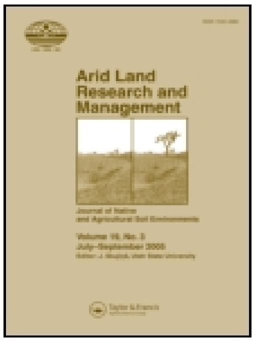

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Uprooted buffelgrass thatch reduces buffelgrass seedling establishment

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ABSTRACT

Buffelgrass (*Pennisetum ciliare* (L.) Link), a non-native perennial bunchgrass, invades ecologically intact areas of the Sonoran Desert. It competitively excludes native plants and increases fire frequency and intensity. Since the 1990s, whole buffelgrass plants have been manually uprooted and removed to control the invasion in southern Arizona. Uprooting plants results in bare, disturbed soil which promotes buffelgrass seed germination. This study examined whether leaving entire uprooted buffelgrass plants (thatch) on a field site reduces future buffelgrass establishment compared to removing uprooted plants from the site. A secondary goal was to determine whether light reduction and autoallelopathy were major factors in the negative effect of thatch on buffelgrass seedling density. Field plots with an average of 8,095 kg/ha thatch had 1.9 buffelgrass seedlings/m^2 which was significantly fewer than the 2.9 seedlings/m^2 in plots without thatch. Thatched portions of thatch plots (50% of their total area) had only 0.7 seedlings/m^2. In the greenhouse, which reduced outdoor light intensity by 35.2%, buffelgrass seeds sown in bare soil resulted in significantly higher seedling density than beneath buffelgrass thatch. Potential autoallelopathic chemicals leached from partially decomposed buffelgrass thatch and leached thatch had an intermediate but not significant ($p = 0.09$) effect on seedling numbers. Results suggest that leaving uprooted buffelgrass plants has the benefit of reducing seedling establishment in the area disturbed by uprooting.

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Autoallelopathy; invasive species; shading; southern Arizona

Introduction

The easy establishment, drought tolerance, and forage value of buffelgrass (*Pennisetum ciliare* (L.) Link), an African perennial C_4 bunchgrass, caused its promotion and seeding in warm climates worldwide (Miller et al. 2010; Marshall, Lewis, and Ostendorf 2012; Lyons et al. 2013). Since the mid-1980s, it has become increasingly evident that buffelgrass spreads into undisturbed natural areas and causes significant ecological harm (Olsson et al. 2012). Buffelgrass invasions can displace native vegetation through competition for water, nutrients, and space; and displacement is more rapid following fire (e.g., Stevens and Fehmi 2009; Miller et al. 2010; Olsson et al. 2012). While the true size of the current buffelgrass

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invasion appears unknown, the extent seems likely to be at least many tens of millions of hectares worldwide (based on Marshall, Lewis, and Ostendorf 2012).

The potential for further wide-scale invasion and conversion to buffelgrass monocultures makes its removal a critical component of land management programs designed to protect and restore native vegetation. Although buffelgrass can be effectively controlled with herbicides (Dixon, Dixon, and Barret 2002; Tjelmeland, Fulbright, and Lloyd-Reilley 2008), manual control by uprooting plants with hand tools remains a common treatment method. Manual removal avoids the need for certification to handle herbicides and can be performed at all stages of phenology. Current manual control practice includes placing uprooted plants in compact piles to prevent the plants and seeds from being transported by wind and water. On treatment areas closer to roads, uprooted plants are often bagged and hauled off-site.

Uprooting buffelgrass plants can result in prolific seedling establishment in the following growing season. This pattern arises from the dense seedbank (Hacker 1989) and increased germination rates in disturbed areas (Búrquez-Montijo, Miller, and Martínez-Yrízar 2002; Brenner and Kanda, 2013). If newly established buffelgrass plants are removed or sprayed before they produce a significant number of seeds, then fewer seedlings establish each successive season (Rutman and Dickson 2002). Therefore, control programs would be more effective if post-treatment seedling establishment was minimized. Placing uprooted plants on the disturbed soil surface to create a thatch layer may reduce seedling establishment after the disturbance. This is supported by field observations that few buffelgrass seedlings emerge from thatch of uprooted parent plants or in dense stands of mature buffelgrass plants.

Shading of seed by thatch is a likely mechanism for reduced seedling numbers, but allelopathic chemicals in thatch may also contribute to reductions. For example, buffelgrass seed germination is about 30% higher for seeds exposed to light compared to those kept in complete darkness (Pandeya and Jayan 1978) and is about 40% higher for seeds on a bare soil surface than buried seeds (Mutz and Scifres 1975). Crutchfield, Wicks, and Burnside (1985) suggested that the shading by straw or mulch lowered the germination rate of many weed species and seeds germinating under mulch may not receive enough photosynthetically active light to grow vigorously into healthy seedlings. In addition, rain leachates of buffelgrass shoots and root exudates inhibited the germination of several plant species including *Setaria italica* (L.) P. Beauv. and *Pennisetum americanum* (L.) Leeke, which are closely related to buffelgrass (Hussain et al. 2011). Buffelgrass root exudates also appeared to limit growth of neighboring buffelgrass seedlings (Hussain, Naqvi, and Ilahi 1982).

Our field study evaluates the response of buffelgrass seedling establishment to the direct effect of applying thatch to areas disturbed by uprooting adult plants. In a controlled greenhouse study, we also evaluate the potential processes of thatch light reduction and allelopathy (thatch leachate) as the mechanism for the response to thatch.

Methods

Field plot thatch study

The study site was located in the Santa Catalina Mountains north of Tucson, Arizona (32°20′ N, 110°49′W) at an average elevation of 1,100 m asl near the boundary of the Sonoran Upland and Desert Grassland vegetation types (Brown 1994). Dominant vegetation included buffelgrass, saguaros (*Carnegiea gigantea* (Engelm.) Britton & Rose), palo verdes

(*Parkinsonia microphylla* Torr.), velvet mesquite (*Prosopis velutina* Woot.), and ocotillo (*Fouquieria splendens* Engelm.). There was little precipitation (13.2 mm) at the field site from 1 February to 30 June 2012 (Woodard and Crimmins 2013). Rain favorable for germination (203.7 mm) fell from 1 July to 31 September during the summer rainy season. Dry conditions during the fall of 2012 (6.1 mm from 1 October to 30 November) possibly contributed to the death of a small percentage of seedlings in plots.

We established sixty 2 × 2 m plots in six blocks of ten plots each (Table 1; Jernigan et al. 2013) in areas which averaged 50% buffelgrass cover. Treatments of either leaving thatch or removing it and leaving bare soil were randomly assigned within blocks defined by aspect. From mid-March to mid-May of 2012, all buffelgrass plants in the plots were completely uprooted with hand tools. Buffelgrass plants within 1 m of plot edges were also uprooted to limit influence of surrounding mature buffelgrass plants. The uprooted plants had produced an abundance of mature seeds, some of which were still attached to the plants.

Uprooted plants were removed off-site for the bare treatment ($n = 30$). For the thatch treatment ($n = 30$), we laid uprooted plants in their natural form over the soil disturbance caused by uprooting. Thatch thickness averaged 1.5 cm and thatch cover averaged 50% of the plot area. Thatch cover was estimated through mapping thatch placements using a grid frame. Thatch biomass averaged 8,095 kg/ha based on twenty 40 × 40 cm randomly located plots at a similar adjacent site treated in 2014. We measured light reduction by thatch using a Mastech Digital Illuminance B, 0-200,000 Lux Luxmeter, (Guangdong, China).

Live and dead buffelgrass seedlings were counted between 28 December 2012 and 11 January 2013 (an average of 262 days after the application of thatch treatment) and were recorded as having established under thatch or out in the open.

Estimates of the buffelgrass seedbank were made in April–June 2012 (3–5 weeks post treatment). Nine soil samples per plot (5 cm diameter, 3 cm deep) were collected in a systematic grid pattern. Buffelgrass fascicles and naked caryopses in the soil samples were separated into five classes: yellow fascicles that matured in the winter of 2012, brown fascicles that matured during the summer of 2011, aging fascicles that probably matured before 2011, naked caryopses that had become detached from fascicles (mostly of yellow color), and immature fascicles (most of which had begun to develop in the winter of 2012).

Table 1. Field plot thatch study 2 × 2 m plot allocation and latitude-longitude coordinates.

Plots	Slope Aspect	Coordinates
Bare (five replications) Thatched (five replications)	West	32° 20.271'N 110° 49.435'W
Bare (five replications) Thatched (five replications)	West	32° 20.185'N 110° 49.452'W
Bare (five replications) Thatched (five replications)	East	32° 20.260'N 110° 49.482'W
Bare (five replications) Thatched (five replications)	East	32° 20.147'N 110° 49.527'W
Bare (five replications) Thatched (five replications)	South	32° 20.097'N 110° 49.508'W
Bare (five replications) Thatched (five replications)	South	32° 20.055'N 110° 49.501'W

Note: Bare plots had buffelgrass uprooted and removed from the plot. Thatched plots had buffelgrass uprooted and laid over the uprooting disturbance. Plots were randomly assigned to be thatched or bare in areas that averaged 50% buffelgrass cover.

Greenhouse thatch-leachate experiment

We used a randomized design to evaluate thatch and thatch leachate influence of seedling emergence. The experiment had four treatment groups with seven replicates each: bare soil irrigated with distilled water (control), bare soil irrigated with leachate from the thatch, a ~1.5 cm-thick layer of thatch that had been leached, and a ~1.5 cm-thick layer of unleached thatch. Greenhouse sunlight reduction was 35.2% and temperatures were between 16°C (night) and 35°C (day). In each 3.8 L pot, twenty buffelgrass fascicles (collected on 14 October 2011 near Sahuarita, Arizona; 31°57′N, 110°59′W) were planted with the base of the seed 1 cm deep in potting soil (Sunshine Professional growing Mix; Sun Gro Horticulture Canada Ltd., Seba Beach, Canada). Based on a previous trial (unpublished data), planting seeds very shallowly in soil helped equalize soil moisture among greenhouse treatments.

Partially decomposed buffelgrass thatch (gray colored rather than yellow uprooted plants) was collected on 14 June 2013 near Tucson, Arizona (32°19′N, 110°49′W). A 14 cm diameter circle (the pot diameter) of thatch, 1.5 cm thick, weighed 29 g. Leachate and leached thatch were created by submerging 29 g (fresh weight) of thatch pieces (≤3 cm long) in 600 ml of distilled water in six batches and kept at room temperature (22°C). After 24 hours, the leachate was drained through unbleached coffee filters and refrigerated at ~ 5°C. Leached thatch was dried in an oven for 48 hours at 70°C, and stored for later use in the leached thatch treatment.

Irrigation began 6 July 2013 with application of 600 mL distilled water to each pot (equal to 39 mm of rainfall). On 7 and 8 July, the bare-soil-leachate pots each received 200 mL of distilled water followed by 100 mL of leachate, while pots of the other three treatments received 300 mL of distilled water (equal to 19.5 mm of rainfall). After irrigation on 8 July, the soil of all pots reached saturation. On 9, 10, and 11 July we added 100 mL of leachate to bare-soil-leachate pots and 100 mL of distilled water to pots of the other three treatments. We carried out a final count of buffelgrass seedlings on 28 July (8 days after treatment).

Statistical methods

The field plot thatch study data were analyzed using a two-way Analysis of Variance (ANOVA) for the randomized complete block design. The greenhouse thatch leachate study data were analyzed using one-way ANOVA along with Tukey's HSD pairwise tests for the simple randomization design. For all analyses, we used an alpha level of $p < 0.05$ as a significant difference. Statistical analyses were carried out using JMP (ver. 9.0, SAS Institute Inc., Cary, NC, U.S.A.), and R (ver. 3.0.3, R Foundation for Statistical Computing, Vienna, Austria).

Results

Field plot thatch study

Thatch reduced buffelgrass seedling density, but did not affect the density of seed in the soil seedbank. At the full plot-scale, the average of 1.9 ± 0.3 SE seedlings/m^2 in the thatched plots was significantly less than the average of 2.9 ± 0.3 SE seedlings/m^2 in the bare (control) treatment plots (Table 2 and Figure 1). Within the thatched plots, the average

Table 2. Results of the two-way ANOVA comparing the effects of thatch treatment and slope aspect on the density of seedlings in field plots.

	df	Sum of squares	Mean square	*F* Ratio	Prob >*F*
Aspect	2	1.44	0.72	0.25	0.78
Thatch Treatment	1	14.02	14.02	4.77	0.03
Aspect*Thatch Treatment	2	0.04	0.02	0.01	0.99
Error	54	158.59	2.94		

of 0.7 ± 0.2 SE seedlings/m^2 observed beneath thatch were significantly less ($p < 0.001$) than the 3.2 ± 0.4 SE seedlings/m^2 in the non-thatch covered portion of the plots (Figure 1). Seedling density in non-thatch covered portions of thatch treatment plots was similar to seedling density in bare (control) treatment plots (Figure 1). Neither the aspect nor the interaction of aspect and treatment had significant effects on seedling density.

Thatched plots had an average thatch cover of $50.2 \pm 1.7\%$ SE as determined from field-drawn thatch maps. Thatch cover values did not differ significantly between aspects ($p = 0.77$). In areas covered by thatch, the average thatch thickness was 1.5 cm and the average reduction of sunlight by thatch was 82.6% (Figure 2). Light reduction by thatch increased steeply to ~ 3 cm of thickness, after which there was limited additional reduction. Minimal thatch movement (<2 cm) was observed in the ~260 days between thatch placement and seedling counting based on maps made at the time of thatch placement.

At the full-plot scale, an average of 0.04 ± 0.02 SE dead buffelgrass seedlings/m^2 were observed in thatched plots, while an average of 0.12 ± 0.04 SE dead seedlings/m^2 were observed in bare plots. The difference was not significant ($p = 0.07$). Within the thatched plots, an average of 0.01 ± 0.01 SE dead buffelgrass seedlings/m^2 were observed beneath thatch, while an average of 0.07 ± 0.03 SE dead seedlings/m^2 were observed in the non-thatch covered portion of the plots. The difference was not significant ($p = 0.12$).

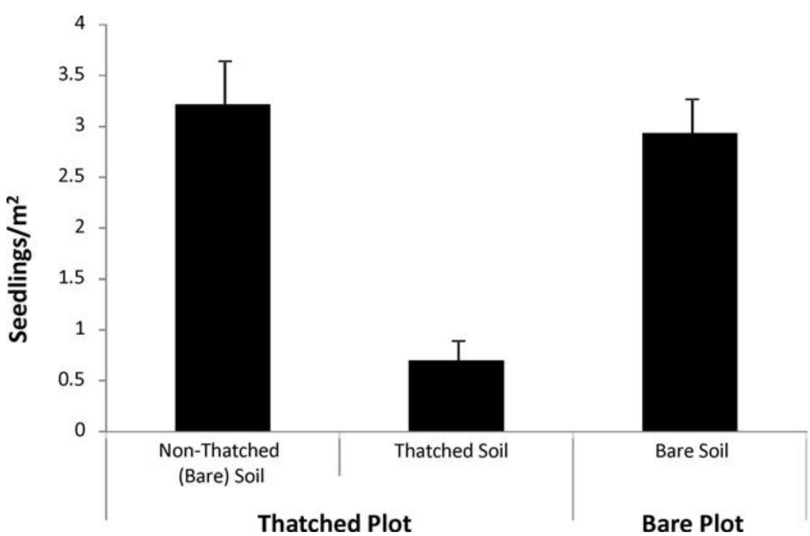

Figure 1. The mean seedling density counted in bare (control) plots, the nonthatched portion of thatched plots, and the thatched portion of thatched plots in the field plot thatch study. Error bars represent one standard error of the mean.

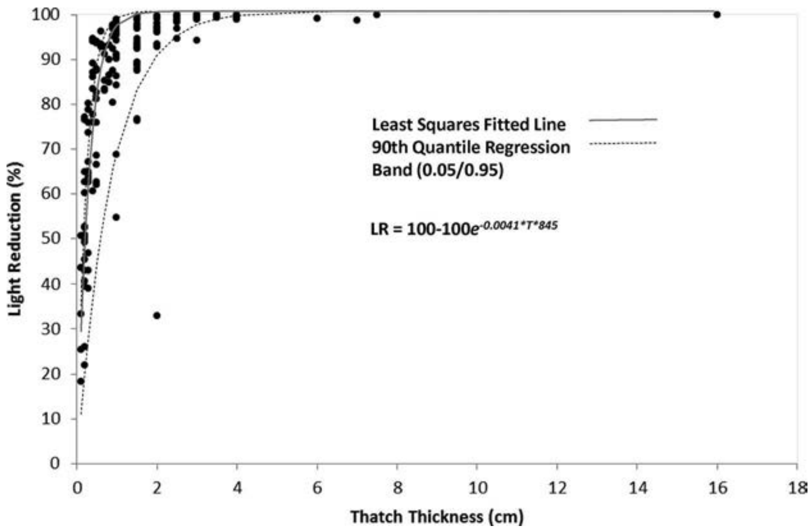

Figure 2. The relationship between light reduction from thatch and thatch thickness where LR is the percent light reduction, −0.0041 is the estimated transmittance constant, *T* is the Thatch Thickness, and 845 converts *T* into g/m^2. We measured sunlight reduction using a Mastech Digital Illuminance B, 0-200,000 Lux Luxmeter, (Guangdong, China) that did not differentiate photosynthetically active radiation (PAR).

Table 3. ANOVA results comparing germination in bare soil containers irrigated with distilled water, bare-soil containers irrigated with thatch leachate, containers with leached thatch, and containers with unleached thatch in the thatch leachate experiment.

Source	*df*	Sum of squares	Mean square	*F* Ratio	Prob >*F*
Treatment	3	62.11	20.70	4.07	0.02
Error	24	122.00	5.08		

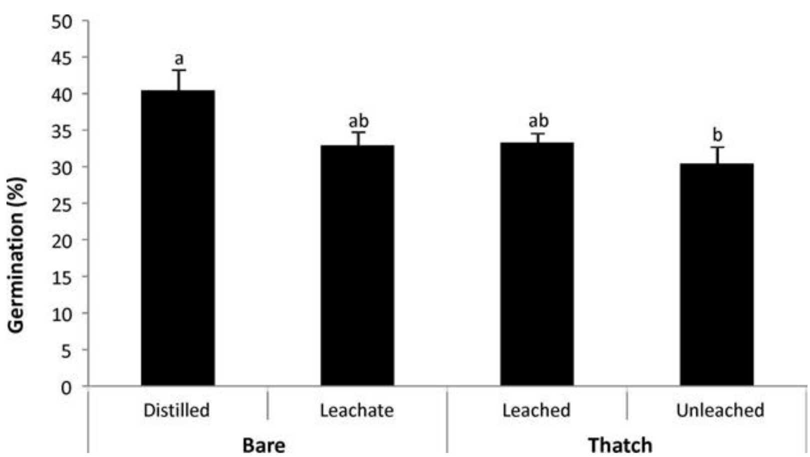

Figure 3. The germination in bare soil containers irrigated with distilled water (control), bare soil containers irrigated with thatch leachate, containers with leached thatch, and containers with unleached thatch in the thatch leachate experiment. Error bars represent one standard error of the mean. Bars with different letters have means that are significantly different (Tukey's HSD).

There was no significant difference in seed numbers between thatched plots ($n = 30$) with 10,426 ± 958 SE fascicles/m^2 and bare plots ($n = 30$) with 11,123 ± 1,263 SE fascicles/m^2 ($p = 0.57$). We also found no significant difference in the average number of abundant yellow seeds (65.6% of all seeds counted) between thatched and bare plots ($p = 0.78$).

Greenhouse thatch-leachate experiment

Only the unleached thatch, which combined shade with autoallelopathy, had fewer seeds germinate than the bare soil control treatment. The 40.4 ± 2.8% SE germination of seeds in the bare soil control-distilled-water treatment was significantly greater ($p = 0.018$; Table 3) than the 30.4 ± 2.3% SE germination of seeds in the unleached thatch treatment (Figure 3). Germination of seeds in the leachate and leached thatch treatments did not differ significantly and were intermediate between that of the bare soil and unleached thatch treatments.

Discussion

Leaving uprooted buffelgrass plants in place resulted in one-third fewer seedlings (1.9 vs. 2.9 seedlings/m^2; Figure 1) compared to moving uprooted plants off site. This practice reduces the need for follow-on control efforts as well as potentially saving time compared to moving uprooted plants. Covering the soil disturbed by uprooting with thatch results in a treatment similar to the known best practices for land conservation with thatch distributed across the site and directly applied to the most disturbed soil (Whisenant 2002). The thatch effect should be long-lasting because the buffelgrass thatch remains on the landscape for several years (3 +) based on observations during the summer of 2014 of a site treated during 2011.

The inhibitory effect of our field thatch treatment was bigger than expected. There were <3 times fewer seedlings directly under the thatch compared to in bare areas. Previous laboratory studies observed buffelgrass germination as about 40% lower for buried seeds compared to seeds on a bare soil surface (Mutz and Scifres 1975) and about 30% lower for seeds kept in complete darkness compared to those exposed to light (Pandeya and Jayan 1978).

We found equivocal evidence that reduced light beneath the thatch negatively influenced buffelgrass seedling density. In the greenhouse, there was ~20% decrease in seedling emergence under thatch than on bare soil. This difference would likely be greater in outdoor settings because the 35% light reduction by the greenhouse and a few mm of soil was equivalent to the light reduction from 1–2 mm of thatch. Similarly, we found indeterminate evidence to support an autoallelopathic effect on seedling emergence. Neither leachate alone nor leached thatch significantly reduced emergence compared to bare soil, and emergence was only significantly reduced by unleached thatch. This suggests a possible additive effect of shade and allelopathy. However, the reduced light intensity in the greenhouse compared to outside may have limited the expression of seedling emergence in the bare soil and leachate treatments.

A role for light reduction in reducing germination is consistent with the general control of weed seedling with rye straw (Creamer et al. 1996), and the suppression of seedling emergence for another invasive grass (*Eragrostis lehmanniana* Nees) in the Sonoran Desert

(Sumrall et al. 1991; Roundy, Taylorson, and Sumrall 1992). An autoallelopathic effect is consistent with leachate suppression of germination on other species and reduced growth of buffelgrass seedling from neighboring plant root exudate (Hussain, Naqvi, and Ilahi 1982; Hussain et al. 2011). It is possible that the leachate from the "older" thatch was less effective than from fresh thatch used in the field plots. However, allelopathic effects have been thought to increase as byproducts of bacterial decay of the biomass (Liebl and Worsham 1983).

At first glance, the negative effect of thatch on buffelgrass seedling establishment is inconsistent with the expectation of increased establishment in arid and semi-arid settings given the greater soil moisture under plant litter. For example, Loydi et al.'s (2013) meta-analysis study noted a general pattern in which plant litter tends to have a facilitative effect on germination in more arid environments and an inhibitory effect on germination in more mesic environments. However, we found fewer dead seedlings under thatch (2% dead based on density of live and dead seedlings) than in unthatched control plots (4% dead). While our experimental design did not track individuals to allow assessment of mortality and survival, our data at least implies that while thatch may reduce germination, thatch may also enhance survival of seedlings by maintaining soil moisture.

Among the many other factors that could reduce seedling establishment, temperature and pathogens have been indicated in other studies. Thatch moderates temperatures of underlying soil in comparison with bare soil. Hacker and Radcliff (1989) found that high fluctuations of temperature and higher temperatures generally lead to increased buffelgrass germination. Lower daytime soil temperatures resulting from shading and insulation by thatch could explain higher germination in our bare plots than in our thatched plots. The cooler, more-moist microclimate under thatch might also allow fungal pathogens to proliferate and play a major role in the death of buffelgrass seeds similar to cheatgrass (Beckstead, Miller, and Connolly 2012). The thatch cover may also attract seed predators or herbivorous animals (Hulme, 1994).

It is important to consider the long-term fate of invaded areas that have been manually treated and covered with thatch. Abella, Chiquoine, and Backer (2013) found that native plant species, rather than buffelgrass or other exotic plant species were dominant where buffelgrass had annual chemical and manual treatment. We observed some native forbs growing through thatch on our field plot thatch study site. Many of the other potentially dominant invasive exotic plant species of the Sonoran Upland region, such as Lehmann lovegrass, fountaingrass (*Pennisetum setaceum* (Forssk.) Chiov.) and natal grass (*Melinis repens* (Willd.) Zizka), may be limited by thatch because their seeds germinate more readily in bare ground.

From a practical standpoint, our field data suggest that a thickness above 3 cm of thatch offers little additional shading of the soil surface (Figure 2). While the principal mechanisms remain undecided, our results imply that covering more of a site with thatch seems likely to result in an additional reduction in buffelgrass seedlings. In addition to putting thatch over the disturbance caused by uprooting plants, seedling control might be maximized by also placing thatch over areas where germination seems most likely, such as at the base of rock outcroppings that harvest rain water.

Buffelgrass thatch reduced buffelgrass seedling density by one-third. While the reduction may seem modest, when it is combined with the time potentially saved by not removing plants and the decreased erosion potential, thatching appears to be a substantially better manual control practice than moving the thatch into piles or off-site. Even small increases in efficiency may increase the area restored or reduce project costs (e.g., Rowe 2010). Future research to better establish the fate of buffelgrass seeds beneath thatch and determine dominant causes of seedling mortality will allow better targeting of invasive species control.

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