HERBICIDE CONTROL AND SEED BANK

DYNAMICS OF OLD WORLD BLUESTEM

By

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Combining glyphosate with burning or mowing improves control of the invasive grass Old World bluestem (*Bothriochloa ischaemum*)

ABSTRACT The invasive grass Old World bluestem (OWB; *Bothriochloa ischaemum*) threatens native plant and animal diversity, but traditional control methods of using only herbicides have had limited success. I used single, double, and triple applications of glyphosate in various combinations with and without a mowing or burning (prior to the herbicide applications) to determine the most effective treatment for controlling OWB for future restoration. Overall control of OWB was assessed by responses of OWB cover, frequency of live crowns, visual obstruction, and density of basal and reproductive tillers. One year after treatment, burning and mowing prior to a single herbicide application improved the amount of OWB control compared to a single herbicide treatment. Burning or mowing with two herbicide applications provided more OWB control relative to plots that received a double herbicide application without burning or mowing. The burn and mow double herbicide treatments did not exhibit an increase in reproductive tiller density or visual obstruction a year after treatment, whereas plots that received only two herbicide applications did. Burning or mowing with two herbicide treatments provided similar amounts of OWB control compared with the triple herbicide treatment. Combining burning or mowing with herbicide applications provided more effective OWB control than any herbicide applications that were not preceded by burning or mowing. Burning and mowing likely improves glyphosate effectiveness by altering OWB structure

so that plants are shorter with active regrowth, and clear of standing dead material, enhancing herbicide deposition and translocation, improving overall control.

Introduction

Non-native species have been transported by humans into new habitats for a variety of reasons such as landscaping ornamentals, erosion control, and livestock forage (Sax et al., 2005). Following introduction, many of these non-native species escape their original planting, invading and establishing in native ecosystems resulting in altered community structure and ecosystem function (Mooney & Hobbs, 2000; Gurevitch & Padilla, 2004), as well as increasing the risk to threatened and endangered species (Wilcove et al., 1998). Therefore, attention should be focused on invasive species eradication and restoration of invaded systems to restore ecosystem function, native biodiversity, and protect threatened and endangered species (Packard & Mutel, 2005).

In the central and southern Great Plains, Old World bluestems (OWB) [*Bothriochloa bladhii* (Retz.) S.T. Blake and *Bothriochloa ischaemum* (L.) Keng] are a group of non-native, perennial, warm-season grasses that were introduced from Europe and Asia (Harlan, 1952). Old World bluestems are usually planted in monocultures for cattle forage or hay production because they establish easily and tolerate both drought and heavy grazing (Harlan, 1952; Coyne & Bradford, 1986). Currently, OWBs have been introduced into 16 states, mostly in the southern United States (USDA, 2007), and have been widely utilized as perennial vegetation for soil stabilization in Conservation Reserve Program (CRP) plantings, roadside rights-of-way, and pasture grass for hay production. The actual amount of land area planted to OWB, not only in CRP seed mixes but also voluntary plantings by land managers remains unknown, but White and Dewald (1996) estimated that over one million ha were planted to OWBs from 1985 to 1995 in Texas and Oklahoma.

Despite the popular use of OWB by land managers, recent research suggests that OWB monocultures do not provide suitable habitat for most native wildlife species. In Kansas, monocultures of OWB had a lower bird species richness and abundance and lower arthropod availability than native mixed grass prairie (Hickman et al., 2007). Another study concluded that OWB monocultures supported lower abundance and diversity of rodents than native vegetation (Sammon & Wilkins, 2005). In northern Texas, swift foxes (*Vulpes velox)* avoided CRP fields planted to OWB (Kamler et al., 2003). OWB also negatively affects native vegetation by reducing native plant diversity as much as 30% after invasion (Gabbard & Fowler, 2006).

The widespread use of OWB and increased awareness that OWB have undesirable and unknown effects on native grassland biodiversity have private land managers and government agencies expressing interest in controlling OWB and restoring those sites to native vegetation. However, controlling OWB for future restoration has proven to be exceedingly difficult. Four studies have evaluated OWB control methods with variable degrees of success (Medlin et al., 1998; Harmoney et al., 2004; Harmoney et al., 2007; Simmons et al., 2007). Adequate control requires more than one herbicide application per year or a combination of herbicide and tillage (Medlin et al., 1998; Harmoney et al., 2004; Harmoney et al., 2007). Medlin et al. (1996) used glyphosate plus two tillage treatments and was able to control OWB by 85–99% one year after treatment. Tillage, however, is not always an appropriate control method, especially for prairie remnants or areas that have rocky ground and have high erosion potential, or contain rare species (Packard & Mutel, 2005). Glyphosate has been found to be the most effective herbicide for controlling OWB (Harmoney et al., 2004; Harmoney et al., 2007). Glyphosate applied once during the spring provided 43% control of OWB by the end of the first year following application (Harmoney et al. 2004). Applying glyphosate twice during a single growing season increased control to 90% after the first frost (Harmoney 2007). Simmons et al. (2007) tested the independent effects of mowing, burning, and glyphosate and found that mowing did not reduce the cover of OWB relative to non-treated areas, a year after treatment was applied. Burning and glyphosate did reduce OWB cover, but neither reduced cover by more than 50%, which was necessary for successful restoration of invaded areas (Packard & Mutel, 2005).

Combining mowing and burning with herbicide could improve OWB control because studies with other invasive and weedy species noted greater success of control when mechanical and chemical treatments were combined rather than applied individually (Bradley & Hagood, 2002; Renz & DiTomaso, 2004). Mechanical treatments, such as mowing, followed by herbicide application increased control of several perennial invasive plants, such as Canada thistle (*Cirsium arvense*), cordgrasses (*Spartina spp.*), tropical soda apple (*Solanum viarum*), and perennial pepperweed (*Lepidium latifolium*) (Hunter, 1996; Mislevy et al., 1999; Bradley & Hagood, 2002; Hedge et al., 2003; Renz & DiTomaso, 2004). Burning, in combination with herbicide applications, increased control of many invasive species such as tall fescue (*Festuca arundinacea*), Bermuda grass (*Cynodon dactylon*), dalmatian toadflax (*Linaria *genistifolia*), and giant mimosa (*Mimosa pigra*) (Masters et al., 2001; Lesica & Martin, 2003).

Effectiveness of foliar applied herbicides, such as glyphosate, requires a lethal dose of herbicide to be translocated from the actively growing leaves to the root system (Hunter, 1996). Previous research has shown that glyphosate translocation increases when herbicide is deposited on the lower leaves in the canopy (McWhorter & Hanks, 1993; Renz & DiTomaso, 2004). Renz and DiTomaso (2004) concluded that mowing changes plant canopy structure such that a greater leaf area exists in the bottom third of the canopy thus increasing glyphosate translocation and enhanced control. I hypothesized that burning or mowing followed by herbicide applications will alter plant canopy structure to allow for more effective glyphosate translocation and provide equal or greater control of OWB relative to single and multiple applications of herbicides alone (i.e. without mowing or burning. Therefore, mu objective was to determine how herbicide timing, number of applications, and the combination of mechanical and herbicide treatments affect OWB monocultures, in order to determine the most effective treatment combinations for controlling OWB for subsequent restoration.

Methods

Research was conducted at the Marvin Klemme Range Research Station (35° 22' N, 99° 04' W), in western Oklahoma, USA. The station was primarily composed of upland prairie with rolling hills and native vegetation dominated by mixed- and shortgrass prairie species. The area receives approximately 76 cm of precipitation per year, with an average summer high temperature of 34.2° C (Brock et al., 1995). The OWB control study was conducted in a 6.5-ha field previously cultivated for wheat

(*Triticum aestivum*) and converted to a monotypic stand of OWB in 1989 (Gunter et al., 1995). Currently, vegetative cover of the field is almost exclusively OWB with small patches of buffalograss (*Buchloe dactyloides*) and scattered forbs (personal observation).

In 2007, single, multiple, and combined treatments of glyphosate, burning, and mowing were applied throughout the growing season. The experimental design was an incomplete factorial randomized block design. Due to constraints of space, not all possible combinations factors were tested, but treatments were selected based on previous research (McWhorter & Hanks, 1993; Renz & DiTomaso, 2004 Harmoney et al., 2004; Harmoney et al., 2007 Simmons et al., 2007). Each treatment was replicalcated four times. Treatments were stratified in that all burned and mowed plots were grouped together within each replication, but randomized within each grouping to effectively apply each treatment. A total of 11 combinations of glyphosate, burning, and mowing were applied to plots of 10 x 10–m (table 1). In 2007, treatments with single, double, and triple applications of glyphosate were applied at three different timings: early (18 May), middle (2 August), and late (1 September) growing season. The single herbicide treatment was applied during the middle (2 August) timing. The two double application treatments were applied at the early and middle timings(double-herbicide-early-middle) or at the early and late timings (double-herbicide-early-late). The triple treatment had an herbicide application at each timing: early, middle, and late growing season (triple-herbicde). The burning for the burn-single-herbicide application treatments occurred early (18 May) and was followed by an herbicide application 4–5 weeks later, when OWB had regrown to the 4 to 5 leaf stage (Harmoney and Hickman 2004). The burn double herbicide treatments occurred at two different timing combinations: 1) an early

(18 May) burn followed by an herbicide application (28 June) with an additional herbicide application late (1 September) (burn-early-double-herbicide) and 2) an early (18 May) application and middle burn (25 July) followed by an herbicide application (30 August) (burn-middle-double-herbicide). The treatment timing of the combined mowing and herbicide treatments were the same timing as the combined burn and herbicide treatments except mowing was substituted for burning and designated as mow-early-double-herbicide and mow-middle-double-herbicide.

Glyphosate (Roundup WeatherMAX, Monsanto, St. Louis, MO) was applied at a rate of 2.125-kg ai/ha, (mixed with 0.232-g of ammonia sulfate) using a R&D EXD-203s bicycle sprayer with 11002 AirMix 110° fan nozzles, approximately 20–25 cm above the vegetation. The early herbicide treatment was applied when OWB had 4–5 fully formed leaves (Harmoney & Hickman, 2004). I conducted all burning in favorable weather conditions with relative humidity above 40%, winds below 30-km/hr, and temperature between 20–30 °C. Burning was applied with a combination of ring and strip head fire technique. Each mow treatment was applied with a tractor mounted mower.

The vegetation sampling method was a modification of those used by Harmoney et al. (2004). A 1 x 1–m quadrat divided into 100 subquadrats (10 x 10–cm each) and frequency determined by counting the number of subquadrats that contained living OWB crowns. Three frequency readings were recorded per plot during each sampling period. To determine basal tiller density all tillers were counted in five randomly selected 10 x 10–cm subquadrats for each plot. Tiller density was recorded three times in every plot. A 0.5 x 0.5–m frame was used to quantify reproductive tiller density, percent OWB cover and percent herbicide control of OWB, with three readings of each per plot. Percent

OWB cover was visually estimated and classified into one of eight foliar cover classes (0; < 1%; 1–5%; 6–25%; 26v50%; 51–75%; 76–95%; >96%). Midpoint values for each cover class were used in analysis (Daubenmire, 1959). Vegetation structural measurements were recorded using a digital visual obstruction technique developed by Limb et al. (2007). During 2007, vegetation sampling occurred at end of season (November). In February 2008, all plots were burned to remove standing dead litter. The vegetation sampling in 2008 occurred at the end of the growing season (October).

Data for end of season 2007 and 2008 were analyzed using an ANOVA procedure with an LSD post hoc at the $p < 0.05$ significance level, to test for differences among treatments for: frequency of live crowns, OWB cover, basal tillers, reproductive tillers, and vegetative structure (SAS 9.1 2003). Data was analyzed separately for end of year 2007 and end of year 2008. Relative importance value (RIV) was used to determine the overall control for each treatment, by combining all response variables into an index. The index value represents control levels of OWB, with lower values indication a greater amount of control. The relative importance value index was calculated for each plot using the formula derived from Mozdzer et al. (2008).

$$\mathrm{RIV} = \left[\left(\frac{f}{F}\times 100\right)+\left(\frac{c}{C}\times 100\right)+\left(\frac{b}{B}\times 100\right)+\left(\frac{r}{R}\times 100\right)\right]$$

Where f = mean frequency of live OWB crowns within each plot, F = maximum frequency of live OWB crowns per plot, c = mean percent cover of OWB within each plot, C = maximum percent cover of OWB within each plot, b = mean number of basal tillers within each plot, B = maximum number of basal tiller within each plot, r = mean number of reproductive tillers within each plot, and R = maximum number of reproductive tillers within each plot. A regression analysis was performed to test for relationships between end of second year RIV and OWB structure at the last herbicide application.

Results

End of first year (2007)

At the end of the first year (2007), all treatments significantly reduced OWB cover compared with the untreated control ($p \leq 0.05$) (Fig. 1). The triple-herbicide-application treatment, both double herbicide application treatments (double-herbicide-early-middle and double-herbicide-early-late), and all double herbicide applications with a mow or burn (mow-early-double-herbicide, mow-middle-double-herbicide burn-early-double-herbicide, and burn-middle-double-herbicide) had the lowest OWB cover. The mow-single-herbicide and burn-single-herbicide treatments significantly reduced OWB frequency and basal tiller density compared with the single-herbicide treatment (Fig. 2 and 3). All treatments with two herbicide applications regardless of mowing and burning, and the triple-herbicide treatment had similar low values for cover, frequency of crowns, and basal tillers, except for the double-early-middle-herbicide treatment which had slightly higher values for percent cover, frequency of crowns, and basal tillers. All treatments except the single-herbicide treatment significantly reduced the number of basal tillers relative to the control ($p \leq 0.05$) (Fig. 3). Three treatments had no reproductive tillers at the end of the first year: triple-herbicide, double-early-late-herbicide and burn-early-double-herbicide treatment (Fig. 4).

Visual obstruction was reduced relative to the control in all treatments except in the single-herbicide treatment and the double-early-late-herbicide treatment. The double-early-late-herbicide treatment had 57% greater visual obstruction relative to the other double and triple herbicide treatments ($p \leq 0.05$) (Fig. 5). Overall there were 6 treatments with less than 5% cover and 10 crowns/m^2 at the end of the first year (triple-herbicide, both mow double herbicide, both burn double herbicide, and the double-early-late-herbicide treatment).

End of second year (2008)

At the end of the second year (2008), only two treatments, the triple-herbicide and the burn-middle-double-herbicide treatments, maintained a similar amount OWB cover and frequency as the end of 2007 (Fig. 6 and 7). Both double herbicide application treatments had less OWB cover compared with the single-herbicide treatment. The triple-herbicide treatment resulted in an even greater reduction of OWB cover, by at least 40%, relative to both double herbicide application treatments. Both mow double herbicide and both burn double herbicide application treatments reduced OWB cover by 77–88% and 90–98%, respectively, which was a greater reduction compared to the 32–51% reduction for both double herbicide application treatments. Both mow double herbicide application and both burn double herbicide application treatments had similar OWB cover as the triple herbicide application treatment ($p \leq 0.05$). Compared to treatments with a single herbicide application, the burn-single-herbicide treatment had the lowest number of basal tillers and had similar basal tiller density as most of the other double herbicide application treatments (Fig. 8). Two treatments had less than 75 basal tillers/m^2: triple-herbicide-treatment, and burn-middle-double-herbicide treatment (Fig. 8).

The mow-single-herbicide, burn-single-herbicide and both double herbicide application treatments had significantly more reproductive tillers and greater visual obstruction relative to the control ($p \leq 0.05$) (Fig. 9 and 10). Those four treatments had 4–7 times more reproductive tillers and 2–3 times greater visual obstruction compared to the control. In contrast, both mow double herbicide application and both burn double herbicide application treatments had visual obstruction and reproductive tiller density that were not higher than the control.

The RIV showed positive relationship with visual obstruction after the last herbicide application, but only 15% of the RIV variation was explained by the visual obstruction ($p = 0.013$, $r^2 = 0.15$) (Fig. 11). Overall, both mow and both burn double herbicide application treatments consistently had lower OWB cover, reproductive tillers, and visual obstruction compared with both double herbicide application treatments.

Discussion

These results suggest that mowing or burning prior to an herbicide application increases the control of OWB. In both Harmoney et al. (2004) and my study, a single application of glyphosate did not reduce OWB frequency or basal tiller density. However, if a mechanical pretreatment (mowing or burning) was applied prior to glyphosate application, OWB frequency and tiller density were significantly lower after the first season. Simmons et al. (2007) tested the independent effects of mowing, burning, and glyphosate (one and two applications) on OWB cover and concluded that two mowing events had no effect on OWB cover, but a growing season burn reduced OWB cover by 30% one year after treatment. Simmons et al. (2007) also reported that two applications of glyphosate reduced OWB cover by 50%, which is similar to the 32% and 51% cover reductions for the double herbicide treatments in my study. Combining mechanical and chemical treatments resulted in a greater reduction in OWB cover: 77–88% and 90–98%

for the treatments that combined two herbicide applications plus a mow or burn prior one of herbicide application, respectively. Independently, mowing, burning, and two glyphosate applications were not effective at controlling OWB; however, all treatments that combined mowing or burning with double herbicide applications resulted in a greater level of control of OWB. Our results support the conclusion of other studies that suggest combining mechanical treatments with chemical treatments can improve control of perennial invasive and weedy species (Mislevy et al., 1999; Adams & Galatowitsch, 2006; Renz & DiTomaso, 2006).

One reason for the increased control could be that the combined treatments increased herbicide effectiveness and reduced OWB vigor. After the first season, all treatments with two or three herbicide applications reduced OWB cover, frequency, and basal tiller density, with similar effectiveness. By the end of the second season, all mow and burn double herbicide application and the triple-herbicide treatments maintained relatively low OWB cover, frequency, and basal tiller number compared to the other treatments. Both double herbicide application treatments had relatively low OWB frequency and basal tillers, but had relatively high cover. In addition to high OWB cover, the both double herbicide application treatments also had reproductive tiller density and visual obstruction greater than the untreated control. I propose that this phenomenon is most likely caused by intraspecific competitive release. OWB has high intraspecific competition and aggressively resprouts (Schmidt et al. 2008). The surviving OWB plants in the double herbicide application treatments were vigorous enough to take advantage of the low density of OWB plants and reduced intraspecific competition and thus were able to grow taller and produce more reproductive tillers compared with untreated control

(Aguiar et al., 2001) (fig 12). Even though the all mow and burn double herbicide application treatments applied the same quantity of herbicide as the double herbicide application treatments, the mow and burn double herbicide application treatments reduced OWB vigor and did not exhibit the competitive release exhibited as in the double herbicide application treatments.

The reduced vigor and greater overall reduction of OWB for the combined treatments might be attributable to an increase in herbicide effectiveness due to the prior mowing and burning, which lowered plant structure, removed standing dead, and produced young regrowth. There was a positive relationship between OWB structure at last herbicide application and OWB control at the end of second year (Fig.. 11). This suggests plots that were mowed or burned, had shorter OWB structure when sprayed leading to a greater amount of OWB control compared with plots that were not mowed or burned, which had taller OWB structure when sprayed. Renz and DiTomaso (2004) suggested that mechanically reducing plant structure prior to an herbicide application, increased the amount of herbicide deposited on the basal third of the plant, which improves control because basal leaves are more efficient at translocating herbicide to the roots than upper leaves (McWhorter & Hanks, 1993). Only 15% of the OWB control variation was explained by structure in my study, so other factors may also explain the increased OWB control for the combined mechanical and chemical treatments.

The combined treatments were sprayed 4 or 5 weeks after mowing or burning and the OWB regrowth was at an earlier growth stage than the OWB regrowth from the first application of the double herbicide treatments that were sprayed 11 and 19 weeks after first treatments. Glyphosate is more readily absorbed in plants at a younger phenological stage than plants at an older phenological stage (Camacho & Moshier, 1991). Mowing and burning also decreased the amount of standing dead (i.e. last years growth and previously controlled plants still standing), which can intercept the herbicide and reduce herbicide effectiveness by decreasing the contact with living leaves (Wolf et al., 2000; DiTomaso et al., 2006). Burning removed a greater amount of standing dead than mowing (personal observation). The burn herbicide treatments consistently provided slightly greater OWB control, possibly due to less herbicide interception by standing dead compared with the mow herbicide treatments that had greater amounts of standing dead. The greater overall control of OWB by the combined mechanical and chemical treatments is possibly due to the effects of prior mowing or burning that decreases the amount of standing dead, reduces plant structure, and promotes regrowth.

Management implications

A single herbicide application does not adequately control OWB, even with prior mowing or burning. Two herbicide applications do effectively control OWB for the first year, but the control does not persist in the following year because OWB cover, reproductive tillers, and vertical structure increase in the second year. The burn and mow double herbicide applications treatments improved overall OWB control after the second year with no significant increase of cover, frequency, basal tillers, reproductive tillers, and structure relative to the end of the first year. Triple-herbicide treatment also provided similar OWB control after the second year as the burn and mow double herbicide applications but used less herbicide, suggesting that a mow or burn combined with herbicide applications can reduce the amount of herbicide required without sacrificing the level of OWB control. The burn plus herbicide application treatments consistently provided more OWB control compared with the mow plus herbicide application treatments. The difference in the effectiveness of the treatments might be attributed to greater biomass and standing dead removed by burning. The most effective combined treatment was the burning in combination with two herbicide applications one early in the season, followed by a middle season burn and the second herbicide application 4 weeks later applied to young regrowth.

Conclusion

Combining mowing or burning with two applications of glyphosate, with one application 4 or 5 weeks after mowing or burning, is more effective at controlling OWB compared with only using glyphosate applications. Effects of two herbicide applications combined with a mow or burn does not exhibit increased cover, reproductive tiller density, or vertical structure in the following year as some of the herbicide only treatments exhibited. A prior mowing and burning treatment might have increased herbicide effectiveness by lowering plant structure, removing standing dead and producing regrowth, which allowed for more efficient herbicide absorption and translocation. This study supports the conclusion of other studies in that combining mechanical and chemical treatments improves the control of perennial invasive and weedy plant species (Bradley & Hagood, 2002; Lesica & Martin, 2003; Renz & DiTomaso, 2004).

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Table 1. Treatment table, list each treatment, timing of herbicide, mowing, and burning applications for each treatment, treatment abbreviations, and the description of each treatment.

treatment	herbicide timing	mechanical and herbicide timing	treatment abbreviations	description
single herbicide	Middle 2 Aug.		M	one herbicide application at the mid timing
burn single herbicide		Early 18 May	Burn+E	spring burn followed by herbicide application 4 weeks later
mow single herbicide		Early 18 May	Mow+E	spring mow followed by herbicide application 4 weeks later
double herbicide	Early, Late 18 May, 1 Sept.		E,L	two herbicide application at the early and late timing
	Early, Middle 18 May, 2 Aug.		E,M	two herbicide application at the early and mid timing
burn double herbicide	Late 1 Sept.	Early 18 May	Burn+E, L	spring burn followed by herbicide application 4 weeks later, with an additional herbicide application at the late timing
	Early 18 May	Middle 25 July	E,Burn+M	herbicide application early, and a mid burn with a herbicide application 4 weeks later
mow double herbicide	Late 1 Sept.	Early 18 May	Mow+E, L	spring mow followed by herbicide application 4 weeks later, with an additional herbicide application at the late timing
	Early 18 May	Middle 25 July	E,Mow+M	herbicide application early, and a mid mow with a herbicide application 4 weeks later
Triple herbicide	Early, Middle, Late 18 May, 2 Aug. 1 Sept		E,M,L	Herbicide application early, mid, and late
control			control	No herbicide applications

Fig. 1

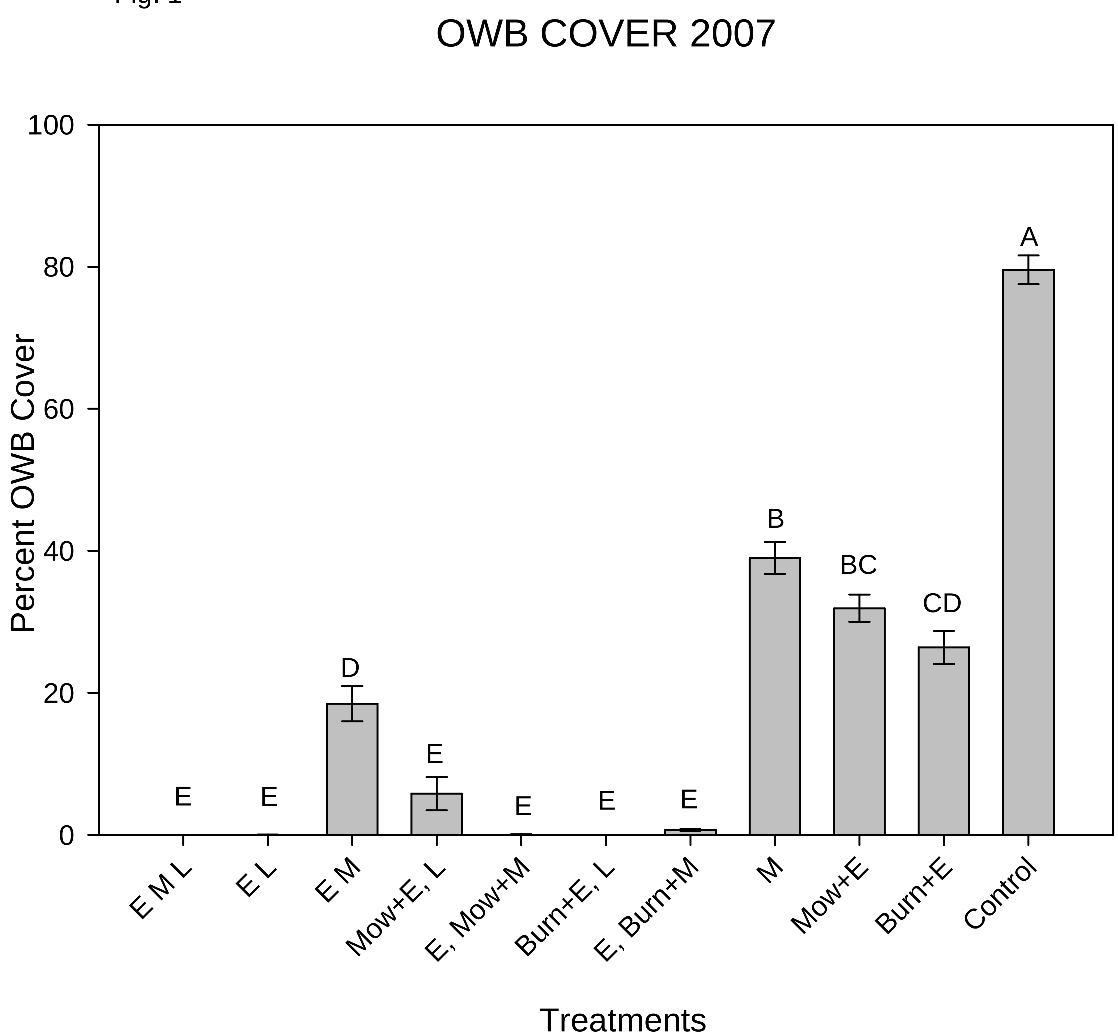


Fig. 1 Percent cover of OWB at end of season 2007. Different letters indicate significant difference ($p < 0.05$), E = early season herbicide application, M =middle season herbicide application, L = late season herbicide application, Mow+E = early season mow followed by a herbicide application, Mow+M = middle season mow followed by a herbicide application, Burn+E = early season burn followed by a herbicide application, Burn+M = middle season burn followed by a herbicide application

Fig. 2

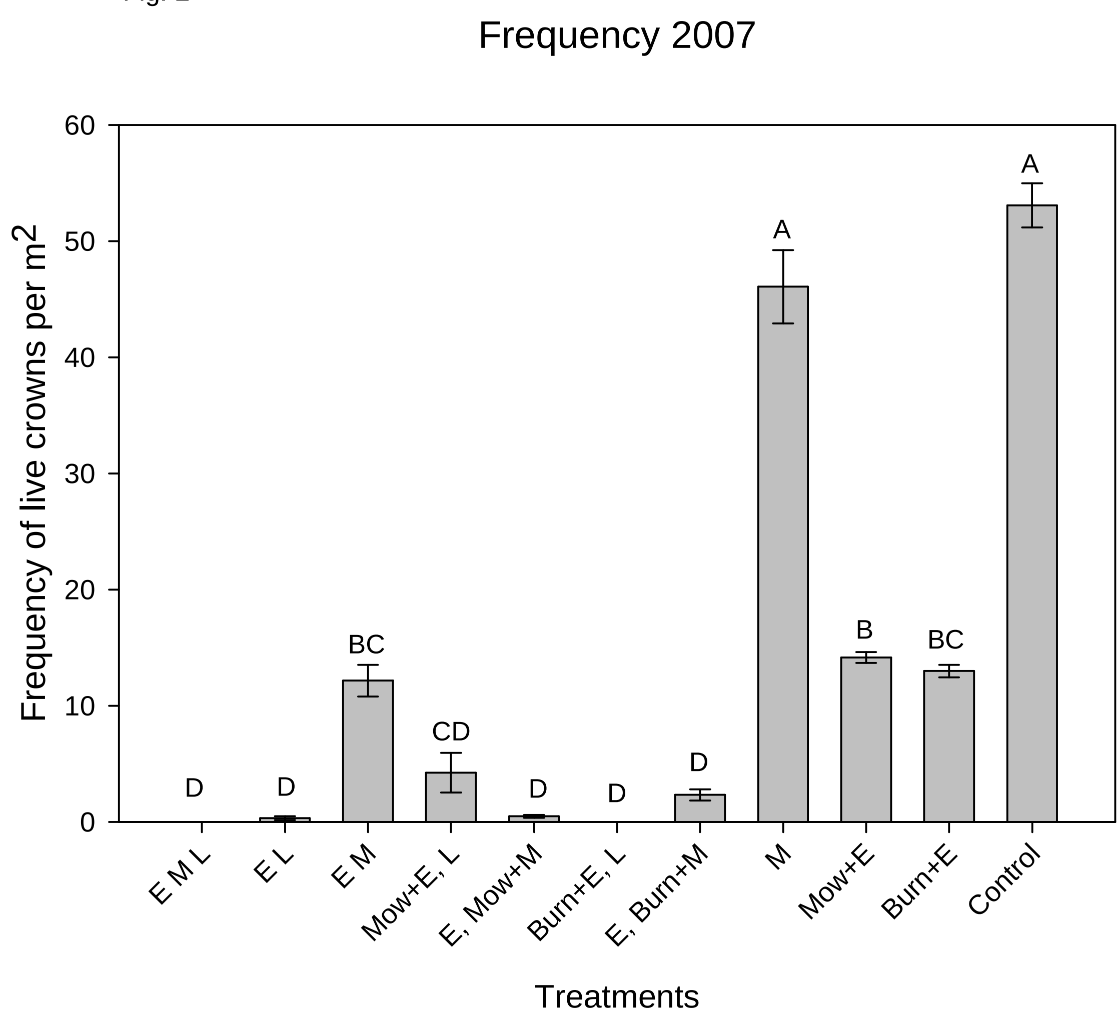


Fig 2. Frequency of live OWB crowns (per m^2) at end of season 2007. Different letters indicate significant difference ($p < 0.05$), E = early season herbicide application, M =middle season herbicide application, L = late season herbicide application, Mow+E = early season mow followed by a herbicide application, Mow+M = middle season mow followed by a herbicide application, Burn+E = early season burn followed by a herbicide application, Burn+M = middle season burn followed by a herbicide application

Fig. 3

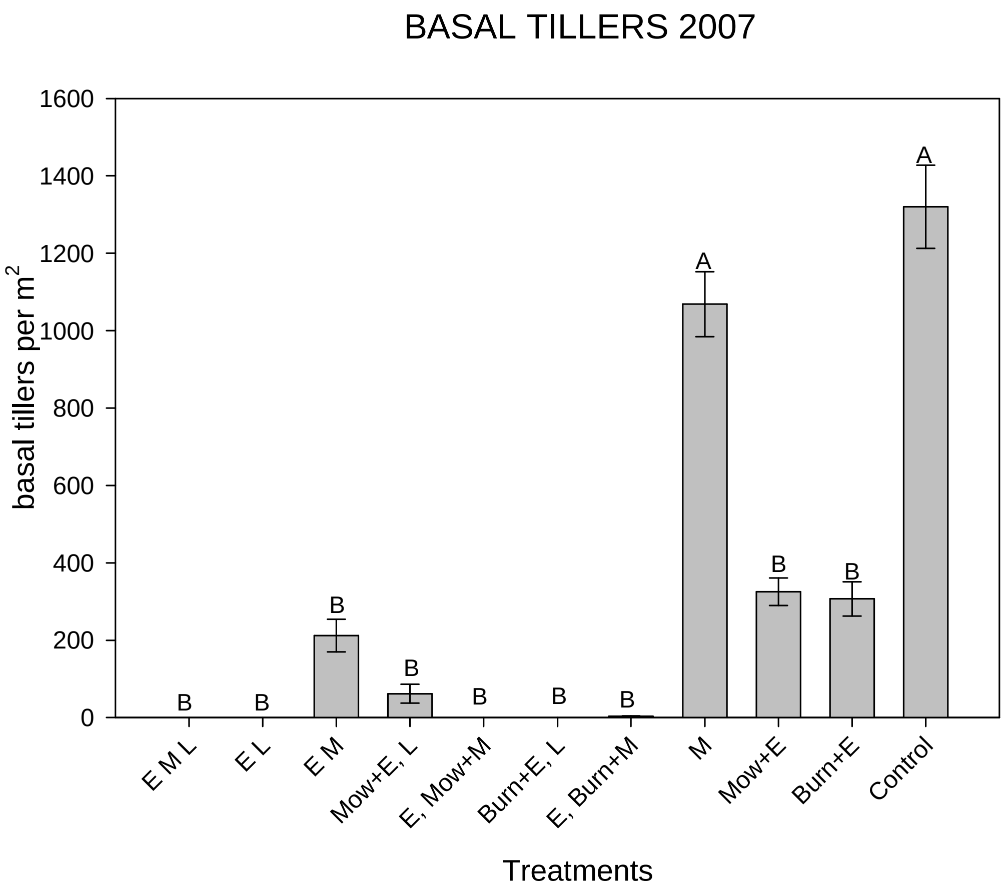


Fig 3. Basal tiller density (per m^2) of OWB at end of season 2007. Different letters indicate significant difference ($p < 0.05$), E = early season herbicide application, M =middle season herbicide application, L = late season herbicide application, Mow+E = early season mow followed by a herbicide application, Mow+M = middle season mow followed by a herbicide application, Burn+E = early season burn followed by a herbicide application, Burn+M = middle season burn followed by a herbicide application

Fig. 4

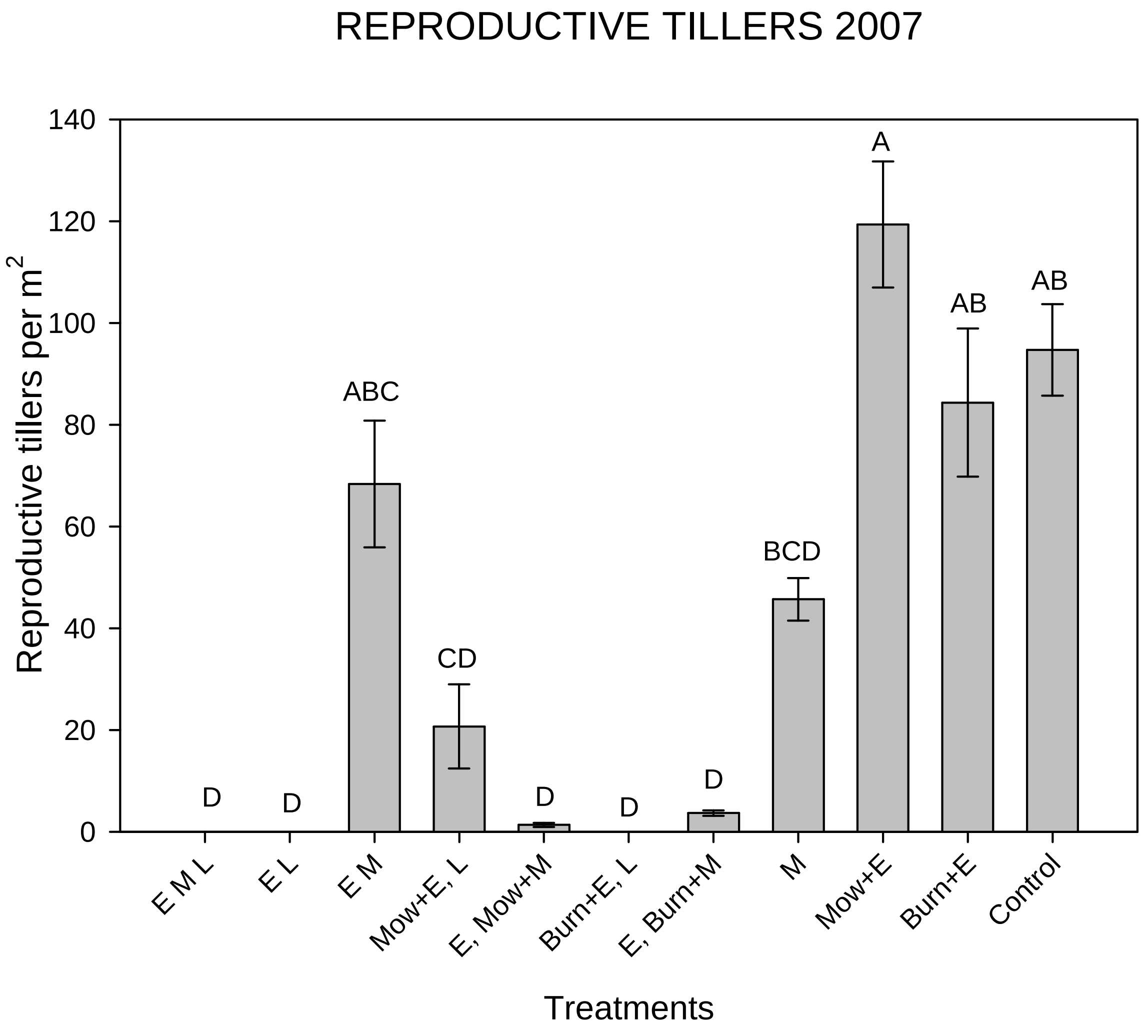


Fig 4. Reproductive tiller density (per m^2) of OWB at end of season 2007. Different letters indicate significant difference ($p < 0.05$), E = early season herbicide application, M =middle season herbicide application, L = late season herbicide application, Mow+E = early season mow followed by a herbicide application, Mow+M = middle season mow followed by a herbicide application, Burn+E = early season burn followed by a herbicide application, Burn+M = middle season burn followed by a herbicide application

Fig. 5

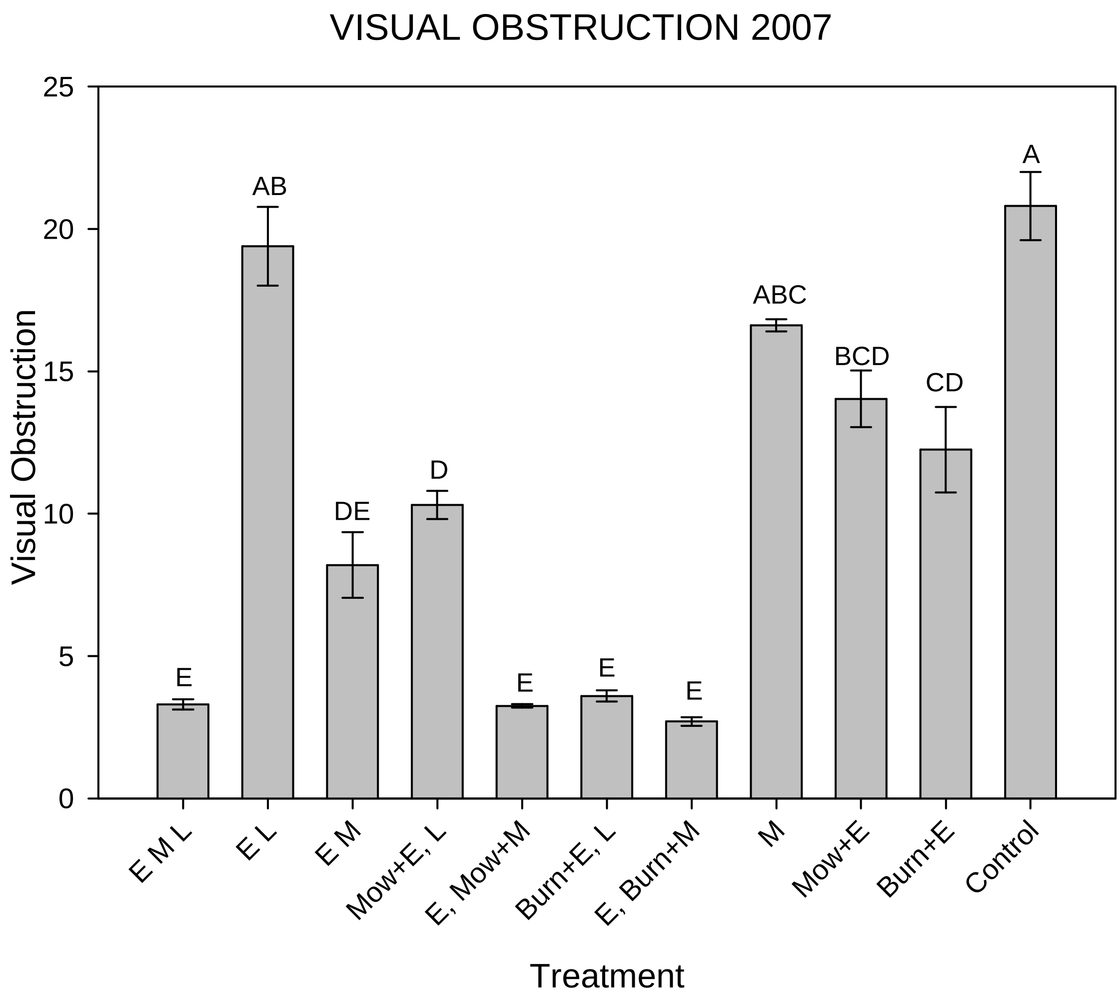


Fig 5. Visual obstruction at end of season 2007. Different letters indicate significant difference ($p < 0.05$), E = early season herbicide application, M =middle season herbicide application, L = late season herbicide application, Mow+E = early season mow followed by a herbicide application, Mow+M = middle season mow followed by a herbicide application, Burn+E = early season burn followed by a herbicide application, Burn+M = middle season burn followed by a herbicide application

Fig. 6

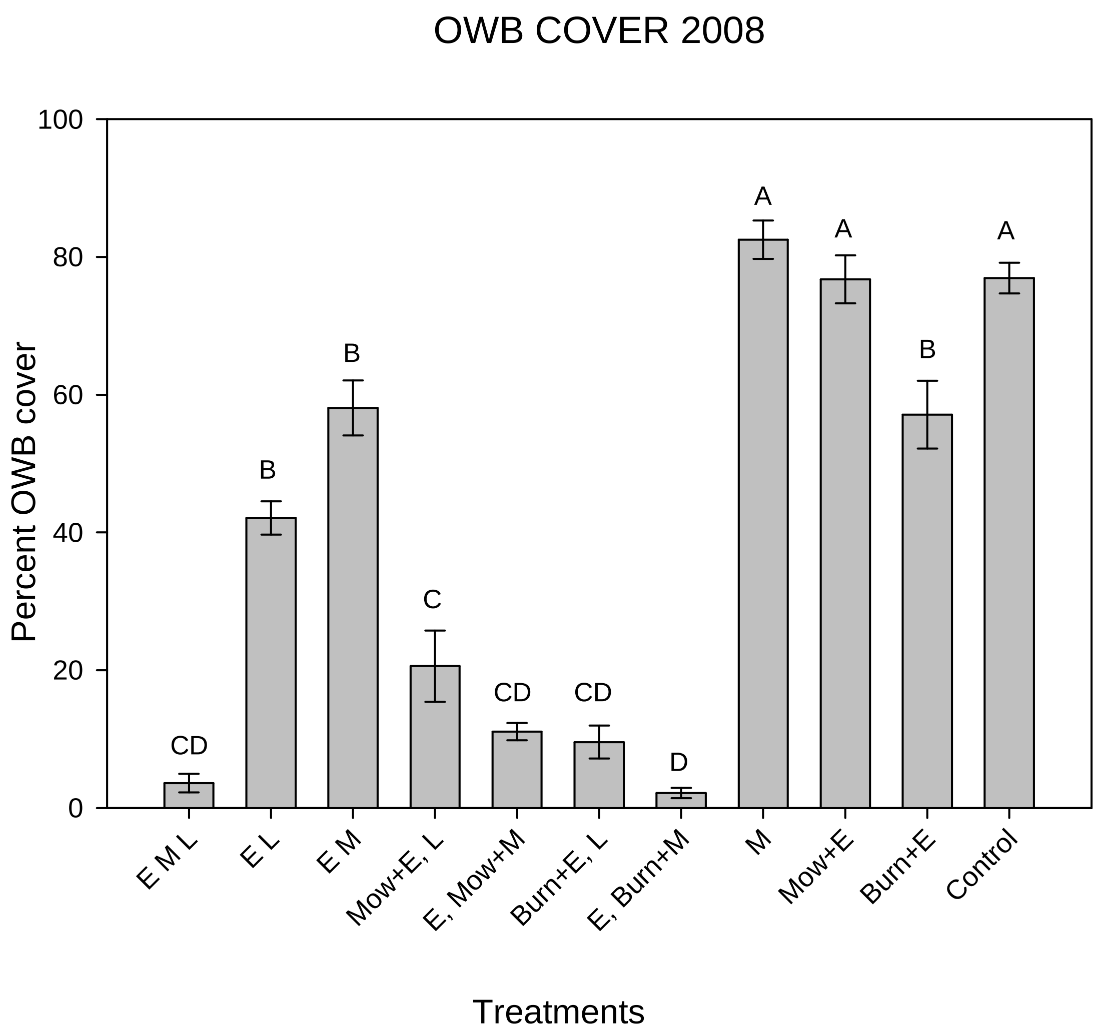


Fig 6. Percent cover of OWB at end of season 2008. Different letters indicate significant difference ($p < 0.05$), E = early season herbicide application, M =middle season herbicide application, L = late season herbicide application, Mow+E = early season mow followed by a herbicide application, Mow+M = middle season mow followed by a herbicide application, Burn+E = early season burn followed by a herbicide application, Burn+M = middle season burn followed by a herbicide application.

Fig. 7

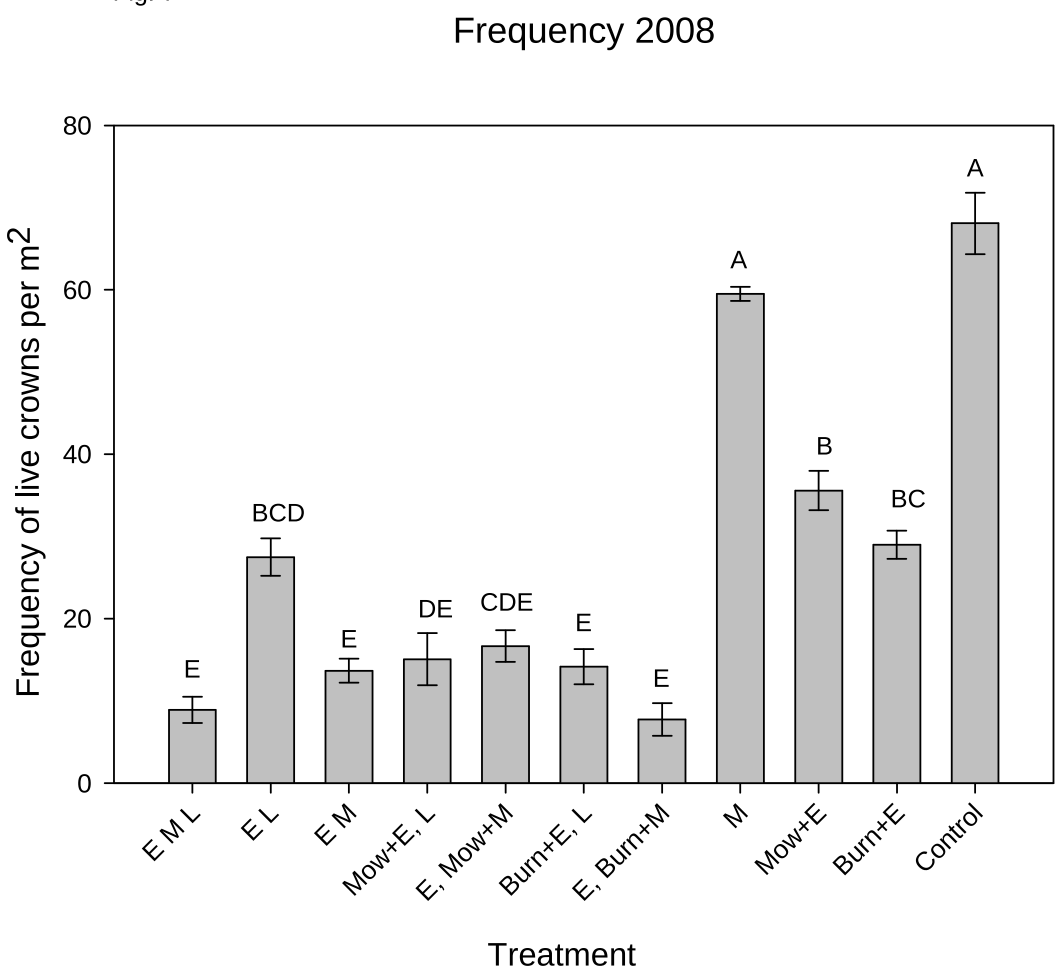


Fig 7. Frequency of live OWB crowns (per m^2) at end of season 2008. Different letters indicate significant difference ($p < 0.05$), E = early season herbicide application, M =middle season herbicide application, L = late season herbicide application, Mow+E = early season mow followed by a herbicide application, Mow+M = middle season mow followed by a herbicide application, Burn+E = early season burn followed by a herbicide application, Burn+M = middle season burn followed by a herbicide application

Fig. 8

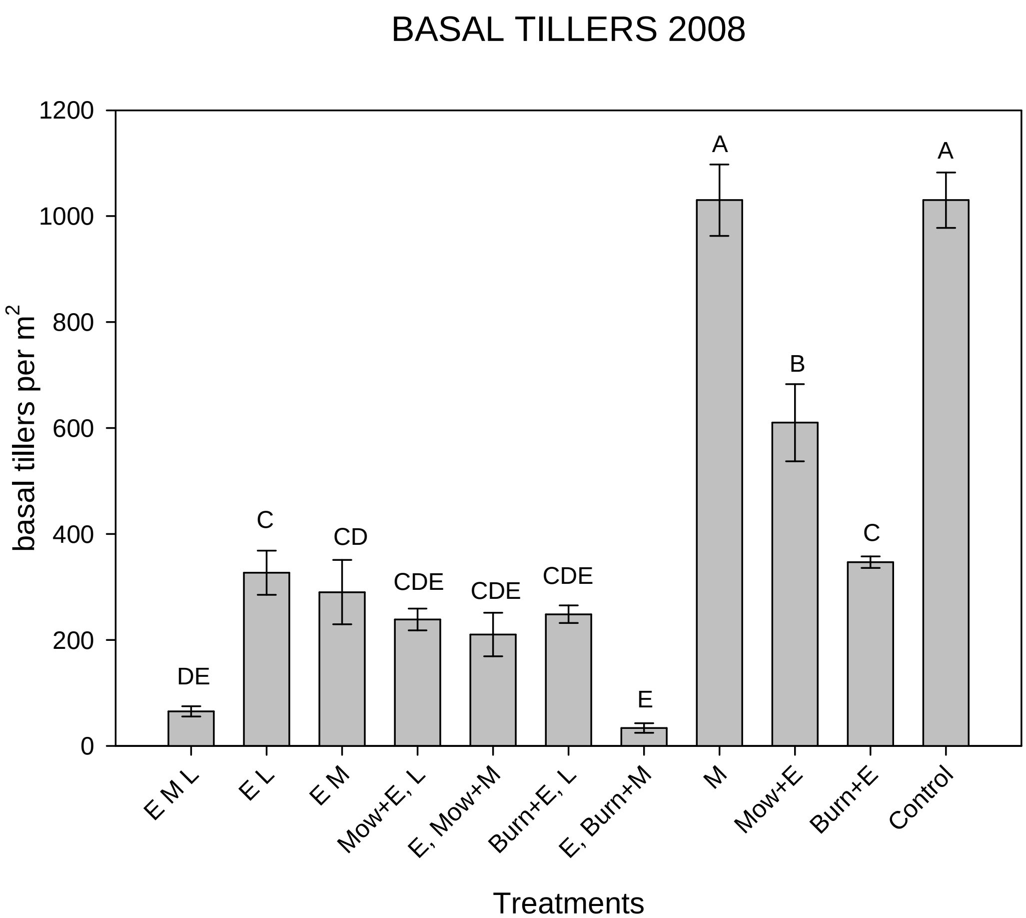


Fig 8. Basal tiller density (per m^2) of OWB at end of season 2008. Different letters indicate significant difference ($p < 0.05$), E = early season herbicide application, M =middle season herbicide application, L = late season herbicide application, Mow+E = early season mow followed by a herbicide application, Mow+M = middle season mow followed by a herbicide application, Burn+E = early season burn followed by a herbicide application, Burn+M = middle season burn followed by a herbicide application

Fig. 9

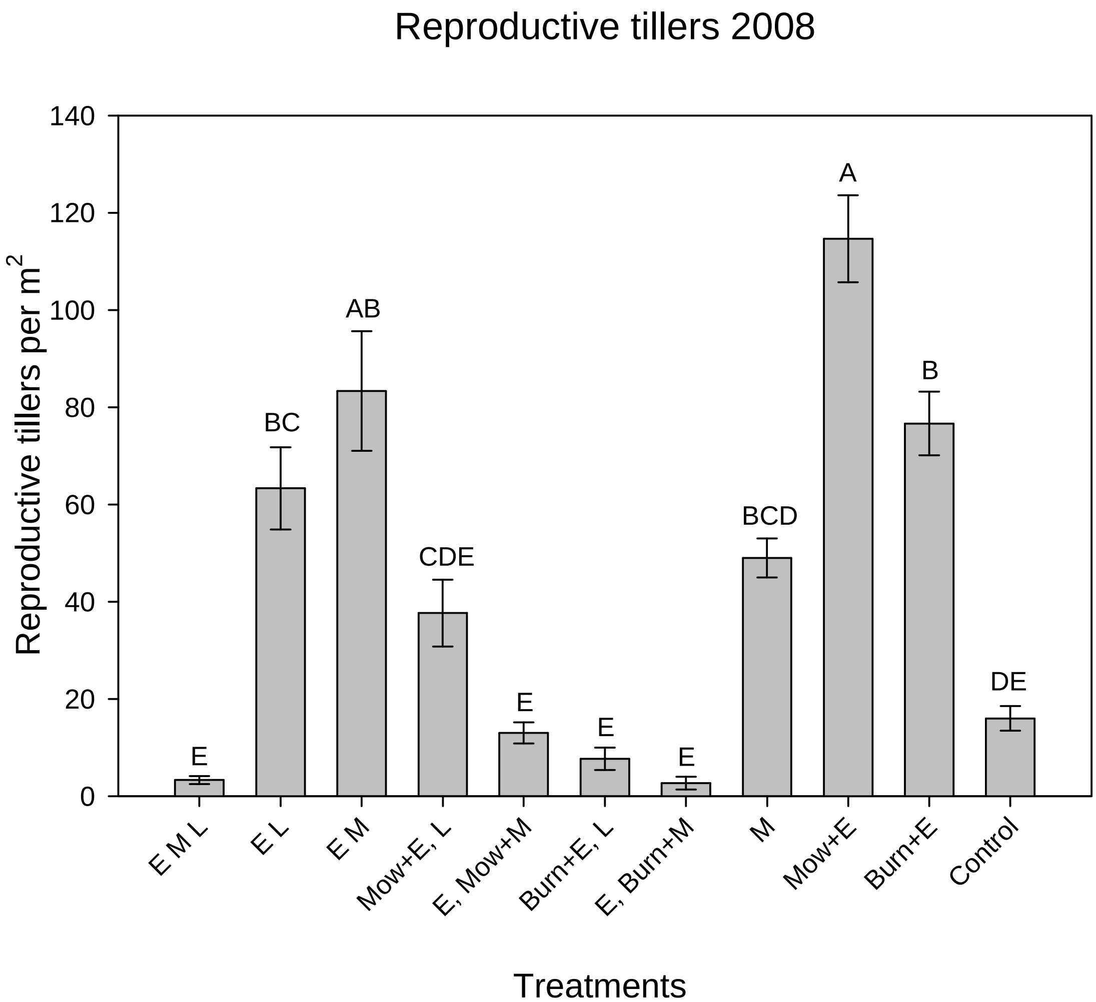


Fig 9. Reproductive tiller density (per m^2) of OWB at end of season 2008. Different letters indicate significant difference ($p < 0.05$), E = early season herbicide application, M =middle season herbicide application, L = late season herbicide application, Mow+E = early season mow followed by a herbicide application, Mow+M = middle season mow followed by a herbicide application, Burn+E = early season burn followed by a herbicide application, Burn+M = middle season burn followed by a herbicide application.

Fig. 10

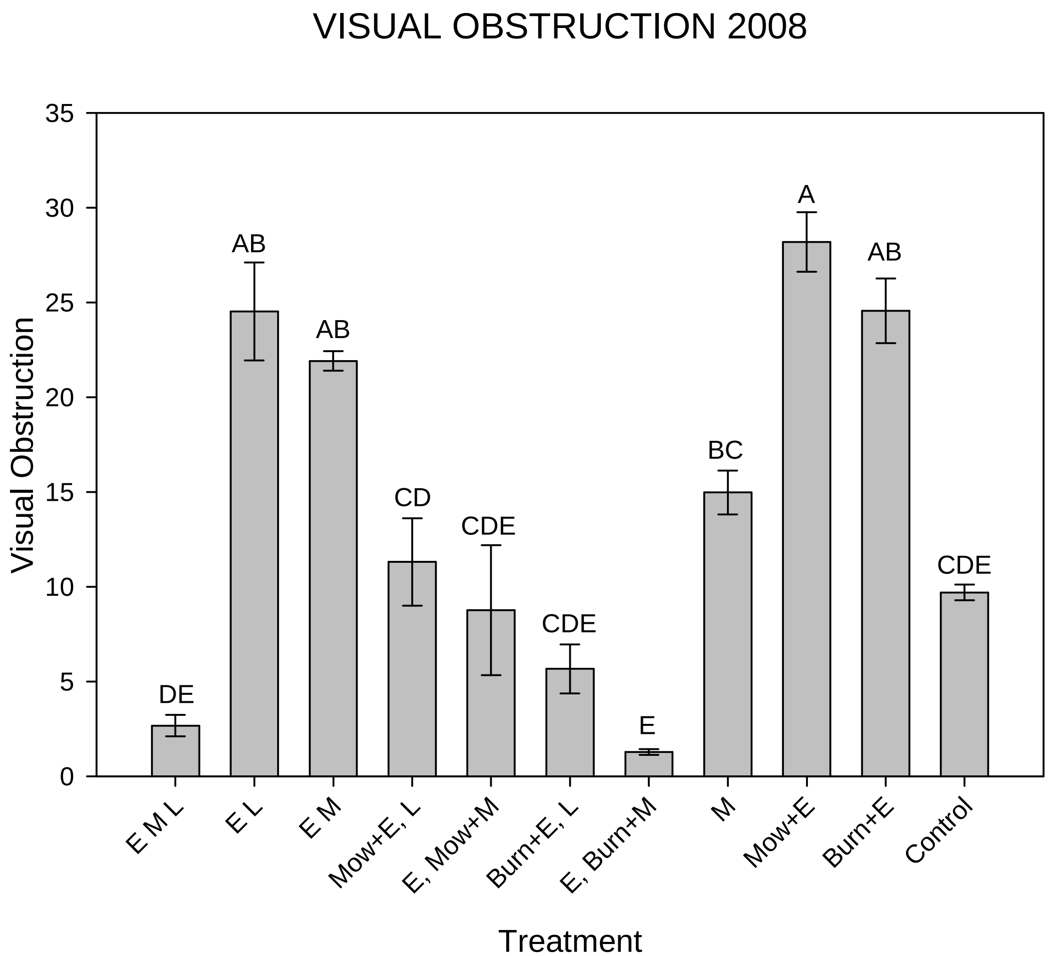


Fig 10. Visual obstruction at end of season 2008. Different letters indicate significant difference ($p < 0.05$), E = early season herbicide application, M =middle season herbicide application, L = late season herbicide application, Mow+E = early season mow followed by a herbicide application, Mow+M = middle season mow followed by a herbicide application, Burn+E = early season burn followed by a herbicide application, Burn+M = middle season burn followed by a herbicide application.

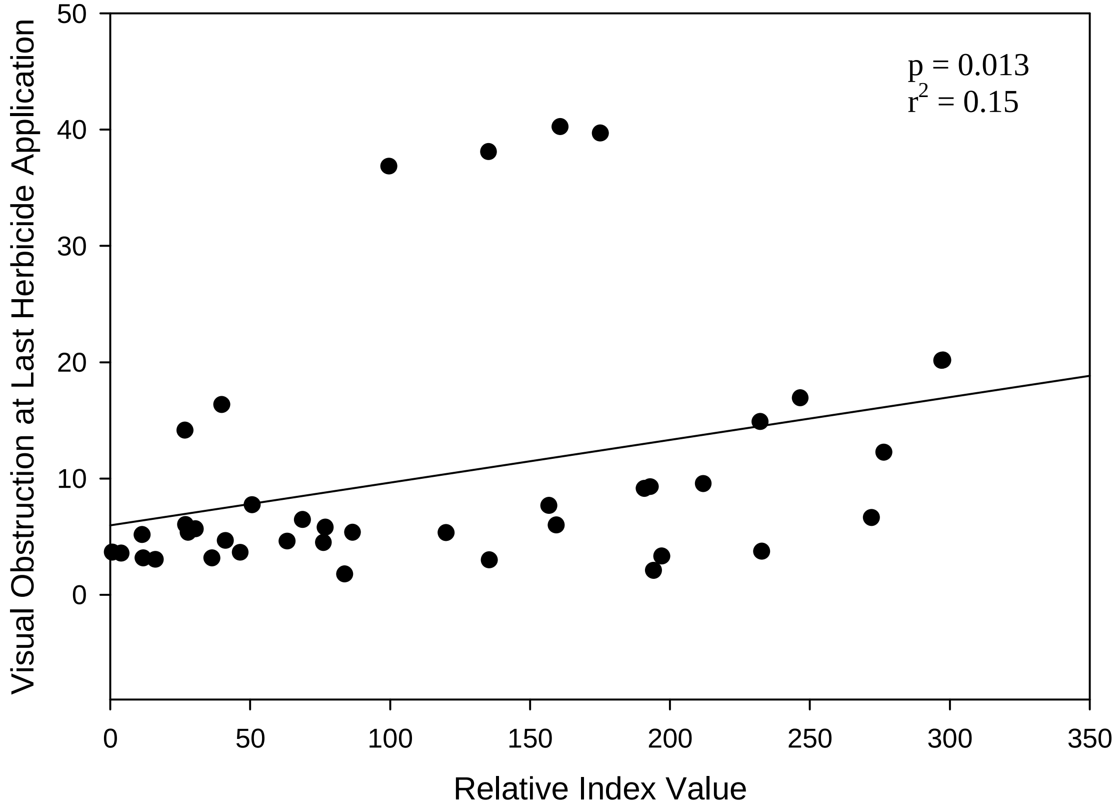
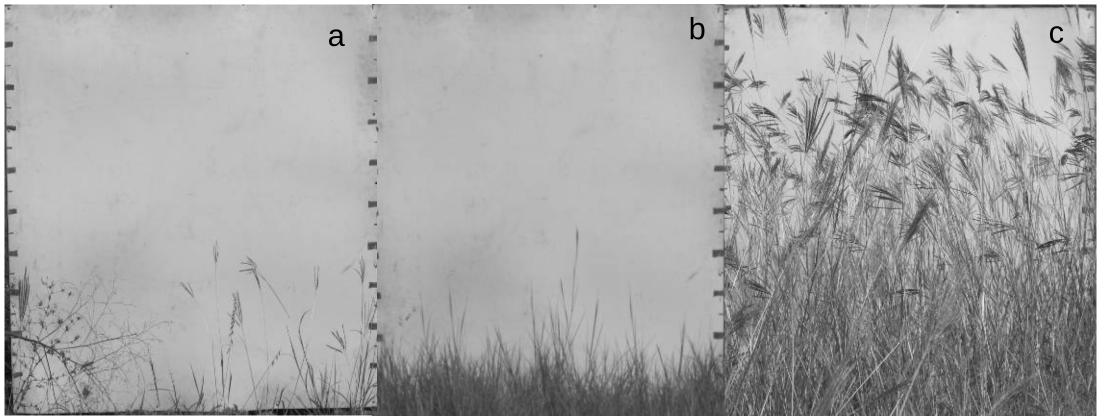


Fig 11. Relationship between visual obstruction at last herbicide application and relative important value (RIV) of OWB.

Fig. 12

Visual Obstruction



Visual obstruction photos from sample of treatments a) Burn double herbicide, timing early burn with an herbicide application 4 weeks after, with in additional application late b) control treatment c) Double herbicide, Early, middle timing.

Chapter II

Aboveground plant community and seed bank composition along an invasion gradient

ABSRACT Invasive species are known to reduce diversity and abundance in a native plant community, but, it is unclear how aboveground invasion effects the native seed bank. My objective was to assess effects of invasion by the exotic grass old world bluestem (OWB; *Bothriochloa spp.*) on native aboveground plant species composition and seed bank diversity and abundance. The aboveground plant and seed bank communities were sampled along a invasion gradient of OWB. Old world bluestem invasion had differential effects on native diversity and abundance in the aboveground plant community and seed bank. Native aboveground species diversity and cover showed a steep declined as OWB cover increased. There was a slight decline in native seed diversity, and no change in native seed density as invasion increased. OWB seed density increased with increasing invasion. I hypothesize that as OWB invasion increases native aboveground plants decrease in diversity and abundance, but native seed bank diversity and density does not decline, but over time as native seeds are lost, and the a lack of native seed replenishment from the aboveground community, native seed bank diversity and density will decline.

Introduction

The soil seed bank is a reservoir of viable seeds under the soil surface that remains dormant until conditions are favorable for germination (Fenner & Thompson, 2005). Soil seed banks are a dynamic system, with seeds constantly lost through germination, death, or predation, while other seeds are added via seed dispersal and seed rain (Nathan & Casagrandi, 2004; Arrieta & Suarez, 2005; Fenner & Thompson, 2005). The seed bank represents the potential future vegetation of an area following a disturbance, or death of an existing plant (Leck et al., 1989).

Seed bank dynamics are effected by a variety of interacting factors, such as seed dispersal, seed rain, germination, disturbance and microsite characteristics (Eriksson & Ehrlen, 1992; Kinucan & Smeins, 1992; Bertiller & Aloia, 1997; Coulson et al., 2001). Land use and disturbance regimes also can have a profound effect on the composition and diversity of the seed bank (Kinucan & Smeins, 1992). Microsite attributes such as slope, aspect, and amount of bareground or litter influence seed bank composition through differential seed input and germination (Bertiller, 1992; Dalling & Hubbell, 2002; Kalamees & Zobel, 2002). The quantity of seeds in the seed rain, distance and direction of seed movement are also important factors in seed bank formation (Kalamees & Zobel, 2002).

Generally, there is low similarity between plant species represented in the aboveground vegetation relative to the species in the seed bank, and similarity can vary depending on the plant community (Hopfensperger, 2007). The density of seeds in seed banks, especially in grasslands, tends to have a high degree of heterogeneity, with wide fluctuations in seed densities over short distances (Fenner & Thompson, 2005). For instance, the seed banks of some plant species have a clumped distribution near parent plants due to limited seed dispersal mechanisms (Jensen, 1998). Annual grasslands in semi-arid regions, tend to have higher similarity between the seed bank and aboveground vegetation compared with other ecosystems (Olano et al., 2005). However, in grasslands of the Great Plains, the dominant perennial grasses are often poorly represented in the seed bank (Kinucan & Smeins, 1992; Hild et al., 2001). In contrast, some species, mostly annuals and small seeded species, make up a small percentage of the aboveground vegetation but tend to be more abundant in the seed bank (Leck et al., 1989; Bertiller & Aloia, 1997). The similarity between the aboveground plant composition and the seed bank composition can also depend upon other factors such as disturbance, management, and presence of invasive species (Hopfensperger, 2007).

Invasion by non-native plant species is typically observed first in the aboveground plant community and found to alter community composition and ecosystem structure and function (Mooney & Hobbs, 2000). However, this apparent aboveground invasion also can result in unobserved alterations in the composition and abundance of the seed bank community (Witkowski & Wilson, 2001; Holmes, 2002; Krinke et al., 2005; Giantomasi et al., 2008). Invasive plant species tend to produce large and persistent seed banks, with the density of the invasive seeds generally increasing as aboveground abundance and seed production of the invasive increases (Mason et al., 2007; Cline et al., 2008), resulting in the invasive species becoming the dominant species in both the aboveground and seed bank communities (Cox & Allen, 2008).

Currently the understanding of the relationship between aboveground invasion by exotic plant species and native seed bank diversity is unclear (Vila & Gimeno, 2007).

Some authors reported lower diversity and abundance of native seeds in an invaded area compared with uninvaded areas (Holmes, 2002; Cline et al., 2008). Other researchers have concluded that large viable native seed banks can exist under invaded areas (Ghorbani et al., 2007; Fourie, 2008). However, native seed banks under invaded areas are typically missing many dominant species, although ruderal and pioneer species are abundant (Bossuyt et al., 2007; Vosse et al., 2008).

Old World bluestems (OWB, *Bothriochloa spp.*) are a group of non-native, perennial, warm-season grasses that reproduce mainly by seeds but also vegetatively by stolons and rhizomes (Harlan, 1952; Schmidt & Hickman, 2006). These grasses were introduced to the United States from Eurasia for use as forage for cattle (Harlan, 1952). Currently, OWBs have been introduced into 16 states, mostly in the southern United States (USDA, 2008) and have been widely promoted and utilized as perennial cover crop for soil stabilization in Conservation Reserve Program (CRP), roadside rights-of-way, and pasture grass for hay production for grazing animals. Old World bluestems have escaped their original plantings, have invaded native prairies, and have been shown to reduce diversity of native plants, grassland birds, and small mammals (Sammon & Wilkins, 2005; Adams & Galatowitsch, 2006; Gabbard & Fowler, 2006; Hickman et al., 2007).

My objective was to assess the effect of OWB invasion on native mixed-grass prairie by quantifying diversity and abundance of the aboveground plant species community and the seed bank community over a range of increasing aboveground invasion by the exotic OWB. Another objective was to assess composition and species similarity between the seed bank and aboveground plant community. By quantifying the seed bank and aboveground plant community in areas of differing levels of OWB invasion, I addressed the following questions: does OWB aboveground cover correlate with the density of OWB seeds in the seed bank and, is native seed bank and aboveground plant community diversity and abundance affected by increasing OWB aboveground cover? The results of this study could provide insight on which stage of invasion, if any, the native seed bank is capable of natural recovery of a native aboveground plant community after successful eradication of OWB.

Methods

Study site

The research was conducted on 129.5 ha of the Marvin Klemme Range Research Station. (35° 22' N, 99° 04' W) in western Oklahoma. The study site is primarily an upland mixed-grass prairie with rolling hills and the native vegetation is dominated by perennial grasses such as side-oats grama [*Bouteloua curtipendula* (Michx.) Torr.], blue grama [*Bouteloua gracilis* (Willd. ex Kunth) Lag. ex Griffiths], little bluestem [*Schizachyrium scoparium* (Michx.) Nash], buffalograss [*Bouteloua dactyloides* (Nutt.) J.T. Columbus], and common forbs are western ragweed (*Ambrosia psilostachya* DC.), annual broomweed [*Amphiachyris dracunculoides* (DC.) Nutt.], and Texas croton [*Croton texensis* (Klotzsch) Müll. Arg.]. During the study period (March-August 2008) the site received 43 cm of precipitation with an average high temperature of 28.2° C and average low temperature of 13.3°C. Longterm averages of the area are 76 cm of precipitation annually, with an average summer high temperature of 34.2° C and an average winter low of 4.4° C (Brock et al., 1995). The soils are silty clay loams of the Cordell series. The site is composed of five pastures under differing management regimes. One pasture (46 ha) has been managed for the past eight years with patch burning using a four year fire return interval with cattle grazing season-long (May to October) at a moderate stocking rate. The second pasture (56 ha) was aerially sprayed with picloram and 2,4-D (Grazon P+D^{tm}) in 2001 and 2004 for musk thistle (*Carduus nutans*) control and has been grazed season long by cattle at a moderate stocking rate (May to Oct). A remnant pasture of 6.2 ha has not been grazed or burned for at least 50 years. Old world bluestem was first introduced to this site in 1989 in two monoculture plantings (6.5 ha and 1 ha), that have been managed for hay production (Gunter et al., 1995).

Sampling

In November 2007, the entire 129.5 ha area was scouted for populations of OWB with line transects of variable lengths. All populations of OWB were marked with a handheld GPS unit and classified as either having high (> 5 populations for a 20 m section of the transect) or low (< 5 populations for a 20 m section of the transect) levels of OWB invasion, in order to ensure a gradient of OWB invasion. Fifteen sites with high levels of invasion and 15 with low levels of invasion were randomly selected for seed bank sampling. An additional 15 sites, not invaded by OWB also were selected for a total of 45 sampling locations. Plots of 10 x 20 m were established for vegetation and seed bank sampling, and all plots were at least 75 m from other plots.

Aboveground vegetation sampling

Within each 10 x 20 m plot (n = 45), 15 subplots of 1 m^2 were used to visually estimate the percent cover of plant species. Aboveground foliar cover of each plot was sampled twice (early May and late August) in 2008. Because some plant species are only present in the aboveground vegetation during early season (cool season grasses and early spring forbs), while other plants (warm season grasses and forbs) are just emerging and reach peak biomass later in the year, the two data sets (May and August) were pooled into one data set, to attain an accurate measurement of aboveground vegetation and seed bank species similarity. The highest cover value of each species during the two sampling periods was used in the analysis (Hickman et al., 2004). Scientific nomenclature of all plant species follows the USDA PLANTS database (USDA, 2008).

Seed bank sampling

The seed bank was sampled during March 2008 with a 9 cm diameter soil core to a depth of 5 cm, 4 soil cores were taken in each of the 15 subplots (1 m^2) and were pooled, for a total of 60 soil cores from each 10 x 20 m plot. Each sample was sieved through a 4 mm sieve to remove coarse material and 0.5 mm sieve to remove fine material. Sieved samples were spread on top of 26 x 54 cm trays filled with 10 cm of sterile potting soil and 5 cm of vermiculite and covered with an additional thin layer of vermiculite (approximately 1 cm deep). The trays were placed in a greenhouse at temperature of 20–25°C. An additional four trays filled with potting soil and vermiculite were randomly placed around the greenhouse as controls to account for seed contamination in the greenhouse. The seed bank composition of each sample was assessed by direct germination method (Gross, 1990; TerHeerdt et al., 1996). All emerged seedlings were identified to species, if possible, counted, and removed after positive identification. Those seedlings that could not be identified were transplanted to a new pot and grown until identification was possible. Germination began 15 April 2008 and after 60 days the soil within the trays was stirred to stimulate more germination.

Seedlings were recorded until no new seedlings had emerged for a period of one week (19 August 2008).

Data analysis

Regression analysis was used to determine the relationship between aboveground OWB cover and the density of OWB seeds in the seed bank, as well as native species diversity, evenness, and richness, for both the seed bank and the aboveground vegetation (SPSS 16). The mean percent cover, species richness, and seed density (seeds/m^2) for each plot was used in the analysis. Native diversity and evenness were calculated using the Shannon diversity (H′) and Pielou's index of evenness. Only native species were included in the calculations (Magurran, 1988). Sorenson similarity index was used to determine the similarity of between species in the seed bank and aboveground community (Magurran, 1988). All species detected in the seed bank and aboveground vegetation were classified into one of eight functional groups, using the USDA Plants database (appendix 1). The "dominant native perennial grasses" functional group contained all perennial grass species which averaged greater than 5% cover in the uninvaded plots. The other native perennial grasses were classified as "non-dominant grasses."

Regression analysis was performed to test for relationships between OWB aboveground cover and seed density, as well as the cover and seed density of each functional group. The species similarity between the species in the aboveground vegetation and the species in the seed bank was determined using the Sorenson similarity index (Magurran, 1988). A regression analysis was used to assess the relationship between aboveground species composition and seed bank species similarity, and aboveground OWB cover.

Results

A total of 134 species were detected in the aboveground plant community. Germinated seeds totaled 30 462 with 112 species recorded in the seed bank. Sixty-eight species were found in both the aboveground and seed bank communities with 44 and 90 species unique to the aboveground plant community and the seed bank, respectively. The average seed bank density was 6 020 seeds/m^2 for all plots.

Aboveground species composition

Native perennial grasses and perennial forbs comprised 76% of total vegetation cover. The dominant perennial grasses *Bouteloua curtipendula, B. gracilis, Buchloe dactyloides*, *Schizachyrium scoparium, Aristida purpurea*, and *Andropogon gerardii* comprised 44% of the aboveground composition (appendix 2). In addition to OWB, 12 invasive species were recorded representing 4% of the total vegetation cover. Excluding OWB, *Bromus* sp. was the most abundant invasive species. In the invaded plots, aboveground OWB cover ranged from 1–61% cover. Native species diversity and evenness decreased as OWB increased ($p = 0.0001$, $r^2 = 0.31$ and $p = 0.0001$, $r^2 = 0.41$, respectively) (Fig. 1a, b). Native species richness averaged 32 species per plot and showed no relationship with OWB cover ($p = 0.502$, $r^2 = 0.011$) (Fig. 1d). Native species cover had a negative relationship with increasing OWB cover ($p = 0.0001$, $r^2 = 0.51$) (Fig. 1c).

The cover of native dominant perennial grasses and native annual forbs had a negative relationship with OWB cover ($p = 0.0001$, $r^2 = 0.43$ and $p = 0.01$, $r^2 = 0.14$, respectively) (Fig. 2a,c). Native perennial forb cover showed a weak negative correlation with OWB cover ($p = 0.08$, $r^2 = 0.07$) (Fig. 2b). The cover of non-dominant perennial grasses was not reduced as OWB cover increased ($p = 0.91$, $r^2 = 0.0001$) (Fig. 2d).

Seed bank

Seeds of native, non-dominant perennial grasses and annual forbs represented 66% of the total seed bank density. Unlike the aboveground plant community, native dominant perennial grasses were not abundant in the seed bank, and each species had a low average seed density, ranging from 6–57 seeds/m^2. Four species, *Sporobolus asper, Bothriochloa ischaemum*, *Bromus* sp. and *Chloris verticillata*, comprised 48% of the total seed bank, with the native grass *S. asper* making up the largest proportion of the total seed bank (appendix 1). A total of 17 non-native species were detected, with OWB and *Bromus* sp. being the most abundant in the seed bank, and together accounted for 91% of the invasive seed bank and 20% of the total seed bank. In the invaded areas OWB formed a large seed bank (averaging 1 076 seeds/m^2 but ranged from 10–4481 seeds/m^2) and OWB seed density was related positively to OWB cover ($p = 0.001$, $r^2 = 0.58$) (Fig. 3). Native seed diversity and evenness showed a negative relationship with OWB cover ($p = 0.042$ $r^2 = 0.093$, and $p = 0.004$, $r^2 = 0.18$, respectively) (Fig. 4, a, b).

Total native seed density showed no relationship with aboveground OWB invasion ($p = 0.17$, $r^2 = 0.042$) (Fig. 4c). There was high variation in native seed densities with the invaded plots at 797–24 869 seeds/m^2 and uninvaded plots at 1 059–10 011 seeds/m^2. The invaded plots had on average almost twice the density of native seeds compared with the uninvaded plots. The increased seed densities can be contributed to the non-dominant perennial grasses such as *S. asper, Chloris verticillata, Bothriochloa* *laguroides,* and *Sporobolus cryptandrus,* which collectively represented 60% of the native seed density in the invaded plots. For example, *S. asper* average seed density increased by 1 420 seeds/m^2 in the invaded plots compared with the uninvaded plots. The other non-dominant perennial grasses, *C. verticillata, B. laguroides,* and *S. cryptandrus,* had twice the density of seeds in the invaded plots compared with the uninvaded plots. Despite the increased densities of those species, native seed density was not related to aboveground OWB cover ($p = 0.17$, $r^2 = 0.042$) (Fig. 4c). The seed density for all functional groups was not related to aboveground OWB cover (data not shown), neither was native species richness ($p = 0.19$, $r^2 = 0.039$) (Fig. 4d). The average Sorenson similarity index between the species in the aboveground vegetation and the seed bank was low, averaging 0.38 (range 0.59–0.16) and was not related to aboveground OWB cover ($p = 0.38$, $r^2 = 0.017$) (Fig. 5).

Discussion

Generally, the native diversity of the aboveground plant community and seed bank declined as aboveground OWB cover increased; however, the magnitude of the reduction in native diversity was less for the seed bank than the aboveground plant community. Results indicate that there was a dense seed bank in this mixed-grass prairie study, with an average density of 6 020 seeds/m^2, and a large range in seed density (797–24 869 seeds/m^2). These values were similar to the values found in other studies in mixed-grass prairies (Leck et al., 1989; Romo & Bai, 2004; Cline et al., 2008). Old World bluestem was one of the dominant species found in the seed bank, along with three other grasses, two native (*S. asper* and *C. verticillata*) and one other non-native invasive grass, *Bromus* sp., supporting other studies that have found only a few species dominating the seed bank of the invaded sites (Wearne & Morgan, 2006). Although *Bromus* sp., an invasive annual grass, formed a dense seed bank, it did not contribute much to the aboveground cover.

The dominant perennial grasses in the aboveground vegetation, *Bouteloua curtipendula, B. gracilis, Buchloe dactyloides,* and *Schizachyrium scoparium* averaged 44% cover per plot in the aboveground species composition whereas they only represented 5.5% of the seeds in the seed bank. Perennial, high seral grass species such as these have often been shown to be absent or at low densities in seed banks (Kinucan & Smeins, 1992; Romo & Bai, 2004). In contrast, four other native perennial grasses all lower seral species, *S. asper, C. verticillata, Bothriochloa laguroides, S. cryptandrus,* were not well represented in the aboveground plant community but had seed densities 18 times greater than the dominant grasses. Native annual forbs also were disproportionately represented in the seed bank relative to their low cover in the aboveground vegetation. Native perennial forbs showed the opposite trend, in that they were abundant in the aboveground vegetation and at low density in the seed bank. These results were not surprising because annual species rely on yearly seed germination to be represented in the aboveground plant community, and tend to accumulate in the seed bank because of high levels of seed production (Bertiller & Aloia, 1997). Thus, there was a low similarity between species in the aboveground vegetation and species in the seed bank, which is typical for most seed banks (Hopfensperger, 2007). The low similarity is most likely related to the differential abundance of some species in the aboveground plant community (e.g. dominant perennial grasses and perennial forbs), relative to the seed bank composition.

The dominant perennial grasses had the highest percent cover of any functional group in the uninvaded plots, but as OWB cover increased, the cover of the dominant grasses decreased, and OWB became the most abundant species. The dominant grasses had the greatest decline in cover than any other native functional group. OWB has been shown to be highly competitive and is capable of reducing the height and biomass of *Bouteloua curtipendula, Schizachyrium scoparium,* and *Andropogon gerardii* (all dominant perennial grasses in the present study) in a greenhouse study (Schmidt & Hickman, 2006). All major native functional groups (dominant grasses, annual, and perennial forbs) exhibited decline in canopy cover as OWB invasion increased, with the exception of the non-dominant perennial grasses. Overall native cover showed steep declines as OWB invasion increased.

These results indicate that as the level OWB invasion increased, there was a loss of native plant diversity. Native species richness did not show a correlation with OWB invasion; however, reduced native species diversity, evenness, and cover were closely related to increasing OWB cover suggesting that although the number of native species present in the aboveground plant community does not decline, their abundances are reduced with increasing cover of OWB. Field studies have shown that OWB invasion reduces diversity and abundance of native plants regardless of environmental conditions and management practices such as burning and grazing, except under dense tree cover (Reed et al., 2005; Gabbard & Fowler, 2006). Reed et al. (2005) suggests that OWB is capable of changing the condition of the surrounding soil, which enhances its ability to compete with other native plants. I hypothesize that OWB's aggressiveness, competitiveness, and wide environmental tolerance allows OWB to decrease native plant species diversity and abundance, as invasion levels increases.

Old World bluestem is capable of forming a large seed bank (up to 4 481 seeds/m^2). Recent studies have shown that other invasive species tend to have large seed banks, their seed densities generally increase as aboveground abundance increases, due to greater seed production, which can result in the invasive species dominating the seed bank (Krinke et al., 2005; Fourie, 2008; Vosse et al., 2008). Similarly, in this study, I found OWB capable of becoming the most abundant species in the seed bank. For example, in plots with greater than 15% OWB cover, OWB seeds were the most abundant species in 9 of the 11 seed bank plots. Other invasive species have been observed to be the most dominant seed in the seed bank. The results suggest that as OWB cover increases, OWB seed density also increases, resulting in OWB becoming the dominant species in both the aboveground plant community and the seed bank.

Although native seed bank diversity and evenness statistically declines as aboveground invasion increased, the regression was relatively weak, with aboveground OWB invasion explaining only 9 and 18%, respectively, of the variation in native seed diversity and evenness. Regression analyses also indicated that native seed bank density and seed density of all native species functional groups were not related to aboveground OWB invasion. This suggests that increasing cover of OWB has a minimal effect on the native seed bank, inconsistent with results from several studies that found decreases in native seed diversity, native seed density, or both in invaded areas (Holmes, 2002; Bossuyt et al., 2007; Cline et al., 2008). However, other studies have found that diversity and/or density of native species were not different or were only slightly reduced from invaded and uninvaded areas (King & Buckney, 2001; Mason et al., 2007). For example, Holmes and Cowling (1997) showed that in areas that were recently, heavily invaded (>80% cover, <25 years), native seed diversity was similar to the uninvaded areas, but in areas with a long history of invasion (>25 years), there was a significant reduction in native seed diversity. Because some species produce a persistent seed bank and can remain viable for over ten years, native seed diversity can persist in soil after heavy invasion (Fourie, 2008). OWB was first introduced at Klemme Research Range 19 years before this study was conducted, and it is unknown how long OWB has existed in the sampled plots (Gunter et al., 1995). One limiting factor in OWB invasion might be a lack of efficient long distance dispersal (Gabbard & Fowler, 2006). It is unlikely that OWB invasion has existed long enough to observe a drastic reduction of native seed density and diversity decreased, suggesting that as OWB invasion increases, OWB seed density increases, but native seed bank diversity and density are maintained until native seeds lose their viability in the soil over time.

Given that a large native seed bank exists under the invaded area (average 5 315 seeds/m^2), I propose there is potential for natural restoration from the native seed bank after successful OWB eradication in invaded prairies. Although natural recovery to a high serial plant community might be difficult (Bossuyt et al., 2007), because 86% of the native seed bank in the invaded plots was composed of non-dominant grasses and annual forbs, and the dominant aboveground species were at low densities in most plots. Reinvasion also might be possible with the large seed bank of OWB in the invaded areas. Therefore, a short period of opportunity might exist for natural restoration since a large native seed bank can exist during the early stages of invasion when OWB invasion does not affect native seed density, and low OWB seed densities exist. Importantly, the possibility for natural recovery decreases as invasion increases due to increased OWB seed densities. Unfortunately, the high degree of variability in native seed bank density limits the ability of restoration attempts to depend solely on a large native seed bank for natural recovery (Vosse et al., 2008).

The findings suggest that OWB invasion had differential effects on native diversity and abundance in the aboveground vegetation compared with the seed bank. Increasing OWB invasion showed a greater reduction of native diversity and abundance in the aboveground plant community compared with native seed bank, which supports the findings of Holmes and Cowling (1997) that aboveground invasion reduced the native aboveground plant diversity more quickly than the native seed bank diversity. A similar lag between the seed bank and aboveground vegetation has been described in successional change from one plant community to a different plant community, in which seeds of the previous plant community persist in the soil even though that plant community no longer exists (Davies & Waite, 1998). Aboveground invasion may have similar effects on native seed bank diversity and density as aboveground successional change.

Based on the results of the present study and conclusions of other studies, I hypothesize that invasion by an invasive species affects the native aboveground plant community, the native seed bank, and the invasive seed bank differentially. As an invasive species increases in abundance in the aboveground vegetation, native species in the aboveground plant community decrease in diversity and abundance, through a variety of interactions, including competitive interactions (Mooney & Hobbs, 2000). Increasing invasion has a direct effect on invasive seed density with the increased seed input from a greater production of seed by the invasive species (Witkowski & Wilson, 2001). Unlike the native aboveground vegetation, invasive plants and their seeds do not directly interact with the existing native seeds, as they do with the native aboveground plants. Therefore, increasing aboveground invasion has minimal direct effect on native seed density and diversity, but as aboveground native diversity and abundance decrease with invasion, so do native seed production and input into the seed bank (Wearne & Morgan, 2006). Initially, after an area has been heavily invaded, the aboveground vegetation might have low density and diversity of native plants, but because some native species persist in the soil for many years, the native seed bank is capable of maintaining a high diversity and density of native seeds. Over time as native seeds are lost through death, predation, or possibly germination, the reduction and lack of native seed replenishment from the native aboveground plants, result in a loss of native seed bank diversity and density as time since invasion increases.

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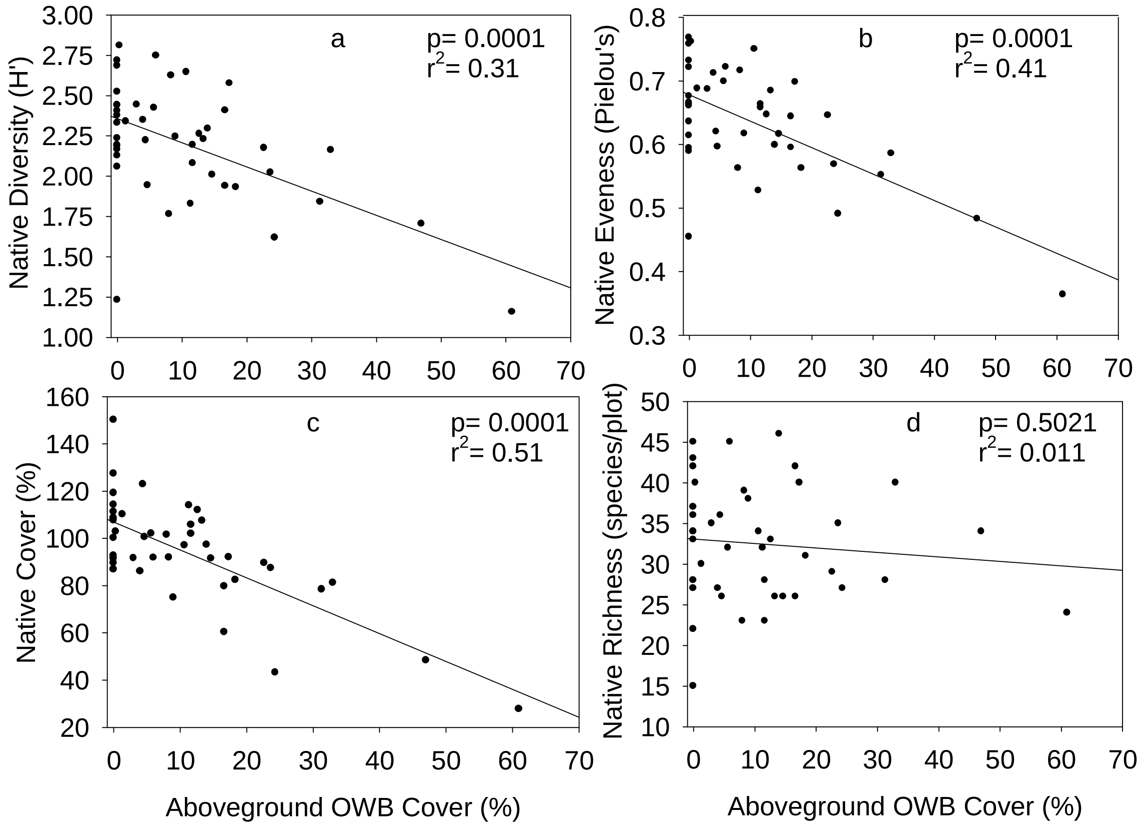

Fig.1. Regression analysis of the relationship between mean aboveground percent cover of OWB and a) mean Shannon diversity index of native aboveground plant species composition b) mean Pielou's evenness index of aboveground native plant species composition c) mean percent cover of aboveground native plant species composition and d) mean richness of aboveground native species.

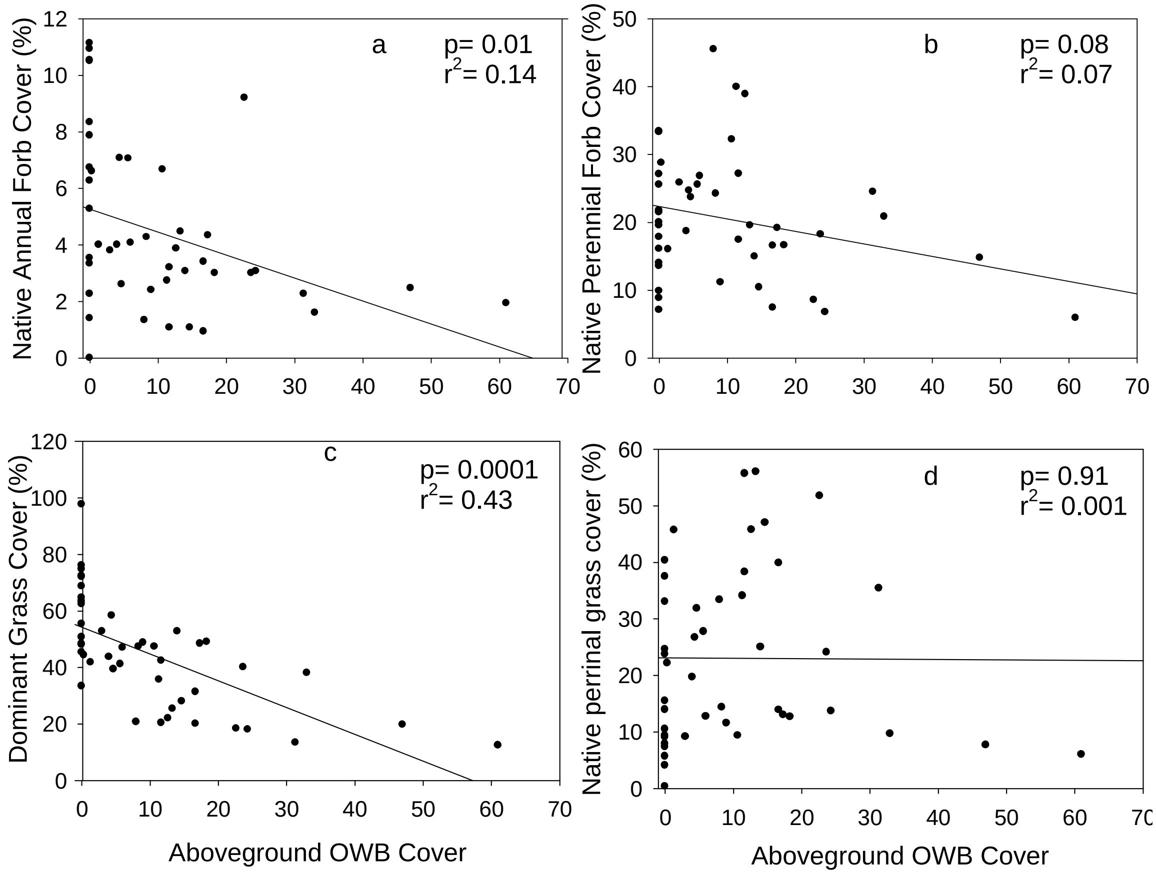

Fig. 2. Regression analysis of the relationship between mean aboveground percent cover of OWB and percent cover of native functional groups a) mean native annual forbs b) mean native perennial forbs c) mean native dominant grass and d) mean native non-dominant grasses.

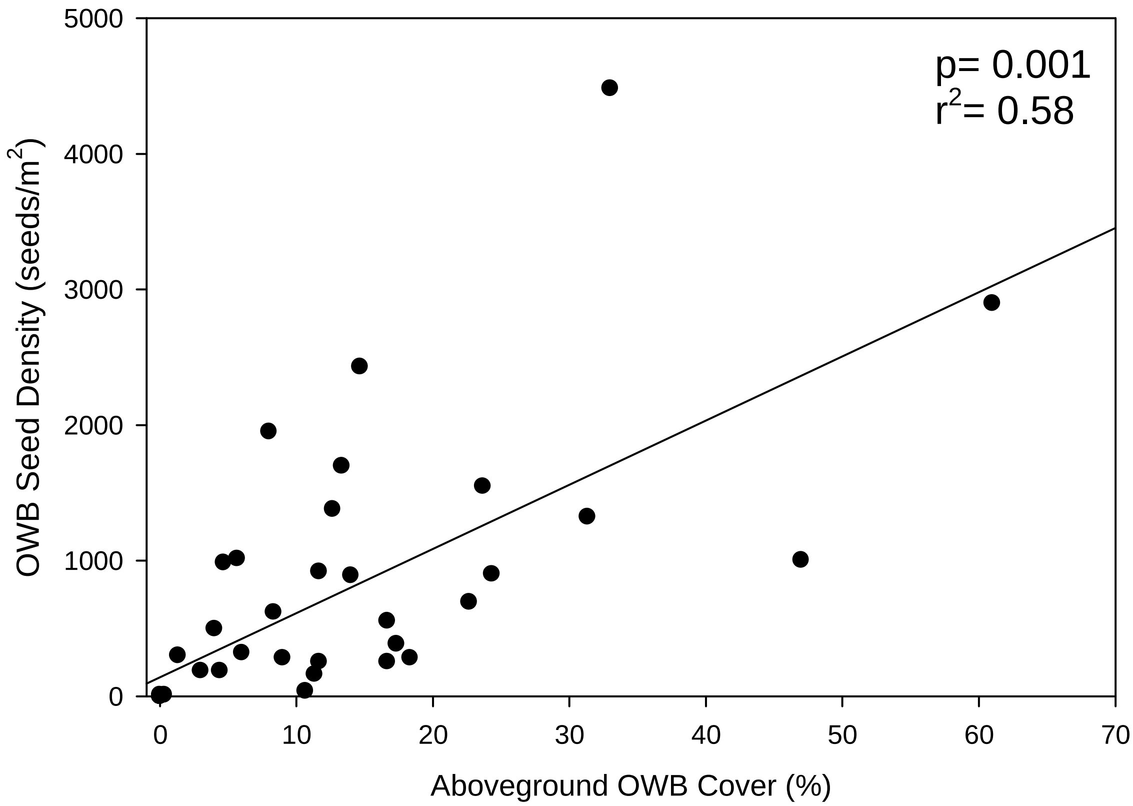

Fig. 3. Regression analysis of the relationship between mean aboveground percent cover of OWB and mean density of OWB seeds in the seed bank.

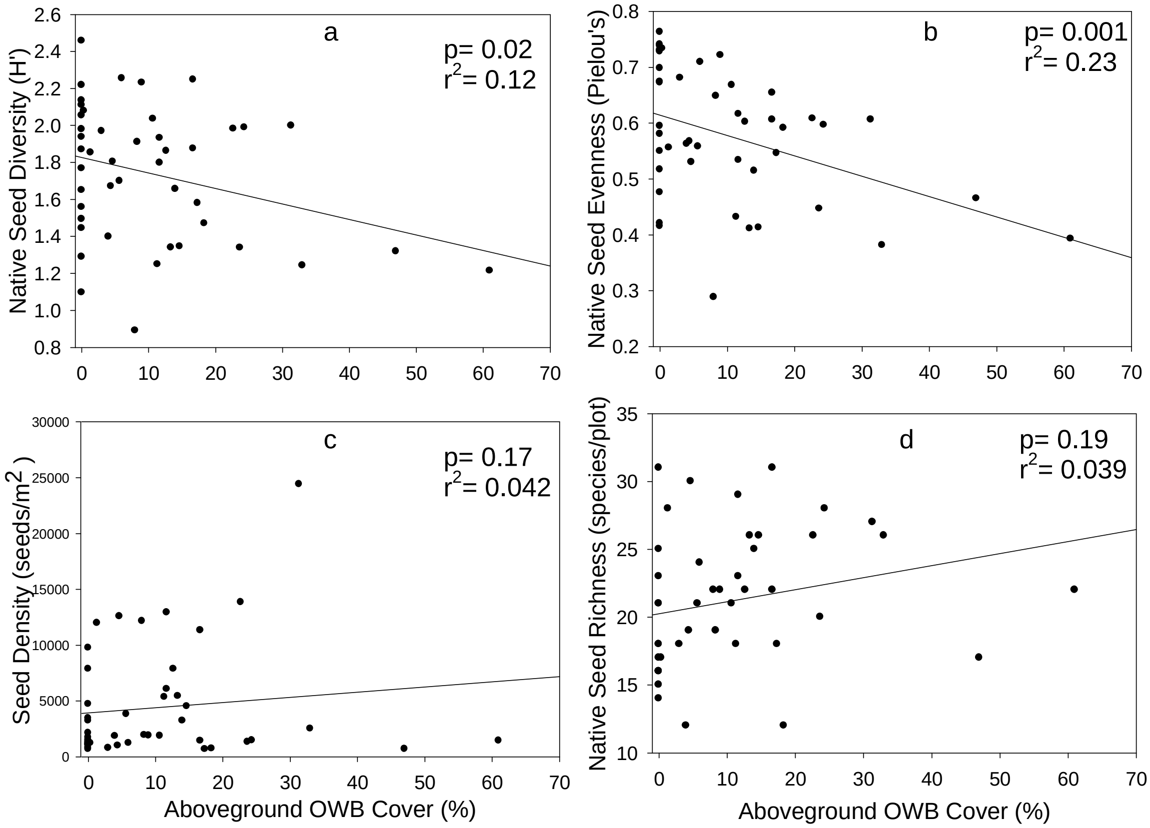

Fig. 4. Regression analysis of the relationship between mean aboveground percent cover of OWB and a) mean Shannon diversity index of native seeds b) mean Pielou's evenness index of native seeds c) mean density of native seeds (seeds/m^2) and d) mean richness of native seeds.

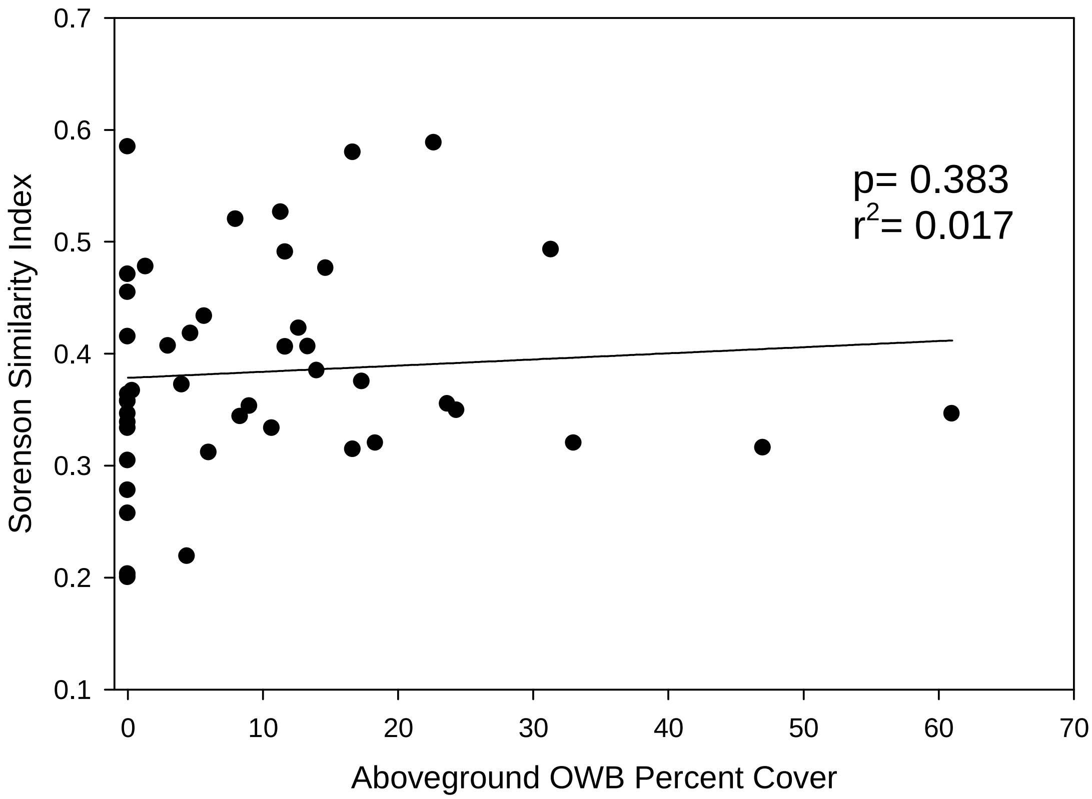

Fig. 5. Regression analysis of the relationship between mean aboveground percent cover of OWB and the Sorenson similarity index between the aboveground species and the seed bank species

Appendix 1. Mean seed density (seeds/m^2) of species recorded in the seed bank community at different levels of aboveground OWB invasion

Scientific Name	Uninvaded		1–10		11–20		21–30		>30	
	Percent invasion by OWB									
	Mean seed density (Standard error)									
Native dominant grasses										
Schizachyrium scoparium	89.7	*(56.4)*	35.2	*(17.3)*	25.8	*(21.6)*	15.6	*(15.6)*	112.5	*(129.9)*
Buchloe dactyloides	63.6	*(18.5)*	46.1	*(33.5)*	71.9	*(22.1)*	53.1	*(30.8)*	25.8	*(26.3)*
Bouteloua curtipendula	8.0	*(3.1)*	9.4	*(5.3)*	62.5	*(28.6)*	18.7	*(9.4)*	9.4	*(7.7)*
Bouteloua gracilis	18.7	*(10.9)*	10.9	*(6.4)*	0.0	*(0)*	0.0	*(0)*	68.0	*(78.5)*
Andropogon gerardii	16.1	*(12)*	0.0	*(0)*	0.0	*(0)*	0.0	*(0)*	0.0	*(0)*
Aristida purpurea	2.0	*(1.9)*	0.8	*(0.8)*	4.7	*(3.9)*	0.0	*(0)*	7.0	*(8.1)*
Native non-dominant grasses										
Sporobolus asper	235.0	*(78.1)*	1262.0	*(809)*	1974.8	*(561.4)*	1096.7	*(1073)*	2160.0	*(2302)*
Chloris verticillata	155.0	*(52.5)*	780.0	*(454.6)*	521.0	*(176.6)*	1527.9	*(1471)*	449.9	*(383.1)*
Sporobolus cryptandrus	198.0	*(53.2)*	472.0	*(302)*	274.2	*(105.2)*	434.3	*(424.9)*	157.0	*(51.2)*
Bothriochloa laguroides	147.0	*(44.2)*	361.0	*(72)*	467.1	*(123.1)*	275.0	*(70.6)*	236.7	*(112.3)*
Bouteloua hirsuta	695.0	*(359.5)*	275.0	*(137.8)*	110.1	*(36.6)*	56.2	*(28.1)*	79.7	*(52.7)*
Carex sp.	167.4	*(142.3)*	60.1	*(31.9)*	85.9	*(32.7)*	187.5	*(164.2)*	656.2	*(696.4)*
Tridens albescens	0.7	*(0.6)*	18.0	*(10.2)*	96.1	*(59)*	415.6	*(392.1)*	447.6	*(456.7)*
Tridens muticus	0.7	*(0.6)*	144.0	*(130.7)*	25.8	*(13.4)*	0.0	*(0)*	0.0	*(0)*
Tridens flavus	2.0	*(1.9)*	0.0	*(0)*	55.5	*(41.3)*	18.7	*(18.7)*	0.0	*(0)*

Eleocharis sp.	0.7	*(0.6)*	11.7	*(8.1)*	16.4	*(5.4)*	9.4	*(0)*	16.4	*(18.9)*
Poa arachnifera	1.3	*(0.9)*	10.9	*(10.9)*	1.6	*(1.1)*	28.1	*(28.1)*	0.0	*(0)*
Sorghastrum nutans	0.0	*(0)*	11.7	*(11.7)*	0.0	*(0)*	15.6	*(15.6)*	11.7	*(13.5)*
Setaria sp.	1.3	*(1.3)*	10.2	*(6.9)*	8.6	*(8.6)*	9.4	*(9.4)*	0.0	*(0)*
Typha sp.	8.7	*(3.9)*	2.3	*(1.2)*	4.7	*(3.2)*	0.0	*(0)*	4.7	*(3.1)*
Elymus smithii	0.0	*(0)*	12.5	*(12.5)*	0.0	*(0)*	0.0	*(0)*	2.3	*(2.7)*
Dichanthelium oligosanthes	3.3	*(2)*	0.0	*(0)*	8.6	*(8.6)*	0.0	*(0)*	0.0	*(0)*
Juncus. sp	0.0	*(0)*	0.0	*(0)*	0.0	*(0)*	0.0	*(0)*	9.4	*(10.8)*
Schedonnardus paniculatus	2.7	*(2)*	0.0	*(0)*	1.6	*(1.6)*	0.0	*(0)*	0.0	*(0)*
Panicum obtusum	0.0	*(0)*	0.0	*(0)*	0.0	*(0)*	0.0	*(0)*	2.3	*(2.7)*
Native perennial forbs										
Oxalis stricta	26.1	*(16.6)*	220.3	*(121.6)*	257.0	*(110.7)*	524.9	*(303.2)*	105.5	*(111.2)*
Nothoscordum bivalve	169.4	*(86.4)*	32.8	*(10.3)*	47.7	*(30.8)*	3.1	*(3.1)*	0.0	*(0)*
Ambrosia psilostachya	15.4	*(7.7)*	18.0	*(7.8)*	54.7	*(25.4)*	34.4	*(13.6)*	37.5	*(15.3)*
Phyla lanceolata	1.3	*(0.9)*	3.1	*(1.8)*	3.1	*(1.8)*	3.1	*(3.1)*	35.2	*(22.3)*
Artemisia ludoviciana	0.7	*(0.6)*	0.8	*(0.8)*	7.8	*(7)*	18.7	*(18.7)*	0.0	*(0)*
Physalis heterophylla	10.7	*(7.6)*	0.0	*(0)*	7.8	*(5.5)*	3.1	*(3.1)*	2.3	*(2.7)*
Cuscuta sp.	4.7	*(2.8)*	10.9	*(3)*	3.1	*(1.8)*	0.0	*(0)*	0.0	*(0)*
Oxalis violacea	0.0	*(0)*	9.4	*(7)*	1.6	*(1.6)*	0.0	*(0)*	0.0	*(0)*
Symphyotrichum ericoides	1.3	*(0.9)*	0.8	*(0.8)*	3.1	*(2.4)*	0.0	*(0)*	2.3	*(2.7)*
Physalis pumila	7.4	*(7.1)*	0.0	*(0)*	0.0	*(0)*	0.0	*(0)*	0.0	*(0)*
Vernonia baldwinii	2.0	*(1.9)*	1.6	*(1.1)*	2.3	*(2.3)*	0.0	*(0)*	0.0	*(0)*
Scutellaria resinosa	5.4	*(3.1)*	0.0	*(0)*	0.0	*(0)*	0.0	*(0)*	0.0	*(0)*
Erysimum asperum	0.0	*(0)*	3.9	*(3.9)*	0.0	*(0)*	0.0	*(0)*	0.0	*(0)*
Lithospermum arvense	2.0	*(1.9)*	0.8	*(0.8)*	0.0	*(0)*	0.0	*(0)*	0.0	*(0)*

Oputia sp.	0.0	*(0)*	0.0	*(0)*	1.6	*(1.1)*	0.0	*(0)*	0.0	*(0)*
	0.0	*(0)*	0.0	*(0)*	0.0	*(0)*	0.0	*(0)*	0.0	*(0)*
Native annual grasses	0.0	*(0)*	0.0	*(0)*	0.0	*(0)*	0.0	*(0)*	0.0	*(0)*
	0.0	*(0)*	0.0	*(0)*	0.0	*(0)*	0.0	*(0)*	0.0	*(0)*
Panicum capillare	24.1	*(12.5)*	49.2	*(22.1)*	17.2	*(8.1)*	109.4	*(104.7)*	63.3	*(65.9)*
Vulpia octoflora	6.0	*(3.5)*	3.9	*(2.4)*	0.0	*(0)*	18.7	*(18.7)*	2.3	*(2.7)*
Eriochloa contracta	0.0	*(0)*	0.0	*(0)*	0.0	*(0)*	3.1	*(3.1)*	0.0	*(0)*
Native annual forbs										
Helenium microcephalum	0.7	*(0.6)*	0.8	*(0.8)*	2.3	*(1.7)*	0.0	*(0)*	1305.0	*(1507)*
Conyza canadensis	392.4	*(295.8)*	70.3	*(20.7)*	207.8	*(127.4)*	253.1	*(143.5)*	23.4	*(15.6)*
Croton sp.	115.8	*(24.2)*	165.6	*(54.2)*	252.3	*(90.6)*	109.4	*(50)*	210.9	*(141.2)*
Euphorbia prostrata	1.3	*(1.3)*	7.0	*(4.3)*	31.2	*(23)*	3.1	*(3.1)*	482.8	*(514.8)*
Plantago sp.	58.9	*(19)*	59.4	*(23.4)*	85.9	*(30.7)*	78.1	*(27.2)*	49.2	*(25.1)*
Ammannia coccinea	2.0	*(1.4)*	3.9	*(3.2)*	3.9	*(3.2)*	6.2	*(6.2)*	302.3	*(341.9)*
Solanum rostratum	8.0	*(6.4)*	50.8	*(27)*	111.7	*(43.6)*	78.1	*(41.3)*	65.6	*(31.2)*
Amphiachyris dracunculoides	22.1	*(9.5)*	36.7	*(22.2)*	71.9	*(21.2)*	12.5	*(12.5)*	42.2	*(28.5)*
Acalypha ostryifolia	32.1	*(29.7)*	0.0	*(0)*	41.4	*(23.1)*	0.0	*(0)*	0.0	*(0)*
Euphorbia marginata	1.3	*(0.9)*	2.3	*(1.7)*	10.9	*(6.3)*	28.1	*(16.2)*	11.7	*(13.5)*
Verbena bracteata	1.3	*(0.9)*	3.1	*(1.8)*	13.3	*(10.9)*	9.4	*(5.4)*	11.7	*(10.2)*
Euphorbia dentata	20.8	*(18.7)*	0.8	*(0.8)*	11.7	*(9.5)*	0.0	*(0)*	4.7	*(5.4)*
Centaurea americana	8.0	*(4.5)*	9.4	*(4.9)*	6.2	*(3.3)*	3.1	*(3.1)*	2.3	*(2.7)*
Helianthus annuus	22.8	*(22)*	0.0	*(0)*	0.0	*(0)*	0.0	*(0)*	0.0	*(0)*
Polygonum pensylvanicum	0.0	*(0)*	0.0	*(0)*	0.0	*(0)*	0.0	*(0)*	14.1	*(12.9)*
Geranium carolinianum	1.3	*(1.3)*	4.7	*(4.7)*	1.6	*(1.6)*	6.2	*(6.2)*	0.0	*(0)*
Tetraneuris linearifolia	6.0	*(2.8)*	2.3	*(1.7)*	5.5	*(3.2)*	0.0	*(0)*	0.0	*(0)*
Gaura mollis	6.7	*(4.4)*	6.2	*(5.5)*	0.8	*(0.8)*	0.0	*(0)*	0.0	*(0)*
Verbena dakotaka	3.3	*(1.8)*	1.6	*(1.6)*	3.1	*(2.4)*	0.0	*(0)*	2.3	*(2.7)*

Linum rigidum	3.3	*(1.8)*	1.6	*(1.1)*	0.8	*(0.8)*	3.1	*(3.1)*	0.0	*(0)*
Leucospora multifida	0.0	*(0)*	0.8	*(0.8)*	1.6	*(1.6)*	3.1	*(3.1)*	2.3	*(2.7)*
Coreopsis tinctoria	1.3	*(0.9)*	1.6	*(1.1)*	0.8	*(0.8)*	0.0	*(0)*	0.0	*(0)*
Solanum ptycanthum	0.0	*(0)*	0.0	*(0)*	0.0	*(0)*	3.1	*(3.1)*	0.0	*(0)*
Polanisia dodecandra	0.0	*(0)*	0.0	*(0)*	0.0	*(0)*	3.1	*(3.1)*	0.0	*(0)*
Lepidium sp.	0.0	*(0)*	1.6	*(1.6)*	0.0	*(0)*	0.0	*(0)*	0.0	*(0)*
Aster subulatus	0.0	*(0)*	0.8	*(0.8)*	0.8	*(0.8)*	0.0	*(0)*	0.0	*(0)*
Palafoxia rosa	0.0	*(0)*	1.6	*(1.1)*	0.0	*(0)*	0.0	*(0)*	0.0	*(0)*
Ambrosia trifida	0.0	*(0)*	0.0	*(0)*	0.8	*(0.8)*	0.0	*(0)*	0.0	*(0)*
Pluchea odorata	0.0	*(0)*	0.8	*(0.8)*	0.0	*(0)*	0.0	*(0)*	0.0	*(0)*
Monolepis nuttalliana	0.0	*(0)*	0.0	*(0)*	0.0	*(0)*	0.0	*(0)*	0.0	*(0)*
Native legumes										
Schrankia nuttallii	0.0	*(0)*	0.0	*(0)*	0.0	*(0)*	0.0	*(0)*	2.3	*(2.7)*
Dalea purpurea	0.0	*(0)*	1.6	*(1.1)*	0.0	*(0)*	0.0	*(0)*	0.0	*(0)*
Strophostyles helvula	0.0	*(0)*	0.8	*(0.8)*	0.0	*(0)*	0.0	*(0)*	0.0	*(0)*
Psoralea tenuiflora	0.7	*(0.6)*	0.0	*(0)*	0.0	*(0)*	0.0	*(0)*	0.0	*(0)*
Astragulus sp.	0.7	*(0.6)*	0.0	*(0)*	0.0	*(0)*	0.0	*(0)*	0.0	*(0)*
	0.0	*(0)*	0.0	*(0)*	0.0	*(0)*	0.0	*(0)*	0.0	*(0)*
Native woody	0.0	*(0)*	0.0	*(0)*	0.0	*(0)*	0.0	*(0)*	0.0	*(0)*
	0.0	*(0)*	0.0	*(0)*	0.0	*(0)*	0.0	*(0)*	0.0	*(0)*
Salix sp.	5.4	*(1.8)*	3.9	*(1.8)*	1.6	*(1.1)*	3.1	*(3.1)*	11.7	*(0)*
Populus deltoides	6.0	*(4.5)*	1.6	*(1.1)*	4.7	*(2.4)*	3.1	*(3.1)*	0.0	*(0)*
Ulmus americana	0.0	*(0)*	0.8	*(0.8)*	0.8	*(0.8)*	0.0	*(0)*	0.0	*(0)*
Celtis sp.	0.0	*(0)*	0.0	*(0)*	0.8	*(0.8)*	0.0	*(0)*	0.0	*(0)*
Invasive perennial grasses										

Bothriochloa ischaemum	0.0	*(0)*	529.6	*(160.5)*	769.4	*(211.3)*	1046.7	*(257)*	2425.0	*(924)*
Sorghum halepense	0.0	*(0)*	0.0	*(0)*	7.0	*(7)*	0.0	*(0)*	72.6	*(83.9)*
Cynodon dactylon	12.1	*(4.2)*	11.7	*(6.1)*	38.3	*(15.2)*	0.0	*(0)*	4.7	*(5.4)*
Invasive annual grasses										
Bromus sp.	533.6	*(319.1)*	396.8	*(199)*	985.0	*(488.6)*	106.2	*(92.2)*	178.1	*(139)*
Panicum miliaceum	2.0	*(1.9)*	0.8	*(0.8)*	0.0	*(0)*	0.0	*(0)*	2.3	*(2.7)*
Invasive forbs										
Mollugo verticillata	16.1	*(10.7)*	4.7	*(3.2)*	36.7	*(21.6)*	106.2	*(106.2)*	11.7	*(10.2)*
Amaranthus blitoides	18.1	*(12.8)*	19.5	*(12.2)*	8.6	*(2.9)*	6.2	*(3.1)*	28.1	*(17.1)*
Melilotus officinalis	0.0	*(0)*	0.0	*(0)*	16.4	*(16.4)*	0.0	*(0)*	60.9	*(66.8)*
Stellaria media	0.0	*(0)*	56.2	*(56.2)*	0.8	*(0.8)*	0.0	*(0)*	0.0	*(0)*
Capsella bursa-pastoris	0.0	*(0)*	0.0	*(0)*	1.6	*(1.1)*	3.1	*(3.1)*	49.2	*(56.8)*
Carduus nutans	10.0	*(2.8)*	14.8	*(12.3)*	11.7	*(6.1)*	6.2	*(3.1)*	0.0	*(0)*
Chenopodium album	16.1	*(15.5)*	0.0	*(0)*	0.8	*(0.8)*	9.4	*(5.4)*	0.0	*(0)*
Taraxacum officinale	0.7	*(0.6)*	2.3	*(1.2)*	4.7	*(4.7)*	3.1	*(3.1)*	0.0	*(0)*
Daucus sp.	0.0	*(0)*	0.0	*(0)*	7.0	*(7)*	0.0	*(0)*	0.0	*(0)*
Convolvulus arvensis	1.3	*(1.3)*	0.0	*(0)*	0.0	*(0)*	0.0	*(0)*	0.0	*(0)*
Lactuca serriola	0.0	*(0)*	0.8	*(0.8)*	0.0	*(0)*	0.0	*(0)*	0.0	*(0)*
Rumex crispus	0.7	*(0.6)*	0.0	*(0)*	0.0	*(0)*	0.0	*(0)*	0.0	*(0)*
Lamium amplexicaule	0.0	*(0)*	0.0	*(0)*	0.0	*(0)*	0.0	*(0)*	0.0	*(0)*

Appendix 2. Mean percent cover of species recorded in the aboveground plant community at different levels of aboveground OWB invasion

	Percent invasion by OWB				
Scientific Name	**Uninvaded**	**1–10**	**11–20**	**21–30**	**>30**
	---------------------------------Mean percent cover (Standard error)---------------------------				
Native dominant grasses					
Bouteloua cutripendula	9.98 *(2.4)*	13.52 *(4.5)*	14.81 *(2.6)*	16.33 *(9.2)*	8.25 *(2.5)*
Bouteloua gracilis	17.71 *(3.6)*	10.78 *(2.7)*	5.31 *(1.7)*	5.00 *(2.6)*	0.42 *(0.2)*
Aristida purpurea	12.14 *(2.4)*	12.01 *(2.6)*	4.00 *(1.5)*	0.67 *(0.4)*	4.77 *(2.4)*
Buchloe dactyloides	8.52 *(3.1)*	5.77 *(2)*	4.70 *(1.5)*	3.33 *(2.3)*	1.33 *(0.7)*
Schizachyrium scoparium	6.62 *(4.2)*	1.70 *(1.2)*	5.97 *(3)*	0.00 *(0)*	5.02 *(5.8)*
Andropogon gerardii	8.19 *(4.8)*	0.67 *(0.5)*	0.42 *(0.3)*	0.11 *(0.1)*	1.08 *(1.3)*
Bothriochloa laguroides	4.46 *(1.1)*	8.37 *(1.6)*	10.67 *(1.5)*	10.22 *(2.6)*	5.50 *(1.4)*
Sporobolus asper	3.15 *(1.2)*	4.20 *(2)*	11.87 *(2.9)*	5.78 *(3.4)*	5.58 *(4.3)*
Bouteloua hirsuta	5.43 *(2.4)*	2.76 *(1.1)*	2.20 *(0.8)*	1.33 *(1)*	0.75 *(0.9)*
Chloris verticillata	0.77 *(0.3)*	1.15 *(0.7)*	2.89 *(1.1)*	6.89 *(6.7)*	0.25 *(0.2)*
Elymus smithii	0.05 *(0)*	0.59 *(0.6)*	0.82 *(0.6)*	2.80 *(1.4)*	1.08 *(1.3)*
Tridens muticus	0.39 *(0.3)*	1.31 *(0.9)*	1.76 *(1.2)*	0.00 *(0)*	0.00 *(0)*
Panicum obtusum	0.48 *(0.5)*	0.53 *(0.4)*	0.14 *(0.1)*	1.44 *(1.4)*	0.08 *(0.1)*
Setaria sp.	0.04 *(0)*	0.81 *(0.8)*	0.44 *(0.3)*	0.84 *(0.8)*	0.02 *(0)*
Sporobolus cryptandrus	0.50 *(0.2)*	0.95 *(0.4)*	0.20 *(0.1)*	0.22 *(0.2)*	0.00 *(0)*
Erioneuron pilosum	0.99 *(0.3)*	0.67 *(0.3)*	0.06 *(0.1)*	0.00 *(0)*	0.00 *(0)*
Tridens albescens	0.02 *(0)*	0.06 *(0.1)*	0.04 *(0)*	0.07 *(0.1)*	0.92 *(1.1)*
Elymus virginicus	0.26 *(0.3)*	0.00 *(0)*	0.56 *(0.5)*	0.00 *(0)*	0.08 *(0.1)*
Tridens flavus	0.00 *(0)*	0.00 *(0)*	0.47 *(0.3)*	0.00 *(0)*	0.42 *(0.5)*

Sorghastrum nutans	0.33	*(0.2)*	0.00	*(0)*	0.17	*(0.2)*	0.00	*(0)*	0.00	*(0)*
Schedonnardus paniculatus	0.13	*(0.1)*	0.14	*(0.1)*	0.03	*(0)*	0.00	*(0)*	0.00	*(0)*
Dichanthelium oligosanthes	0.05	*(0)*	0.03	*(0)*	0.19	*(0.2)*	0.00	*(0)*	0.00	*(0)*
Paspalum setaceum	0.00	*(0)*	0.00	*(0)*	0.00	*(0)*	0.22	*(0.2)*	0.00	*(0)*
Spartina pectinata	0.00	*(0)*	0.00	*(0)*	0.03	*(0)*	0.00	*(0)*	0.00	*(0)*
Carex sp.	0.00	*(0)*	0.06	*(0.1)*	0.08	*(0.1)*	0.44	*(0.4)*	0.68	*(0.8)*
Native perennial forb										
Ambrosia psilostachya	4.31	*(1)*	7.91	*(2.9)*	9.89	*(2.9)*	3.40	*(1.8)*	4.68	*(2.7)*
Gutierrezia sarothrae	2.62	*(0.8)*	2.42	*(0.8)*	1.38	*(0.7)*	1.00	*(0.7)*	1.83	*(0.9)*
Artemisia ludoviciana	0.63	*(0.3)*	1.78	*(0.8)*	0.68	*(0.3)*	1.11	*(1.1)*	2.08	*(1.8)*
Calylophus lavandulifolia	1.09	*(0.5)*	2.29	*(0.7)*	0.96	*(0.4)*	0.13	*(0.1)*	1.08	*(1.1)*
Cirsium undulatum	0.40	*(0.2)*	0.66	*(0.4)*	1.43	*(0.4)*	0.91	*(0.9)*	0.27	*(0.2)*
Symphyotrichum ericoides	0.72	*(0.3)*	0.32	*(0.2)*	0.71	*(0.4)*	0.11	*(0.1)*	1.50	*(1.2)*
Oxalis stricta	0.07	*(0)*	0.59	*(0.3)*	1.22	*(0.4)*	1.22	*(1.1)*	0.22	*(0.1)*
Opuntia macrorhiza	0.47	*(0.2)*	1.23	*(0.7)*	0.56	*(0.5)*	0.00	*(0)*	0.00	*(0)*
Physalis heterophylla	0.35	*(0.2)*	0.06	*(0)*	0.79	*(0.3)*	0.49	*(0.3)*	0.57	*(0.4)*
Calylophus serrulatus	0.34	*(0.2)*	0.22	*(0.2)*	0.26	*(0.1)*	0.11	*(0.1)*	1.28	*(1.4)*
Sisyrinchium campestre	0.62	*(0.2)*	0.74	*(0.3)*	0.36	*(0.3)*	0.07	*(0)*	0.13	*(0.1)*
Gaura longiflora	0.16	*(0.1)*	0.28	*(0.1)*	0.23	*(0.1)*	0.78	*(0.7)*	0.42	*(0.4)*
Evolvulus nuttallianus	0.89	*(0.3)*	0.68	*(0.3)*	0.21	*(0.1)*	0.00	*(0)*	0.03	*(0)*
Liatris punctata	0.41	*(0.1)*	0.51	*(0.3)*	0.18	*(0.1)*	0.00	*(0)*	0.45	*(0.4)*
Paronychia jamesii	0.66	*(0.2)*	0.59	*(0.2)*	0.19	*(0.1)*	0.00	*(0)*	0.10	*(0.1)*
Krameria lanceolata	0.71	*(0.4)*	0.56	*(0.3)*	0.11	*(0.1)*	0.00	*(0)*	0.00	*(0)*
Hymenoxys scoposa	0.54	*(0.2)*	0.64	*(0.2)*	0.09	*(0)*	0.04	*(0)*	0.02	*(0)*
Asclepias viridis	0.23	*(0.1)*	0.42	*(0.2)*	0.24	*(0.1)*	0.11	*(0.1)*	0.33	*(0.2)*
Tragia ramosa	0.32	*(0.1)*	0.48	*(0.3)*	0.19	*(0.2)*	0.11	*(0.1)*	0.17	*(0.2)*
Castilleja sessiliflora	0.29	*(0.2)*	0.74	*(0.3)*	0.16	*(0.1)*	0.00	*(0)*	0.00	*(0)*

Ratibida columnifera	0.24	*(0.2)*	0.12	*(0.1)*	0.09	*(0.1)*	0.56	*(0.3)*	0.00	*(0)*
Hedyotis nigricans	0.39	*(0.3)*	0.25	*(0.2)*	0.15	*(0.1)*	0.02	*(0)*	0.10	*(0.1)*
Gaillardia suavis	0.03	*(0)*	0.10	*(0.1)*	0.23	*(0.1)*	0.04	*(0)*	0.43	*(0.5)*
Chrysopsis villosa	0.33	*(0.2)*	0.07	*(0.1)*	0.03	*(0)*	0.02	*(0)*	0.25	*(0.3)*
Machaeranthera pinnatifida	0.31	*(0.1)*	0.20	*(0.1)*	0.03	*(0)*	0.00	*(0)*	0.10	*(0.1)*
Calylophus hartwegii	0.24	*(0.2)*	0.26	*(0.2)*	0.08	*(0.1)*	0.00	*(0)*	0.00	*(0)*
Vernonia baldwinii	0.00	*(0)*	0.03	*(0)*	0.49	*(0.4)*	0.00	*(0)*	0.00	*(0)*
Solanum carolinense	0.00	*(0)*	0.00	*(0)*	0.03	*(0)*	0.44	*(0.4)*	0.00	*(0)*
Polygala alba	0.00	*(0)*	0.11	*(0.1)*	0.05	*(0)*	0.22	*(0.2)*	0.00	*(0)*
Hymenopappus scabiosaeus	0.05	*(0)*	0.12	*(0.1)*	0.06	*(0)*	0.13	*(0.1)*	0.02	*(0)*
Yucca glauca	0.15	*(0.1)*	0.01	*(0)*	0.01	*(0)*	0.11	*(0.1)*	0.03	*(0)*
Solanum elaeagnifolium	0.05	*(0)*	0.00	*(0)*	0.23	*(0.1)*	0.00	*(0)*	0.00	*(0)*
Dyssodia pentachaeta	0.21	*(0.2)*	0.01	*(0)*	0.03	*(0)*	0.00	*(0)*	0.00	*(0)*
Leucelene erciodies	0.05	*(0.1)*	0.17	*(0.1)*	0.00	*(0)*	0.00	*(0)*	0.00	*(0)*
Penstemon albidus	0.15	*(0.1)*	0.00	*(0)*	0.06	*(0.1)*	0.00	*(0)*	0.00	*(0)*
Lithospermum caroliniense	0.00	*(0)*	0.03	*(0)*	0.00	*(0)*	0.00	*(0)*	0.17	*(0.2)*
Solidago canadensis	0.17	*(0.2)*	0.00	*(0)*	0.00	*(0)*	0.00	*(0)*	0.00	*(0)*
Engelmannia peristenia	0.00	*(0)*	0.00	*(0)*	0.00	*(0)*	0.00	*(0)*	0.17	*(0.2)*
Solidago missouriensis	0.12	*(0.1)*	0.00	*(0)*	0.01	*(0)*	0.00	*(0)*	0.00	*(0)*
Scutellaria resinosa	0.07	*(0)*	0.00	*(0)*	0.03	*(0)*	0.00	*(0)*	0.00	*(0)*
Cuscuta sp.	0.02	*(0)*	0.04	*(0)*	0.03	*(0)*	0.00	*(0)*	0.00	*(0)*
Oxalis violacea	0.04	*(0)*	0.04	*(0)*	0.01	*(0)*	0.00	*(0)*	0.00	*(0)*
Salvia azurea	0.00	*(0)*	0.03	*(0)*	0.06	*(0.1)*	0.00	*(0)*	0.00	*(0)*
Gaura villosa	0.10	*(0.1)*	0.00	*(0)*	0.00	*(0)*	0.00	*(0)*	0.00	*(0)*
Mirabilis linearis	0.10	*(0.1)*	0.10	*(0.1)*	0.00	*(0)*	0.00	*(0)*	0.00	*(0)*
Zinnia grandiflora	0.00	*(0)*	0.00	*(0)*	0.10	*(0.1)*	0.00	*(0)*	0.00	*(0)*
Cucurbita foetidissima	0.10	*(0.1)*	0.00	*(0)*	0.00	*(0)*	0.00	*(0)*	0.00	*(0)*
Ferocactus sp.	0.10	*(0.1)*	0.00	*(0)*	0.00	*(0)*	0.00	*(0)*	0.10	*(0.1)*
Nothoscordum bivalve	0.10	*(0.1)*	0.10	*(0.1)*	0.00	*(0)*	0.00	*(0)*	0.00	*(0)*

Cirsium ochrocentrum	0.00	*(0)*	0.00	*(0)*	0.10	*(0.1)*	0.00	*(0)*	0.00	*(0)*
Achillea millefolium	0.00	*(0)*	0.10	*(0.1)*	0.00	*(0)*	0.00	*(0)*	0.00	*(0)*
Kuhnia eupatorioides	0.00	*(0)*	0.10	*(0.1)*	0.00	*(0)*	0.00	*(0)*	0.00	*(0)*
Galium virgatum	0.10	*(0.1)*	0.00	*(0)*	0.00	*(0)*	0.00	*(0)*	0.00	*(0)*
Phyla lanceolata	0.00	*(0)*	0.00	*(0)*	0.00	*(0)*	0.00	*(0)*	0.10	*(0.1)*
Allium sp.	0.00	*(0)*	0.00	*(0)*	0.01	*(0)*	0.00	*(0)*	0.00	*(0)*
Native annual grasses										
Panicum capillare	0.08	*(0.1)*	0.06	*(0)*	0.03	*(0)*	0.13	*(0.1)*	0.00	*(0)*
Native annual forbs										
Linum rigidum	1.06	*(0.3)*	1.23	*(0.3)*	0.30	*(0.1)*	0.40	*(0.4)*	0.27	*(0.1)*
Croton sp.	1.00	*(0.3)*	0.48	*(0.1)*	0.53	*(0.2)*	0.33	*(0.2)*	0.37	*(0.2)*
Grindelia squarrosa	0.16	*(0.1)*	0.52	*(0.3)*	0.79	*(0.3)*	0.80	*(0.3)*	0.22	*(0.2)*
Euphorbia marginata	0.01	*(0)*	0.29	*(0.2)*	0.22	*(0.1)*	1.33	*(1.3)*	0.33	*(0.3)*
Eriogonum annuum	0.56	*(0.2)*	0.54	*(0.2)*	0.09	*(0.1)*	0.02	*(0)*	0.00	*(0)*
Amphiachyris dracunculoides	0.49	*(0.2)*	0.11	*(0.1)*	0.25	*(0.1)*	0.11	*(0.1)*	0.17	*(0.2)*
Hedeoma drummondii	0.67	*(0.3)*	0.18	*(0.1)*	0.25	*(0.2)*	0.00	*(0)*	0.00	*(0)*
Coreopsis tinctoria	0.34	*(0.1)*	0.42	*(0.3)*	0.16	*(0.1)*	0.02	*(0)*	0.02	*(0)*
Conyza canadensis	0.20	*(0.2)*	0.03	*(0)*	0.03	*(0)*	0.67	*(0.7)*	0.00	*(0)*
Plantago patagonica	0.19	*(0.1)*	0.25	*(0.1)*	0.07	*(0)*	0.20	*(0.2)*	0.05	*(0.1)*
Erigeron strigosus	0.12	*(0.1)*	0.04	*(0)*	0.11	*(0)*	0.33	*(0.2)*	0.10	*(0.1)*
Plantago sp.	0.30	*(0.2)*	0.02	*(0)*	0.08	*(0)*	0.00	*(0)*	0.05	*(0)*
Centaurea americana	0.11	*(0.1)*	0.09	*(0)*	0.09	*(0)*	0.04	*(0)*	0.10	*(0.1)*
Helianthus annuus	0.43	*(0.4)*	0.00	*(0)*	0.00	*(0)*	0.00	*(0)*	0.00	*(0)*
Thelesperma filifolium	0.12	*(0.1)*	0.03	*(0)*	0.03	*(0)*	0.00	*(0)*	0.17	*(0.2)*
Solanum rostratum	0.00	*(0)*	0.01	*(0)*	0.01	*(0)*	0.22	*(0.2)*	0.10	*(0.1)*

Aster subulatus	0.00	*(0)*	0.00	*(0)*	0.00	*(0)*	0.33	*(0.3)*	0.00	*(0)*
Geranium carolinianum	0.02	*(0)*	0.04	*(0)*	0.00	*(0)*	0.13	*(0.1)*	0.08	*(0.1)*
Euphorbia missurica	0.13	*(0.1)*	0.06	*(0)*	0.00	*(0)*	0.00	*(0)*	0.00	*(0)*
Palafoxia rosa	0.00	*(0)*	0.08	*(0.1)*	0.09	*(0.1)*	0.00	*(0)*	0.00	*(0)*
Monarda citriodora	0.07	*(0.1)*	0.04	*(0)*	0.00	*(0)*	0.00	*(0)*	0.00	*(0)*
Triodanis perfoliata	0.00	*(0)*	0.00	*(0)*	0.00	*(0)*	0.11	*(0.1)*	0.00	*(0)*
Euphorbia prostrata	0.00	*(0)*	0.01	*(0)*	0.03	*(0)*	0.02	*(0)*	0.05	*(0.1)*
Acalypha ostryifolia	0.00	*(0)*	0.00	*(0)*	0.03	*(0)*	0.00	*(0)*	0.00	*(0)*
Euphorbia dentata	0.02	*(0)*	0.00	*(0)*	0.00	*(0)*	0.00	*(0)*	0.00	*(0)*
Lepidium sp.	0.00	*(0)*	0.01	*(0)*	0.00	*(0)*	0.00	*(0)*	0.00	*(0)*
Verbena sp.	0.00	*(0)*	0.00	*(0)*	0.01	*(0)*	0.00	*(0)*	0.00	*(0)*
Native legumes										
Psoralea tenuiflora	1.34	*(0.4)*	0.90	*(0.4)*	1.72	*(0.6)*	0.44	*(0.4)*	2.28	*(2.1)*
Astragalus sp.	0.43	*(0.2)*	0.22	*(0.1)*	0.22	*(0.2)*	0.67	*(0.5)*	0.70	*(0.5)*
Schrankia nuttallii	0.00	*(0)*	0.14	*(0.1)*	0.11	*(0.1)*	0.13	*(0.1)*	0.33	*(0.3)*
Dalea purpurea	0.06	*(0)*	0.11	*(0)*	0.22	*(0.1)*	0.00	*(0)*	0.13	*(0.1)*
Strophostyles helvula	0.10	*(0.1)*	0.00	*(0)*	0.03	*(0)*	0.00	*(0)*	0.00	*(0)*
Dalea aurea	0.02	*(0)*	0.07	*(0)*	0.00	*(0)*	0.00	*(0)*	0.00	*(0)*
Chamaecrista fasciculata	0.00	*(0)*	0.06	*(0.1)*	0.01	*(0)*	0.00	*(0)*	0.00	*(0)*
Lupinus texensis	0.02	*(0)*	0.00	*(0)*	0.03	*(0)*	0.00	*(0)*	0.00	*(0)*
Acacia angustissima	0.02	*(0)*	0.00	*(0)*	0.00	*(0)*	0.00	*(0)*	0.00	*(0)*
Native woody										
Rhus glabra	0.02	*(0)*	0.00	*(0)*	0.00	*(0)*	0.00	*(0)*	0.60	*(0.7)*
Ulmus sp.	0.00	*(0)*	0.03	*(0)*	0.00	*(0)*	0.00	*(0)*	0.02	*(0)*
Celtis sp.	0.00	*(0)*	0.02	*(0)*	0.01	*(0)*	0.00	*(0)*	0.02	*(0)*

Invasive perennial grasses										
Bothriochloa ischaemum	0.00	*(0)*	4.56	*(0.9)*	14.08	*(0.8)*	23.56	*(0.5)*	43.08	*(8)*
Cynodon dactylon	0.00	*(0)*	0.17	*(0.1)*	0.08	*(0.1)*	0.33	*(0.2)*	2.75	*(3)*
Sorghum halepense	0.00	*(0)*	0.00	*(0)*	0.06	*(0.1)*	0.00	*(0)*	0.00	*(0)*
Invasive annual grasseses										
Bromus sp.	3.10	*(1.7)*	2.48	*(1.2)*	4.51	*(1.1)*	1.24	*(1.1)*	0.65	*(0.5)*
Invasive forbs										
Carduus nutans	0.14	*(0.1)*	1.56	*(1.5)*	1.28	*(1.1)*	2.22	*(2.2)*	0.00	*(0)*
Medicago lupulina	0.00	*(0)*	0.00	*(0)*	0.06	*(0.1)*	0.00	*(0)*	0.25	*(0.3)*
Convolvulus arvensis	0.00	*(0)*	0.00	*(0)*	0.03	*(0)*	0.11	*(0.1)*	0.10	*(0.1)*
Capsella bursa-pastoris	0.00	*(0)*	0.00	*(0)*	0.00	*(0)*	0.11	*(0.1)*	0.00	*(0)*
Taraxicum officinale	0.00	*(0)*	0.00	*(0)*	0.11	*(0.1)*	0.00	*(0)*	0.00	*(0)*
Melilotus officinalis	0.00	*(0)*	0.00	*(0)*	0.08	*(0.1)*	0.00	*(0)*	0.00	*(0)*
Tragopogon dubius	0.00	*(0)*	0.01	*(0)*	0.06	*(0)*	0.00	*(0)*	0.00	*(0)*
Chenopodium album	0.05	*(0)*	0.00	*(0)*	0.00	*(0)*	0.00	*(0)*	0.02	*(0)*
Lactuca serriola	0.00	*(0)*	0.00	*(0)*	0.03	*(0)*	0.00	*(0)*	0.00	*(0)*
Amaranthus blitoides	0.00	*(0)*	0.01	*(0)*	0.00	*(0)*	0.00	*(0)*	0.00	*(0)*

VITA

Scott Gallup Robertson

Candidate for the Degree of

Master of Science

Thesis: HERBICIDE CONTROL AND SEED BANK DYNAMICS OF OLD WORLD BLUESTEM

Major Field: Natural Resource Ecology and Management

Biographical:

Personal Data:

Education:

I completed the requirements for the Bachelors of Science in wildlife ecology and management from Oklahoma State University, Stillwater, Oklahoma in May 2006. I completed the requirements for the Master of Science in Natural Resource Ecology and Management at Oklahoma State University, Stillwater, Oklahoma in May, 2009.

Professional Memberships:

The Wildlife Society
Society for Rangeland Management
Ecological Society of America

Name: Scott Gallup Robertson　　Date of Degree: May, 2009

Institution: Oklahoma State University　　Location: Stillwater, Oklahoma

Title of Study: HERBICIDE CONTROL AND SEED BANK DYNAMICS OF OLD WORLD BLUESTEM

Pages in Study: 72　　Candidate for the Degree of Master of Science

Major Field: Natural Resource Ecology and Management

Scope and Method of Study:
The invasive grass Old World bluestem (OWB; *Bothriochloa ischaemum*) threatens native plant and animal diversity. I used single, double, and triple applications of glyphosate in various combinations with and without a mowing or burning to determine the most effective treatment for controlling OWB for future restoration. Also I assessed the affects of OWB invasion on native species diversity and abundance of the aboveground plant community and seed bank community.

Findings and Conclusions:
One year after treatment, burning and mowing prior to a single herbicide application improved the amount of OWB control compared to a single herbicide treatment. Burning or mowing with two herbicide applications provided more OWB control relative to plots that received only two herbicide application. The burn and mow double herbicide treatments did not exhibit an increase in reproductive tiller density or visual obstruction a year after treatment, whereas plots that received only two herbicide applications did. Burning or mowing with two herbicide treatments provided similar amounts of OWB control compared with the triple herbicide treatment. Combining burning or mowing with herbicide applications provided more effective OWB control than the herbicide only treatments. Regarding the seed bank, native aboveground species diversity and cover showed a steep declined as OWB cover increased. There was a slight decline in native seed diversity, and no change in native seed density as invasion increased. OWB seed density increased with increasing invasion. I hypothesize that as OWB invasion increases native aboveground plants decrease in diversity and abundance, but native seed bank diversity and density does not decline, but over time as native seeds are lost, and the lack of native seed replenishment from the aboveground community, native seed bank diversity and density will decline.

ADVISER’S APPROVAL: Karen Hickman