The effects of initial vegetation composition, seed availability, fire and competition on herbaceous species recruitment in savannas and savanna restoration

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INTRODUCTION & STUDY SYSTEM

• Species composition of savannas and grasslands is highly affected by disturbance, seed availability, species traits, and competition.

• Models based on ecological filters envision community assembly as a narrowing down of the potential pool of species that could be present in a given community; this narrowing down is due to biotic and abiotic constraints or filters (Fattorini & Halle 2004).

• Fire is an ecological filter that can act to contract or expand niche space. Many species are fire-adapted and their persistence in a community may be dependent on recurring disturbance via fire (Bond and Keeley 2005). Fire can also eliminate species that do not have the traits necessary to regenerate after fire.

• This study examined the joint effects of initial species composition and competition reduction (through fire, clipping, or mechanical clearing) on community assembly by examining germination and establishment rates of seeds added to manipulated plots. The following hypotheses were tested:

- H1. Native species germination and establishment will be higher in native-dominated than invasive-dominated plots.
- H2. Native species germination and establishment will be higher in manipulated than unmanipulated plots. Specifically, establishment will be higher in burned than clipped or mechanically cleared plots.
- H3. Prescribed fire and clipping are equally effective at reducing invasive grass density.

• There are many factors to consider when choosing species for restoration projects such as germination rate, establishment success, and resistance to invasion from exotic species (Funk 2008). This study examined germination and survival rates of several native species with a variety of traits. Possible mechanisms that may determine species success, i.e., high germination and/or survival rates, include:

- *Similarity to invader* - the concept of limiting similarity predicts that species that are similar to the invader (share niche and resource space) will exclude invasive species from the restored community.
- *Rapid growth and establishment* - early successional and/or fast growing species are ideal for restoration as they can get to the site earlier than the invaders, pre-empting niche space.
- *Dissimilar to the invader* - species with different traits from the invader (e.g. different growth forms) will be able to coexist with the invader, increasing native species diversity

STUDY SITE

Balcones Canyonlands National Wildlife Refuge (BCNWR) on the eastern edge of the Edwards Plateau in central Texas

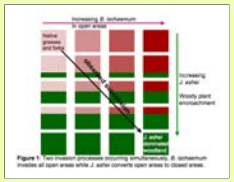


Figure 1. Two invasion processes occurring simultaneously. *B. ischaemum* invades all open areas while *J. ashei* canopy converts open areas to closed areas.

• There are two invasion processes that occur simultaneous in central Texas: woody plants, primarily *Juniperus ashei*, encroach on savannas while the grass *Bothriochloa ischaemum* invades areas that are still open (Fig 1). Mechanical clearing can slow or reverse woody plant encroachment; however, *B. ischaemum* often invades in sites that have been cleared of *J. ashei*, preventing the restoration of a native-dominated open system.

• There is as yet no satisfactory control of *B. ischaemum*, although intense warm-season fires may be effective (Simmons et al. 2007).

METHODS

Plots were set up in two sites to examine the effects of initial vegetation composition and manipulation on added species germination and establishment rates (below, Table 1)

Grassland site– abandoned agriculture field initially dominated by the non-native invasive grass *Bothriochloa ischaemum*. Treatments were a combination of manipulation (burn, clipping, unmanipulated) and initial vegetation composition (native or invasive dominated).
Restoration goal: Restore native savanna by removing *B. ischaemum* and promoting native species richness

Woodland site - site initially dominated by the native invasive tree *Juniperus ashei*. Treatments were mechanical clearing with or without fire and woody debris removal.
Restoration goal: Restore native savanna by removing *J. ashei* and promoting native species richness.

Table 1. List of treatments (TR) in the two sites.

Site	TR	Description
Grassland	BI	Burned-Invasive dominated. Warm season, high intensity prescribed fire in July 2009
Grassland	BN	Burned-Native dominated
Grassland	UI	Unmanipulated-Invasive dominated
Grassland	UN	Unmanipulated-Native dominated
Grassland	CI	Clipped-Invasive dominated (unburned)
Woodland	B+MC	Burned plus mechanical clearing of *J. ashei*. Prescribed fire in January 2009.
Woodland	U+MC+R	Unburned, mechanical clearing of *J. ashei*, woody debris removed from plot.
Woodland	U+MC	Unburned, mechanical clearing of *J. ashei*, woody debris left on plot.
Woodland	U	Unmanipulated

grassland site

woodland site

prescribed fire at grassland site

Seeds of 17 species were added in November 2009 to plots in the two sites (Table 1&2) after manipulation. The 2x1-m plots were divided into 50-cm rows spaced 10-cm apart (one species added per row). Plots were monitored for germination in Spring 2010. Survival, new germinants, and the % invasive grass cover in each row were recorded in Spring 2011.
A variety of native species were chosen for seed addition with a mixture of traits (Table 2).
Data were analyzed using generalized linear mixed models, GLIMMIX procedure, SAS 9.2.

Table 2. Species used in seed addition. Listed in approximate order from largest to smallest

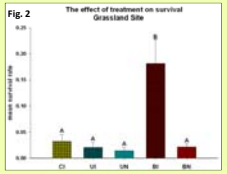
Grasses	Forbs
Schizachryium scoparium	*Ipomopsis rubra*
Bothriochloa ischaemum	*Ratibida columnifera*
Bothriochloa laguroides	*Monarda citriodora*
Leptochloa dubia	*Gaillardia pulchella*
Bouteloua curtipendula	*Liatris mucronata*
Aristida purpurea	*Senna roemeriana*
Aristida purpurea	*Glandularia bipinnatifida*
Hilaria belangeri	*Asclepias asperula*
	Desmanthus illinoensis

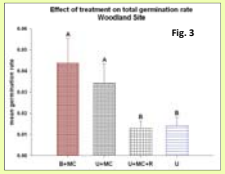
RESULTS

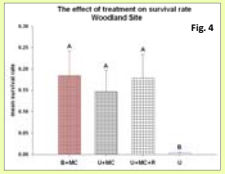
Effects of treatment on total germination & survival rates

There was no difference in total germination rates between treatments at Grassland site. Survival, defined as the number of germinants that survived from Spring 2010 to 2011, was significantly higher in the burned-invasive (BI) treatment (Fig 2).

At the Woodland site, total germination rate was significantly greater in burned plus mechanical clearing (B+MC) and mechanical clearing only (U+MC) plots than in mechanical clearing with debris removal (U+MC+R) or unmanipulated (U) plots (Fig. 3). Mechanical clearing and/or burning were equally effective at promoting native species survival (Fig. 4).







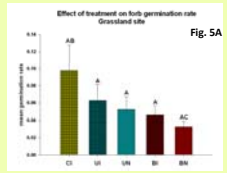
Grasses & forbs, germination & survival

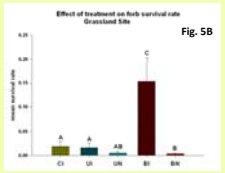
Forbs had a significantly higher germination rate than grasses at both sites ($P < 0.0001$), although at the Grassland site, grasses had a higher survival rate ($P < 0.0001$). The disparity is most likely due to the higher proportion of annual forbs that germinated as opposed to the mostly perennial grasses.

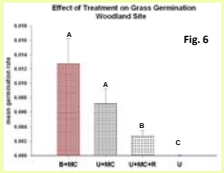
At the Grassland site, forb germination rate in the clipped-invasive (CI) treatment was significantly higher than in the burned-native (BN) treatment ($P = 0.0036$, Fig. 5a). Survival was greatest in the burned-invasive (BI) treatment, indicating that burning may remove a higher amount of invasive grass biomass than clipping (Fig. 5b).

There was a non-significant trend towards higher germination and survival rates in invasive-dominated plots than in native dominated plots within the burned and unburned pairs (Fig. 5AB).

Grasses at the Grassland site were significantly less likely to germinate in the unburned-invasive (UI) treatment than other treatments ($P < 0.01$)







Forb germination rate was uniform across all treatments at the woodland site. Fire and/or cutting significantly increased forb survival as compared to the unmanipulated treatment ($P < 0.0001$).

Cutting and/or burning significantly increased grass germination as compared to the unmanipulated treatment (Fig. 6). Within the unburned plus mechanical clearing treatments, (U+MC and U+MC+R), leaving woody plant debris following cutting significantly increased grass germination rates (Fig. 6), indicating that grasses benefit from protection by woody debris.

Effect of treatment on individual species germination and survival

The forbs with the highest germination and survival rates included the tall *Ipomopsis rubra* and *Ratidbida columnifera*, as well as the quickly growing *Gaillardia pulchella* and *Monarda citriodora*.

The grasses with the highest germination and survival rates included: the native conger to the invader, *Bothriochloa laguroides* and the quickly growing *Aristida purpurea*.

The invasive *Bothriochloa ischaemum* had a significantly higher survival rate than the other grass species added ($P < 0.001$).

There was a significant treatment by species interaction ($P < 0.0001$): *Gaillardia pulchella* had a higher germination rate in burned plots (BI, BN), whereas *Ipomopsis rubra* dominated in unburned plots (CI, UI, UN) (Fig. 7)

There was a significant treatment by species interaction ($P < 0.0001$): the native *Bothriochloa laguroides* had a higher germination rate in disturbed plots (BI, BN, CI), while the invader *Bothriochloa ischaemum* had higher germination in unburned-invasive (UI) treatment (Fig. 8)

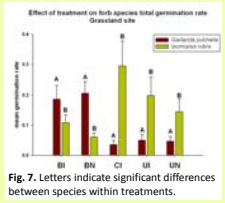


Fig. 7. Letters indicate significant differences between species within treatments.

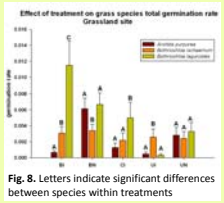


Fig. 8. Letters indicate significant differences between species within treatments

Bothriochloa ischaemum

Burned-invasive plots post fire, note high number of *Gaillardia pulchella* and *Monarda citriodora* seedlings

Ipomopsis rubra, note height

Ratibida columnifera

Gaillardia pulchella

RESULTS CONTINUTED

There was a small but significant negative relationship between the number of germinants on a row and the % invasive grass cover on that row (Fig. 9, ANCOVA P=0.01, slope = -0.027).

There was no significant effect of species identity in a row and the % invasive grass cover in that row. However, given that as the total number of germinants increases, invasive grass cover decreases (Fig. 9), species with high germination rates should be most effective at preventing grass invasion.

Fire effectively reduced invasive grass cover. Burned-invasive plots were not significantly different from burned-native or unburned-native plots (Fig. 9). Clipped-invasive plots also had significantly less invasive grass cover than unburned-invasive plots (Fig. 9). However the effect was much smaller that that of burning.

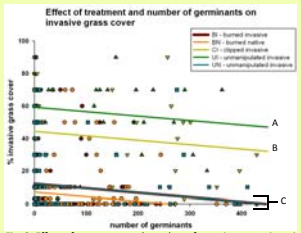


Fig. 9. Effect of treatment and number of germinants on invasive grass cover. Number of germinants refers to the total number of seeds germinated on a row (spring 2010 + spring 2011 seedlings), % invasive grass cover refers to the % of that row covered by *B. ischaemum* in spring 2011. Only the top 3 forbs and grasses data included. Different letters indicate significant differences among treatment means (intercepts in graph).

DISCUSSION

• Native species germination and establishment were not higher in native-dominated plots. Within burned plots, germination and establishment were greater in invasive-dominated than in native plots. Native plant community members are better competitors post fire than the invasive grass.

• Fire and competition reduction (clipping or clearing) are equally effective at increasing native species germination rates. However, fire is more effective than clipping at increasing survival rates, particularly of forbs. Burning most likely removes a higher proportion of invasive grass biomass than clipping alone, which accounts for higher native species establishment.

• Adding seeds alone in the absence of disturbance is not an effective restoration strategy. Native communities in central Texas may be more structured by disturbance regime than by seed limitation.

• The concept of limiting similarity is the most likely mechanism to explain the high establishment success of *Bothriochloa laguroides* in burned or clipped plots with pre-exiting *Bothriochloa ischaemum*.

• *Ipomopsis rubra* is a tall and thin forb with large seeds. It was most likely successful in unburned-invasive dominated plots because it is very dissimilar to the invader. Future monitoring will determine whether *I. rubra* can persist in invasive-dominated communities in the long term.

• Fire disturbance favors species that have traits that allow them to establish and grow rapidly, such as the forb *Gaillardia pulchella*.

• The invader *B. ischaemum* had a significantly higher survival rate than other grasses, indicating a possible invasion mechanism, and highlighting the importance of long-term monitoring of restoration efforts.

• Warm season prescribed fire is more effective than competition reduction alone (clipping) in reducing *B. ischaemum* density. Fire most likely removes a higher proportion of invasive biomass than clipping.

MANAGEMENT IMPLICATIONS

• Land managers should consider using warm-season prescribed fires to control the invasive grass *B. ischaemum*.

• When removing *Juniperus ashei*, prescribed fire and cutting are both effective at promoting native species recruitment. If cutting is used, the woody plant debris should be left in place to increase grass species germination.

unburned plot in burned matrix

• The native perennial *Gaillardia pulchella* is an excellent choice for rapid establishment in post-burn sites.

• Seed mixes should contain a variety of grasses and forbs to promote both rapid initial germination and long-term survival.

• Although warm-season prescribed fires are effective at controlling *B. ischaemum*, their use must be carefully monitored (many plots that were supposed to remain unburned in this experiment were accidentally burned due to fast moving fire behavior).

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