

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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*First author: Associate Research Professor, Department of Environmental and Occupational Health, University of Nevada, Las Vegas, NV 89154-3064; second author: Research Assistant, Department of Environmental and Occupational Health, University of Nevada, Las Vegas, NV 89154-3064; and third author: Restoration Ecologist, National Park Service, Saguaro National Park, 3693 Old Spanish Trail, Tucson, AZ 85730. Corresponding author's E-mail: scott.abella@unlv.edu

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

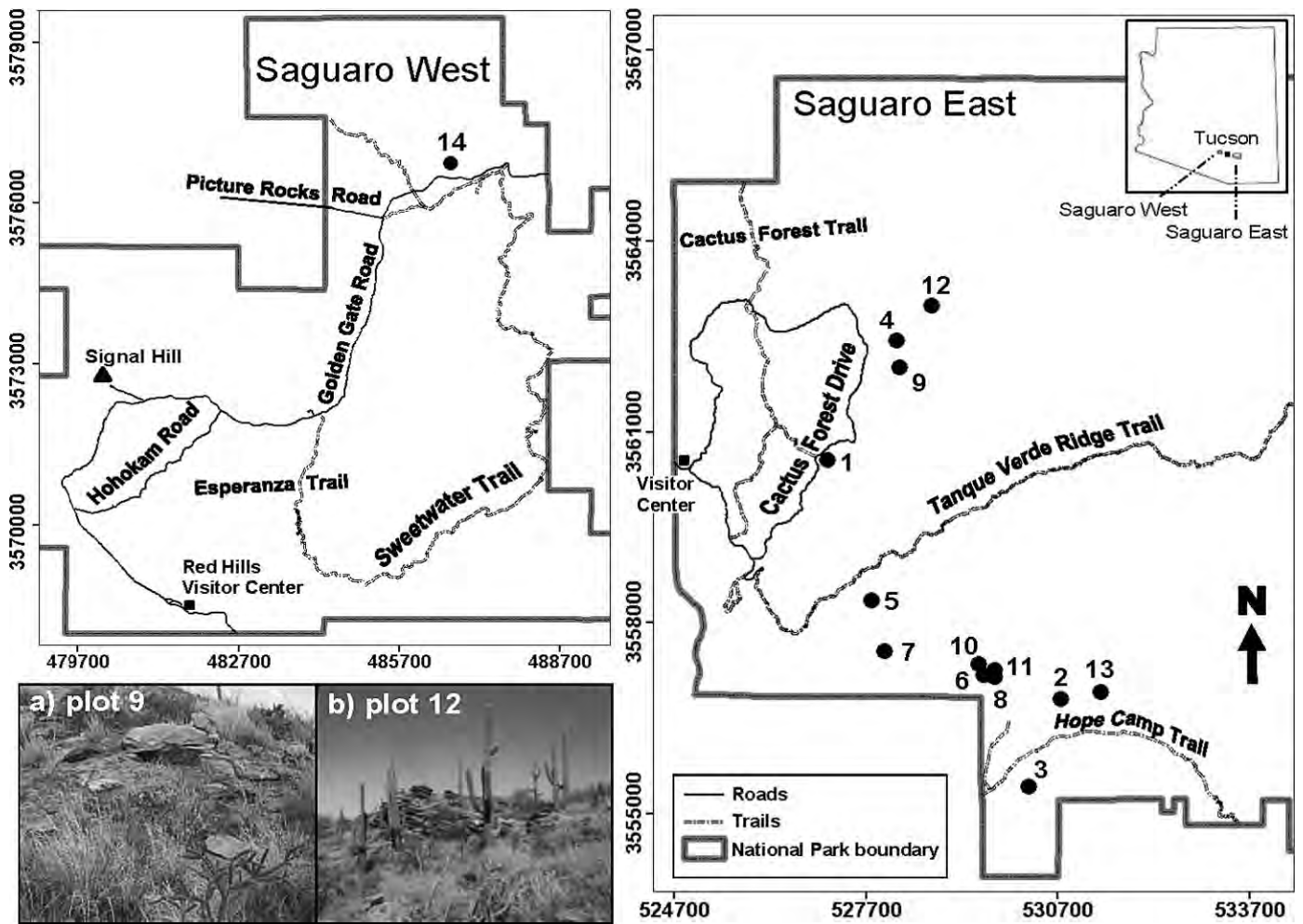


Figure 1. Location of the study area in Saguaro National Park units west and east of Tucson, AZ (inset, top right), and study sites with site numbers corresponding to descriptions in Appendix 1. Photos by L. P. Chiquoine, 2011.

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 echinochloidea* 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

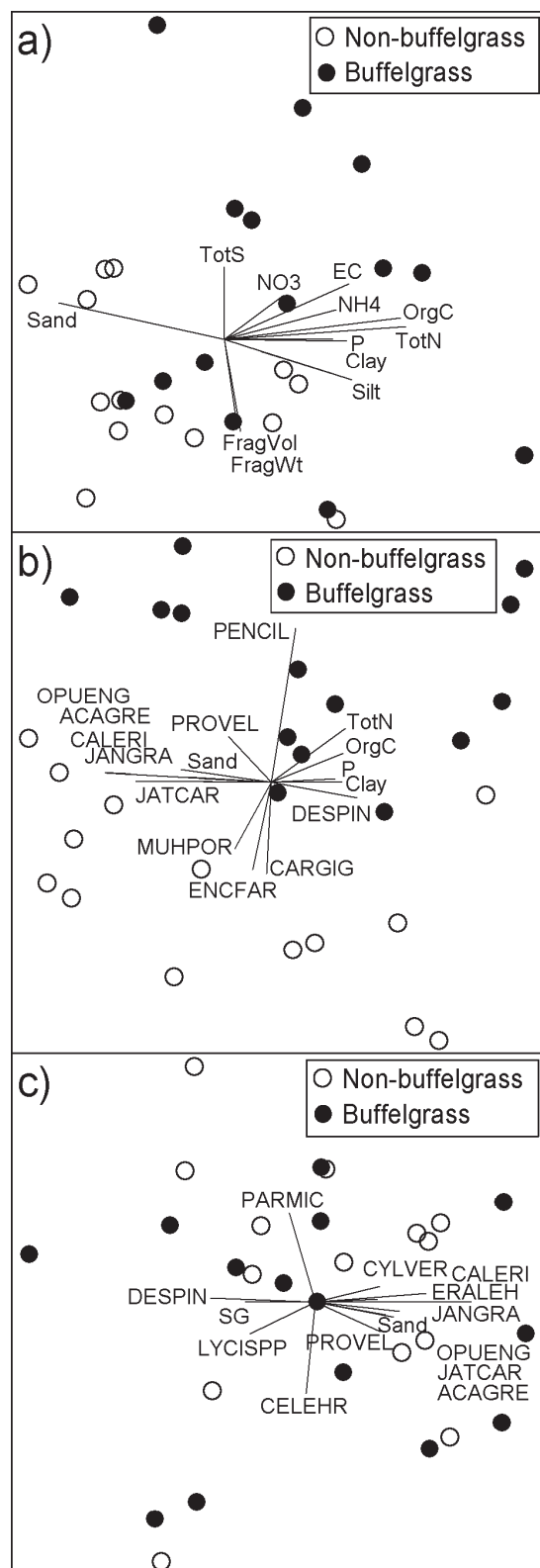


Figure 2. Ordination of (a) soil properties; (b) vegetation, including buffelgrass; and (c) vegetation, excluding buffelgrass, in buffelgrass and nonbuffelgrass patches of Saguaro National Park,

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 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 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.