SEED DISPERSAL AND OVERLAND FLOW:

THE ROLE OF RAINFALL IN THE PROLIFERATION

OF SERICEA LESPEDEZA, A NON-NATIVE

INVASIVE LEGUME

By

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Abstract: Sericea lespedeza is an invasive legume native to eastern Asia. Although it was initially introduced for forage and erosion control, it has since become a widespread problem, especially in prairie areas, forming dense monocultures and reducing abundances of more palatable native plants. While much work has been done on identifying methods of controlling sericea, less is known about the biology of the plant itself. One particular knowledge gap concerns the methods by which sericea seeds are dispersed. It has been suggested that water, specifically overland flow, may play a role in sericea's dispersal. To test this hypothesis, I set out transects at Oklahoma State University's Range Research Station, and the Joseph H. Williams Tallgrass Prairie Preserve, with six seed traps per transect. Each transect consisted of six seed traps located downslope from a patch of sericea. Slope and sericea density varied for each transect, from 2° to 16° slope, and 10% to nearly 100% upslope sericea. I also set out batches of UV tagged sericea seeds along slopes of varying intensities at the Range Research Station and monitored their movement across a 1-m quadrat. Seed movement was compared with rainfall data obtained from the local Mesonet station. Both experiments were analyzed using generalized linear mixed modeling (GLMM). Seed counts in the traps decreased with distance from the sericea patch, though slope did not affect seed numbers. UV tagged seeds also were more likely to be found within 50cm from their starting location, and were more affected by rainfall quantity when close to their source as well. Rainfall is likely a vector for the dispersal of sericea seeds, though its impact does not appear to be affected by slope. New sericea seedlings are most likely to germinate in areas adjacent to existing patches, but seeds can still disperse up to at least 7-m away, a further distance than has been previously reported.

Key Words: Sericea lespedeza, lespedeza cuneata, seed dispersal, overland flow

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER I

REVIEW OF LITERATURE

Biological Characteristics of Sericea

Sericea lespedeza [*Lespedeza cuneata* (Dum. Cours.) G. Don], also known as Chinese Bush Clover, is a leguminous forb native to eastern Asia. Sericea is a long-lived warm season perennial, with a shrub-like growth form of around 0.5-1m tall (Zheng, 2004). As a mature plant, it has coarse woody stems with a dense accumulation of alternate trifoliate leaves of up to 3cm long (Cummings et al., 2007). Sericea has a deep taproot system (Ohlenbusch & Bidwell, 2007), allowing it to be highly drought-tolerant, though it grows best under conditions with an annual precipitation of at least 762mm. It is known to grow under a wide variety of soil conditions, though is mostly found on deep clay or loamy soils with a pH of 6-6.5 (Brandon et al., 2004; Cummings et al., 2007), and can be found growing anywhere from roadsides and crop fields to along slopes and streambanks (Zheng, 2004).

As sericea plants grow, they produce increased amounts of tannins, astringent polyphenolic biomolecules, which then bind to the proteins in the plant, making the mature plants less palatable to grazers (Donnelly & Anthony, 1970). Sericea also contains high amounts of lignin, complex organic polymers found in the support tissues of most plants and increase their rigidity, which also negatively affects digestibility (Hawkins, 1959). In addition to sericea's defenses against grazing, it is also known to produce allelopathic chemicals from its roots, as well as in leaf residues, that may reduce competition from neighboring plants (Kalburtji & Mosjidis, 1993a). Allelopathy is a phenomenon common in plants in which chemicals exuded by one organism influences the growth or survival of other organisms around it, and is considered to be an important factor in species distribution and the success of invasive plants. In particular, sericea residues have been shown to inhibit both the germination and growth of cool-season grasses (Kalburtji & Mosjidis, 1993b) as well as the growth of warm-season grasses (Kalburtji & Mosjidis, 1992). As a legume, sericea is also capable of forming associations with nitrogen-fixing rhizobia. In its native range, sericea has been shown to be highly promiscuous, and is known to associate with several different genera of rhizobia, including *Bradyrhizobium*, *Mesorhizobium*, *Rhizobium*, and *Sinorhizobium* (Gu et al., 2007).

Sericea lespedeza is capable of utilizing several different reproductive methods. The plants produce both chasmogamous flowers, which are outcross-pollinated, as well as self-pollinated cleistogamous flowers (Woods et al., 2009). According to Donnelly (1955), chasmogamous flowers produce approximately 40% more seed than cleistogamous flowers. Sericea plants are also able to spread vegetatively through perennial crown buds (Stevens, 2002). While the exact flowering time of sericea seems to vary by region, several studies have reported flowering to begin in July, with seed set occurring by September or October (Schutzenhofer, 2009; Czarapata, 2005). Sericea seed pods are small (2.5-3.5mm) and contain only a single seed per pod (Zheng, 2004). However, they are capable of producing around 6,500 seeds per plant (Woods et al., 2009). Little is known about the dispersal mechanisms of sericea seeds. They have no obvious morphological adaptations for dispersal, being small and oval-shaped with no wings, plumes, or barbs, though Quick et al. (2016) still found that both wind and animal fur likely act as dispersal vectors. Wind dispersal is more localized, with a maximum dispersal distance of 3-m, while epizoochory may be a vector for longer distance dispersal. Additionally, seeds have occasionally been found in the feces of several species, making endozoochory another potential factor (Eddy, 2003). Water runoff and vehicle movement may also be potential vectors for sericea seed dispersal (Silliman & Maccarone, 2005). Seeds have a low germination rate of only about 20% (Pieters, 1939), but this may be increased by scarification, which allows better water penetration through the normally impermeable seed coat (Logan et al., 1969). If left intact, seeds are thought to remain viable in the soil for 20 or more years (Czarapata, 2005).

Sericea as an Invasive Species

Sericea was first brought to the United States in 1896, to the North Carolina Agriculture Experiment Station (Heath et al., 1985). However, little was done with it until 1924, when it was brought again from Japan by the USDA to the Arlington Experiment Farm in Virginia (Ohlenbusch & Bidwell, 2007). Initially, it was deliberately planted for erosion control and ground cover, stabilizing soil on highway rights-of-way and reclaimed minelands (Heath, 1985). It was later introduced into the Midwest and southeastern United States in the 1930s and 1940s as forage for cattle (McGraw and Hoveland 1995). Populations of sericea are currently found in 31 states, including Hawaii, and it is considered a Noxious Weed in Kansas and Colorado (USDA 2021). In Oklahoma, it can be found growing in all parts of the state except for the panhandle (Ohlenbusch & Bidwell, 2007).

Unfortunately, like many exotic forages, these traits that initially made sericea seem favorable also give it several advantages as an invasive species (Scasta et al., 2015). Its adaptability to drought, and poorer quality and acidic soils allow it to establish populations in disturbed areas that may be less suitable for native plants (Vermeire et al., 2007; Mosjidis, 1997). Once established, sericea forms dense monotypic stands (Eddy and Moore 1998), reducing native species abundance by shading them out (Brandon et al., 2004). Sericea further stresses competing native plants by utilizing a greater amount of water than most other warm-season plants to produce an equivalent amount of biomass (Cummings et al., 2007). Furthermore, leaf area of sericea exceeds that of native tallgrass prairie species, which may further help it in gaining an advantage over other plants in resource acquisition (Allred et al., 2010).

In addition to its physical properties, its chemical properties also help it to outcompete native plants and establish dominance. The high tannin content of mature sericea makes it less likely to be grazed than some other plants, resulting in overgrazing of desirable native plants while sericea is able to continue to grow and spread, and the allelopathic chemicals it produces are capable of further reducing germination and growth of neighboring plants (Kalburtji & Mosjidis, 1992, 1993a, 1993b; Dudley & Fick, 2003). Not only does sericea restrict the growth of other plants, it also facilitates its own growth by altering soil conditions, especially during initial establishment, and making it easier for it to spread to new areas (Coykendall & Houseman, 2014; Crawford & Knight, 2016). Another factor contributing to sericea's success as an invasive is its reproductive output. Not only is sericea visited more often by insect pollinators than native lespedezas (Woods et al., 2012), it also produces around five times as many seeds. This overabundance of seed production when compared with native congeners strongly implies that propagule pressure is an important factor in sericea's success as an invasive. Additionally, the fact that it can utilize both chasmogamous and cleistogamous methods of reproduction means that seeds will still be produced under a wide variety of environmental conditions (Woods et al., 2009). Overall, sericea has invaded at least 3.5 million ha of land in the United States (Duncan, 2005). Of these, the tallgrass prairie ecosystem, of which only around 4% remains of its original extent, has seen significant damage from sericea invasions, with losses of native grass and forb abundances of up to 92% (Eddy and Moore 1998).

But plants are not the only parts of the ecosystem impacted by sericea invasion. According to Eddy & Moore (2008), areas invaded by sericea also have fewer invertebrate species than intact tallgrass prairie. Furthermore, while wildlife like quail may occasionally use sericea for food and cover, sericea seeds have little nutritional value for them (Cummings et al., 2007). Moreover, the northern bobwhite (*Colinus virginianus*) preferentially places its nests in areas where sericea has been treated with herbicide (Brooke et al., 2016). The reductions in native plant diversity caused by sericea may also indirectly impact the fitness of wildlife species that require those plants (Cummings et al., 2007). In addition to impacts on wildlife, sericea has also been shown to alter the soil bacteria and soil fungi communities in areas that have been invaded (Yannarell et al., 2011). Therefore, the repercussions of sericea invasion have the potential to negatively affect the entire ecosystem, and likely extend beyond what little is already known.

In light of these effects, methods to control the continued invasion of sericea lespedeza into rangeland and prairie areas have been sought. One of the most common ways of dealing with invasive plants is through the use of herbicides, which come in a wide variety of specificities and target a number of different mechanisms to inhibit plant growth, meaning certain herbicides will be more effective at suppressing specific plant species than others. Several studies have shown triclopyr and fluroxypyr to be the most successful at controlling sericea, with metsulfuron providing a moderate success rate as well (Altom et al., 1992; Koger et al., 2002). It has also been suggested that pre-emergence herbicides, which are applied before seedlings begin sprouting and kill them as they emerge, may also be an effective method for dealing with sericea seedlings (Farris & Murray, 2009). However, due to sericea's extensive seed bank, follow-up herbicide applications are required in order to maintain control over the population, potentially leading to high expenses in both time and money (Cummings et al., 2007). In addition, treatment effectiveness has been shown to decrease as plants mature (Farris & Murray, 2009). Furthermore, herbicide application may have negative non-target effects on desirable native plants in the affected area.

Biological controls are a potential alternative to chemical control methods. This involves using a natural enemy of the target species to help manage its population and spread, though if the potential control agent is not specific enough it may have negative effects on non-target species as well. One biological control agent that has been proposed for sericea is that of the lespedeza webworm (*Tetralopha scortealis*), which was found to reduce seed production by 98% (Eddy et al., 2003), though it has also been found to feed on native lespedezas as well. Additionally, a study simulating the effects of herbivory on sericea did not observe any reductions in population growth rate (Schutzenhofer & Knight, 2007). Therefore, it seems unlikely that biological control methods will prove to be a viable option for managing sericea.

In many areas, grazing and burning have often been used as management practices. However, thus far both grazing and burning alone have proven unsuccessful in preventing the spread of sericea. As cattle tend to avoid consuming sericea, it will persist in pastures while native grasses and forbs are over-grazed. Furthermore, when sericea is consumed, its seeds may then be spread through manure (Cummings et al., 2007). Spring burning has been shown to both decrease seedling survival as well as increase the density of existing sericea patches (Koger, 1996; Cummings et al., 2007). It has been reported that summer burns may be relatively effective at suppressing sericea, though better results are achieved when used in conjunction with other treatment methods, such as herbicide application (Alexander et al., 2018; Gatson et al., 2018). One suggested combination treatment is the patch burn grazing system, where smaller areas are burned, leading to higher grazing intensity in the recently burned areas, including grazing of the more palatable sericea regrowth. This method not only reduces sericea invasion rates, but also increased diversity across the pasture (Cummings et al., 2007b), and may prove to be a viable management strategy.

The most effective way to prevent sericea invasion is to ensure that it does not gain a foothold in the first place. Studies have shown that restoration of disturbed lands to native grasses and forbs can reduce sericea's ability to dominate a landscape (Walder et al., 2019; Foster et al., 2015; Wohlwend et al., 2019). There is also research being done into using geospatial modeling to identify invasion patterns and areas that are more likely to be at risk for invasion (Mikhailova et al., 2016; Lemke et al., 2013), as well as using hyperspectral imagery to determine the locations of current patches, which would be far more efficient in surveying large areas than ordinary field surveys (Wang et al., 2008). While multispectral imagery is unlikely to be able to distinguish sericea from other vegetation in pastures, the many narrower infrared bands captured by hyperspectral sensors may be more able to detect the differences between species (Jensen, 2007). In particular, the spectral signature of sericea was found to be distinguishable from fescue along the red edge (Wang et al., 2008). This information can then be used to help managers know where is most crucial to focus their efforts, and at the least potentially slow further spread of this invasive plant.

CHAPTER II

SEED DISPERSAL AND OVERLAND FLOW: THE ROLE OF RAINFALL IN THE PROLIFERATION OF SERICEA LESPEDEZA, A NON-NATIVE INVASIVE LEGUME

Introduction

Introduced and invasive species are perhaps one of the most well-known issues in natural resource management today. An invasive species is defined as a species that is not endemic to a given ecosystem, and whose presence causes harm either environmentally, economically, or to human health (USDA, 2021). Humans have long facilitated the transportation of organisms from one location to another, either by deliberate introductions for reasons ranging from agriculture to escaped ornamental plants and exotic pets, or by unintentional ones, such as the transport of organisms in ballast water. Significant amounts of money have been spent in the attempt to control or eradicate these invasive populations (Pimentel et al., 2005).

For an introduced species to become invasive, there are several factors needed to occur in combination for this potentially invasive species to thrive. Species traits that are generally acknowledged to facilitate invasion include growth and reproductive rate, tolerance of varying environmental conditions, lack of natural predators, and dispersal ability (Kolar & Lodge, 2001; Rejmanek, 2000). Though invasions may only consist of a small number of individuals at first, they eventually begin to dominate the new area and may even extirpate some of the native species completely.

Once introduced to a site, a species' dispersal ability will then determine how well and how quickly it will continue to spread to other sites. Many animals are motile and can disperse under their own power, but for other creatures, especially plants, some type of dispersal vector is needed to facilitate arrival at a new location. Plant seeds disperse through a variety of methods, both biotic and abiotic, the most well known of which are dispersal by wind, water, and animals, as such seeds often possess specialized adaptations, such as a pappus or barbs, to better enable such movements (Vittoz & Engler, 2007). However, plants may often have more than one dispersal method. Primary dispersal describes the method by which seeds initially leave the plant, while secondary dispersal describes their fates after they reach the ground (Bochet, 2015). These secondary dispersal methods may be particularly important in understanding the dispersal of seeds which have no other obvious adaptations for other dispersal methods.

In particular, dispersal via overland flow caused by rainwater runoff, or bythisochory, may be a potentially important secondary dispersal method for many species (Sarneel, 2016). Several studies have examined the viability of this method, both in the field, and through the use of rainfall simulators in the lab. In general, seed size and shape, as well as slope intensity and soil particle size are all important factors in determining how far a seed will travel, with smaller and rounder seeds generally traveling farther (Cerdà, & García-Fayos, 1997; Cerdà, & García-Fayos, 2002; Han et al., 2011; Bochet, 2015). Given the importance that propagule pressure, the number of individuals of a given species introduced into a non-native region, is considered to have on the ability of a plant species to become invasive (Lockwood et al., 2005; Houseman et al., 2014), it would follow that an understanding of a species' main dispersal methods may help in identifying strategies to curb their spread.

First introduced to the United States in 1896, Sericea lespedeza [*Lespedeza cuneata* (Dum. Cours.) G. Don] is an invasive legume native to Asia (Ohlenbusch et al., 2001). Since then, there have been several other deliberate introductions, as sericea was initially utilized as forage for livestock, as well as for erosion control and revegetation of areas such as abandoned mine sites and roadways (Silliman and Maccarone, 2005; Wolf et al., 2018). However, the environmental dangers posed by this invasive species have only been recognized within the last few decades. Once sericea is present in an area, it forms dense stands, reducing abundance and diversity of native plants (Eddy et al., 2003). Additionally, cattle prefer to avoid feeding on sericea when possible, likely due to its high tannin content which makes it more difficult for them to digest and resulting in decreased grazing income for cattle owners (Eddy et al., 2003).

Most research on sericea has focused on methods for controlling local infestations. However, routine management practices such as grazing, prescribed fire, and herbicide have not individually proved effective in controlling sericea in the long term (Cummings et al., 2007). Some research has shown that late summer burns and patch burning methods may be more effective at controlling sericea spread than conventional burning practices (Alexander et al., 2018; Gatson et al., 2018; Cummings et al., 2007). However, herbicide treatments are ineffective at one-year post application, and therefore require a constant effort for consistent control, making this method both economically unfeasible and potentially hazardous to desirable native plants (Sherril, 2019; Koger et al. 2002).

While much attention has been paid to the treatment and control of sericea, less focus has been given to the physical attributes of the plant itself. For instance, despite the fact that sericea produces approximately five times as many seeds as its native congeners (Woods et al., 2009), almost nothing is known about its methods of seed dispersal, though it has been observed to spread vegetatively through perennial crown buds (Stevens, 2002). Considering high propagule pressure is expected to increase invasibility of a species (Houseman et al., 2014), it follows that dispersal must also be an important piece in understanding sericea lespedeza invasion. However, with its small, rounded seeds, sericea has no obvious mechanisms to facilitate dispersal. Quick et al. (2016) investigated the potential of wind and mammal dispersal, and found that both may influence its spread, though their relative magnitudes may be different, with wind only dispersing seeds over very short distances. Other studies have suggested that dispersal by water through overland flow may influence the spread of sericea (Hearth, 2015; Silliman & Maccarone, 2005). At present, little has been done to examine this possibility. My hypothesis is that overland flow is an important dispersal mechanism for the seeds of sericea lespedeza. Therefore, the goal of this study is to understand the role that overland flow plays in the seed dispersal of sericea lespedeza, looking specifically at rainfall and slope intensity. To accomplish this, the placement of seed traps and tracking of tagged seeds along slopes where sericea is present was used to assess the extent of sericea seed dispersal.

Methods

Study Areas

Joseph H. Williams Tallgrass Prairie Preserve

At 39,650 acres, the Tallgrass Prairie Preserve (TGP) (36°50′31″N, 96°25′08″W) is the largest remaining area of protected tallgrass prairie. The TGP is located at the southern end of the Flint Hills ecoregion, an area that is mainly uncultivated due to the large amounts of exposed limestone. The average temperature for the area is 15.3°C, with an average annual high of 33.9°C and low of -3.9°C. Average rainfall is 1191.3 mm. Restoration began with the purchase of the land by The Nature Conservancy in 1989. Currently, the TGP utilizes a patch-burn system as part of their conservation efforts. Additionally, the Preserve also houses a herd of approximately 2,500 bison, which graze the majority of the Preserve, with cattle grazing about one third of the area. Currently, one of the primary threats to this region are invasive plants such as sericea lespedeza (*Lespedeza cuneata*).

Oklahoma State University Range Research Station

The Range Research Station (RRS) (36°03'52.6"N, 97°13'52.1"W) is located to the southwest of Stillwater, Oklahoma. The average temperature for the area is 14.8°C, with an average annual high of 34.4°C and a low of -1.1°C. The average rainfall is 932.2 mm. The Station consists of nine properties of various sizes, for a total of approximately 5,000 acres. It is in the western part of the Cross Timbers ecoregion, and is made up of upland deciduous forest, savannah, and tallgrass prairie. The Research Station is managed using a patch-burn system that includes cattle and goat grazing. Additionally, the soil in this region is less rock-strewn than that of the Flint Hills.

Seed Trap Experiment

In order to examine the influence of slope on seed dispersal distance, a seed trapping experiment was conducted. Funnel traps were constructed out of a plastic funnel set into a PVC pipe, with a gauze bag attached to the bottom to collect the seeds (Chabrerie & Alard, 2005). Transects of 7.6 m were located downslope from patches of sericea, with traps placed at 1.52 m intervals, for a total of six traps per transect. Sites were selected by visual identification of sericea patches with sufficient area clear of sericea located downslope. Individual sericea plants adjacent to the placement of the transect were removed to prevent the addition of seeds from outside the focal patch. A total of 27 transects were set up, with 14 at the RRS and 13 at the TPP. Transects were placed in a combination of “small,” “medium,” and “large” sericea patch size, and “low,” “medium,” and “high” slope. A small sericea patch was defined as 1-4m^2, medium size as 4-8m^2, and large as <8m^2. Low slope was 0-3° slope, medium was 3-6° slope, and high was greater than 6° slope. Slope data was obtained from a DEM, and the range of slopes across study sites was between 0-26.5° at RRS and 0-56° at TPP. Slope categories were determined from the quantile distribution of slope at TPP. Traps were set out in late September, before sericea began seeding, and seeds were collected weekly from October 16, 2019 to December 12, 2019.

Seed Tagging Experiment

A seed tagging experiment was conducted to determine the effect of rainfall on the movement of sericea seeds. Sericea seeds were coated in ultraviolet powder UVXPBR, to allow for identification in the field using ultraviolet light, by placing seeds in bags with the UV powder and agitating them until all seeds were covered entirely. After marking, 500 seeds were placed along the upslope edge of 20 randomly selected transects at the RRS, which were oriented to run parallel to slope direction. Transects had slopes ranging from 1.52° to 14.09°, with an average slope of 2.6° across the pasture. Using a one-meter quadrat divided into discrete distances of 16.7 cm, seeds were counted weekly for each distance category from July 6, 2020 to September 18, 2020. Rain amount was tracked through the Oklahoma Mesonet station located at the RRS.

Analysis

For the seed trap experiment, main effects of sericea patch size, slope, sample week, and trap distance were tested using generalized linear mixed modeling (GLMM), as well as the interactions of patch size by slope, and week by distance. The main effects tested in the seed tagging experiment were slope, sample date, distance category, and rainfall, with interactions between date by distance, date by rainfall, and distance by rainfall. The response variable in both experiments was seed count, and models for both experiments also included a random effect to account for site differences.

For both experiments, Akaike weights were used to determine which statistical distribution best fit the data. The distributions tested were Poisson, negative binomial, zero-inflated Poisson, and zero-inflated negative binomial. These distributions were selected because the response variable was the count of seeds (Zuur et al., 2009). Models were run in R 3.6.3 (R Core Team, 2020) using the package "glmmADMB" (Fournier et al., 2012; Skaug et al., 2016). Chi-squared likelihood ratio tests were run to determine the significance of interaction and main effects through sequential removal of terms and comparison between models using the R packages "bbmle" (Bolker and R Development Core Team, 2020) and "lmtest" (Zeileis & Hothorn, 2002).

Results

In total, 703 seeds were collected across all seed traps. The greatest number of seeds collected in a given week was 136, in the week of November 11, 2019. Additionally, 486 seeds were collected at the closest trap distance of 0 m, and 22 were collected at the furthest trap distance of 7.6 m. The greatest number of seeds recovered from a single trap was at the TGP with 25 seeds in the 0 m trap, the week of December 2, 2019.

The negative binomial model was selected for modeling seed counts from the seed trap experiment (Table 1). Seed count increased until the fifth week of the experiment, November 11, 2019, and decreased towards the end ($\chi2 = 16.15$, df = 1, $p = 0.012$) (Figure 1). Additionally, seed count decreased with distance of the trap from the focal sericea patch ($\chi2 = 140.34$, df = 1, $p < 0.001$) (Figure 2). Patch size, slope, and the interaction terms of patch size by slope and week by distance did not influence seed counts (Table 2).

By the end of the seed tagging experiment, 244 of the initial 10,000 UV tagged seeds remained detectable in the plots. On average, 87.4% of the seeds detectable in the plots were located within the closest distance category to initial placement, with only 0.35% found beyond 50 cm. The highest number of seeds lost after a rain even was an average of 400 per plot during the first week after seeds were placed. For the remainder of the experiment, seed loss varied from between 0 and 32 seeds per plot (Figure 3). Total rainfall over the sampling period was 290 mm, with a minimum of 0 mm and a maximum of 99 mm between sampling days (Figure 4).

The zero-inflated negative binomial model was selected for modeling seed counts (Table 3). For the seed tagging experiment, the majority of recaptured seeds were found in the first distance category, nearest the starting position of the seeds, and were rarely recaptured past 50 cm. Seed count was also more strongly affected by rainfall at closer distances to the seed source ($\chi2 = 6.34$, df = 1, $p < 0.05$). Seed count decreased sharply between seed placement and initial sampling, but decreased at a much slower rate the weeks following ($\chi2 = 209.82$, df = 1, $p < 0.001$) (Figure 5). Neither slope nor the interaction terms of date by rainfall or date by distance influenced seed counts (Table 4).

Discussion

I hypothesized that slope degree and rainfall amount would positively influence seed dispersal in sericea lespedeza. While rainfall was found to impact seed dispersal, slope degree did not. I also determined that sericea seed numbers were related to the date and distance at which sampling occurred.

Rainfall events decreased the overall seed count in the seed tagging experiment. Rainfall had the greatest effect on seed count in the first two distance categories, though this may be because there were not enough seeds present in the remainder of the sampling area for any difference to be noticeable. Bochet (2015) also suggests that seeds may become trapped in soil after rainfall events, which could lead to fewer seeds being found at further distances. Overall, each rainfall event decreased the number of seeds counted in the sampling area, and seed numbers did not change much during weeks with no recorded rain. While the total rainfall amount per sampling period does not reduce seed numbers by a constant rate, it is possible that the intensity of the rain events has a greater impact on seed dispersal than merely the total amount of rain that falls, as suggested by Han et al. (2011).

Seed dispersal through overland flow from rainfall events, or bythisochory, is usually considered a complementary dispersal method, as it occurs once the seed has already fallen from the parent plant (Vittoz & Engler, 2007). The distance traveled in a single rainfall event is likely to be fairly short, at least when compared to dispersal via wind or animals (Vittoz & Engler, 2007). Furthermore, as rainfall events heavy or intense enough to move seeds in this way may occur multiple times post seed fall, total dispersal distances for this method are rarely documented due to the difficulty of following individual seeds. However, these multiple dispersal events may build up over time before the seed enters the seed bank. Other factors, such as soil type and ground cover, may also impact dispersal potential, both positively and negatively. For example, seeds may travel further on bare ground, but may be more likely to enter the seed bank if the soil is porous (Chambers & MacMahon, 1994).

In both experiments, sampling date was a significant factor in determining seed counts. The seed traps collected few seeds in the first weeks of the experiment in October, but increased in overall seed numbers until the fifth week of the experiment, in November, after which numbers began to decrease again. This indicates that seed fall of sericea lespedeza is likely greatest around November, but that sericea can continue to drop its seeds through December. However, this may vary between different years and regions, as previous studies have stated sericea seed set as occurring as early as September or October (Schutzenhofer, 2009; Czarapata, 2005). Knowing when seed set is likely to occur may help in determining the optimal time to treat sericea, especially if herbicides are being used. The continued presence of seeds in traps through

December could also point to continued movement of seeds over time after dropping from the parent plant.

The seed tagging experiment, on the other hand, demonstrates that overall seed count decreased as time went on from the initial placement of the UV tagged seeds. The initial drop in seed count was quite large, with over half of the placed seeds not located upon the first sampling day following initial placement at all sites. Further changes in seed counts occurred more gradually over the remaining sampling period. This indicates that seeds are either being removed from the sampling area or are entering the soil seed bank, and that the first rainfall event after the seed is dropped from the plant may have the greatest impact. As seed counts changed over time at all distances, sericea seeds are equally capable of entering the seed bank both where they initially fall, and after dispersing various distances as well.

I also found evidence that these dispersal distances may be further than previously expected. In both experiments, the greatest number of seeds were found directly adjacent to the seed source. In the seed tagging experiment, smaller numbers of seeds were also consistently found up to about 50 cm. However, the seed trap experiment showed that seeds could still be found up to at least 7.6 m away from sericea patches. Quick et al. (2016) investigated wind dispersal and also found that sericea only tends to move about 0.5 m, though seeds were also found as far away as 3 m. Therefore, while most seeds may tend to stay relatively close to where they drop from the plant, small numbers will still end up several meters away. So, although most spread is likely to be slow, sericea can still potentially establish new patches at some distance away. And given the high numbers of seeds that sericea produces (Woods et al., 2009), even if only a relatively small number of seeds per plant disperse further away, the total number of seeds capable of dispersing longer distances may still be quite high if the parent patch is large, thereby increasing the likelihood of successfully establishing a new patch.

While I found no evidence that slope intensity impacts sericea seed dispersal, rainfall did reduce the number of experimentally placed seeds, particularly when seeds were nearer to the point of initial placement. Primary seed dispersal refers to the initial movement of seeds from the parent plant to the initial landing site, while secondary dispersal is defined as any significant further movement from that initial site (Bochet, 2015). Therefore, rainfall may serve as a vector for the secondary dispersal of sericea, particularly in the immediate aftermath of primary dispersal. Additionally, given the continued movement of sericea seeds over time in both experiments, sericea may well be capable of undergoing multiple instances of secondary dispersal before either germinating or becoming part of the seed bank. Furthermore, I have found that sericea is able to disperse at least twice as far as the 3 m wind dispersal reported by Quick et al. (2016). Therefore, while most sericea is still most likely to germinate close to established patches, managers should remain aware of the possibility of new sericea seedlings appearing away from prior sericea patches, especially if there has been significant rain in late Fall while plants are seeding. Future research should work to determine the relationship of rain intensity, soil type, and vegetation density to seed movement, as well as the germination rate of seeds collected at farther distances, to determine the likelihood of new patches establishing. Sericea's high propagule pressure and its ability to grow in a wide variety of conditions make it a difficult plant to get rid of once it has been established. Understanding where and how far sericea seeds are likely to travel may at least help in preventing further spread of this invasive species.

Table 1. Comparison of Akaike weights for the full model seed trap data to determine the best fit distribution among Poisson (P), negative binomial (NB), zero-inflated Poisson (ZIP), and zero-inflated negative binomial (ZINB).

Model	ΔAIC	Model df	Weight
NB	0	14	0.73
ZINB	1.9	15	0.27
ZIP	336.8	14	<0.001
P	653.2	13	<0.001

Table 2. Chi-squared likelihood ratio tests for interaction terms and main effects of seed trap data to determine effects on seed count.

Source	df	χ^2	p-value
Sericea*Slope	4	0.328	0.988
Week*Distance	1	0.124	0.725
Sericea	2	2.374	0.305
Slope	2	2.74	0.254
Week	1	16.15	0.012
Distance	1	140.34	<0.001

Table 3. Comparison of Akaike weights for the full model seed tagging data to determine the best fit distribution among Poisson (P), Negative Binomial (NB), and Zero-Inflated Negative Binomial (ZINB).

Model	**ΔAIC**	**Model df**	**Weight**
ZINB	0	11	1
NB	16.5	10	<0.001
P	2031.1	9	<0.001

Table 4. Chi-squared likelihood ratio tests for interaction terms and main effects of seed tagging data to determine effects on seed count.

Source	**df**	**χ^2**	**p-value**
Date*Rainfall	1	0	1
Date*Distance	1	1.04	0.308
Distance*Rainfall	1	6.34	0.012
Slope	1	0.26	0.610
Date	1	209.82	<0.001

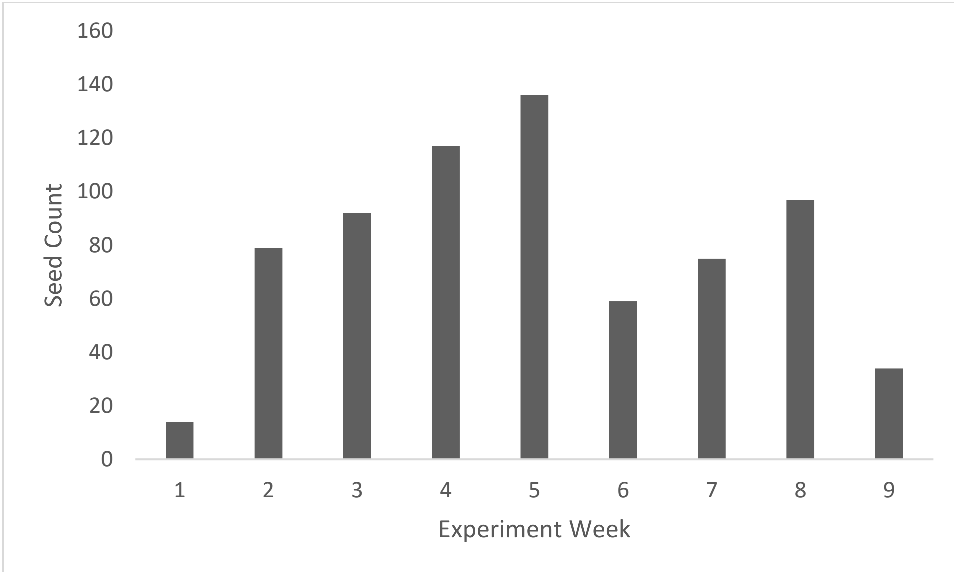

Figure 1. Total seed counts in traps of all distances by week since sampling began

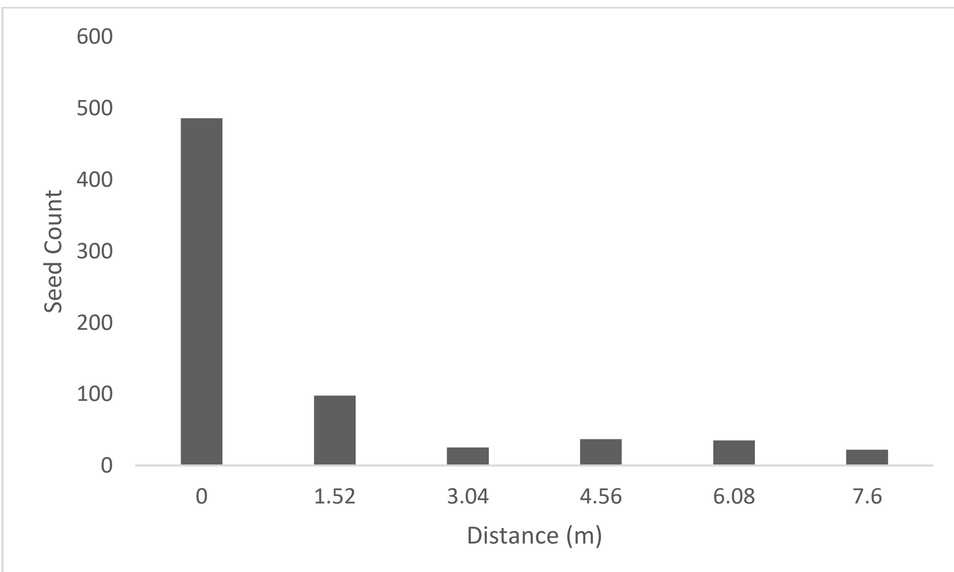

Figure 2. Total seed counts at each trap distance over the entire sampling period.

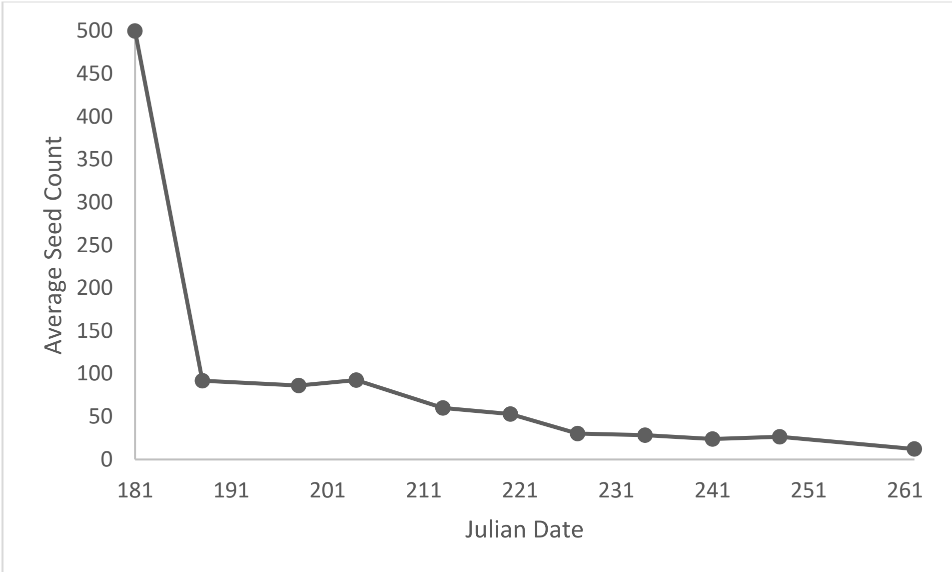

Figure 3. Average number of seeds per plot by Julian date over the course of the seed tagging experiment.

Figure 4. Rainfall per day by Julian date in millimeters since placement of UV tagged seeds.

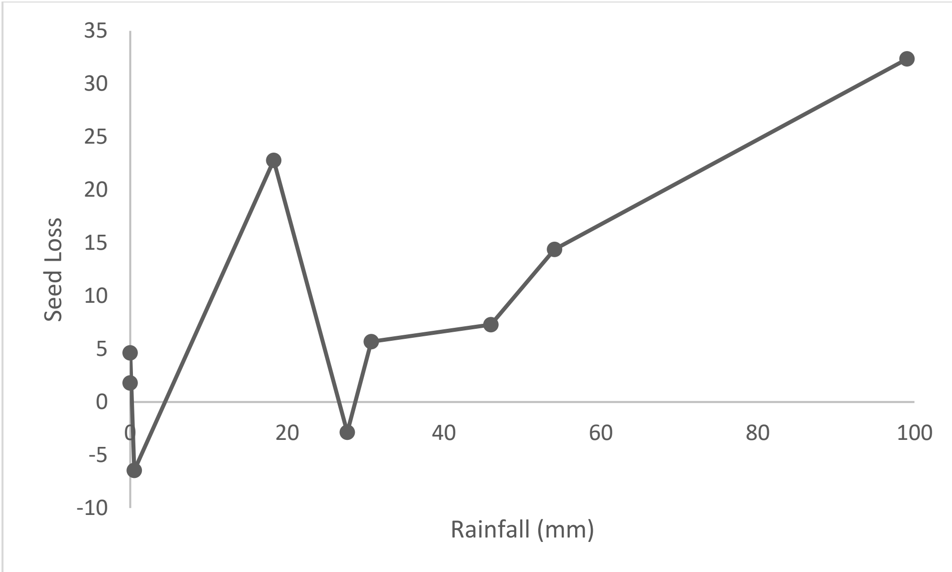

Figure 5. Average number of seeds lost per plot over rainfall events of increasing quantity.

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VITA

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