REDUCING INVASION BY TARGETING VULNERABLE LIFE STAGES: EFFECTS OF FIRE ON SURVIVORSHIP OF *LESPEDEZA CUNEATA*

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REDUCING INVASION BY TARGETING VULNERABLE LIFE STAGES: EFFECTS OF FIRE ON SURVIVORSHIP OF Lespedeza Cuneata

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ABSTRACT

There is growing interest in whether invasive species may be controlled by targeting key life stages or by tailoring different management strategies to the specific characteristics of particular life stages. In this study, I test whether fire targeted at seed or seedling stages of sericea can increase mortality and potentially limit the spread of this invader. Two field experiments were performed manipulating the timing of fire and a laboratory experiment was conducted that quantified germination rates. The field experiments revealed that seedling survivorship varied with timing of burns and plant age, but these variables only accounted for a small amount of the variability in survivorship ($R^2 = 0.09, P = 0.032$), suggesting that sericea seedlings quickly reach a size from which they can resprout. At the seed stage, fire greatly enhanced cumulative germination in the field burns. In contrast, the lab experiment showed that fire inflicted extremely high mortality on sericea seeds, suggesting that, in the field, seeds gain protection from fire as they mix with soil and that fire may increase germination due to enhanced resource availability. Taken together, my results illustrate that, although targeting vulnerable life stages is a sound strategy for invasive species control, careful preliminary studies may be needed to unravel complex interactions between biotic and abiotic variables before effective solutions can be devised.
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INTRODUCTION

All invaders possess unique characteristics that allow successful invasion into native ecosystems. For example, one invader may be particularly adept in competing for resources while another may be resistant to drought or disturbances, but be a poor competitor. Despite such differences, all species share several key demographic features such as survivorship, growth rate, and fecundity (Ramula et al. 2008). These features coupled with transitions between key life stages may offer an opportunity to utilize alternative management practices designed to target vulnerable life stages (Gurevitch et al. 2011; Schutzenhofer and Knight 2007). Presumably, if vulnerable life stages can be identified, the intensity of control measures could be minimized while maximizing control of invaders. Although such a strategy would likely be advantageous to native ecosystems, there are few examples of such targeted management. In this study, I examine the possibility that fire, a common and characteristic management tool, can be modified to disrupt certain demographics by targeting potentially vulnerable life stages of an invasive legume in the Great Plains.

Sericea (*Lespedeza cuneata* ([Dum.-Cours.] G. Don)) is an herbaceous, long-lived perennial legume initially introduced as a forage crop to the United States in 1896 from Eastern Asia (Cummings et al. 2007). Since then, it has spread throughout the Eastern United States partly from widespread use as an erosion deterrent on roadsides and as a pasture crop, as well as its high propagule production, strong competitive ability, and tolerance of a wide range of environmental conditions. The spread of sericea into the Great Plains has had a profound impact on grasslands by suppressing native plant species. A study in the Chautauqua Hills, Kansas shows that, within 5 to 7 years of invasion, sericea reduces the biomass of native forbs and
grasses by 92% and the diversity from 27 native species to 8 when compared to uninfested areas (Eddy and Moore 1998).

Over the past decade, land managers have attempted to control the spread of sericea by using various methods including herbicides, grazing, and fire. A single application of herbicide is largely ineffectual against sericea over the long term because, although mature plants can be eliminated, sericea’s high propagule production of up to 6000 seeds per plant per year creates an extensive seed bank from which new plants will germinate (Woods et al. 2009). Consequently, frequent herbicide application is necessary to maintain sericea in low abundance. Traditional burning has also proved ineffectual in controlling sericea. For example, a field burn in the spring once every three years resulted in an increase in sericea cover from 5 to 16% (Cummings et al. 2007). However, it is unclear how these measures affected various life stages as they only focused on disturbance effects on mature sericea stands.

Despite the limited success of control measures other than repeated application of herbicide, little is known about how typical disturbance regimes influence the demographics of sericea. For example, fire is a common management tool in grasslands typically favoring native species which are adapted to prairie fires. Although sericea plants are thought to resprout following fire (Ohlenbusch 2007), young plants may not have sufficient reserves to resprout following removal of shoots by fire. Consequently, the timing of prescribed burns might be utilized to induce mortality at a key life stage. However, there are very little data available on fire-induced mortality at different life stages for sericea.

In addition to effects on immature plants, fire may alter germination rates. Anecdotal information suggests that fire may stimulate sericea germination (Ohlenbusch 2007). However,
Bell and Koerner (2009) found that sericea seed viability drops significantly at 225°C and is unviable at 250°C, while Martin et al. (1975) report that 4 minutes of exposure to moist or dry heat between 90 and 110°C is lethal to sericea seeds. With prairie fires burning up to 411°C (Engle et al. 1993), sericea seed may be vulnerable to fire, but these effects have not yet been quantified under field conditions.

It is possible that burning sericea could kill enough seedlings at vulnerable life stages and consume enough seeds to offset any potentially stimulatory effect of fire on seedling germination and prevent population spread. However, the efficacy of such a management strategy is limited by the lack of data from coordinated field and laboratory studies to isolate the vulnerable life stages and to resolve the apparent discrepancy between anecdotal and laboratory results. In this study, I addressed the following questions: 1) Does fire have suppressive or facilitative effects on sericea recruitment? 2) Is this suppressive or facilitative effect on sericea recruitment due to changes in seed germination or seedling survivorship? 3) At what size or life stage does sericea become insensitive to burning? To test these ideas, I manipulated the timing of prescribed burns to quantify the probability of mortality on sericea plants of different ages under field conditions. In addition, I quantified the germination rates of sericea seeds under different burning conditions in the lab.
2.1 Field Experiment

In order to test the effect of fire on sericea at different life stages, a burn experiment was conducted at the University of Kansas Field Station (39.05°N, 95.19°W). The experiment was located in a former agricultural field that had undergone natural conversion to tallgrass prairie since 1956.

In March 2010, ninety 1 by 1 m plots were arrayed in a grid with 0.5 m between plots. Nine different burn and seed addition treatment combinations were applied in a randomized, complete block design to account for underlying spatial variability and each treatment replicated ten times. Sericea seed, collected in 2009 from a previous experiment adjacent to the experimental plots (Houseman, unpublished data), were sown by hand into the six burn treatment plots in each block as well as an unburned control at a rate of 4000 seeds per m². The timing of burns was manipulated so that each block contained plots burned on 21 April, 25 May, 21 June, 21 July, and 4 September of the first growing season (2010) and 21 April of the second growing season (2011). Within each burned plot, a tallgrass prairie burn was simulated using a propane torch to ignite the vegetation. The target temperature of the burns was 350 to 400°C, which was within the typical range of prairie burns (Gibson et al. 1990; Hobbs et al. 1991; Middleton 2002; Engle et al. 1993). Temperature was monitored using temperature-sensitive paint (Tempil, South Plainfield, NJ, USA) applied to aluminum strips that were placed within the plot prior to the burn. Each block also contained an unseeded control burned on 21 April, 2010, and an unseeded, unburned control.
Plots were monitored until sericea germinants were positively identified on 14 April, 2010. Cohorts throughout the first growing season were established to quantify the effect of burning on plants of different ages. Every twenty days throughout the growing season, up to four sericea seedlings were randomly marked with metal rings in each plot. To maintain cohort discreteness, all unmarked seedlings within plots were pulled every ten days to ensure that each marked seedling was no more than ten days old. First-year survivorship was quantified on 4 November, 2010. Second-year germination data were taken 17 April, 2011. A final survivorship census of marked seedlings was taken at the end of the second growing season on 2 August, 2011. In the event that a ring was not found, its corresponding data point was dropped from the analysis.

To test the effect of burn timing on survivorship, I used a multiple regression with plant age at time of burn (plant age) and days elapsed since the first sericea germinated (timing of burn) as independent variables using MYSTAT v 12.02.00 (Cranes Software International, Bangalore, India). Differences in cumulative germination between burn treatments were tested with a one-way ANOVA for a randomized complete block design using SAS 9.2 (SAS Institute Inc., Cary, NC, USA). Bonferroni correction was utilized to control for multiple comparisons. Unless otherwise stated, statistical significance was assessed at $P \leq 0.05$.

### 2.2 Fall Burn Experiment

To test the effect of fall burning on sericea germination and establishment, twenty-four 0.5 m by 0.5 m plots were established adjacent to the first experiment. Three treatments (unsown control and seed addition either pre- or post-burn) were replicated eight times in a randomized, complete block design. Seeds were sown at a rate of 5 g per plot. For the pre-burn
treatment, seeds were added 29 October, 2009. The field burn was conducted on 5 November, 2009. After the burn, on 6 November, 2009, the post-burn seeds were added. A one-way, blocked ANOVA was performed in SAS 9.2 (SAS Institute Inc., Cary, NC, USA) to determine the effects of seed addition pre- and post- burn on plant density after two growing seasons.

2.3 Lab Germination Experiment

A laboratory burn experiment was conducted to test how fire, light, or litter influenced sericea germination rates. After a burn, photosynthetic active radiation (PAR) is 100%, but under unburned conditions, standing dead plant material and litter reduces light reaching the seeds and the soil, potentially altering germination rates. The presence of litter may also affect the amount of heat reaching the seeds during the burn, potentially preventing them from being consumed by the fire, or by altering soil chemistry. Thus, four burn treatments were devised to determine whether burning the soil and litter or seed directly influenced germination responses to fire: seed burned with litter on soil, soil and litter burned followed by seed addition, seed burned and then added to unburned soil in the absence of litter, and unburned soil and seed in the absence of litter. All treatments were replicated 12 times in a fully crossed design. The burns were conducted in an aluminum tray the lab with a propane torch (Bernzomatic, Medina, NY, USA) that mimicked the simulated field burn with target temperatures of 350 to 400°C, which were monitored with temperature-sensitive paint (Tempil, South Plainfield, NJ, USA) applied to aluminum strips. PAR was manipulated in the lab germination experiment to reflect burned plots (100% PAR) or unburned plots (field mean PAR = 38%) by covering the trays with 60% shade cloth, which was similar to reduction in light due to litter measured in undisturbed areas in the field experiment. Sieved soil collected from the field site was added to 25 by 25 by 4 cm trays with transparent covers and 100 sericea seeds were added to each treatment. Prior to
sowing, seeds were stratified by placing the trays in a freezer for two weeks after the seed additions and burns to simulate overwintering. The trays were watered daily and monitored for germination. Germination was recorded after 17 days.

The effects of light and burn treatments on the germination rate were tested using a two-factor ANOVA in SAS 9.2 (SAS Institute Inc., Cary, NC, USA) with Bonferroni correction for multiple comparisons.
RESULTS

3.1 Field Experiment

Mean survivorship in unburned control plots ($\bar{x} = 38.2\% \pm 4.6$, $n = 65$), was higher than in any of the burned treatments. The survivorship of plants marked pre-burn was lower than unburned controls in all cases ($\bar{x}_{\text{June}} = 2.5\% \pm 2.5$, $n = 10$, $\bar{x}_{\text{July}} = 12\% \pm 4.1$, $n = 26$, $\bar{x}_{\text{Sept}} = 7\% \pm 1.9$; Figure 1) while the survivorship of plants of all burn treatments marked post-burn were similar to each other ($\bar{x}_{\text{April}} = 31.8\% \pm 3.9$, $n = 75$, $\bar{x}_{\text{May}} = 29\% \pm 4.0$, $n = 80$, $\bar{x}_{\text{June}} = 20.8\% \pm 3.9$, $n = 58$, $\bar{x}_{\text{July}} = 22\% \pm 5.6$, $n = 33$, $\bar{x}_{\text{Sept}} = 1.1\% \pm 1.1$, $n = 23$; Figure 1) except September. The extremely low survivorship of plants marked after the September burn occurred even though sericea continued to germinate through 3 November, 2010. Multiple regression analysis revealed that sericea survivorship was dependent on plant age combined with the timing of burn. However, this relationship explained only a small amount of the variation in sericea survivorship ($R^2 = 0.093$, $P = 0.032$, $F_{2,150} = 7.69$; Figure 2).

The timing of burns had strong effects on cumulative germination through April of the second growing season ($F_{6,54} = 6.27$, $P < 0.0001$). Cumulative germination (mean number of seedlings per plot) of plots burned in April of the first growing season ($\bar{x} = 155.2 \pm 18.3$, $n = 10$), May ($\bar{x} = 193.6 \pm 26.8$, $n = 10$), June ($\bar{x} = 177.9 \pm 30.8$, $n = 10$), July ($\bar{x} = 196.1 \pm 35.2$, $n = 10$), and September ($\bar{x} = 186.7 \pm 25.9$, $n=10$) of the first growing season were similar to each other and higher than the unburned control (Figure 3). In contrast, cumulative germination in the unburned control ($\bar{x} = 77.5 \pm 9.3$, n=10) was similar to the cumulative germination of those plots burned in April of the second growing season ($\bar{x} = 89.9 \pm 12.4$, $n = 10$).
3.2 Fall Burn Experiment

The timing of seed addition had a large effect on sericea density after two growing seasons \((F_{1, 7} = 17.39, P = 0.0042)\). Seed addition post-burn had a higher mean plant density per plot \((\bar{x} = 7.25 \pm 1.1, n = 8)\) than seed addition pre-burn \((\bar{x} = 1.63 \pm 0.6, n = 8)\).

3.3 Lab Germination Experiment

Under laboratory conditions, a reduction from 100% to 40% light availability had very little effect on sericea germination rate \((F_{1, 77} = 0.80, P = 0.37)\). The various burn treatments, however, had an extremely large effect on germination rate \((F_{3, 77} = 423, P < 0.0001; \text{Figure 4})\). Germination rates of unburned seeds added to treatments with burned soil and litter \((\bar{x} = 80.3\% \pm 2.3, n = 24)\) did not significantly differ from unburned control \((\bar{x} = 78.3\% \pm 3.5, n = 24)\). In contrast, when soil, litter, and seed were burned, germination rates were significantly lower \((\bar{x} = 9.5\% \pm 1.4, n = 24)\) than unburned controls and seed only burned treatments were significantly lower \((\bar{x} = 0.46\% \pm 0.21, n = 24)\) than all other treatments.
DISCUSSION

Although fire reduced sericea survivorship in the field burn, this reduction in invasion success was mitigated by enhanced cumulative germination in burned plots. Enhanced germination following burns was surprising given that, in the lab burn, fire greatly reduced germination suggesting that seed-soil mixing in the field likely protects sericea seed from fire. Additionally, laboratory assays indicated that seed viability was unexpectedly high compared to those found in the field (Houseman, unpublished data), which may explain reports of persistent seed banks in sericea (Ohlenbusch 2007; Woods et al. 2009) that repopulate stands eradicated by herbicides. These results illustrate how complex interactions among biotic and abiotic factors complicate potentially detrimental effects of managed disturbance that target specific life stages of invaders.

4.1 Timing of Fire and Survivorship

My results show that unburned sericea plants have the highest survivorship suggesting that, under field conditions, burning has detrimental effects on seedling survivorship. However, only 9% of the variability in survivorship could be explained by plant age and the timing of burn. One explanation for the low explanatory power of plant age on survivorship may have been the additional germination in the rings following the burns. I assumed that every seedling within a ring was a resprout rather than a new germinant. Since each ring encompassed an area of 0.0095 m² of an experimental plot and sericea germinated at roughly 200 per m², it is possible that some rings may have had new germinants, but, given the relatively small area covered by the rings and the sowing density, such an effect could only account for a relatively small amount of noise in the data. Additionally, the removal of sericea seedlings throughout the growing season may have
increased survivorship due to a decrease in competition among seedlings, but previous work suggests that there is little density dependence among seedlings at these densities (Houseman, unpublished data). A more likely explanation is that sericea quickly reaches a size at which it is capable of resprouting after a fire. While fire does not have a strong direct effect on sericea, burning the surrounding environment could lead to an indirect positive effect on survivorship. Since it has been suggested that litter can affect survivorship rates of native plants via changes in competition, increase in predation (Facelli 1994), or other indirect mechanisms, removal of litter by fire could likewise affect the survivorship rates of sericea. Although further experiments will be necessary to unravel such potential explanations, it is clear that fire has weak effects on survivorship presumably because young sericea plants quickly reach a stage from which they can resprout.

4.2 Fire and Germination

Although there are reports that fire stimulates sericea germination rates (Ohlenbusch 2007) there are little or no data from field experiments to quantify the effect of fire on sericea germination. My field experiment suggests that burning does have a direct stimulatory effect on germination since every burn treatment increased the cumulative germination rate of sericea seedlings nearly twofold compared to unburned controls regardless of when the burn occurred. The stimulatory effect of fire on germination in the field could be a result of scarification of the seeds (Herranz 1998), heat shock breaking dormancy like that observed in other plant species (Herranz 1998; Gashaw and Michelson 2002; Baeza and Vallejo 2005), or perhaps the reduction in competition for resources from the removal of aboveground biomass (Potvin, 1993).
While the field burn experiment suggests that burning increases the germination rate of sericea seedlings, the lab burn experiment shows that there was an extremely large negative effect of fire on sericea germination. Interestingly, similar results were obtained from the fall burn experiment showing that plots in which seeds were sown pre-burn resulted in lower plant density after two growing seasons compared to seeds that were sown post-burn. These results are consistent with those from the lab, which show that unburned seeds have the highest germination rate (soil and litter burned = 80%, unburned = 78% compared to 0.46% when seeds were burned). In contrast, the field burn experiment shows that burning results in a flush of germination directly after the burn event and that the cumulative germination of burned plots is significantly higher than unburned controls suggesting that seeds experiencing a burn event in the field may be protected from the detrimental effects of fire by litter, aboveground biomass, or by being mixed into the soil, and that the competitive advantage granted by a disturbance results in a higher overall germination rate of sericea.

The higher cumulative germination in my field burn experiment tends to agree with what is found in the literature regarding legumes subjected to field burns in dry Mediterranean valleys (Baeza and Vallejo 2006). However, a simulated field burn reported that burning could also reduce seedling emergence (Vermeire and Rinella 2009). Except for these few cases, the vast majority of reported results are from laboratory experiments. The high mortality rate of burned seeds and the high germination rate of untreated seeds in my lab burn experiment are in contrast to what is commonly reported in laboratory studies involving heat shock seed treatment (Blank and Young 1998; Gashaw and Michelson 2002; Keeley and Bond 1997; Keeley 1987). Furthermore, the seeds that were sown in trays with burned soil and litter, and presumably exposed to chemical changes of burned soil and litter, did not have a significantly higher
germination rate as other studies would suggest (Blank and Young 1998; Keeley and Bond 1997). Although it is rare for field and laboratory studies to be combined, the fact that burning has strong negative effects in the laboratory but positive effect in the field illustrates how complexities of these interactions can be obscured when using only laboratory assays.

The overall viability of the seeds used in these experiments was somewhat surprising. Previous field experiments suggested that seeds would have a 6-9% germination rate (Houseman, unpublished data) and the cumulative germination from my field experiment shows a germination rate of approximately 3%. Other studies suggest similar values and argue that a substantial seed bank would result in new sericea germination over several years (Ohlenbusch 2007; Woods et al. 2009). Some studies even go so far as to attempt to increase the germination rate of sericea seeds in laboratory experiments by sulphuric acid scarification (Bentley, 1933). However, in the lab burn experiment, seeds treated by being placed into experimental trays with soil and placed in the freezer for two weeks to simulate winter had a 78% germination rate—albeit with steady light, no competition, and daily watering.

This study is not without its limitations including both time and location. The study was conducted over the course of two growing seasons (2010 and 2011) and the results are subject to the conditions of those particular years. It should also be noted that the experiment was conducted at a single site so variation in soils and climate may alter germination and growth rates. Likewise, this experiment necessarily included practical limitations such as the use of simulated burns rather than field-scale burns. Despite these limitations, my results illustrate how fire interacts with environmental variables at early life stages of sericea to influence the spread of this invader in grassland habitats.
LITERATURE CITED


APPENDIX
Figure 1. Field Experiment Second-Year Survivorship

Figure 1. Mean sericea survivorship (+1 standard error) at the end of the second growing season based on the timing of seedling marking in relation to the burns pre-burn (black) or post-burn (gray).
Figure 2. Sericea survivorship in response to plant age and timing of burn (calendar days since first sericea germinated).
Figure 3. Effect of burn timing on mean (± 1 standard error) cumulative germination rates of sericea seedlings from April 2010-April 2011. The arrows denote the time of burn treatments corresponding to their respective color.
Figure 4. Effect of burning on seed, soil, and litter on mean germination of sericea (± 1 standard error) grouped by PAR 100% (gray) and 40% (black).