annual buffelgrass treatment, 3) 2010-2011 (2 years) annual buffelgrass treatment, 4) 2008 single year (4-year-old) buffelgrass treatment, 5) 2011 single year (1-year-old) buffelgrass treatment, 6) control, buffelgrass but no treatment, and 7) control, no buffelgrass and no treatment.

Table F3. Significant differences of total native, buffelgrass and other exotic seed density and species richness between buffelgrass treatments along a treatment gradient for two seed bank methods and two microsites.

Comparing Buffelgrass treatment effects								
Method	Microsite	Vegetation Group	Seed Density			Species Richness		
			<i>df</i>	<i>F</i>	<i>P</i>	<i>df</i>	<i>F</i>	<i>P</i>
Emergence	Brittlebush	Natives	6,14	1.26	0.337	6,14	1.9	0.148
		Other Exotics	6,14	1	0.463	6,14	0.7	0.678
		Buffelgrass	6,14	0.37	0.884	-		
	Interspace	Natives	6,14	0.97	0.478	6,14	0.8	0.567
		Other Exotics	6,14	1	0.463	(No other exotics)		
		Buffelgrass				-		
Extraction	Brittlebush	Natives	6,14	0.21	0.968	6,14	0.9	0.498
		Other Exotics	6,14	8.46	0.001	6,14	5.2	0.005
		Buffelgrass	6,14	1.62	0.215	-		
	Interspace	Natives	6,14	0.28	0.935	6,14	0.6	0.739
		Other Exotics	6,14	0.75	0.617	6,14	0.9	0.501
		Buffelgrass	6,14	10.46	0.000	-		

Table F4. Pearson's correlation co-efficient (r) relationships between vegetation group (duration $\times$ growth habit) seed density and species richness with time since initial buffelgrass treatment and years of buffelgrass treatment.

Time since Treatment											
Seed Density											
Method	Microsite	Annual			Perennial				Total	Other	
		Forb	Grass	Total	Forb	Grass	Shrub	Total	Natives		Exotics
Emergence	Interspace	-0.17	-0.34	-0.19	-	-0.44	-0.44	-0.49	-0.24		0.20
	Brittlebush	-0.50	0.27	-0.47	0.79	-0.06	0.51	0.50	-0.35		-0.79
Extraction	Interspace	0.13	0.09	0.13	0.36	0.15	-0.11	0.14	0.14		-0.59
	Brittlebush	-0.06	0.56	0.19	0.41	-0.60	-0.28	-0.37	-0.15		-0.71
Species Richness											
Method	Microsite	Annual			Perennial				Total	Buffelgrass	Other
		Forb	Grass	Total	Forb	Grass	Shrub	Total	Natives	Presence	Exotics
Emergence	Interspace	-0.43	-0.35	-0.43	-	0.05	-0.44	-0.27	-0.41	-	0.20
	Brittlebush	-0.26	0.19	-0.17	0.79	-0.21	0.27	0.34	-0.08	-0.55	-0.43
Extraction	Interspace	0.05	0.40	0.19	0.59	0.04	0.77	0.46	0.34	-0.54	-0.29
	Brittlebush	0.38	0.38	0.42	-0.58	-0.26	0.54	-0.34	0.25	-0.16	0.57
Years of treatment											
Seed Density											
Method	Microsite	Annual			Perennial				Total	Other	
		Forb	Grass	Total	Forb	Grass	Shrub	Total	Natives		Exotics
Emergence	Interspace	-0.01	-0.25	-0.03	-	-0.37	-0.67	-0.55	-0.10		0.27
	Brittlebush	-0.34	-0.49	-0.40	0.43	0.00	-0.24	-0.19	-0.44		-0.45
Extraction	Interspace	0.30	0.20	0.29	-0.32	0.22	0.17	0.22	0.27		-0.39
	Brittlebush	0.11	-0.18	0.03	-0.34	-0.60	-0.03	-0.29	-0.19		-0.56
Species Richness											
Method	Microsite	Annual			Perennial				Total	Buffelgrass	Other
		Forb	Grass	Total	Forb	Grass	Shrub	Total	Natives	Presence	Exotics
Emergence	Interspace	-0.32	-0.14	-0.30	-	-0.15	-0.67	-0.55	-0.38	-	0.27
	Brittlebush	-0.22	-0.46	-0.31	0.43	-0.34	0.25	0.08	-0.26	0.00	0.00
Extraction	Interspace	-0.51	0.46	-0.33	0.29	-0.28	0.80	0.12	-0.16	0.00	-0.67
	Brittlebush	-0.27	-0.17	-0.27	-0.53	-0.26	0.00	-0.47	-0.38	0.22	-0.18

Table F5. Significant differences across treatments between species richness and seed densities m⁻² species observed in above-ground vegetation and not observed in vegetation for two seed bank methods and two microsites sampled from plots along a buffelgrass treatment gradient in Saguaro National Park. Vegetation categorized by duration and growth habit.

In-vegetation vs. Not in Vegetation	Species Richness			Seed density		
	<i>df</i>	<i>F</i>	<i>P</i>	<i>df</i>	<i>F</i>	<i>P</i>
Emergence (Not in vegetation>In Vegetation)						
Interspace	1,12	3.50	0.086	1,12	4.96	0.046
Annual Forb	1,12	7.73	0.017	1,12	6.50	0.026
Annual Grass	1,12	0.01	0.927	1,12	1.26	0.283
Perennial Forb	(Not detected with emergence)					
Perennial Grass	1,12	0.14	0.712	1,12	0.68	0.427
Shrub	1,12	1.33	0.271	1,12	0.75	0.404
Buffelgrass	(Not detected with emergence)					
Other Exotic	1,12	2.00	0.183	1,12	1.80	0.546
Below Brittlebush	1,12	6.22	0.028	1,12	4.95	0.046
Annual Forb	1,12	23.12	<0.001	1,12	8.77	0.012
Annual Grass	1,12	0.08	0.778	1,12	1.68	0.219
Perennial Forb	1,12	1.00	0.337	1,12	1.00	0.337
Perennial Grass	1,12	0.83	0.381	1,12	0.64	0.441
Shrub	1,12	14.40	0.003	1,12	5.13	0.043
Buffelgrass	1,12	1.80	0.205	1,12	1.09	0.318
Other Exotic	1,12	0.67	0.679	1,12	0.67	0.492
Extraction (In vegetation>Not in Vegetation)	<i>df</i>	<i>F</i>	<i>P</i>	<i>df</i>	<i>F</i>	<i>P</i>
Interspace	1,14	0.22	0.622	1,14	0.01	0.921
Annual Forb	1,14	6.08	0.027	1,14	-	-
Annual Grass	1,14	0.00	1.000	1,14	0.90	0.358
Perennial Forb	1,14	1.00	0.334	1,14	0.02	0.895
Perennial Grass	1,14	0.29	0.599	1,14	1.17	0.297
Shrub	1,14	60.06	<0.001	1,14	12.99	0.003
Buffelgrass	1,14	20.00	<0.001	1,14	5.02	0.042
Other Exotic	1,14	1.62	0.213	1,14	3.54	0.081
Below Brittlebush	1,14	0.14	0.714	1,14	2.72	0.121
Annual Forb	1,14	5.51	0.341	1,14	0.32	0.774
Annual Grass	1,14	0.86	0.369	1,14	2.67	0.124
Perennial Forb	1,14	1.71	0.212	1,14	0.14	0.710
Perennial Grass	1,14	0.31	0.586	1,14	0.07	0.802
Shrub	1,14	42.67	<0.001	1,14	18.76	<0.001
Buffelgrass	1,14	12.80	0.003	1,14	6.13	0.027
Other Exotic	1,14	12.00	0.004	1,14	6.46	0.024

Table F6. Significant differences between two seed bank assessment methods seed densities m⁻² and species richness observed in above-ground vegetation and not observed in vegetation two microsites sampled from plots along a buffelgrass treatment gradient in Saguaro National Park. Vegetation categorized by duration and growth habit.

Emergence vs. Extraction		In vegetation			Not in vegetation		
	<u>Seed Density</u>	<i>df</i>	<i>F</i>	<i>P</i>	<i>df</i>	<i>F</i>	<i>P</i>
Interspace		1,12	15.94	0.001	1,14	96.00	<0.001
Annual Forb		1,12	7.64	0.017	1,14	6.55	0.023
Annual Grass		1,12	3.86	0.073	1,14	1.31	0.271
Perennial Forb		1,12	6.82	0.023	1,14	2.64	0.127
Perennial Grass		1,12	7.33	0.019	1,14	19.60	0.001
Shrub		1,12	17.85	0.001	1,14	13.00	0.003
Buffelgrass		1,12	5.14	0.043	1,14	1.80	0.201
Other Exotic		1,12	3.67	0.080	1,14	2.58	0.131
Below Brittlebush		1,12	35.27	<0.001	1,14	3.64	0.078
Annual Forb		1,12	9.87	0.009	1,14	2.50	0.136
Annual Grass		1,12	3.82	0.074	1,14	4.73	0.047
Perennial Forb		1,12	2.89	0.115	1,14	3.89	0.069
Perennial Grass		1,12	2.77	0.122	1,14	2.95	0.108
Shrub		1,12	22.09	<0.001	1,14	1.95	0.185
Buffelgrass		1,12	6.66	0.024	1,14	1.95	0.184
Other Exotic		1,12	7.16	0.020	1,14	2.85	0.113
	<u>Species Richness</u>	<i>df</i>	<i>F</i>	<i>P</i>	<i>df</i>	<i>F</i>	<i>P</i>
Interspace		1,12	202.34	<0.001	1,14	94.18	<0.001
Annual Forb		1,12	68.22	<0.001	1,14	53.12	<0.0001
Annual Grass		1,12	5.19	0.042	1,14	7.11	0.018
Perennial Forb		1,12	16.67	0.015	1,14	19.60	0.001
Perennial Grass		1,12	7.64	0.017	1,14	13.00	0.003
Shrub		1,12	165.78	<0.001	1,14	18.00	0.001
Buffelgrass		1,12	48.00	<0.001	1,14	2.00	0.179
Other Exotic		1,12	29.45	<0.001	1,14	3.00	0.105
Below Brittlebush		1,12	82.71	<0.001	1,14	48.86	<0.001
Annual Forb		1,12	55.74	<0.001	1,14	35.30	<0.001
Annual Grass		1,12	6.85	0.023	1,14	7.00	0.019
Perennial Forb		1,12	17.24	0.001	1,14	13.07	0.003
Perennial Grass		1,12	11.17	0.006	1,14	5.54	0.034
Shrub		1,12	54.45	<0.001	1,14	14.08	0.002
Buffelgrass		1,12	12.65	0.004	1,14	4.50	0.052
Other Exotic		1,12	20.08	<0.001	1,14	2.67	0.125

Table F7. Significant differences between two microsite (interspace and brittlebush) species richness and seed densities m⁻² observed in above-ground vegetation (above) and not observed in vegetation (below) for two seed bank assessment methods microsites.

Between Microsite In- Vegetation differences	Species Richness			Seed Density		
	<i>df</i>	<i>F</i>	<i>P</i>	<i>df</i>	<i>F</i>	<i>P</i>
Emergence						
Annual Forb	1,14	2.57	0.131	1,14	1.83	0.198
Annual Grass	1,14	0.00	1.000	1,14	0.17	0.684
Perennial Forb	1,14	0.08	0.777	1,14	0.12	0.731
Perennial Grass	1,14	1.00	0.334	1,14	1.00	0.334
Shrub	1,14	0.20	0.662	1,14	0.62	0.444
Buffelgrass	1,14	11.11	0.005	1,14	4.40	0.055
Other Exotic	1,14	4.00	0.065	1,14	25.58	0.131
Extraction						
Annual Forb	1,14	6.53	0.023	1,14	0.66	0.431
Annual Grass	1,14	1.33	0.268	1,14	0.00	0.979
Perennial Forb	1,14	0.17	0.689	1,14	0.96	0.343
Perennial Grass	1,14	0.50	0.491	1,14	2.33	0.149
Shrub	1,14	0.29	0.601	1,14	0.00	1.000
Buffelgrass	1,14	0.00	1.000	1,14	6.12	0.267
Other Exotic	1,14	0.00	1.000	1,14	0.27	0.611
Between Microsite Not- In- Vegetation differences	Species Richness			Seed Density		
	<i>df</i>	<i>F</i>	<i>P</i>	<i>df</i>	<i>F</i>	<i>P</i>
Emergence						
Annual Forb	1,14	3.12	0.099	1,14	2.71	0.122
Annual Grass	1,14	0.00	1.000	1,14	0.05	0.834
Perennial Forb	1,14	3.00	0.105	1,14	3.00	0.105
Perennial Grass	1,14	0.00	1.000	1,14	0.71	0.412
Shrub	1,14	0.00	1.000	1,14	0.20	0.662
Buffelgrass	1,14	1.00	0.334	1,14	1.00	0.334
Other Exotic	1,14	0.00	1.000	1,14	0.00	1.000
Buffelgrass						
Annual Forb	1,14	0.50	0.491	1,14	0.00	0.995
Annual Grass	1,14	0.11	0.744	1,14	0.68	0.424
Perennial Forb	1,14	0.47	0.503	1,14	4.12	0.062
Perennial Grass	1,14	0.07	0.800	1,14	0.74	0.405
Shrub	1,14	0.33	0.573	1,14	1.75	0.207
Buffelgrass	1,14	1.00	0.334	1,14	1.80	0.201
Other Exotic	1,14	0.11	0.744	1,14	1.72	0.210

Table F8. Pearson's correlation co-efficient (r) relationships between vegetation group (duration $\times$ growth habit) seed density and species richness also observed in above-ground vegetation surveys with time since initial buffelgrass treatment and years of buffelgrass treatment.

Time since treatment											
Seed Density											
Method	Microsite	Annual Forb	Grass	Total	Perennial Forb	Grass	Shrub	Total	Total Natives	Other Exotics	
Emergence	Interspace	-0.40	0.07	-0.24	-	0.44	-0.70	-0.48	-0.31	-	
	Brittlebush	-0.15	0.36	0.34	-	-0.06	0.49	0.49	0.44	-0.78	
Extraction	Interspace	-0.07	-0.23	-0.09	-0.15	-0.32	-0.31	-0.39	-0.14	-0.59	
	Brittlebush	-0.15	0.57	0.14	0.47	-0.44	-0.32	-0.33	-0.23	-0.73	
Species Richness											
Method	Microsite	Annual Forb	Grass	Total	Perennial Forb	Grass	Shrub	Total	Total Natives	Buffelgrass Presence	Other Exotics
Emergence	Interspace	0.03	0.40	0.14	-	0.55	-0.70	-0.35	-0.04	-	#DIV/0!
	Brittlebush	0.05	0.39	0.29	-	-0.40	0.22	-0.05	0.24	-0.55	-0.55
Extraction	Interspace	-0.25	0.28	-0.09	0.50	-0.13	0.58	0.53	0.13	-0.56	-0.39
	Brittlebush	0.07	0.39	0.23	-0.15	-0.31	0.05	-0.23	0.10	-0.45	0.39
Years of treatment											
Seed Density											
Method	Microsite	Annual Forb	Grass	Total	Perennial Forb	Grass	Shrub	Total	Total Natives	Other Exotics	
Emergence	Interspace	-0.35	0.00	-0.24	-	0.13	-0.55	-0.49	-0.32	0.00	-
	Brittlebush	0.27	-0.39	-0.32	-	0.07	-0.25	-0.23	-0.27	0.00	-0.46
Extraction	Interspace	0.07	-0.12	0.06	-0.12	-0.58	-0.09	-0.21	0.03	0.00	-0.40
	Brittlebush	0.18	-0.17	0.11	-0.29	-0.65	-0.13	-0.25	-0.18	0.00	-0.55
Species Richness											
Method	Microsite	Annual Forb	Grass	Total	Perennial Forb	Grass	Shrub	Total	Total Natives	Buffelgrass Presence	Other Exotics
Emergence	Interspace	-0.09	0.27	0.00	-	0.00	-0.55	-0.55	-0.21	-	-
	Brittlebush	0.45	-0.27	0.17	-	-0.22	0.15	0.00	0.15	0.00	0.00
Extraction	Interspace	-0.74	0.08	-0.69	0.68	-0.59	0.34	-0.16	-0.55	0.10	-0.53
	Brittlebush	-0.52	0.39	-0.41	-0.27	-0.38	-0.22	-0.53	-0.59	0.31	-0.18

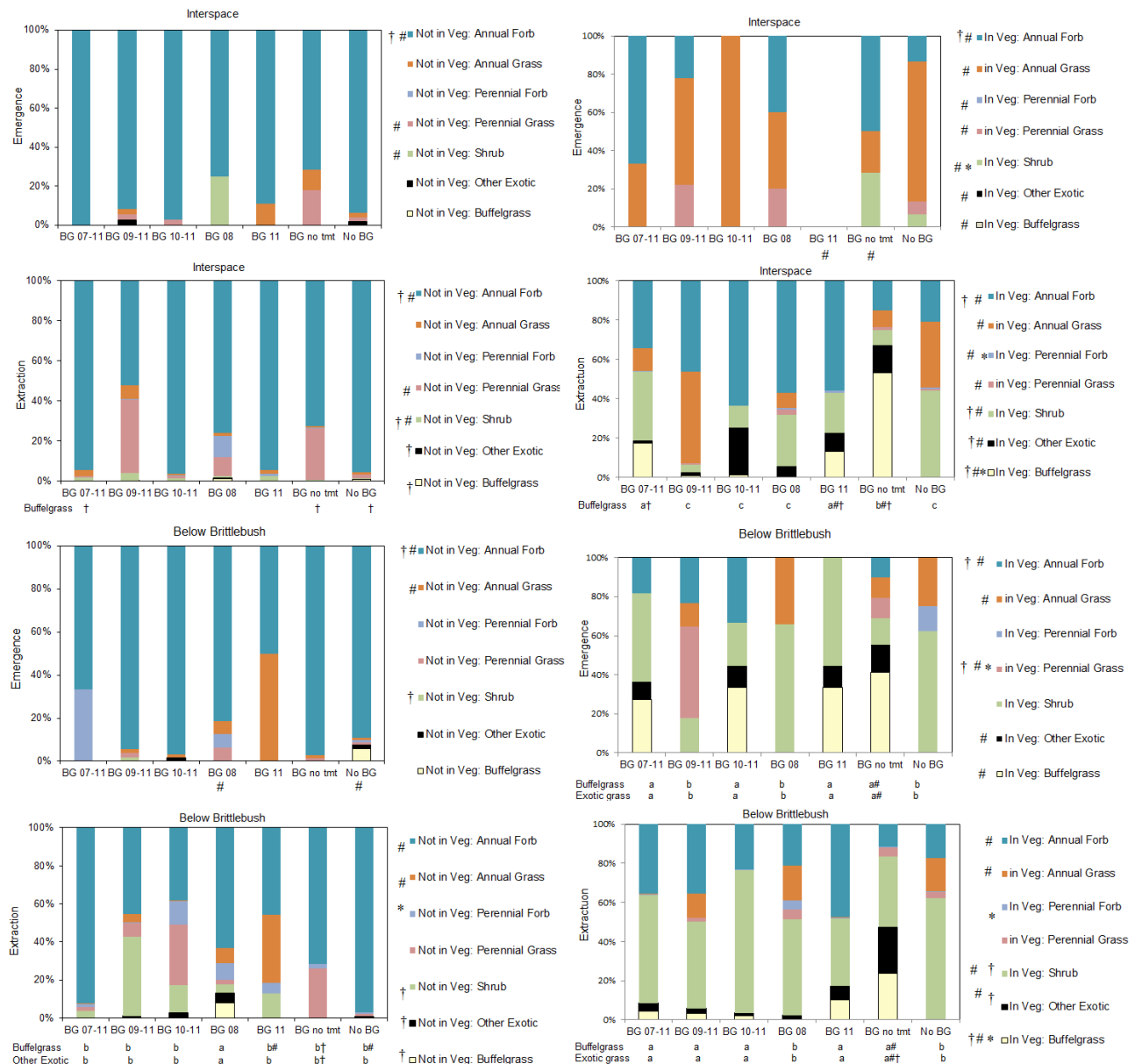


Figure F1. Relativized seed densities of species observed and not observed in above-ground vegetation for two seed bank assessment methods from two microsites in 0-5 cm soil seed bank along a buffelgrass treatment gradient in Saugaro National Park, Sonoran Desert. Treatment abbreviations along x axis: BG = buffelgrass, with the numbers following describing the year(s) in which BG was treated. Vegetation grouped by duration × growth habit. # = Indicates significant differences between seed bank assessment method within microsite and vegetation group (in-vegetation or not-in-vegetation). * Indicates significant differences between microsites within seed bank assessment method and within vegetation group (in-vegetation or not-in-vegetation). For example, within emergence, greater shrub densities from species which occurred in above ground vegetation were detected within below brittlebush microsites compared to interspace microsites. † Indicates significant differences between species detected within above-ground vegetation and species not detected within above-ground vegetation within microsites and within seed bank assessment method. For example, emergence within below brittlebush microsite detected greater annual forb seed densities of species that were not detected within the above-ground vegetation versus densities which occurred in above-ground vegetation. Letter groups denote significant differences between groups.

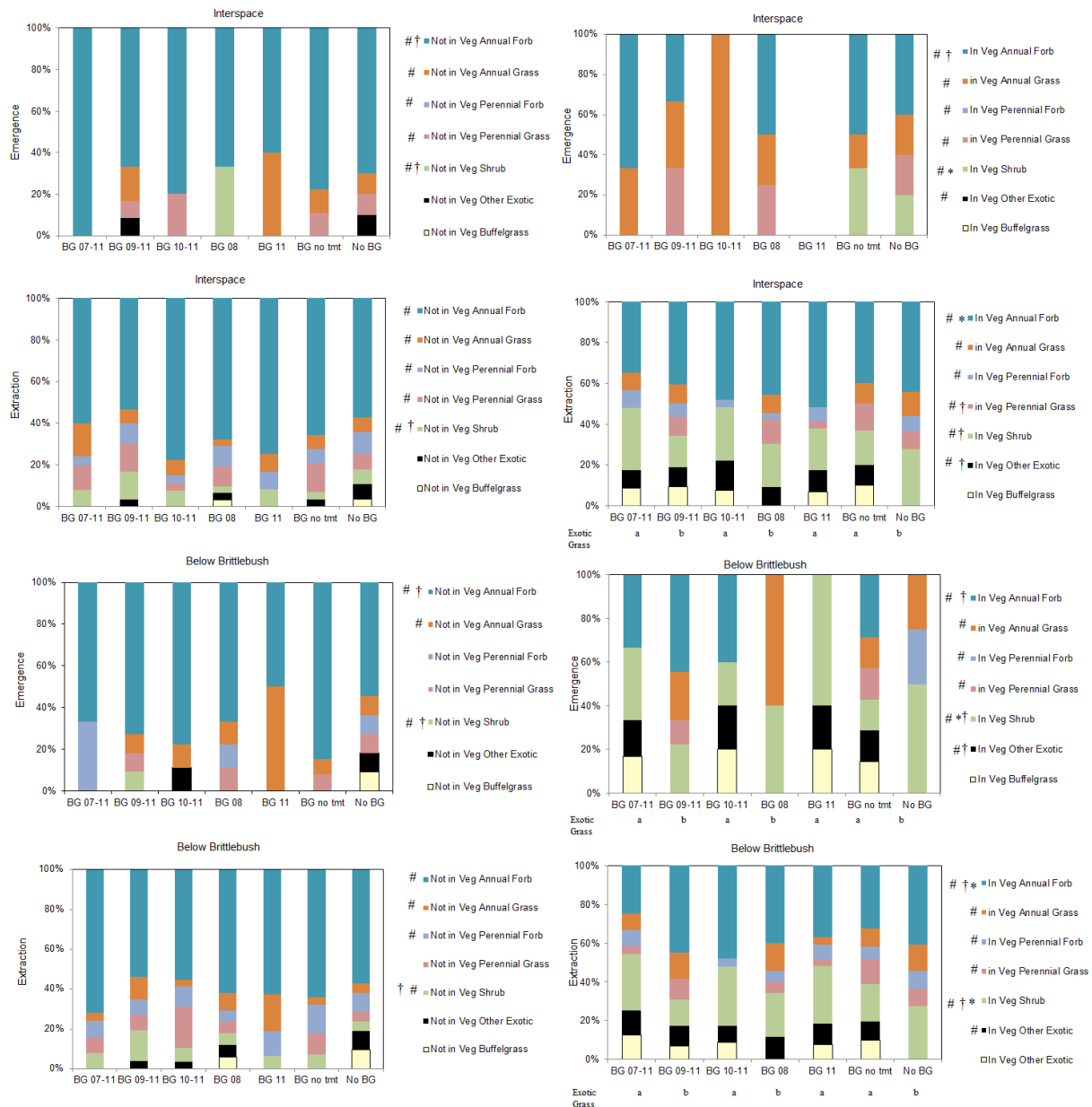


Figure F2. Relativized species richness of species observed and not observed in above-ground vegetation for two seed bank assessment methods from two microsites in 0-5 cm soil seed bank along a buffelgrass treatment gradient in Saugaro National Park, Sonoran Desert. Treatment abbreviations along x axis: BG = buffelgrass, with the numbers following describing the year(s) in which BG was treated. Vegetation grouped by duration × growth habit. # Indicates significant differences between seed bank assessment method within microsite and vegetation group (in-vegetation or not-in-vegetation). * Indicates significant differences between microsites within seed bank assessment method and within vegetation group (in-vegetation or not-in-vegetation). For example, within emergence, greater shrub densities from species which occurred in above ground vegetation were detected within below brittlebush microsites compared to interspace microsites. † Indicates significant differences between species detected within above-ground vegetation and species not detected within above-ground vegetation within microsites and within seed bank assessment method. For example, emergence within below brittlebush microsite detected greater annual forb seed densities of species that were not detected within the above-ground vegetation versus densities which occurred in above-ground vegetation. Letter groups denote significant differences between groups.

Appendix G. Additional Peer-Reviewed Resources

Sonoran Desert Ecology

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