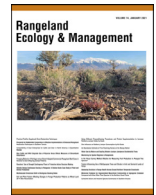




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Using Locally Adapted Seeds to Restore Native Plants and Arthropods After Plant Invasion and Drought[☆]

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ABSTRACT

Non-native plants alter conditions and can reduce the effectiveness of restoration tools. Under these conditions, adding native, locally adapted seeds to favor establishment of native plant communities may provide a potential restoration strategy. We explored the efficacy of soil disturbance and the addition of native seed to restore native plant and arthropod communities in landscapes dominated by Kleberg bluestem (*Dichanthium annulatum* [Forssk.] Stapf, Old World bluestem grasses, OWB) in summers 2011–2013; our study coincided with severe drought. We compared vegetation and arthropods on disked plots with and without seed (experimental plots), as well as plots within adjacent, undisturbed OWB monocultures. Adding seeds increased cover of native plants and reduced cover of OWBs relative to unseeded plots and undisturbed OWB monocultures. Most of the plants we recorded in seeded plots were not included in the seed mix; we hypothesize that arthropods may have been consuming the added seed rather than the seed bank, permitting native plants in the seed bank to establish. Adding seed also increased arthropod species richness, which was more pronounced as drought severity decreased. During severe drought, arthropod abundance in experimental plots was comparable with undisturbed OWB monocultures, despite the absence of vegetation after disking. However, as drought subsided, undisturbed OWB monocultures had more arthropods than experimental plots. Non-native arthropods, particularly herbivores, were positively associated with OWBs; adding seed was associated with reduced dominance of both OWBs and nonnative arthropods. Reducing dominance of OWBs by adding seed was also associated with reduced dominance of some predators that consume non-native arthropod prey. Understanding how communities respond to multiple disturbances seems especially important to inform restoration strategies given that changes in climate patterns and establishment of invasive species are likely to be more common and widespread.

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Introduction

The establishment of invasive plants in native landscapes can alter ecosystem function and community characteristics through changes in plant composition and soil properties (D'Antonio and Vitousek 1992; Ehrenfeld 2002; Levine et al. 2003; Callaway and Ridenour 2004; Heneghan et al. 2008). Invasive plants often reduce

richness of native plants and change vegetation structure (Levine et al. 2003; Vilà et al. 2011), which can have concomitant effects on the future success of native plants. Changes in the composition of litter or presence of nitrogen-fixing bacteria following plant invasion may alter soil fertility and seedling establishment (Vitousek 1990; Alpert and Maron 2000; Ehrenfeld 2002; Vinton and Goergen 2006; Wolkovich et al. 2009). Allelopathic chemicals produced by invasive plants inhibit mycorrhizal symbionts (Callaway and Ridenour 2004; Koger and Bryson 2004; Stinson et al. 2006; Callaway et al. 2008; Wolfe et al. 2008). These compounding changes create challenges when managers seek effective tools to reduce the dominance of an invasive plant.

Invasive plants may create feedback loops that inhibit traditional restoration strategies, such as prescribed fire (D'Antonio and Vitousek 1992; Bryson and Carter 2004; Vinton and Goergen 2006; Alba et al. 2015). In areas dominated by invasive plants, removing

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the existing plant community through some sort of disturbance (e.g., grazing/mowing, fire, herbicide, disking) can alter succession, changing the availability of appropriate growing conditions (e.g., light exposure and soil temperature), potentially resulting in growth of a different suite of plants than those currently present (Luken 1990). Disking mixes the seed bank but can also favor invasive species (Hobbs and Huenneke 1992; D'Antonio et al. 1999). The existing seed bank may not be sufficient to restore the diversity of native plants if invasive species and only a few native species dominate (e.g., Robertson and Hickman 2012). Given that competition and seed limitation can reduce restoration and recovery of native plants (DiVittorio et al. 2007), adding seeds of native plants to areas dominated by invasive plants can alter competitive relationships and promote establishment of native species (Pywell et al. 2002, 2007).

Changes in the structure and composition of native plant communities can have concomitant shifts in arthropod communities, especially because of their limited mobility and specialized relationships with plants for food, cover, and sites for reproduction (Kremen et al. 1993). Different functional groups could demonstrate contrasting responses to plant invasion (e.g., Mitchell and Litt 2016; Andersen et al. 2019), where predators and detritivores could benefit from structural changes in vegetation (e.g., Kappes et al. 2007; Pearson 2009; Alerding and Hunter 2013; Lau 2013) and herbivores could be affected negatively due to reductions in food resources (Burghardt and Tallamy 2015; Mitchell and Litt 2016; Andersen et al. 2019). Arthropods provide important ecosystem services, such as pollination, decomposition, and seed dispersal (Wilson 1987; Archer and Pyke 1991; Brussaard 1997), and changes in arthropod communities associated with invasion could also alter the integrity of these services.

Old World bluestems (OWBs, *Bothriochloa* Kuntze and *Dichanthium* Willem. spp.) are a group of warm-season perennial grasses that were introduced as cattle forage and have become dominant in the central and southern United States (Kartesz and BONAP 2015; USDA-NRCS 2019; Wied et al. 2020). Where dominant, OWBs reduce the diversity of native plants (Gabbard and Fowler 2007), arthropods (Woodin et al. 2010; Cord 2011; Mitchell and Litt 2016; Bhandari et al. 2018a, 2018b, 2018c), and other wildlife (Sammon and Wilkins 2005; Hickman et al. 2006; Grahmann et al. 2018). Attempts to reduce the dominance of OWBs with prescribed fire have had varying success, as OWBs may alter the frequency and intensity of fire (Reed et al. 2005), and any restorative effects typically are short-lived (Berg 1993; Simmons et al. 2007; Ruckman et al. 2011; Twidwell et al. 2012; Reemts et al. 2019). Dee et al. (2016) found that yellow bluestem (*Bothriochloa ischaemum* [L.] Keng) initially declined after mowing but reestablished once mowing ceased. Herbicides generally reduce dominance of OWBs in the short term but may impede restoration success through the loss of native plants (Harmony et al. 2004, 2007; Mittelhauser et al. 2011; Ruffner and Barnes 2012).

When OWBs dominate aboveground vegetation, they are also dominant in the seed bank belowground (Robertson and Hickman 2012). Native plant species persist in the seed bank in the face of OWB invasion, but continued inputs of OWB seeds with increased time since invasion may limit restoration potential (Robertson and Hickman 2012). We developed a field-based experiment to test the efficacy of seeding with locally adapted propagules and soil disturbance (disking) for reducing the dominance of OWBs. Seeding and soil disturbance have not been evaluated for OWBs but may provide an alternative restoration tool to fire and herbicides. We also were interested in understanding how these restoration techniques would affect native plant and arthropod communities. To understand the diversity of arthropod-related changes, we focused on responses of different functional groups (herbivores, decomposers, predators, and ants).

In 2011, a severe drought event coincided with and persisted throughout our study (NDMC-UNL 2014). Drought conditions can limit the competitive ability of native plants (Everard et al. 2010; Larios et al. 2013), especially given that OWBs tolerate drought conditions (White and Dewald 1996; Bhat et al. 2011; Liu et al. 2017; Wied et al. 2020). However, we know relatively little about how severe drought could affect seed banks and, therefore, restoration success (Ooi 2012). The drought provided us with the opportunity to test the efficacy of restoration treatments under extreme conditions, which is especially important in the face of changes in climatic patterns (Ooi 2012). Drought also may limit food resources (Frampton et al. 2000; Scheirs and De Bruyn 2005; McCluney and Sabo 2009; Buchholz et al. 2013), altering composition of the arthropod community.

We predicted that we would observe more species of native plants with seeding. We also predicted that if abundance and species richness of native plants increased and OWBs were less dominant with seeding, we would observe subsequent increases in abundance and species richness of arthropods. We expected the benefits of restoration treatments to increase as drought severity decreased. Understanding how multiple stressors combine to affect native plants and arthropods may improve our ability to implement robust restoration tools.

Methods

Study site

We conducted our research at the Welder Wildlife Refuge (28.12155°N, 97.442808°W), a 3 157-ha refuge located 12 km northeast of Sinton, southern Texas. The vegetation was classified historically as a mesquite-buffalograss community but is now dominated by Kleberg bluestem (*Dichanthium annulatum* [Forssk.] Stapf). We determined the soil type to be a Victoria Clay, a calcareous, slightly to moderately alkaline Ustert clay commonly encountered in the landscape (USDA-SCS 1979).

Study design

We established fifty 6 × 9-m experimental plots in an undisturbed area dominated by OWBs. Plots were separated by 1.5-m buffers, and the entire area was bordered by a 2-m-wide firebreak. We selected plot placement, plot size, and buffer size based on the maneuverability of disking equipment used to maintain buffers and prepare the treatment plots. We also established five 6 × 9-m plots at random in an undisturbed part of the OWB monoculture away from the experimental plots, to serve as a reference (hereafter referred to as "OWB plots"). These reference OWB plots were spatially separated to facilitate disking of the experimental plots. We determined that plots were dominated by Kleberg bluestem (> 90% canopy cover) by visually estimating canopy cover to the nearest 5% on two 1-m² quadrats placed randomly within each plot in 2011, one wk before treatment.

We explored soil disturbance alone and in combination with planting a native, locally adapted seed mix (Table 1). We randomly assigned seeding treatments to experimental plots and established 25 plots with seed and 25 plots without (50 total experimental plots, all with soil disturbance). Soil disturbance consisted of disking with an off-set disk at a depth of 15 cm; all 50 plots were disked once in June 2011, which removed all standing vegetation. We planted a mixture of native seeds on 25 of the 50 plots at a rate of 13.0 kg•ha⁻¹ of pure live seed, using a native seed drill (Truax Flex III, Truax Company, New Hope, MN). The species and quantities included in the seed mix were based on native plants observed during pretreatment vegetation sampling (canopy cover by species, see earlier) or selected by

Table 1
Species composition of the native seed mix used for restoration treatments.

| Common name | Species name | Variety | % of seed mix | Pure live seed (kg•ha ⁻¹) |
|----------------------------------|---|------------|---------------|---------------------------------------|
| Slender grama | <i>Bouteloua repens</i> (Kunth) Scribn. & Merr. | Dilley | 34.81 | 4.48 |
| Tallow weed blend | <i>Plantago</i> L. spp. | Divot | 13.05 | 1.68 |
| Texas grama | <i>Bouteloua rigidisetata</i> (Steud.) Hitchc. | Atascosa | 11.31 | 1.46 |
| Buffalograss | <i>Bouteloua rigidisetata</i> (Steud.) Hitchc. | Texoka | 6.61 | 0.85 |
| Little bluestem | <i>Schizachyrium scoparium</i> (Michx.) Nash | Common | 6.53 | 0.84 |
| Sideoats grama | <i>Bouteloua curtipendula</i> (Michx.) Torr. | Haskell | 3.48 | 0.45 |
| Pink pappusgrass | <i>Pappophorum bicolor</i> Fourn | Maverick | 3.31 | 0.43 |
| Whiplash pappusgrass | <i>Pappophorum vaginatum</i> Buckley | Webb | 3.05 | 0.39 |
| Bristlegrass | <i>Setaria</i> P.Beauv.spp. | Catarina | 2.44 | 0.31 |
| Hairy grama | <i>Bouteloua hirsuta</i> Lag. | Chaparral | 1.83 | 0.24 |
| Multiflowered false Rhodes grass | <i>Trichloris pluriflora</i> Fourn | Common | 1.74 | 0.22 |
| Arizona cottontop | <i>Digitaria californica</i> (Benth.) Henr. | La Salle | 1.74 | 0.22 |
| Hall's panicum | <i>Panicum halli</i> Vasey var. <i>halli</i> | Oso | 1.74 | 0.22 |
| Canada wildrye | <i>Elymus canadensis</i> L. | Lavaca | 1.65 | 0.21 |
| Hooded windmillgrass | <i>Chloris cucullata</i> Bisch. | Mariah | 1.13 | 0.15 |
| Green sprangletop | <i>Leptochloa dubia</i> (Kunth) Nees | Van Horn | 0.87 | 0.11 |
| Big sacaton | <i>Sporobolus wrightii</i> Munro ex Scribn. | Falfurrias | 0.87 | 0.11 |
| Shortspike windmillgrass | <i>Chloris x subdolichostachya</i> Müll. Berol (pro sp.) [cucullata x verticillata] | Welder | 0.78 | 0.10 |
| Dwarf prairie clover | <i>Dalea nana</i> Torr. ex A. Gray | Cuero | 0.78 | 0.10 |
| Sand dropseed | <i>Sporobolus cryptandrus</i> (Torr.) A. Gray | N/A | 0.78 | 0.10 |
| Awnless bush sunflower | <i>Simsia calva</i> (Engelm. & A. Gray) A. Gray | Plateau | 0.44 | 0.06 |
| Partridge pea | <i>Chamaecrista fasciculata</i> (Michx.) Greene | Lark | 0.35 | 0.04 |
| Engelmann daisy | <i>Engelmannia pinnatifida</i> A. Gray ex Nutt | Eldorado | 0.35 | 0.04 |
| Wild tanton | <i>Desmanthus virgatus</i> (L.) Willd. | Sabine | 0.17 | 0.02 |
| False Rhodes grass | <i>Trichloris crinita</i> (Lag.) Parodi | Kinney | 0.17 | 0.02 |

South Texas Natives (Kingsville, TX, see Table 1). Initially, we also explored several treatments to modify soil chemistry (e.g., additions of carbon, powdered lime, sulfur) with and without seed; however, we did not detect evidence of treatment effects (all tests: $P > 0.13$, Mitchell 2014) and instead focused our analysis on the effects of soil disturbance with and without the addition of native seeds (disked and seeded, disked and unseeded). We also made comparisons to the OWB plots (undisked and unseeded).

Precipitation data

We collected rainfall data from a weather station located 386 m from the study area. We quantified precipitation by month from the start of the water year (October), 2010–2013. We used the Palmer Drought Severity Index (NCDC-NOAA 2014) as a measure of drought severity for each field season (June–August) in the study.

Vegetation sampling

We measured canopy cover of vegetation on two 1-m² quadrats in each plot every month after seeding during summers 2011–2013 (June–August). Quadrats were placed at random within each plot for each sampling period but always were at least 1 m from plot boundaries to avoid edge effects. We visually estimated canopy cover (≤ 1 -m tall) by species to the nearest 5% within the same 1-m² quadrats and later combined species-specific cover values into two cover classes: forbs (herbaceous plants) and native grasses. Woody plants represented < 1% of all plants recorded and were not considered for analysis. We used species richness and canopy cover as measures of community richness and structure, respectively. No vegetation grew during the first 2 mo after treatment due to severe drought. As such, we did not analyze vegetation data from 2011.

Arthropod sampling

We sampled arthropods after completing vegetation sampling (monthly, June–August during 2011–2013) in each plot within the same 1-m² quadrats. We used three sampling techniques to collect arthropods and waited 24 h between each technique to allow the arthropod community to recover. First, we placed two pitfall traps (266-mL plastic cups) randomly within each quadrat and filled each halfway with propylene glycol. Pitfall traps were collected 24 h later. We then collected arthropods on the vegetation using a vacuum sampler (Rincon-Vitova Insectaries, Ventura, CA). We vacuumed each quadrat for 90 sec and transferred specimens into a plastic bag with cotton balls soaked with ethyl acetate to prevent predation. Finally, we extracted arthropods from the soil using Berlese-Tullgren funnels (BioQuip Model 2845, Bio-Quip, Compton, CA, modified with a smaller-diameter mesh filter [0.32 × 0.32 cm]). We collected 473 mL of soil from each quadrat, placed soil in a funnel, and exposed soil to sunlight for 48 h to facilitate extraction.

We identified all arthropods to the lowest taxonomic unit; when possible, we identified to morphospecies (Oliver and Beatie 1996). We determined arthropod taxa as native or nonnative based on online records of distribution in North America (<http://bugguide.net>). We quantified richness and abundance of arthropods as measures of overall community composition and structure. We also designated each arthropod to a functional group that represented the taxon's feeding guild (Appendix A). We classified herbivores as taxa that subsist on living plant tissue but also included fungivores that fed on fungi in living plant tissues, as these arthropods were supported by the green food web. We classified decomposers as taxa that subsist on either dead organic matter or consume microorganisms (i.e., bacteria and fungi) that break down organic matter (Brussaard 1997). We classified predators as species that consume living animals, in whole or in part, to complete their life cycle; we considered parasitoids as predators for the purpose of this study. We considered ants as a separate functional group due to the taxa's varied role in ecosystems (Wilson 1987; Brussaard 1997). We removed immatures or larval taxa that dif-

ferred in diet from their adult stages due to a lack of taxonomic resolution; these taxa represented < 1% of individuals collected.

Data analysis

We analyzed differences in vegetation and arthropod characteristics among experimental plots (disked, then seeded or unseeded) and OWB plots (undisked and unseeded) using generalized linear mixed models. We considered treatment (seeded, unseeded, or OWB plots) and drought severity (using year as a proxy) as independent factors in models. We also explored evidence for a two-way interaction (treatment • year), but removed this term from final inferential models when $P > 0.10$. We accounted for repeated sampling (i.e., sampling monthly [June–August] each summer and over multiple years) and considered covariance structures in each model (no within-group covariance, compound symmetric, and first-order autoregressive), selecting the most appropriate based on AIC value. To analyze difference in arthropod abundance (overall and by functional group), we used a Poisson distribution and a log link. We provide means and 95% confidence intervals (95% CI) in the text as estimates of effect sizes and precision and include all test statistics (F for overall effects, t and z for specific comparisons based on linear and Poisson models, respectively) and P values in tables. All analyses were completed in R (R v. 3.1.2, R Foundation for Statistical Computing, Vienna, Austria) using the lme, nlme, and MASS packages (Venables and Ripley 2002; Bates et al. 2014; Pinheiro et al. 2018).

Results

Precipitation

Total annual rainfall measured 32.3 cm, 62.5 cm, and 69.1 cm for 2011, 2012, and 2013, respectively. Annual rainfall on the study site represented 36% of the long-term average in 2011, 69% in 2012, and 76% in 2013. Drought severity was extreme (< -4.00) in 2011, moderate (-3.99 to -3.00) in 2012 and no drought (-1.99 to 1.99) in 2013 (NCDC-NOAA 2014).

Vegetation

We identified 53 plant species, including 17 species of native grasses, 4 invasive grasses, 30 forbs, and 2 woody plants (Appendix B). Kleberg bluestem and hogwort (*Croton capitatus* Michx.) were common in all plots (see Appendix B). We observed seven species that were included in the native seed mix (*Bouteloua curtipendula* [Michx.] Torr., *B. repens* [Kunth] Scribn. Ex Vasey, *Chloris cucullata* Bisch., *Elymus canadensis* L., *Panicum halli* Vasey var. *halli*, *Pappophorum bicolor* Fourn., *Setaria* P. Beauv. spp.), but these species represented only 2% of all plants observed in seeded plots (see Appendix B).

In seeded plots, richness of native plants was 2.6× higher (95% CI = 2.2–3.1) and cover of native grasses was 426.8× higher (102.5–1 777.3, Figs. 1a and 1b, Table 2), compared with OWB plots. Similarly, disking alone increased species richness of native plants (2.1×, 1.7–2.5) and native grass cover (60.5×, 14.5–252.1), compared with OWB plots (see Figs. 1a and 1b). Cover of native forbs increased by 46.1× (12.5–169.2) in disked plots and 58.0 times (15.8–213.4) times in seeded plots, compared with OWB plots; forb cover in seeded plots increased further as drought subsided (see Fig. 1c). Dominance of OWBs was lower in seeded plots (see Fig. 1d). Specifically, seeded plots had 98.5% less OWB cover (90.0–99.8% decline), compared with OWB plots during moderate drought; this reduction was similar when drought subsided (see Fig. 1d). Disking alone reduced cover of OWB to some degree, but there was substantial variation in this response (see Fig. 1d).

Table 2

Factors affecting vegetation characteristics on experimental plots (disked, then unseeded/seeded) and Old World bluestem plots (undisturbed OWB monocultures) based on generalized linear mixed models, southern Texas, summers 2012–2013. We used year as a proxy for drought severity and removed the interaction term from final inferential models when $P > 0.10$. For models that include the interaction term, denominator $df = 272$ for the yr effect.

| Vegetation variable | Treatment | | Yr | | Treatment • Yr | |
|---------------------|------------|---------|-------------|---------|----------------|---------|
| | $F_{2,52}$ | P | $F_{1,274}$ | P | $F_{1,272}$ | P |
| Species richness | 62.41 | < 0.001 | 10.25 | 0.002 | | |
| Native grass cover | 39.17 | < 0.001 | 30.34 | < 0.001 | | |
| Forb cover | 53.75 | < 0.001 | 1.39 | 0.240 | 8.94 | < 0.001 |
| OWB cover | 38.08 | < 0.001 | 4.10 | 0.044 | 5.44 | 0.005 |

Table 3

Factors affecting arthropod characteristics on experimental plots (disked, then unseeded/seeded) and Old World bluestem (OWB) plots (undisturbed OWB monocultures) based on generalized linear mixed models, southern Texas, summers 2011–2013. We used linear and Poisson models for richness and abundance, respectively. We used year as a proxy for drought severity and removed the interaction term from final inferential models when $P > 0.10$. For models that include the interaction term, denominator $df = 381$ for the yr effect.

| Arthropod variable | Functional group | Treatment | | Yr | | Treatment • Yr | |
|--------------------|------------------|------------|---------|-------------|---------|----------------|---------|
| | | $F_{2,52}$ | P | $F_{2,383}$ | P | $F_{2,338}$ | P |
| Richness | Total | 3.18 | 0.050 | 112.40 | < 0.001 | | |
| | Herbivores | 1.44 | 0.245 | 146.50 | < 0.001 | | |
| | Decomposers | 5.49 | 0.007 | 57.09 | < 0.001 | | |
| | Predators | 0.71 | 0.495 | 107.22 | < 0.001 | | |
| | Ants | 2.03 | 0.142 | 4.56 | 0.011 | | |
| Abundance | Total | 32.18 | < 0.001 | 1 077.78 | < 0.001 | 307.18 | < 0.001 |
| | Herbivores | 39.40 | < 0.001 | 951.47 | < 0.001 | 108.88 | < 0.001 |
| | Decomposers | 13.23 | < 0.001 | 864.70 | < 0.001 | 55.06 | < 0.001 |
| | Predators | 4.04 | 0.023 | 145.59 | < 0.001 | 46.47 | < 0.001 |
| | Ants | 1.65 | 0.202 | 8.95 | < 0.001 | | |

Arthropods

We captured 36 588 arthropods, representing 35 orders, 209 families, and 456 species in the experimental plots (see Appendix A). In contrast, we captured 20 821 arthropods, representing 23 orders, 109 families, and 155 species in OWB plots (Appendix C). Species richness of arthropods in experimental plots did not differ from OWB plots (disked: $t_{52} = -0.84$, $P = 0.41$; seeded: $t_{52} = 0.62$, $P = 0.54$), but richness increased as drought severity decreased. Specifically, we recorded 1.7× more arthropod species m^{-2} (95% CI = 1.6–1.9) during moderate and no-drought conditions compared with severe drought (Fig. 2a). Although we did not observe any living vegetation in experimental plots during severe drought (2011), abundance of arthropods in these disturbed areas was comparable with undisturbed OWB plots (disked: $z = -0.83$, $P = 0.41$; seeded: $z = -0.24$, $P = 0.81$, see Fig. 2b). As drought severity decreased, however, OWB plots had more arthropods than experimental plots (see Figs. 2c and 2d). OWB plots had 1.3× more arthropods m^{-2} (1.2–1.5) during moderate drought and 3.5× more (3.1–4.0) when drought conditions subsided, compared with seeded plots (see Figs. 2c and 2d).

We did not detect differences in richness of herbivorous arthropods on the basis of treatment over time (treatment • year, $F_{4,379} = 1.58$, $P = 0.18$) or among treatments (Table 3). However, richness of herbivores was 6.1× higher in all plots (4.9–7.7), as drought conditions subsided between 2011 and 2013. During severe drought (2011), we did not detect differences in abundance of herbivorous arthropods between experimental and OWB plots (disked: $z = 0.86$, $P = 0.39$; seeded: $z = -1.15$, $P = 0.25$). In comparison, as drought severity decreased, OWB plots consistently had more arthropods than experimental plots; OWB plots had 3.1× more herbivores m^{-2} (2.1–4.6) during moderate drought and 7.2× more (4.9–10.7) when drought conditions subsided, compared

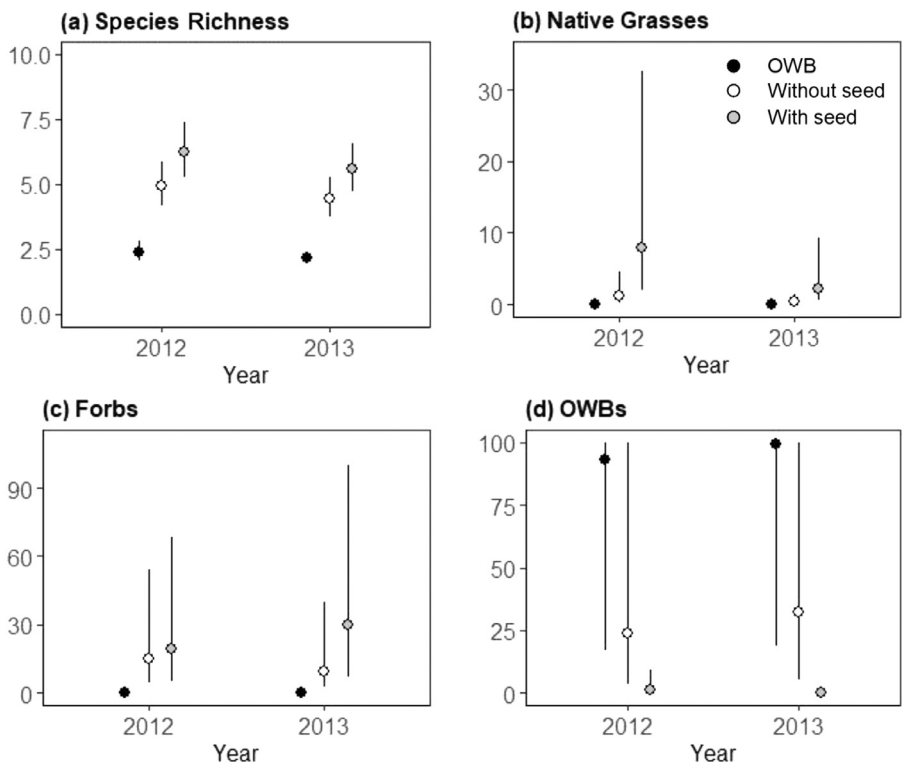


Fig. 1. Vegetation characteristics (means and 95% confidence intervals) for Old World bluestem plots (black) and unseeded (white) and seeded (gray) experimental plots, including species richness of plants (species•m⁻²) and canopy cover by cover class (%), southern Texas, summers 2011–2013. See Table 2 for test statistics and P values.

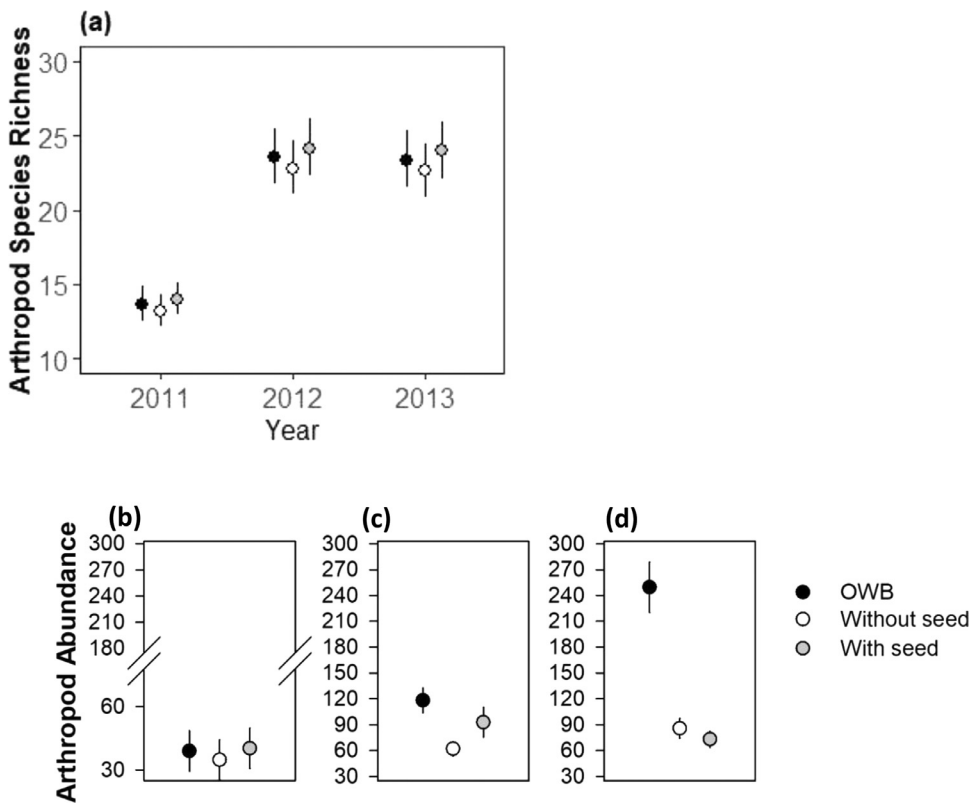


Fig. 2. Arthropod characteristics (means and 95% confidence intervals) for Old World bluestem plots (black) and unseeded (white) and seeded (gray) experimental plots, including total species richness (species•m⁻²) and abundance of arthropods (individuals•m⁻²), southern Texas, summers 2011–2013. See Table 3 for test statistics and P values.



Fig. 3. The invasive leafhopper (*Balclutha rubrostriata*) alongside a floret of Kleberg bluestem (*Dichanthium annulatum*).

with seeded plots. Differences in the abundance of herbivores were driven by the invasive red-streaked leafhopper (*Balclutha rubrostriata*) and generalist mites (Mochlozetidae), which represented 32% (2 355 individuals) and 18% (1 330) of all herbivores collected in experimental plots, respectively (see Appendix A). In contrast, these two herbivorous taxa represented 43% (1 844) and 51% (2 238) of all herbivores collected in OWB plots (see Appendix C).

Richness of decomposer arthropods differed between experimental and OWB plots (see Table 3); OWB plots had 1.2 \times more species m^{-2} (1.1–1.4) than seeded plots and 1.3 \times more species m^{-2} (1.1–1.5) than unseeded plots. Richness of decomposer arthropods was also higher as drought conditions subsided between 2011 and 2013 (1.5 \times higher, 1.4–1.7). In contrast, the density of decomposers differed by treatment and drought severity (see Table 3). During severe drought, abundance of decomposers was 1.4 \times higher on OWB plots compared with seeded plots (1.1–1.9) and 1.5 \times higher on OWB plots compared with unseeded plots (1.1–2.0). During moderate drought, disking and adding seed increased decomposer abundance by 1.8 \times (1.4–2.2) compared with OWB plots, whereas we did not detect differences between OWB plots and disking alone ($z = 1.07$, $P = 0.29$). However, decomposer abundance was higher on all experimental plots than OWBs plots once drought conditions subsided in 2013 (disked: 1.7 \times , 1.3–2.1; seeded: 1.4, 1.2–1.8). Differences in the abundance of decomposers between experimental and OWB plots were driven mainly by invasive pillbugs (*Armadillidium vulgare*), which represented 48% (4 933 individuals) of all decomposers collected (see Appendix A).

We did not detect differences in richness of predator arthropods between experimental and OWB plots (see Table 3), but the richness of predators was 2.0 \times higher (1.8–2.2) as drought conditions subsided (between 2011 and 2013). We detected little difference in predator abundance between experimental and OWB plots during severe drought (disked: $z = -1.1$, $P = 0.27$; seeded: $z = 0.13$, $P = 0.41$), but this changed as drought severity decreased (see Table 3). During moderate drought, OWB plots had 2.0 \times more predators (1.7–2.4) compared with seeded plots and 1.7 \times more predators (1.4–2.0) compared with unseeded plots. As drought conditions subsided in 2013, OWB plots had 1.7 \times more predators (1.3–2.3) compared with seeded plots, but we did not detect a difference from unseeded plots ($z = 0.06$, $P = 0.95$). Predatory mites (Anystidae) and thrips (*Aeolothrips* spp.) were the most dominant taxa in all plots (Mitchell 2014).

We did not detect differences in species richness of ants among treatments, but richness declined as drought subsided (see Table 3); we collected 24% fewer ant species (8–37% fewer) in 2013, compared with 2011. We also did not detect differences in ant abundance between experimental and OWB plots (see Table 3). Ant abundance was highest during severe drought and declined by 36% (14–53% fewer) as drought subsided in 2011.

Discussion

Exploring effectiveness of restoration treatments is especially important in the face of compounding disturbances—in our case, drought and plant invasion. We documented increased species richness, cover of native plants, and reduced dominance of invasive plants following a combination of soil disturbance and seeding of native plants, even during drought. These changes in vegetation resulted in increased presence and abundance of native arthropod species 1 yr after treatment, highlighting the short-term benefits of disking and adding native seed to improve habitat for grassland invertebrates.

LaForgia et al. (2018) documented increases in native forbs and decreases in exotic annual grasses, both aboveground and belowground, during drought; we found additional restorative benefits of seeding in the face of drought conditions. Although we observed more species and increased cover of native plants after adding locally adapted seed, most of the plants we recorded in seeded plots were early successional and drought-tolerant species (see Appendix B) not included in the seed mix. The observed seed effect suggests that plant composition may have been influenced by factors other than the seeding treatment. We hypothesize that arthropods may have been responsible. For example, *Solenopsis geminata*, a native, granivorous fire ant, increased in abundance following the addition of seed (Mitchell 2014). Harvester ants (*Pogonomyrmex* spp.), although uncommonly collected during the study ($\sim 3\%$ of all individuals), were sampled exclusively in seeded plots (see Appendix A). Although granivores could reduce the effectiveness of seeding as a restoration treatment (MacDougall and Wilson 2007; Linabury et al. 2019), the arthropods may have been consuming the added seed rather than the seed bank, permitting native plants in the seed bank to establish.

Differences between experimental and OWB plots in the abundance of plant-feeding arthropods were driven largely by two taxa: an invasive leafhopper (red-streaked leafhopper, *B. rubrostriata*) and generalist mite (Mochlozetidae) dominated OWB plots as drought severity decreased (see Appendix C, Mitchell and Litt 2016). The native range of the invasive red-streaked leafhopper overlaps with the native range of many OWBs, and in the United States the hopper has been reported where OWBs are dominant (Zahniser et al. 2010; Morgan et al. 2013). We collected most of these leafhoppers ($\sim 99\%$) when OWBs were in flower. Interestingly, the invasive red-streaked leafhopper is similar in size and shape to flowers of Kleberg bluestem (Fig. 3). OWBs may serve as a plant host in the invasive red-streaked leafhopper's introduced range, and leafhoppers may use flowers to avoid predation. In addition to altering the arthropod composition in our sites, the invasive red-streaked leafhopper is a concern for the sugarcane industry (Haboosong et al. 2006; Liu and Piper 2016) and reducing

the densities of OWBs is therefore also desirable where susceptible crops are grown.

Like the herbivorous arthropods, differences among treatments in the abundance of decomposer arthropods were driven by an invasive arthropod, a pillbug (*Armadillidium vulgare*, Isopoda). Pillbugs outcompete native decomposers and alter decomposition rates where they are dominant (Ellis et al. 2000; Frouz et al. 2008; Singer et al. 2012). OWBs are reportedly more “woody” (i.e., higher C:N ratios) than native grasses (Reed et al. 2005), and decomposers may find native plant litter more palatable. Mitchell and Litt (2016) reported higher densities of the pillbug in communities dominated by native grasses when compared with communities dominated by OWBs, despite similar quantities of litter. Pillbugs may consume seeds when litter is scarce (Saska 2008), and seeding may have provided a supplementary food source.

We suspect the lower abundance of predatory arthropods in seeded plots compared with unseeded plots and undisturbed OWB plots may be due to the presence of generalist and non-native prey. We found an abundance of mites in OWB plots (Mochlozetidae and Anystidae), which may serve as an important prey item for small predators, such as *Aeolothrips* spp. (Bailey 1951). Homogenization of plants or prey may have negative consequences for the complexity and productivity of food webs (Olden et al. 2004; deHart and Strand 2012; Hansen et al. 2009; Lenda et al. 2017; Sterzyńska et al. 2017; Baranová et al. 2018). As a result of reducing OWB dominance, native plant cover may have increased the diversity of prey for some generalist predators, like spiders (Araneae) and harvestmen (*Vonones* spp.), which were more abundant with seeding (see Appendix A).

Implications

We examined the potential of seeding locally adapted plants to restore native grassland communities impacted by an invasive grass and observed reduced dominance of the invasive grass, increased cover of native plants, and subsequent changes in the community of native arthropods, even in the face of drought. We hypothesize that granivorous arthropods altered the effectiveness of our seeding treatment but also may have improved restoration outcomes if seeds provided a supplementary food source. Sampling arthropod communities before restoration may help determine which tools would be most successful. Nonnative arthropods were dominant in both experimental and OWB plots; additional effort may be needed to increase native arthropods even after seeding or restoration techniques have increased native plant diversity. Shifts in the composition of the arthropod community due to plant invasion and drought can alter food availability for native grassland fauna (Hickman et al. 2006; Litt and Steidl 2010; Woodin et al. 2010). Because changes in climate patterns and establishment of invasive species are likely to be more common and widespread, management strategies that aim to restore vegetation communities and habitat for other organisms will likely require an understanding of how communities respond to multiple disturbances.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary Materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.rama.2021.03.003.

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