POPULATION ECOLOGY AND MANAGEMENT OF THE INVASIVE PLANT, *LESPEDEZA CUNEATA*

by

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ABSTRACT

Despite reports that sericea lespedeza (*Lespedeza cuneata* (Dumont) G. Don., Fabaceae) is one of the worst invasive plants across much of the North American Great Plains, most of the detailed work documenting its biology and ecology was performed in the context of its uses in soil stabilization and reclamation or as a forage crop. In this dissertation, I used a field experiment and spatially explicit computer simulations to investigate the persistence and spread of an invasion of *L. cuneata* in a native prairie site.

Chapter 1 describes an experiment in which I tested how the timing of mowing and the local application of herbicide influence the abundance and occupancy of *L. cuneata*. By collecting data on adult individuals and stems I found that herbicide limited increases in the abundance, average size, and spread of adult plants; but the timing of mowing had little impact on adults. Large increases in juvenile occupancy and abundance in plots with high seed production (late-mown and unsprayed) suggested that, without soil disturbance, recruitment is affected more by new seed input than a soil seed bank. The effectiveness of treatments varied among years for both adults and juveniles. This result, particularly in light of the large increases in plots where *L. cuneata* was not sprayed, indicates that continual management efforts over multiple years are necessary to control established infestations.

Collecting data on stem density or the spatial position of plants requires more effort than collecting presence/absence data without any reference to space. In Chapter 2, I used the spatially explicit data set from the field experiment and statistical models to address how different levels of sampling effort by land managers can influence predictions of spread under managed and unmanaged conditions. I found that density-based models that included simple spatial information provided more reliable estimates of colonization, persistence, and changes in abundance within local infestations. Under managed conditions, the effect of herbicide was so strong that it essentially negated the predictive value of model variables.

Models which simulate the spread of weeds in fields and their response to control treatments frequently assume that all plants in the population are found and treated. In Chapter 3, I developed a simulation model to address the importance of three factors that could influence the spread of *L. cuneata*: 1) the spatial distribution of the population, 2) treatment intensity, and 3) the detectability of local infestations. The model indicated that imperfect detectability can reduce the overall effectiveness of control when treatment intensity is low. The negative impact of imperfect detectability can be outstripped however, when intensive treatment leads to large declines in weed spread and abundance.

By integrating the results of a field experiment, statistical models, and simulation models, this research provides a comprehensive examination of the population ecology of invasion of *L* .cuneata in native tall grass prairies. It also suggests approaches for monitoring and management.

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INTRODUCTION

Biological invasions have received an increasing amount of attention in both scientific and popular literature in the decades following Elton's (1958) recognition of their potential global threat. Invasive species can negatively impact native populations and alter community structures in a wide range of habitats (Parker et al. 1999, Sakai et al. 2001, Sala et al. 2001, MacDougall and Turkington 2004a & b, Minchinton 2006), and some species have been linked to changes in ecosystem-level processes (Ehrenfeld 2003, Olden et al. 2004, Mooney and Hobbs 2005, Prater 2006). In addition to expensive control programs, the costs associated with biological invasions include the degradation of habitat and losses in agricultural and rangeland productivity (Lodge 2006). A conservative estimate of these costs exceeds $120 billion in the United States alone (Pimentel et al. 2005).

Ecologists working at several spatial scales and levels of inquiry contribute to the study of invasive species. Landscape ecologists have measured and predicted the movement and distribution of species across regional scales (Peterson et al. 2003, Kapustka 2005). The discipline of community ecology has provided a theoretical framework for predicting habitats that may be particularly susceptible to invasion and has proposed mechanisms that could slow the invasion process (MacDougall and Turkington 2004a, Harrison et al. 2006). Finally, population ecologists have studied the demography, life history, and ecological interactions of invasive species in order to make more realistic predictions about their spread and persistence (Crawley 1986, Sakai et al. 2001).

A major challenge in invasion biology is that the specific risks associated with allowing the establishment and spread of an exotic species are not recognized until after the species has become a problem. In fact, Simberloff (2003) has argued that the very measures meant to prevent the spread of exotic species may be responsible for the failures to prevent their establishment. In particular, the World Trade Organization's (WTO) Agreement on the Application of Sanitary and Phytosanitary Measures requires that nations attempting to exclude an exotic species must first quantify the threat it poses to the native habitat or economy (National Research Council 2000). Such an assessment requires information on population biology that may take a long time to acquire. In the end, the paucity of population biology data on invasive plants leads to management decisions that are often based on incomplete knowledge of the biological or ecological factors that influence the populations' growth rates, spread, and persistence. Thus, population ecologists can make an important contribution by doing observations, experiments, and models that focus on the spread and control of important invasive species. Knowledge gained from such research can allow us to make more realistic predictions about invasions and may be the key to limiting further spread or even eradicating invasive plants.

When invasive plant species become established in natural areas, rangelands, and pastures, substantial losses in both forage value and wildlife habitat have been observed (Thompson 1996, Sheley et al.1998, Masters and Sheley 2001). For example, sericea lespedeza (*Lespedeza cuneata* (Dumont) G. Don. (Fabaceae)) is an exotic plant of increasing concern in the Great Plains of North America and is cited as one of the greatest threats to the tall grass prairie (The Nature Conservancy 2001). The overarching goal of my dissertation research was to study this species' population ecology in order to better understand its local persistence and spread. Since developing appropriate practices for controlling *L. cuneata* populations is of current practical importance I also explain how the results of my study may affect management decisions in natural areas and rangeland settings.

Basic Biology of Sericea Lespedeza

Lespedeza cuneata is a perennial, deciduous legume with erect, ascending stems that grow from 0.5-2.0 m in height. Individual plants are single stemmed during the first year of growth and increase their number of stems with age. In Kansas, adult plants typically produce 1 to 5 stems, but large individuals produce in excess of 30 stems (personal observation). New growth arises each year from a single, knobby caudex located 2.5-8.0 cm belowground. During establishment the species allocates much of its resources to its root system, producing a taproot that can reach nearly 1.5 m belowground. The root system also includes lateral and fibrous growth that is thought to increase the species' competitive ability and drought resistance (Ohlenbusch and Bidwell 2001). Like other leguminous species, it maintains a mutualistic relationship with *Bradyrhizobium* species and is capable of nitrogen fixation. Hoveland and Donnelly (1985) report that soil inoculation may be necessary to establish *L. cuneata* as a forage crop in areas where it has been absent for more than three years.

Lespedeza cuneata typically flowers from mid-July to early October, with fruit and seed development beginning in mid-August in eastern Kansas (personal observation). The species produces chasmogamous flowers which are often cross-fertilized and cleistogamous flowers that are exclusively self-fertilized (Donnelly 1979). Flowers are borne along the entire length of the stem and produce a single seeded fruit. Plants are prolific seed producers, with each stem producing up to 1,000 seeds (Ohlenbusch and Bidwell 2001). Very little information on seed dispersal exists, but human activities such as mowing and haying likely contribute most to long-distance dispersal (Munger 2004). The species is slow to establish, and its seedlings are poor competitors in dense vegetation (Hoveland and Donnelly 1985) which is likely due to its relatively high light and high temperature requirements (Mosjidis 1990) and possibly to the presence of germination inhibitors in its seed coat (Logan et al. 1969). Vegetative spread, though noted in *L. cuneata*, appears to be minimal with most workers citing the regrowth of new stems from the existing root rather than spreading rhizomes or stolons (Stevens 2002).

History of Sericea Introduction and Invasion

Lespedeza cuneata's native distribution extends from central to eastern Asia and south to Australia (Global Invasive Species Database 2005). It was first introduced into the U.S. in 1896 and was widely used for pasture by the late 1940's (Ohlenbusch and Bidwell, 2001). In the 1930's, the United States Department of Agriculture proposed its use as a forage crop for cattle and wild game populations and for erosion control (Pieters 1950), and it is still used for these purposes primarily in the southeastern United States. Although *L. cuneata* seedlings are highly palatable and have high crude protein levels (Petersen and Hill 1991), the plants mature quickly, becoming woody and accumulating tannins. Over time this leads to a decline in the forage value in pastures and a reduction in the degree to which grazing and foraging by native herbivores controls the spread of *L. cuneata* populations in natural systems (May and Jones 2000). It grows well in disturbed areas, pastures, and grasslands and has become established in at least 35 states in the U.S. ranging from the East Coast to Nebraska and Kansas and north to Minnesota (USDA, NRCS 2005). A review of rangeland weeds reported that *L. cuneata* affects at least 3.5 million ha in the 48 contiguous states (Duncan et al. 2004). In a single Kansas county, the number of sections reported as infested increased 83% over two years; the control cost for one year in this county alone was estimated to be $186,486 (Silliman and Maccarone 2005). It is currently listed as noxious in Kansas and Colorado, but is on the watch lists in Iowa, Missouri, Nebraska, Oklahoma, and Texas (USDA, NRCS 2005).

The presence of *L. cuneata* can lead to a range of negative effects within the invaded community. For example, this exotic plant has been found to dominate and to alter the composition of both plant and insect communities in a Kansas oak savanna (Eddy and Moore 1998) and has hindered re-establishment of native forbs and warm-season grasses in Great Smoky Mountain National Park (Price and Weltzin 2003). In a study of old field plant communities, Brandon et al. (2004) found that established *L. cuneata* could reduce both the richness and percent cover of native species by outcompeting them for light, but that it lost its competitive advantage in fertilized plots. Surprisingly, there have been few studies of *L. cuneata* in native tallgrass prairie communities and even fewer in prairies that are part of natural areas rather than pastures or rangelands.

Dissertation Objectives

The overall goal of my dissertation was to explore how the population ecology of *L. cuneata* affects its local persistence and spread in a natural area. The objectives of the first chapter were basic to plant ecology. Namely, my goal was to investigate the patterns of abundance and occupancy within a population of *L. cuneata* and to determine the effectiveness of common management techniques used to control the abundance and spread of the species. Mowing and herbicide application are typically used to control *L. cuneata* populations (Kansas Department of Agriculture Plant Protection and Weed Control Program 2004). Some studies have recorded changes in stem and/or plant density over time for this species under different treatment regimes (Altom et al. 1992, Koger et al. 2002, Brandon et al. 2004). However, these studies focused primarily on dense, uniform infestations where population increases could be determined by changes in density but not overall occupancy. In contrast, my research was done in an area where *L. cuneata* was well established, but patchily distributed. By collecting data on adult individuals such as occupancy, abundance, and local density I could make inferences about spread and persistence in response to treatment. Including data on average plant size indicated that different treatments could influence either the vigor of individual plants or the age structure of the population. Data on juveniles shed light on mechanisms that affect recruitment in habitats where soil disturbance is minimal. As far as I am aware this is the first study that examined juveniles in a natural area setting.

Concern about the impact and spread of exotic plants has produced a growing body of knowledge about the spatial distribution of numerous invasive species. Spatially explicit data sets with resolutions of 1-5 meters have been used in precision agriculture (Ahrens 1994, Rew and Cousens 2001) and to estimate or model weed spread in arable fields (Marshall 1988, Dieleman and Mortensen 1999, Blumenthal and Jordan 2001). However, such data are lacking for most invasive species. In the second chapter, I use a high resolution (1-m^2), spatially-explicit data set for *L. cuneata* to explore the value of such detailed information for guiding local management decisions of invasive species in natural areas. The goals of the study were: 1) to quantify natural spatial patterns of occupancy and aggregation in a field population, 2) to determine the herbicide effectiveness when the spatial autocorrelation of stem density is taken into account, and 3) to test how different data structures (presence/absence data vs. local density data) and local neighborhood information influence predictions of the occupancy and density of *L. cuneata* under managed and unmanaged conditions. The results, although specific to this study, are likely to be typical of other invasive species and could provide a general approach for incorporating spatially explicit data into monitoring and management programs.

In the third and final chapter I present a cell-based simulation model for predicting the short-term (5 years) local spread of *L. cuneata* under managed and unmanaged conditions. In natural areas, locally applied treatments such as hand pulling and "spot spraying" of herbicides are seen as ways to reduce the economic and ecological costs of management (Humston et al. 2005, Shaw 2005). The overall effectiveness of such treatments depends on the intensity of treatment (i.e., reductions in survival and/or reproduction) and workers' abilities to find and treat all plants within infested sites. If plants in large or dense patches have a higher likelihood of detection than plants in small patches (Williams and Hunt 2002, Kéry 2004, Brown and Noble 2005, Casady et al. 2005) it follows that populations with patchy spatial distributions would likely exhibit greater reductions in response to locally applied management. Thus the goal of this study was to use the simulation model to examine how treatment intensity interacts with the initial spatial distribution of a population and detectability to determine the abundance and spatial extent of an invasive plant. In particular, I determined under what combination(s) of treatment intensity and spatial distribution the detectability of plants is a factor in the overall effectiveness of control.

Taken together, the work presented here represents an important step in providing insight of the population ecology of an important invasive plant. The studies include field experiments, statistical models, and computer simulations that explore the patterns of local spread and persistence for *L. cuneata* under various conditions. The results provide information useful to land managers and suggest the types of data necessary for building a better understanding of the process of invasion.

Chapter 1

Invasive plant management in native prairies: effects of spot spraying of herbicide and timing of mowing on juveniles and adults of *Lespedeza cuneata*

CHAPTER SUMMARY

Lespedeza cuneata is a widely recognized invasive plant of both native grassland and pasture lands, but few studies have documented its spread and persistence in response to management practices. The goal of this study was to determine how herbicide application and the timing of mowing affect the abundance and occupancy of adults and juvenile plants within an established, but patchily distributed, stand of *L. cuneata*. Spot spraying of herbicide led to slight decreases in both adult and juvenile abundance after two years of treatment while adult and juvenile abundances increased two to four-fold in the unsprayed plots. Increases in adult and juvenile occupancy only occurred in plots that were not spot sprayed, while only adult occupancy significantly declined in the sprayed plots. Mowing time by itself had no effect on adult *L. cuneata*. Mowing time did influence juveniles, however, with the largest increases in abundance and occupancy occurring in unsprayed plots that had set seed before the late-season mowing was applied. Under these conditions of no soil disturbance, recruitment from the seed bank appears to be minimal, making new seed input necessary for both the growth and spread at the site. Although the herbicide treatment was effective, the dramatic increases in untreated plots combined with the more modest declines in treated plots suggest that that long-term, continual management is required; and eradication, if possible at all, is a long time in the future.

INTRODUCTION

Invasive species can affect native population and community structures (Parker et al. 1999, Sakai et al. 2001, Sala et al. 2001, MacDougall and Turkington 2004a & b, Minchinton 2006) and have been linked to changes in ecosystem-level processes (Ehrenfeld 2003, Olden et al. 2004, Mooney and Hobbs 2005, Prater 2006). When these changes occur in pastures, rangeland, and natural areas, substantial losses in both forage value and wildlife habitat have been observed (Thompson 1996, Sheley et al.1998, Masters and Sheley 2001). A number of control measures have been effectively used to manage invasive plant populations in rangelands and natural areas (see DiTomaso 2000 and Masters and Sheley 2001 for summaries). Most strategies aim to reduce plant numbers by directly removing or killing individuals (hand pulling and direct herbicide application) or by preventing further growth and spread by altering the environment in a way that may favor native species (fire, mowing, nutrient addition/limitation).

Herbicides are commonly used to control invasive plants used in the United States with approximately 25% of the 400 million ha of rangeland treated, for instance, in 1997 (Bussan and Dyer 1999). Depending on the rate, timing, and mode of application, herbicides can reduce survival, seed production, vegetative spread, and competitive ability of weed species (Bussan and Dyer 1999, Shinn and Thill 2002, Grekul et al. 2005). Broadcast applications of herbicides treat expansive areas by mounting sprayers on either aircraft or ground-based vehicles. For example, this approach has led to some success in controlling *Centaurea maculosa* in western

Montana rangeland (Rice et al. 1997), However, herbicide sprayed in arable fields and pastures has been shown to drift up to eight meters into field boundary vegetation (Marrs and Frost 1997) and negatively impact non-target plant species (Kleijn and Snoeijing 1997, Marrs and Frost 1997). Thus, concerns about how broadcast applications affect beneficial, non-target and indigenous plants have limited their widespread use in natural areas. Other tractor-mounted application regimes such as spraytopping and wick application have been designed to specifically treat target plants over broad areas (Wallace et al. 1998, Grekul et al. 2005). However, these practices can also reduce forage quality if desirable legumes and indigenous plant species are tall enough to be treated or if a broad-spectrum herbicide such as glyphosate is used. “Spot spraying”, where herbicide is applied to individual target plants by using handheld or backpack sprayers, is therefore commonly employed to directly treat target plants while minimizing environmental impact such as off-site drift and damage to non-target plants (Bussan and Dyer 1999, Obermeyer et al. 2001). Including labor costs, spot spraying has also been estimated to be five to seven times cheaper than either ground or aerial broadcast applications (Obermeyer et al. 2001). Such an approach would be appropriate to control small to moderate infestations of invasive plants in rangeland, pastures, and natural areas since maintaining and/or preserving the richness of the existing native community is the goal (Bussan and Dyer 1999).

Mowing and clipping are also commonly used in grassland management and restoration efforts worldwide (Clark and Wilson 2001, Lennartsson and Oostermeijer

2001, Wilson and Clark 2001, Moog et al. 2002). Mowing may be an easier and cheaper control method than spot spraying since the time, financial resources, and labor required are reduced (Magadlela et al. 1995). However, the timing and frequency of mowing could determine which life stages are treated and how effectively the weeds are controlled. Mowing or clipping at pre-bud and early flowering stages can reduce weed populations by decreasing both sexual and vegetative reproduction (Bossard and Rejmánek 1994, Sheley et al. 1999, Rinella et al. 2001). Mowing can also decrease survivorship by limiting carbohydrate reserves (DiTomasso, 2000). However, mowing may also stimulate new stem production in some perennial species if applied too early in the season (Lehtila and Syrjanen 1995, Sheley et al. 1999).

No matter what management practices are used, a common goal is the reduction of seed production. For instance, Meyer and Schmid (1999a, b) found that mowing and clipping before seed set and dispersal effectively controlled *Solidago altissima* in German grasslands. Herbicides can also lead to both the reduction of seed set and to the production of abnormal or inviable seeds (Wallace et al. 1998). However, the presence of dormant seed in the soil (i.e. a seed bank) could also limit the effectiveness of reducing seed input from the previous season (Panetta and Randall 1993, Zamora and Thill 1999, Alexander and Schrag 2003).

Developing appropriate control practices is of current practical importance for *Lespedeza cuneata* (Dumont) G. Don. (Fabaceae), an exotic plant of increasing concern in the Great Plains of North America and cited as one of the greatest threats to the tall grass prairie (The Nature Conservancy 2001). Commonly known as sericea lespedeza or Chinese bushclover, this woody perennial of Asian origin was first introduced into the U.S. in 1896 and was widely used for pasture by the late 1940's (Ohlenbusch and Bidwell, 2001). In the 1930's, the United States Department of Agriculture proposed its use as a forage crop for cattle and wild game populations and for erosion control (Pieters 1950), and it is still used for these purposes primarily in the southeastern United States. This species grows well in disturbed areas, pastures, and grasslands and has become established in at least 35 states in the U.S. ranging from the East Coast to Nebraska and Kansas and north to Minnesota (US Department of Agriculture – Natural Resource Conservation Service, 2005). Although *L. cuneata* seedlings are highly palatable and have high crude protein levels (Petersen and Hill 1991), the plants mature quickly, becoming woody and accumulating tannins. Over time this leads to a decline in the forage value in pastures and a reduction in the degree to which grazing and foraging by native herbivores controls the spread of *L. cuneata* populations in natural systems (May and Jones 2000). Despite concern over its spread in the Great Plains (The Nature Conservancy 2001), very few detailed ecological studies have examined *L. cuneata* in the context of native or degraded grassland communities. However, the species has been found to dominate and to alter the composition of both plant and insect communities in a Kansas oak savanna (Eddy and Moore 1998) and has hindered re-establishment of native forbs and warm-season grasses in Great Smoky Mountain National Park (Price and Weltzin 2003). In a study of old field plant communities, Brandon et al. (2004) found that established *L.*

cuneata could reduce both the richness and percent cover of native species by outcompeting them for light. Therefore, limiting the establishment and spread of *L. cuneata* is important to agronomists, range managers, and conservationists alike.

Mowing and herbicide application have been shown to control *L. cuneata* (Altom et al. 1992, Jordan and Jacobs 2002, Jordan et al. 2002, Stevens 2002, Koger et al. 2002, Brandon et al. 2004, Kansas Department of Agriculture Plant Protection and Weed Control Program 2004). However, few of these studies directly addressed population dynamics (i.e., changes in stem and/or plant density over time) of the species under different treatment regimes (Altom et al. 1992, Koger et al. 2002, Brandon et al. 2004). Further, since the majority of studies on *L. cuneata* focus on control in dense, relatively uniform stands of *L. cuneata* (but see Brandon et al. 2004), they do not address the efficacy of spot spraying on more patchily distributed populations characteristic of a moderate (or growing) infestation. As emphasized by Puth and Post (2005), heavy infestations of invasive weeds are difficult to control and nearly impossible to eradicate (see also Simberloff 2003, Arim et al 2006). Thus, improving our knowledge of how to control *L. cuneata* at early stages of invasion and spread is critically important.

The objectives of this study were therefore to investigate the patterns of abundance and occupancy within an established, but patchily distributed population of *L. cuneata* and to determine how effectively herbicide application and the timing of mowing control the population growth and spread of the species. I also used population data to infer the mechanisms of the persistence and spread of *L. cuneata* at this site. I chose to employ spot spraying over broadcast spraying in order to directly treat individual *L. cuneata* plants while minimizing herbicide effects on desirable plants. Since the study site was owned by the Nature Conservancy and Kansas noxious weed laws require management of the species, all plots had to have some form of treatment applied, and no true control could be incorporated into the study.

MATERIALS AND METHODS

STUDY ORGANISM

Lespedeza cuneata is perennial, deciduous legume. Its erect, ascending stems grow from 0.5-2.0 m in height. New growth arises each year from a single, knobby caudex located 2.5-8.0 cm belowground. During establishment the species allocates much of its resources to its root system, producing a taproot that can reach nearly 1.5 m belowground. Their root system also includes lateral and fibrous growth that is thought to increase the species' competitive ability and drought resistance (Ohlenbusch and Bidwell 2001). While individual plants are single stemmed during the first year of growth, stem number increases with age, and isolated plants with over 100 stems have been documented (Blair, 1933). *Lespedeza cuneata* plants are prolific seed producers, with each stem producing up to 1,000 seeds (Ohlenbusch and Bidwell 2001). At the Kansas study site (see below), adult plants typically produced 1 to 5 stems, with the largest individuals producing more than 30 stems per plant. The species typically flowers from mid-July to early October, with fruit and seed development occurring throughout September at the study site. Vegetative spread, though noted in *L. cuneata*, appears to be minimal with most workers citing the regrowth of new stems from the existing crown root rather than spreading rhizomes or stolons (Stevens 2002).

STUDY SITE

The study was performed at the Welda Prairie, a 52 ha preserve owned by The Nature Conservancy in Anderson County, Kansas USA at the eastern extent of the Kansas

Flint Hills region. With deeper soils and higher annual rainfall than the rest of the Flint Hills (mean = 101 cm, s.d. = 22.1 cm), this site represents one of the more diverse tallgrass prairies in the region. Native grasses such as *Andropogon gerardii*, *Sorghastrum nutans*, and *Panicum virgatum* dominate the prairie, but a high diversity of non-grass species including *Amorpha canescens*, *Echinacea purpurea*, and the globally threatened *Asclepias meadii* also occur at the site. Most of the Anderson county prairies were previously used as native pasture and hay meadows, but there has been disturbance from agriculture and associated activities. My study site was a ~1 ha area within a matrix of high-quality prairie. The specific site had a history of disturbance, being located in the vicinity of a former homestead, which was plowed and cultivated from circa 1945 to 1985. The site is now dominated by several introduced pasture grasses such as *Agrostis stolonifera*, *Bromus inermis*, and *Festuca arundinacea* as well as a number of old field successional species such as *Ambrosia artemisiifolia*, *Helianthus annuus*, and several species of *Solidago* and *Aster*. The site was chosen because it is representative of other disturbed sites within the tallgrass prairie landscape of the Eastern Flint Hills where *L. cuneata* has become established. Initial infestation levels of *L. cuneata* varied across the site, with approximately 20% occupancy and local density ranging from 1-120 stems m^{-2} (median = 4 stems m^{-2}, scale of 1 m^2). These local levels of stem density are similar to those observed at other sites in the Flint Hills as well as sites in other regions where *L. cuneata* is described as established but not completely dominant (Brandon et al. 2004, Blocksome 2006).

EXPERIMENTAL DESIGN AND DATA COLLECTION

A 3456 m^2 study area was established at a site previously invaded by *L. cuneata* (Figure 1.1). A five meter border was mown around this area in June each year in order to minimize seed input from *L. cuneata* outside the study area. In overview, the experimental design consisted of dividing the area into six blocks according to distance from an access road with a large concentration of *L. cuneata*. Each block was then divided into three plots, with each plot randomly receiving one of three mowing treatments: mid-June, late-August, or twice mown. Each plot was then divided in two sub-plots, with one sub-plot receiving a herbicide (spot spraying) treatment and the other receiving no herbicide treatment; hence the mowing and spraying was done in a split-plot experimental design. No true control treatment (i.e., no spraying or mowing) was tested due to the site managers' concerns about spread of *L. cuneata* into the adjacent, high-quality prairie.

The mid-June mowing time used here was chosen because earlier control treatments (spring mowing, grazing, or burning) often lead to an increase in the number of seed-producing stems per individual (Ohlenbusch and Bidwell 2001, US Department of Agriculture – Natural Resource Conservation Service 2005). Mowing late in the season can limit the energy available for allocation to root reserves, overwinter survival, and future growth (Ohlenbusch and Bidwell 2001). The August mowing time was also chosen in an effort to cut plants back before they set seed. In reality, 10% to 25% of reproductive *L. cuneata* plants had set seed by this time each year. All mowing treatments were carried out using a three-blade tractor mower, with a two-meter wide platform. Vegetation was cut to a height of ~10 cm at each mowing period. For subplots assigned herbicide treatments, I used a backpack sprayer to spot spray any *L. cuneata* plants present with a 0.26 g L^{-1} solution of metsulfuron methyl (Escort®, DuPont™ Industries) until all leaf and stem surfaces were coated (as per label instructions for spot spraying). Given the dense vegetation, I estimate that I detected plants that were approximately 12 cm high or taller but may not have sprayed all very small individuals. Herbicide was applied in mid-July of 2002 and the first week of August in 2003. Interplot effects were minimized by establishing a permanent 22 x 2 meter sampling area in the center of each subplot, providing two meters of space between sampling areas. This provided six sampling areas for each treatment combination. In order to more efficiently perform the censuses, each sampling area was divided into 44 1-m^2 quadrats (Figure 1.1). During each census a measuring tape was extended between pins that permanently marked the ends of a 22 meter transect. Quadrats were censused using a 1 x 2 meter counting frame that was moved the along the length of the transect at one meter increments. Data were recorded in each quadrat and summarized for each sampling area before the final analysis.

I recorded the number of adult stems, adult individuals, and juveniles in each quadrat during five census periods: mid-June 2002 (pre-treatment), mid-August 2002, mid-June 2003, mid-August 2003, and mid-June 2004. Preliminary analyses showed no significant differences between June and August within either year, so final analyses were only performed on the June census data. Seedlings and young (non-woody) plants were difficult to distinguish. Therefore, all plants that were ≤ 15 cm tall, non-woody, and not sexually reproductive during a given census were defined as juveniles. The total number of stems or plants provided information about the overall population size within a sampling area while mean and maximum density gave estimates of the intensity of infestation at the 1-m^2 level for each sampling area. The mean density was defined as the average density of stems or individual plants in the occupied quadrats within a plot while the quadrat with the highest number of stems or individual plants represented the maximum density for each sampling area.

I did not record data on the number of stems produced on each individual plant. Thus adult plant sizes were estimated by dividing the number of stems per quadrat by the number of adult plants per quadrat. By having data on both stem number and estimated plant size, I could discern whether changes in density represent changes in the number of individuals within the population, the size of individual plants within the population, or both. Finally, I also calculated the occupancy within a sampling area as the percentage of the 44 quadrats with at least one plant. Initial occupancy was low (mean = 18.4%, s.e. = 1.97%), with no sampling area having more than 48% of its quadrats containing *L.cuneata*.

The population was censused twice yearly because I had initially predicted that the treatments would result in different germination, survival, and branching patterns within a single growing season. However, since no significant variation occurred between June and August within any given year, only the June censuses were included in the final analyses. The mid-June census was performed before any treatments were applied each year.

I used a split-plot design ANOVA to analyze the resulting data. In this analysis, mowing was the whole-plot treatment, and herbicide application was the split-plot treatment. Both treatments were fixed effects while the effect of block was considered random. All analyses were performed using Statistix® 8 (Analytical Software, Tallahassee, FL) with model statements and error terms determined according to Gotelli and Ellison (2004).

I first analyzed the impact of mowing and herbicide on abundance and occupancy after two years of treatment applications. If either mowing time alone or the interaction of mowing and spot spraying was significant in these analyses then Tukey's HSD was used to perform pairwise comparisons of treatments. Finally, I analyzed the change in plant and stem numbers over time (i.e., the degree to which numbers increase or decrease within each treatment). In order to perform the final analysis, I first created data pairs for each response variable. A data pair consisted of measurements of the 2002 and 2004 responses for the same plot. In order to see if a response within each treatment changed over time I used Monte Carlo simulations to randomize the paired data. For each simulation the data values from 2002 and 2004 were randomly reassigned as either first or third year values (1000 simulations). The average observed change in a response (final [2004] measurement – initial [2002] measurement) was compared to its average change in the simulations. The average change for plots with the same treatment combination indicated the trajectory of the response variables through time, with a positive change indicating an increase and a negative change indicating a decrease in the response variable (Gotelli and Ellison 2004). Since a pilot study indicated that herbicide decreased plant survivorship and vigor, all tests involved one-tailed alternative hypotheses. For unsprayed plots, this meant that the observed change would be greater than the simulated change; for sprayed plots, the observed change would be less than the simulated change.

Since spot spraying occurred later in 2003 compared to 2002 it was possible that the effects of management treatments were not consistent from year to year. To examine this question, I also tested whether the treatments influenced the annual change of each response consistently over both annual transitions (2002 to 2003, 2003 to 2004).

RESULTS

ABUNDANCE, DENSITY, AND PLANT SIZE

The timing of mowing treatments did not affect any adult response variable, but herbicide application significantly affected the total abundance of adult plants and adult stems after two years of treatment (Table 1.1). By 2004, the numbers of individual plants and stems were 81% and 91% lower respectively in the sprayed plots compared to the unsprayed plots (Figure 1.2a, b). Tests of the significance of the change in total abundance between 2002 and 2004 showed that the greater number of individual plants and stems in the unsprayed plots resulted primarily from increases in the unsprayed plots (Figure 1.2a, b). A similar result was seen in the analysis of mean density, a measure for tracking abundance in only the occupied quadrats within a plot (Table 1.1; Figures 2c, d). However, while the maximum density of adult individuals decreased 57% in the sprayed plots, it remained stable in the unsprayed plots (Figure 1.2e). In contrast, the maximum density of adult stems increased 13% in the unsprayed plots and declined 73% in the sprayed plots over the course of two years (Figure 1.2f).

A measure of average plant size, the mean number of stems per adult, was also affected by herbicide application (Table 1.1). In 2002 the average adult plant had between three and four stems. After two years of treatment application, the average adult plant in the sprayed plots had approximately half the number of stems (mean = 1.5, s.e. = 0.09) as the average adult plant in the unsprayed plots (mean = 3.3, s.e. = 0.46).

Juvenile abundance was determined by both mowing regime and herbicide application after two years of treatment (Table 1.1). Spot spraying significantly decreased the total abundance of juveniles by the end of the study (Table 1.1; Monte Carlo randomization, $p=0.007$; Figure 1.3). Further, a significant interaction between treatments (Table 1.1) resulted because three times more juveniles were found in the plots that were unsprayed and mowed only in August compared to other treatments (Table 1.2, Figure 1.3). The same pattern was found for maximum density of juveniles, with the unsprayed plots that were mown only in August having at least three times higher maximum density than plots in all other treatment combinations (data not shown).

For all adult abundance and density, the cumulative effect of herbicide resulted from the effect of the 2002 application on the 2003 population (ANOVA results for herbicide effects ranged from $F_{1,15} = 5.59$, $p \leq 0.05$ to $F_{1,15} = 21.49$, $p \leq 0.001$). Individuals and stems both appeared to increase in the unsprayed plots and decrease in the sprayed plots between 2002 and 2003 (Figure 1.2). However, these changes were less pronounced between 2003 and 2004, with evidence of recovery in the unsprayed plots. Treatment effects also varied between years for juveniles. In these test herbicide alone only affected the change in juvenile abundance between 2002 and 2003 ($F_{1,15} = 7.12$, $p \leq 0.05$). Mowing and the interaction of mowing and herbicide affected abundance and density (mean and maximum) over the second transition (ANOVA results for tests ranged from $F_{1,15} = 4.06$, $p \leq 0.05$ to $F_{1,15} = 11.19$, $p \leq 0.01$).

OCCUPANCY

The effect of herbicide application on the occupancy of *L. cuneata* adults within the plots was similar to its effect on adult abundance. By the end of 2004 the percent occupancy of adults was more than two times higher in unsprayed plots compared to spot sprayed plots (Table 1.1, Figure 1.4a). The timing of mowing had no effect on adult occupancy. The results for juvenile occupancy were qualitatively the same as the adult data (Table 1.1). By the end of the study the percentage of quadrats containing juveniles was nearly four times higher in the unsprayed plots (Figure 1.4b).

Treatment effects on occupancy were also variable between each transition for both juveniles and adults. For adults, herbicide was only effective over the first annual transition ($F_{1, 15} = 2.94$, $p \leq 0.001$); but it affected changes in juvenile occupancy over both annual transitions ('02-03: $F_{1, 15} = 15.90$, $p \leq 0.01$; '03-'04: $F_{1, 15} = 9.06$, $p \leq 0.01$). Mowing only influenced the change in juvenile occupancy between 2003 and 2004 ($F_{2, 10} = 9.06$, $p \leq 0.01$).

DISCUSSION

Herbicide had a major effect on abundance and occupancy of *L. cuneata*, while the effects of the timing of mowing were more subtle and primarily affected numbers of juvenile plants. Although herbicide is frequently used to control dense infestations of *L. cuneata* in pastures (Altom et al. 1992, Koger et al. 2002, Brandon et al. 2004), few studies examine the control of this important plant in patchily distributed infestations in natural areas or rangelands. Since the initial occupancy of the study plots was low (< 20%) the site likely represents a growing *L. cuneata* population. This study thus presents data on the efficacy of treating an invasion at the stage where the likelihood of successful control is greater (Simberloff 2003, Puth and Post 2006).

ADULT DYNAMICS

Effects of herbicide on adult abundance were striking: after just two years of treatment, unsprayed plots had more than 5 times the number of individual plants and nearly 12 times the number of adult stems compared to the spot sprayed plots (Figure 1.2). Despite the fact there was little reduction in the abundance of either individual plants or stems in the sprayed plots over time, the large and growing differential between the sprayed and unsprayed plots (Figure 1.2) emphasizes the large effect of the herbicide in this study. Most past work with herbicide control has been performed on dense, uniform stands of the species (Altom et al. 1992, Koger et al. 2002). For example, previous work has shown that a single broadcast application of metsulfuron in Oklahoma pastures led to 70-100% reductions in *L. cuneata* stem density in the first year after treatment (Koger et al. 2002), with adult mortality the primary factor. In the present study, the decline in adult occupancy in the sprayed plots provides evidence that herbicide increased adult mortality (Figure 1.4a).

The number of stems per adult was calculated as a means to estimate the size and vigor of individual plants. While the mean number of stems per adult declined in sprayed plots (2002, 3.1 ± 0.20; 2004, 1.5 ± 0.09; mean ± s.e) it remained largely stable in unsprayed plots (2002, 3.7 ± 1.33; 2004, 3.3 ± 046; mean ± s.e.). At least two possible explanations could account for the difference in stem number. The most obvious explanation is that individual plants that aren't killed experience a reduction in vigor (and stem number) in response to herbicide. Alternatively, since many juvenile plants might not have been spot sprayed (plants ≤ 12 cm in height were difficult to see during herbicide application in mid-July), the reduction in stem number in the sprayed plots could signal a shift in the age structure of sprayed plots following the death of multi-stemmed adults. These untreated juvenile plants could have replaced adult plants that had been killed by the previous year's herbicide application. Further work should track the fate of individuals in order to determine the relative importance of these two processes.

Data on the density of individuals and stems provided information about differences in infestation intensity among plots and indicated "hot spots" (areas of highest infestation) within individual plots. It is noteworthy that the maximum density of adult individuals in the unsprayed plots appeared to be stabilizing in numbers over time, suggesting that this may be the "carrying capacity" for this habitat (Fig. 2e). This result suggests that density-dependent factors may regulate the abundance of individual *L. cuneata* plants at the scale of one meter. Such density-dependence has been reported for *L. cuneata* grown as a forage crop (Hoveland and Donnelly, 1985), but more detailed work needs to be conducted to determine its influence on populations invading natural areas.

JUVENILE AND SEED BANK CONTRIBUTION

In contrast to adult plants, the overall abundance of juveniles responded to both mowing regime and herbicide application. Juvenile abundance was halved when seed input was limited by two years of spot spraying, but it experienced a nearly four fold increase in the unsprayed plots during the same period. Exploring the patterns of juvenile abundance in different treatments gives insight on the impact of current seed input versus the seed bank on seedling recruitment, and suggests that the seed bank contribution is low in this prairie site with minimal soil disturbance.

The logic for this conclusion depends on several factors, including the source of juveniles in different treatment plots. Since a pilot study (Emry, unpublished data) showed that sprayed plants contribute essentially no seed during the year of treatment, most new seedlings and juveniles counted in the sprayed plots during 2003 and 2004 would have been recruited from a seed bank. In contrast, for the unsprayed plots, new seedlings and juveniles could come from two sources: dormant seed in the soil and also new seed production. Approximately 10-25% of plants in the unsprayed plots had set seed before the mid-August mowing treatment was applied. Little is known about seed banks in *L. cuneata*, but workers have speculated that seeds may remain viable in the soil for 20 years (Ohlenbusch and Bidwell 2001). The population at the Welda Prairie has been established for more than 10 years (Dean Kettle*, personal communications*), so if *L. cuneata* had the potential to develop large, persistent, seed banks, then the site should have experienced at least some level of seedling (and juvenile) recruitment even with the absence of new seed input. The decline in juveniles in sprayed plots thus suggests that either germination requirements were not met or that recruitment from the seed bank does not play a major role in increasing the population.

One caveat to this idea is incidental application of herbicide to juveniles and seedlings growing below larger, sprayed plants. Juvenile abundance per quadrat was correlated with both the abundance of adult individuals and stems during each year of the study (Spearman rank correlation; 2002 $r = 0.554$, $p < 0.001$; 2003 $r = 0.649$, $p < 0.001$; 2004 $r = 0.643$, $p < 0.001$) suggesting that the two life stages do occur in the same location. Neither adult nor juvenile abundance varied between the June and August censuses in any year, suggesting that spot spraying adults either failed to kill juveniles or that juvenile mortality was quickly and consistently balanced by recruitment from the seed bank. Though individual plants were not marked and tracked in this study, a simple experiment in which individual juveniles are monitored before and after spot spraying could address this question.

Further evidence that current year seed production, and not seed banks, is essential to increasing juvenile abundance comes from the significant interaction between mowing and spraying (Table 1.1, Figure 1.3). This interaction resulted from the unusually large number of juveniles that occurred in the unsprayed plots that were mown only in August. Flowering and seed production occur along the length of stems and thus tall and/or highly branched plants produce more seeds than short plants with minimal branching. Mowing in June did not increase branching by the mid-August census, but the plants in these plots were 70 – 80% shorter than those in the plots mowed only in August (personal observation). The seed-producing potential of the early-mown plants was therefore lower than plants that were not mowed until August. Since a dramatic increase in juveniles only occurred in unsprayed, late-mown plots, a large amount of seed input must be necessary to increase the juvenile abundance within a population (Figure 1.3). This result provides further evidence that without any obvious soil disturbance the population is seed limited, and that if a seed bank is present, it contributes little to population growth at this site.

New seed input also appears to be necessary for the spread of *L. cuneata*. Increases in occupancy represented the colonization of new quadrats within a plot and could theoretically occur as a result of either seed bank recruitment or new seed input. While juvenile and adult occupancy both increased more than 13% in the unsprayed plots over the course of the study, neither stage experienced an increase in occupancy in the sprayed plots (Figures 4a, b). Thus, from a management standpoint, the presence of a seed bank in *L. cuneata* could slow eradication efforts, but without soil disturbance it may not intensify an infestation in the absence of new seed input. Since soil disturbance often initiates germination and recruitment from a seed bank (Meyer and Schmid 1999b, Grigulis et al. 2001, Moody-Weis and Alexander 2007), dormant seeds may indeed play a much more important role in sites with frequent soil disturbance.

MANAGEMENT IMPLICATIONS

Management strategies such as mowing, grazing, herbicide/pesticide applications, and biocontrol agents are often applied at a large spatial scale. Therefore, the impact of treatments on individual patches or “hotspots” is not always clear. From this study, it appears that the reduced seed input brought on by spot spraying led to lower abundances of *L. cuneata* at the plot level and lower densities (both mean and maximum) in the specific areas of infestation within the plots. The decreased occupancy in spot sprayed plots indicates that limiting seed input can also reduce the area of infestation. However, effective control may hinge on the ability of workers to treat all individuals in a population. Failing to detect and treat plants (especially large and/or highly branched plants) could lead to scattered areas of high seed production and an expanding population. Future studies should address the issue of detectability and its effect on population persistence and growth.

Herbicide, although effective, is expensive. Thus mechanical approaches such as mowing and clipping are often employed as a more cost-effective management strategy for non-desirable plant species (Magadela et al. 1995; Wilson and Clark 2001; Verrier and Kirkpatrick, 2005). For *L. cuneata,* managers and researchers have had conflicting views on mowing. On one hand, summer mowing commonly occurs in many Great Plains prairies as part of mid-summer haying operations. Thus, it is valuable to know the effect of mowing on invasive plant spread, and in particular the effect of mowing in different seasons. Others, however, have documented that mowing actually increases *L. cuneata* levels (Brandon et al. 2004). They proposed that increased light availability following mowing led to increased rates of *L. cuneata* germination and establishment. In the study presented here, I did not address the effectiveness of mowing as a treatment; instead the focus was on how the timing of mowing influenced abundance and occupancy. Further, to my knowledge, workers have not simultaneously examined juvenile and adult responses to mowing treatments. Though the timing of mowing had little effect on the adult population, it had a significantly large and consistent effect on the abundance of juveniles, with the plots mowed only in August having at least three times more seedlings than the other plots.

Finally, it is important to realize that data on the management of pest species can be interpreted from two perspectives. First, one can focus on the cumulative effects of the treatments. In the case of this study, the differences between treatments (especially spot spraying) were large and straightforward. Second, one can focus on the trajectory of the treated populations as well as the variability of treatment effects over time. With respect to this second approach, the small declines observed in the herbicide plots over the course of the study indicate that continual treatment over multiple years, though capable of slowing the spread of *L. cuneata*, may not lead to complete eradication. More importantly, however, is the understanding that the failure to effectively treat infestations, even for a few years, can lead to tremendous increases in both the intensity and the extent of an infestation.

Table 1.1. Effect of mowing regime and herbicide application on *L. cuneata* after two years of treatment (2004 data). Each column represents the results of separate split-plot ANOVA's for adult individuals, adult stems, and juveniles present in 2x22 m sampling areas.

		Sum[1]	**Mean Density**[2]	**Maximum Density**[2]	**Mean Stems/Adult**[3]	**Percent Occupancy**[4]
Adult Individuals						
	df					
Block	5	ns	ns	ns	ns	ns
Mow	2	ns	ns	ns	ns	ns
Mow x Block (error)	10	ns	ns	ns	ns	ns
Spray	1	**	***	**	****	*
Mow x Spray	2	ns	ns	ns	ns	ns
Mow x Block x Spray (error)	15	ns	ns	ns	ns	ns
R^2		56.73%	61.65%	56.19%	86.36%	50.85%
Adult Stems						
	df					
Block	5	ns	ns	ns		
Mow	2	ns	ns	ns		
Mow x Block (error)	10	ns	ns	ns		
Spray	1	***	***	***		
Mow x Spray	2	ns	ns	ns		
Mow x Block x Spray (error)	15	ns	ns	ns		
R^2		63.77%	72.92%	67.68%		
Juveniles						
	df					
Block	5	ns	ns	ns		ns
Mow	2	*	†	*		ns
Mow x Block (error)	10	ns	ns	ns		ns
Spray	1	***	**	****		***
Mow x Spray	2	*	ns	*		ns
Mow x Block x Spray (error)	15	ns	ns	ns		ns
R^2		74.93%	70.31%	79.21%		70.18%

1 Total number of individuals or stems in 44 m^2 plot

2 Determined only by analyzing occupied quadrats within a 44 m^2 plot.

3 Based on the average number of stems per adult per quadrat in the occupied 1-m^2 quadrats within a 44 m^2 plot

4 Percent of the 1-m^2 quadrats within a plot that had at least one individual.

† $0.10 > p > 0.05$

* $0.05 > p > 0.01$

** $0.01 > p > 0.005$

*** $0.005 > p > 0.001$

**** $p < 0.001$

Table 1.2. Total juvenile abundance after two years of treatment application. Each Mowing x Herbicide treatment combination is represented by the mean (±s.e.) of six plots; values with different lowercase letters are significantly different (Tukey's Honest Significant Difference, $p \leq 0.05$). The means for the mowing treatments (±s.e.) are at the bottom of each column. Values denoted with different letters are significantly different (Tukey's HSD, $p < 0.05$).

	Mowing Treatment		
Herbicide	June mown	August mown	Twice mown
Control	47.5 (±28.63)^{b}	166.7 (±49.39)^{a}	39.2 (±11.79)^{b}
Spot Sprayed	10.0 (±6.19)^{b}	9.2 (±3.52)^{b}	5.0 (±4.08)^{b}
Total	28.8 (±15.07)$^{A, B}$	87.9 (±33.48)^{A}	22.1 (±13.14)^{B}

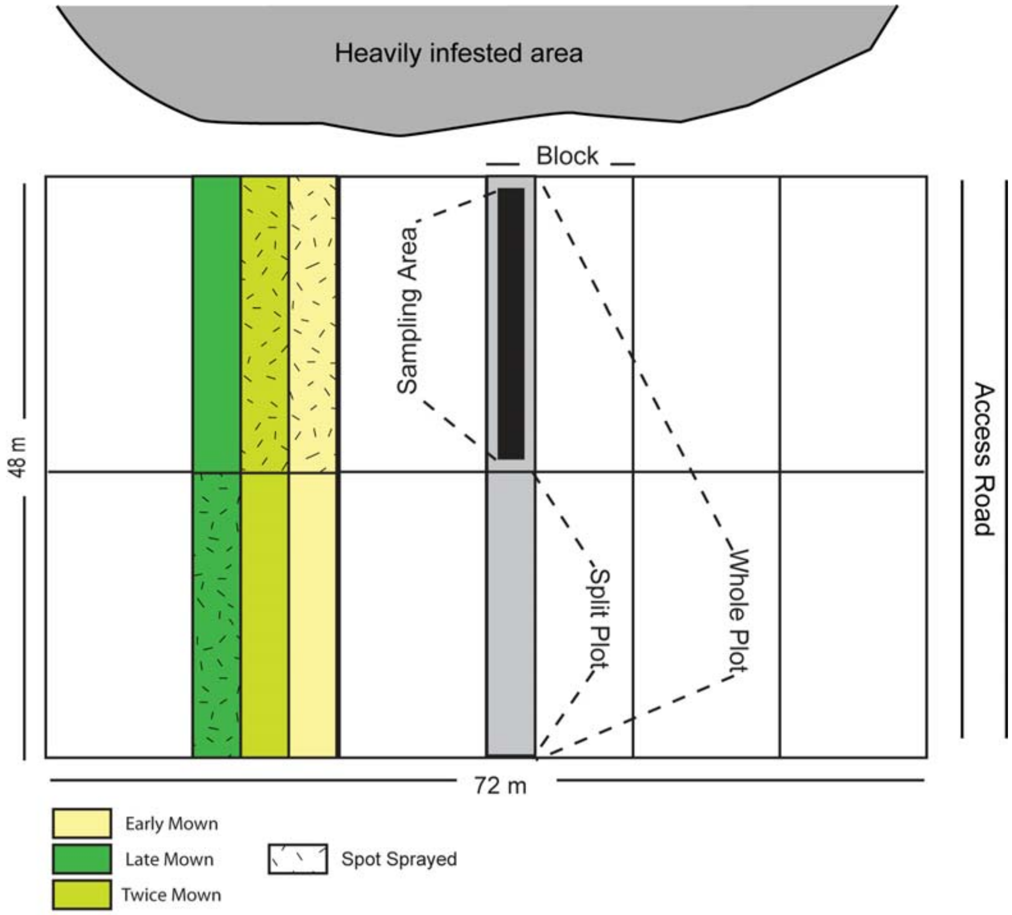

Figure 1.1. Map of the experimental site at Welda Prairie. Three mowing applications served as whole plot treatments, and herbicide application (+/- spot spraying) was the split plot treatment. The treatment arrangement of one block is shown above with colored strips. In order to facilitate data collection each 2x22 m sampling area was further divided into 44 1-m^2 quadrats. The number of adult individuals, adult stems, and juveniles were counted in each quadrat and summarized for the sampling area before the final analysis.

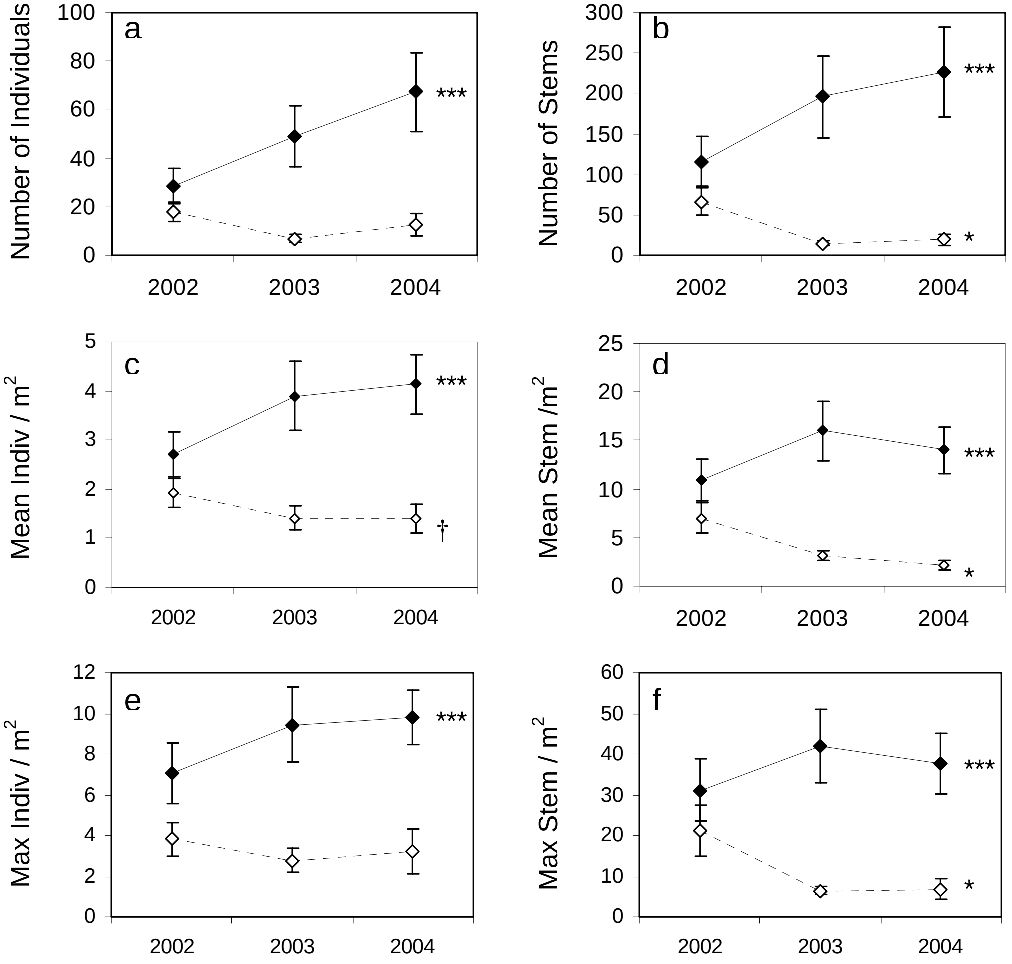

Figure 1.2. Response of *Lespedeza cuneata* adults to herbicide application from 2002-2004. Closed symbols (◆) and solid lines represent unsprayed plots. Open symbols (◇) and dashed lines represent sprayed plots. a, Total number of individuals within a plot; b, total number of stems within a plot; c, mean density of individuals/occupied quadrat; d, mean density of stems/occupied quadrat; e, maximum density of individuals/occupied quadrat; f, maximum density of stems/occupied quadrat within a plot. Points represent the mean (± 1 se) of 18 plots within each treatment. Lines denoted by asterisks indicate a significant change in the response between 2002 and 2004 (one-tailed Monte Carlo randomization test, 1000 simulations). †, $0.10>p>0.05$; *, $p<0.05$; **, $p<0.01$; ***, $p<0.001$

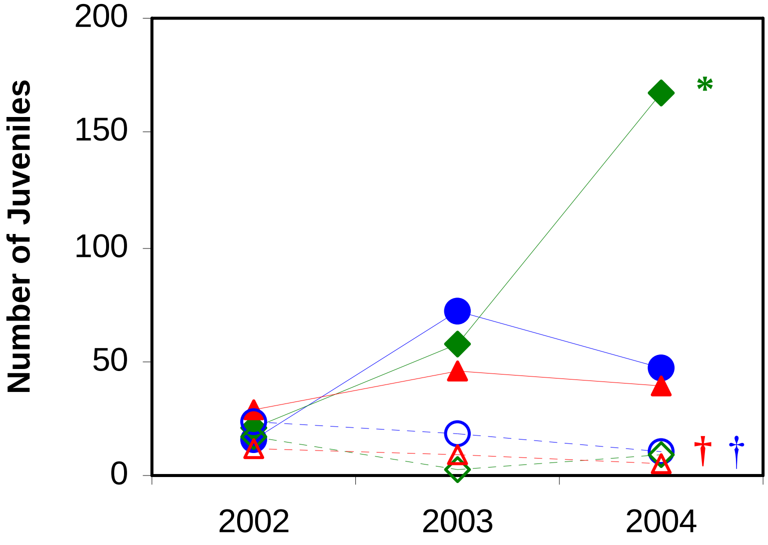

Figure 1.3. The total number of *Lespedeza cuneata* juveniles from 2002 to 2004 in response to each combination of herbicide application and mowing regime. Closed symbols (●,◆,▲) with solid lines represent unsprayed plots while open (○,◇,△) symbols with dashed lines represent sprayed plots. Points represent the mean of six plots within each treatment combination. Error bars were omitted for clarity. Blue circles (●,○) represent early mown plots; Green diamonds (◆,◇) represent late mown plots; Red triangles (▲,△) represent twice mown plots. Lines denoted by asterisk indicate treatments combinations that showed a significant change in the response between 2002 and 2004 (one-tailed Monte Carlo randomization test, 1000 simulations) †, $p<0.10$; *, $p<0.05$. The average increase in all unsprayed plots and the average decrease in all sprayed plots were both significant ($p=0.004$ and $p=0.007$ respectively).

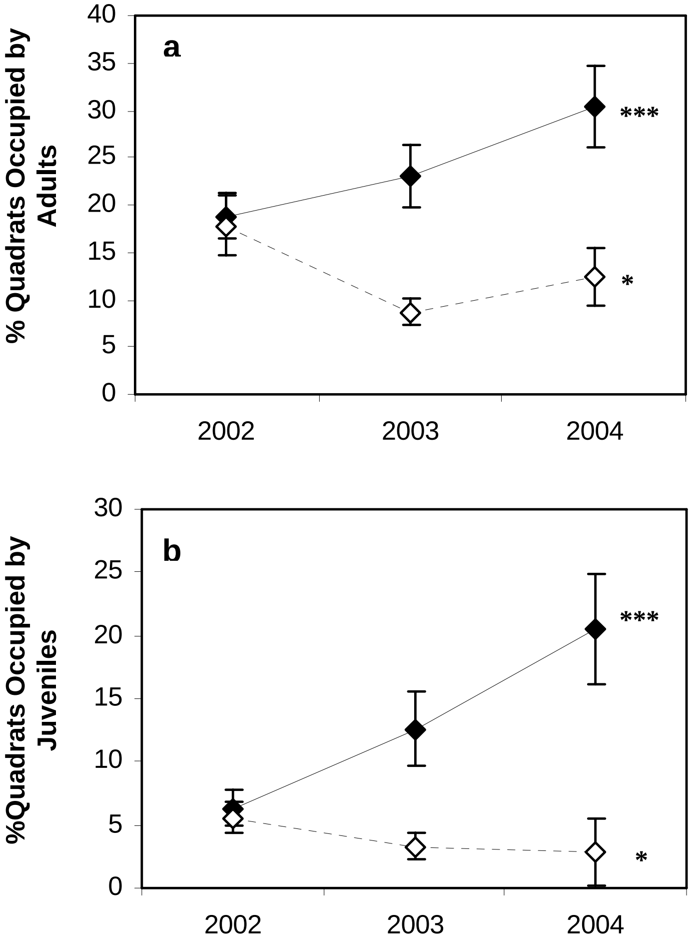

Figure 1.4. Effect of herbicide application on the percent occupancy of: a, adult and b, juvenile *Lespedeza cuneata* from 2002-2004. Points represent the mean (± 1 se) of 18 plots within each treatment condition. Closed symbols (◆) with solid lines represent unsprayed plots while open symbols (◇) with dashed lines represent sprayed plots. Lines denoted by asterisks indicate a significant change in the response between 2002 and 2004 (one-tailed Monte Carlo randomization test, 1000 simulations) *, $p \leq 0.05$; ***, $p \leq 0.001$)

Chapter 2

Quantifying and predicting the local spread of invasive plants: a case study of the exotic legume, *Lespedeza cuneata*

CHAPTER SUMMARY

Concern about the impact and spread of exotic plants has produced a growing body of knowledge about the spatial distribution of numerous species. However, while the bulk of these datasets are regional or landscape in scale, management treatments are often applied locally in an effort to reduce economic and environmental costs. I use *Lespedeza cuneata*, an invasive species in much of the North American Great Plains, to investigate how a high resolution (1-m^2), spatially-explicit data set can be used to guide management decisions at a local scale. The goals of the study were: 1) to quantify natural patterns of occupancy and aggregation in a field population, 2) to determine the herbicide effectiveness when the spatial autocorrelation of stem density is taken into account, and 3) to test how different data structures and local neighborhood information influence predictions of the occupancy and density of *L. cuneata* under managed and unmanaged conditions. Stems at the site exhibited significant spatial autocorrelation, but this did not impact the overall effectiveness of herbicide in reducing stem density. In nearly all models (both presence/absence and density-based) for predicting *L. cuneata* occupancy, the odds of colonization were low while the odds of persistence were high. However, managers using only presence/absence data to predict spread may underestimate future occupancy and the resources required to effectively manage the population. Local stem density had the greatest influence on future stem density under unmanaged conditions. The effectiveness of herbicide negated any predictive value of local density or neighbor abundance, but the fact that only low density sprayed quadrats experienced density

increases raises concerns about detectability of plants during treatment. These results, although specific to this study site, are likely to be typical of other invasive species and could provide a general approach for incorporating spatially explicit data into monitoring and management programs.

INTRODUCTION

Controlling the persistence and spread of invading plant populations is a primary concern of land managers, thereby necessitating an understanding of the spatial distribution of species. Studies of the distribution and spread of invasive plants are often conducted at landscape, county, or regional scales. These investigations have used spatially explicit data to successfully track and predict the distribution of exotic species (Lesica and Miles 2001, Pauchard et al. 2003, Peterson et al. 2003). The knowledge gained from this research has led to the implementation of an increasing number of regional and global control initiatives such as weed-free hay, cleaning agricultural equipment before using it in new areas, and restricting horticultural imports (Pauchard and Shea 2006). However, not all control measures should be applied broadly. Herbicides, for example, can be both economically and environmentally costly, prompting managers to apply them at very local spatial scales (Bussan and Dyer 1999, Clark and Wilson 2001, Shaw 2005). Spot spraying is a control method in which herbicides are precisely applied to individuals or patches of exotic plant species and can be more cost effective than broadly treating entire areas (Heisel and Walter 1999, Masters and Sheley 2001, Shaw 2005).

To understand the consequences of this control method on exotic plant populations, one must understand the local spatial distribution of the invasive species at a site. The fact that plants are rarely evenly distributed in space has long been recognized (Turkington and Harper 1979, Dale 1999). For example, populations of exotic plants often first appear at a site as either discrete patches within disturbances or as linear invasions along environmental gradients, roads, or waterways (Lesica and Miles 2001, Pauchard et al. 2003). By collecting spatially explicit data on plants at a local scale, workers can describe spatial patterns of occupancy and density within populations. This information could, in turn, guide management programs as opposed to basing decisions on the assumption that occupancy and density are evenly distributed across a site. Local-scale, spatially explicit data have, for example, aided in the development of precision agriculture (Ahrens 1994, Rew and Cousens 2001) and methods of estimating and modeling weed spread in arable fields (Marshall 1988, Dieleman and Mortensen 1999, Blumenthal and Jordan 2001).

Despite agriculture's increased use of spatially explicit data in both simulations and field experiments in recent decades, invasive plant studies involving empirically derived, spatially explicit datasets are relatively rare at the local scale. A likely cause of this discrepancy is the considerable effort required to detect and record spatially explicit data on individual species within a diverse plant community in comparison to the effort required to collect data in relatively simple crop fields. Collecting density data is also more time consuming than simply recording the presence or absence of a plant within a sampling area. Since managers of both private and public lands often lack the equipment, personnel, and financial resources to collect such highly detailed and complete datasets, it is relevant to explore how different levels of data resolution at the local scale affect our ability to understand persistence and spread of invasive plants.

Developing appropriate control practices is of current practical importance for *Lespedeza cuneata* (Dumont) G. Don. (Fabaceae). Commonly known as sericea lespedeza or Chinese bushclover, this woody perennial grows well in disturbed areas, pastures, and grasslands and has become established in at least 35 states in the U.S. ranging from the East Coast to Nebraska and Kansas and north to Minnesota (US Department of Agriculture – Natural Resource Conservation Service, 2005). To date, most studies of herbicidal control of *L. cuneata* have been performed on relatively dense, uniform stands (Altom et al. 1992, Koger et al. 2002). Further, such studies have summarized plot level abundance with no reference to how plants were distributed within the population. Though such studies can reveal changes in percent cover, they cannot test the effectiveness of control on a more patchily distributed population or whether control measures influence the spatial distribution of the plants themselves.

In a three year study, I examined both herbicide and mowing effects on juvenile and adult *L. cuneata* plants in a patchily distributed population (Chapter 1). I found that plot-level occupancy and abundance of adult individuals, adult stems, and juveniles were all lower in plots where *L. cuneata* had been sprayed, while mowing effects were minimal. For this study I conducted a complete census and recorded plant density in each 1-m^2 quadrat, yielding a spatially explicit data set for a 3456 m^2 area (48 x 72 m) with one meter resolution. This resolution was large enough to capture the pattern of aggregation but small enough to detect changes in occupancy across the field. This detailed data set provided an ideal opportunity to study the spatial structure of an economically important invasive plant at a scale relevant to a manager charged with controlling the early stages of an invasion. The objectives of this study were three-fold. The first was to describe the natural pattern of occupancy and spatial autocorrelation of stem density within a patchily distributed population of *L. cuneata* prior to any management treatment. The second objective was to determine if herbicide application effectively controlled *L. cuneata* within the field when spatial autocorrelation of stem density is taken into account. I also asked whether herbicide treatments altered patterns of occupancy and spatial distribution. The final objective was to investigate the consequences of different levels of sampling effort on short-term predictions of local occupancy and abundance. More specifically, I explored if the choice of quantitative data over binary data (density vs. presence/absence) or the inclusion of simple spatial data (in the form of neighborhood information) substantially increased our understanding of persistence and local spread of this invasive plant. These comparisons were made under both natural and managed (sprayed) conditions.

MATERIALS AND METHODS

STUDY ORGANISM

Lespedeza cuneata is a perennial, deciduous legume. Its erect, ascending stems grow to 0.5-2.0 m in height. New growth arises each year from a knobby caudex located 2.5-8.0 cm belowground. Individual plants have a single stem during the first year of growth, but this number increases with age; isolated plants with over 100 stems have been documented (Blair, 1933). *L. cuneata* plants are prolific seed producers, with each stem producing up to 1,000 seeds (Ohlenbusch and Bidwell 2001). Though the seeds have been reported to be long-lived (Ohlenbusch and Bidwell 2001), recent work suggests that current seed input has the greatest impact on abundance and density (Fechter 2003, Chapter 1). A more complete description of the species at the study site is given in the first chapter.

STUDY SITE

The field experiment was performed at Welda Prairie in Anderson County, Kansas USA. Welda Prairie is part the Anderson County Prairies, a 52 ha preserve located at the eastern extent of the Kansas Flint Hills region that is owned by The Nature Conservancy and managed by the University of Kansas. Native grasses such as *Andropogon gerardii*, *Sorghastrum nutans*, and *Panicum virgatum* dominate the prairie, but a high diversity of non-grass species such as *Amorpha canescens*, *Echinacea purpurea* and the globally threatened *Asclepias meadii* also occur at the site. Most of the Anderson County Prairies are used as native pasture and hay meadows, but there has been disturbance from agriculture and associated activities.

The study site was part of a ~1 ha area located within a matrix of high-quality prairie. The specific site has a history of disturbance and is representative of other disturbed sites within the tallgrass prairie landscape of the Eastern Flint Hills where *L. cuneata* has become established. The study site was dominated by several introduced pasture grasses such as *Agrostis stolonifera*, *Bromus inermis*, and *Festuca arundinacea* as well as a number of old field successional species such as *Ambrosia artemisiifolia*, *Helianthus annuus* and several species of *Solidago* and *Aster*.

EXPERIMENTAL DESIGN

This study utilized spatially explicit data collected as part of an herbicide and mowing experiment (see Chapter 1). Since mowing effects were not significant for adult abundance or occupancy in the earlier experiment I focus only on herbicide application in the current study. I also only used data from the annual transition when the timing of herbicide application proved to be highly effective (2002 to 2003). In overview, I established a 3456 m^2 study area in October 2001 at a site previously invaded by *L. cuneata* (Figure 2.1). The area was divided into six blocks according to distance from an access road with a large concentration of *L. cuneata*. I divided each block into six 4 x 24 m plots (36 plots total). Half of the plots in each block were randomly selected to be treated with herbicide. In mid-July 2002, I used a backpack sprayer to spot spray any *L. cuneata* plants present in the plot with a 0.26 g L^{-1} solution of metsulfuron methyl (Escort®, DuPont™ Industries) (see Chapter 1). The remaining plots were left untreated.

I performed a complete census of the field population in mid-June in 2002 and 2003. In order to more efficiently perform the censuses, I divided each 4 x 24 m plot into 96 1-m^2 quadrats, and recorded the number of adult stems within each quadrat. Data were also collected on the density of *L. cuneata* individuals, which can consist of one to many stems. However, the analyses presented here are based only on stem densities for two reasons. First, since identifying individuals can be time-consuming, most studies of the species' management are based on either stem density or percent cover. Second, preliminary analyses based on individuals gave very similar results to the analyses of stems. Note that the 2002 census was performed before any treatments were applied, thus it represents a baseline for an established but patchily distributed population.

DATA ANALYSIS

Characterizing Initial Occupancy and Spatial Distribution

I quantified the pretreatment patterns of occupancy and aggregation of stem density using the 2002 census data. Only the 44 quadrats from the central 2 x 22 m sampling area within each of the 36 plots were included in all analyses (n = 1584 quadrats); these sampling areas were the focus of previous analyses (Chapter1). I defined occupancy as the proportion of quadrats within the field that had at least one *L. cuneata* stem present and mean crowding ($\overset{*}{m}$, Lloyd 1967) as the average local density experienced by each stem in a quadrat (see Appendix for explanation of calculations of $\overset{*}{m}$). Since only occupied quadrats were included in the calculation of

m^*, this measure of aggregation was not affected by the large number of unoccupied quadrats. I refer to m^* as an "implicit" measure of aggregation because it gives an estimate of the average number of neighbors experienced by a plant, but does not account for the precise spatial location of those neighbors.

I used Mantel tests to provide another measure of spatial aggregation by determining the degree to which *L. cuneata* density was correlated across two-dimensional space (Smouse et al. 1986, Fortin and Gurevitch 2001, Rew and Cousens 2001). I considered the Mantel test an "explicit" measure of aggregation because the analysis takes the exact spatial location of each quadrat into account and explores whether quadrats that are physically close to each other are more or less similar in density compared to quadrats that are located far from each other. Specifically, the geographic position of each quadrat (i.e., spatial coordinates $\{x, y\}$) represented the distance in meters of the center of each quadrat from the origin of the 48 x 72 m field (Figure 2.1). I also tested for spatial autocorrelation of occupancy by converting the density data to presence/absence data (hereafter, PA) to simulate a reduction in sampling effort. All Mantel tests (and partial Mantel tests discussed later, which allow one to analyze effects while statistically controlling for spatial autocorrelation in the data) were performed using the 'vegan' statistical package in R$^{©}$ (version 2.4.1, R Development Core Team 2006).

Herbicide Effects on Occupancy, Density, and Aggregation

Whether a species is limited by dispersal, competition, or the distribution of available resources, it is difficult to imagine that the density of one quadrat is completely independent of nearby quadrats. For this reason, I used partial Mantel tests to determine if herbicide treatment influenced either the stem density or occupancy of *L. cuneata* (Smouse et al. 1986, Fortin and Gurevitch 2001).

I also explored the degree to which one year of herbicide application could reduce occupancy, decrease mean crowding, or break up patterns of spatial autocorrelation initially exhibited by *L. cuneata*. I first created pairs of data for three response variables; the occupancy, $\overset{*}{m}$, and Mantel's r for the 2 x 22 m sampling areas in the center of each of the 36 plots. Each data pair consisted of measurements for a variable for the same sampling area in 2002 and 2003. In order to see if a response within each treatment changed over time I used Monte Carlo simulations to randomize the paired data. For each simulation the data values from 2002 and 2003 were randomly reassigned as either first or second year values (1000 simulations). The average observed change in a response variable (final [2003] measurement – initial [2002] measurement) was compared to its average change in the simulations. Given the expectation that herbicide would decrease plant survivorship and vigor (as demonstrated in Chapter 1), all tests were done using a one-tailed alternative hypothesis. For unsprayed plots, this meant that the observed change would be greater than the simulated change; for sprayed plots, the observed change would be less than the simulated change. The p-value in each of these tests represents the proportion of simulations that did not fit the specific alternative hypotheses (Table 2.1). In both observed and simulated data, a positive change indicated an increase in the response variable and a negative change indicated a decrease in the response variable. Note that local extinction in three of the sprayed plots meant that aggregation and spatial autocorrelation could only be calculated for 15 of 18 sprayed plots in 2003.

I used correlation to determine if my implicit ($\overset{*}{m}$) and explicit (Mantel *r*) measures of spatial distribution were related. Since the ranges of values for $\overset{*}{m}$, and Mantel *r* were variable across the plots and on different scales I standardized both variables before performing the analysis (*Z*-transformation, Gotelli and Ellison 2004). In this analysis, a positive association would indicate that plots with high mean crowding also exhibit significant positive spatial autocorrelation and that this simpler, implicit measure of aggregation could serve as a reasonable proxy of a more data-intensive explicit measure of spatial aggregation. Lack of an association or a negative association would indicate that the mean crowding index, although easy to calculate, does not provide the same information as a spatially explicit measure of aggregation.

The Role of Spatial and Density Data in Predicting *L. cuneata* Persistence and Spread

In the original study I collected complete census data in a spatially explicit manner at the 1-m^2 scale. I sought to determine the degree to which such detailed data were needed to describe the local persistence and spread of *L. cuneata* in sprayed and unsprayed quadrats. To answer this question I considered two dependent variables: the quadrat-level occupancy and the density of stems of *L. cuneata* in Year$_{t+1}$ (2003). I thus used equations based on two types of statistical models. First, I used logistic regression to explore whether occupancy could be predicted equally well with binary or quantitative data from Year$_t$ (2002), and whether data from neighboring quadrats would improve predictive power. In order to perform these analyses I first converted the stem density values from the original data set into binary values (1's and 0's) to create a data set consisting only of PA data. Second, I used linear regression to evaluate the importance of stem density in Year$_t$, the potential for density dependence, and the role of neighbors in determining stem density in Year$_{t+1}$.

In all models only eight quadrats from each 2 x 22 m sampling areas in the 36 plots were included as data points in the analyses (n = 288) (Figure. 2.2). This choice maximized the sample size while ensuring that the included quadrats were neither neighbors of each other nor did they share any of their neighboring quadrats. The eight quadrats immediately surrounding a quadrat were defined as "neighbors" (Figure 2.2). In preliminary analyses using logistic or linear regression, block had no significant main effects or interactions so the term was dropped from all subsequent models. Preliminary analyses also revealed significant interactions between herbicide treatment and other model terms. Sprayed and unsprayed data were therefore analyzed separately in the final analyses. All analyses were performed using Minitab® Release 14 (Minitab, Inc.).

Predicting Occupancy

To predict occupancy in 2003 based on binary data I used logistic regression to create the following full model:

$$\Pr\left[X_{t+1}=1 \middle| X_t, Y_t\right] = \frac{e^{\beta_0+\beta_1 X_t+\beta_2 Y_t}}{1+e^{\beta_0+\beta_1 X_t+\beta_2 Y_t}} . \qquad \textbf{\textit{Equation 2.1}}$$

In this model the probability that *L. cuneata* will be present in a quadrat in 2003 (i.e., $X_{t+1} = 1$) is a logit function of its occupancy state in 2002 (X_t) and the number of neighboring quadrats that were occupied in 2002 (Y_t).

To predict occupancy in 2003 based on quantitative data I used the same model as in Equation 2.1 above. However, in the quantitative model the probability that *L. cuneata* will be present in a quadrat in 2003 is now a logit function of its own 2002 stem density (X_t) and the total number of *L. cuneata* stems in the neighboring quadrats in 2002 (Y_t).

The selection procedure was the same for both models and followed the general procedure of Quinn and Keough (2002). Deviance (G) represents the degree to which a model varies from the null hypothesis (H_0: all model coefficients are equal to zero; $\beta_0 = 0 \ldots \beta_n = 0$) and provided a method of determining model fit during the selection process. After the full model was run the p-values for all terms were compared, and the term with the highest p-value was dropped. The G and degrees of freedom of the resulting model were then compared to those of the full model, and a Chi-square test was used to determine if the change in G was significant. If so, the dropped term was included in the final model. If the change in G was not significant then the term was permanently dropped. The new model would then become the reference, and the selection process continued. I use the term “persistence” to describe cases where a quadrat occupied in 2002 remained occupied in 2003 and “colonization” to describe cases where an unoccupied quadrat from 2002 contains at least one *L. cuneata* stem in 2003.

Predicting Density

To predict abundance in 2003 I used linear regression and created the following full model:

$$X_{t+1} = \beta_0 + \beta_1 X_t + \beta_2 X_t^2 + \beta_3 Y_t + \varepsilon \ . \qquad \textbf{\textit{Equation 2.3}}$$

In this model the density of *L. cuneata* within an occupied quadrat in the second year of the transition (X_{t+1}) is determined by its density in 2002 (X_t) and the total abundance in the neighboring quadrats in 2002 (Y_t). Work on the species as a forage plant has indicated that growth and local spread may be slower in dense stands (Hoveland and Donnelly 1985). I explored the possibility of density-dependence by including a quadratic term for local density in the model (X_t^2).

After the full model was run, the *p*-values for all terms were compared. I then reran the model after dropping the term with the highest *p*-value. I first calculated the difference between the sums of squares of the regression terms in subsequent models (i.e., $SS_{extra} = Full\ SS_{reg} - Reduced\ SS_{reg}$). I used an *F* test to determine if the change in the variation explained by regressions relative to the residual variation of the full model was significant. If so, then the dropped term was included in the final model. If the change was not significant, then the term was permanently dropped. The selection process continued, using the new model as a reference (Quinn and Keough 2002).

RESULTS

HERBICIDE EFFECTS ON OCCUPANCY, DENSITY, AND AGGREGATION

With only 18% of the quadrats occupied in 2002, the pre-treatment distribution of stem density across the field was strongly right skewed (Figure 2.3, white bars); both occupancy ($r = 0.048$, $p \leq 0.001$) and density ($r = 0.023$, $p \leq 0.05$) exhibited significant positive spatial autocorrelations within the field (Figure 2.1). The random assignment of herbicide treatment, by chance, meant that sprayed plots had fewer quadrats with more than twenty stems in 2002 (prior to treatment) compared to the unsprayed plots (Figure 2.1; Figure 2.3, white bars). However, the effect of spraying on 2003 densities was dramatic: in plots where *L. cuneata* had been sprayed, 2003 stem numbers per quadrat were greatly reduced (Figure 2.3b). In contrast, increases in stem density among the unsprayed quadrats resulted in a larger number of quadrats with more than five stems and a slight flattening of the tail of the 2003 distribution compared to that of 2002 (Figure 2.3a). The Monte Carlo simulations indicated that occupancy and mean crowding increased in the unsprayed plots, and both variables decreased in the sprayed plots from 2002 to 2003 (Table 2.1). Spatial autocorrelation, however, did not significantly change under either treatment (Table 2.1). Partial Mantel tests further revealed that quadrat-level changes in both stem density ($r = 0.0112$, $p < 0.001$) and occupancy ($r = 0.0134$, $p < 0.001$) between 2002 and 2003 were significantly reduced by spraying even after controlling for spatial autocorrelation. These changes can be most easily interpreted by comparing the large differences in frequency distributions of stem density over the 2002-2003 time period for the two treatments (Fig. 2.3).

Spatial autocorrelation (Mantel *r*) and stem mean crowding ($\overset{*}{m}$) were significantly positively correlated across plots in the pretreatment year (2002; $r = 0.4246$, $p < 0.05$). Though the unsprayed plots showed no significant change in their degree of spatial autocorrelation between 2002 and 2003, the sprayed plots had a tendency ($p = .119$) towards a decline in spatial autocorrelation (Table 2.1). The net result was that in 2003, spatial autocorrelation and mean crowding were still positively correlated across the unsprayed plots ($r = 0.6580$, $p \leq 0.01$) but were negatively correlated across plots where *L. cuneata* was sprayed ($r = -0.6003$, $p \leq 0.05$).

THE ROLE OF SPATIAL AND DENSITY DATA IN PREDICTING *L. CUNEATA* PERSISTENCE AND SPREAD

Predicting Occupancy

The full logistic regression model for predicting *L. cuneata* occupancy based on PA data included terms for a quadrat's occupancy in the previous year as well as the occupancy of its neighboring quadrats in the previous year (Equation 2.1). This full model provided the best fit for predicting occupancy in the unsprayed quadrats (Table 2.2, Figure 2.4a). The odds of *L. cuneata* being present in a quadrat in 2003 were 10.5 times higher if it was previously occupied compared to if it had been unoccupied in 2002 (Table 2.2). In the model of the sprayed quadrats the probability that *L. cuneata* would be present was affected only by whether it was present in the previous year (Table 2.2, Figure 2.4b). Similar to the unsprayed quadrats, the odds of *L.*

cuneata persisting in a previously occupied quadrat were 13.8 times higher than the odds that it would colonize an empty quadrat.

The full model for the density-based analyses included three terms describing a quadrat's condition in the previous year: *L. cuneata* density within the quadrat, number of neighboring quadrats occupied by *L. cuneata*, and the total number of *L. cuneata* stems present in neighboring quadrats (Equation 2.2). The models selected for the density-based data again differed for each herbicide treatment. For unsprayed quadrats the probability of *L. cuneata* presence increased with their *L. cuneata* density in the previous year and with the previous total number of stems present in the neighboring quadrats (Table 2.2). More specifically, the odds of *L. cuneata* occupying a quadrat in 2003 increased 1.84 times with each additional stem present in that quadrat in 2002 and 1.16 times for each additional stem present in neighboring quadrats in 2002 (Table 2.2, Figure 2.4c). The probability that *L. cuneata* would be present in sprayed quadrats was only affected by their own stem density levels and not by the abundance of *L. cuneata* in neighboring quadrats (Table 2.2, Figure 2.4d).

The R^2 values from the models predicting *L. cuneata* occupancy in the sprayed quadrats were consistently lower than those predicting occupancy in the unsprayed quadrats (Table 2.2). When *L. cuneata* was left unsprayed, the fit of the PA-based model was nearly identical to that of the density-based (57.9% and 59.9% respectively). In contrast, when spot spraying was applied, the R^2 values were low (16.7% vs. 6.1%) with the PA-based model providing a somewhat better fit than the density-based model.

Predicting Density

The full linear model for predicting *L. cuneata* stem density included terms for a quadrat's density in 2002 (X_t) as well as the total stem abundance in neighboring quadrats in 2002 (Y_t) (Equation 2.3). When *L. cuneata* was not spot sprayed with herbicide, the local stem density within a quadrat in 2002 and the total number of stems in neighboring quadrats in 2002 both significantly predicted density in 2003 (Table 2.3, Figure 2.5a). The small but significant quadratic term reflects the fact that increases in local density were smaller in quadrats where stem density was already high (Figure 2.5a). Under sprayed conditions, the local 2002 density significantly affected the 2003 density (Table 2.3, Figure 2.5b). Quadrats with both the lowest and highest densities in 2002 exhibited the greatest declines by 2003, leading to a small but significant quadratic term (Figure 2.5b). The fit of the models for predicting density in control and sprayed quadrats were strikingly different. While the selected model for the unsprayed quadrats explained over 90% of the variation in 2003 density, less than 10% of the variation in 2003 stem density was explained by the model for the sprayed quadrats (Table 2.3).

DISCUSSION

SPATIALLY EXPLICIT DATA OF EXOTIC PLANTS AND RELEVANCE TO MANAGEMENT

Given the sheer numbers of invasive plant species, it is not surprising that quantitative data on spatial distributions is challenging to obtain. Despite this challenge, a growing body of literature describes species distributions at county (Silliman and Maccarone 2005), regional (Pande et al. 2007, Sanchez-Flores 2007) and national scales (Hooftman et al. 2006, Zhu et al. 2007, Cook et al. 2008). To my knowledge however, this is the first spatially explicit data set of *L. cuneata* at the resolution of 1 m^2; and few studies include data sets at this resolution for other exotic plants (but see Theoharides and Dukes 2007 and Pyšek et al. 2008 for exceptions). Since land managers often work with populations at small spatial scales, basic knowledge of the local patterns of persistence and spread are needed. Therefore, the overall goal of this study was to use a fine-scale, spatially explicit data set to better understand the population spread of an invasive species and explore how local occupancy and abundance could provide useful insights on management.

Lespedeza cuneata is a major threat to pastures, native rangeland, and prairies in a large portion of the North American Great Plains (USFWS 2004). In Kansas alone, more than 200,000 ha are infested in 73 counties (Gordon 2003). Locally scaled management treatment such as spot spraying is often the primary method of control for this species even in broad areas deemed to have high levels of landscape-level infestation (Obermeyer et al. 2001, Silliman and Maccarone 2005). Earlier work has shown that herbicide can reduce *L. cuneata* density and percent cover

(Jordan and Jacobs 2002, Jordan et al. 2002, Stevens 2002, Koger et al. 2002, Brandon et al. 2004, Kansas Department of Agriculture Plant Protection and Weed Control Program 2004). This study (and Chapter 1) confirmed the successful control of the species by herbicide, and by using spatially explicit datasets, analyses presented here emphasize that this result is not affected by the spatial autocorrelation of plant variables.

In addition to decreasing occupancy and local stem density, spot spraying also decreased the level of aggregation in the plots. This tendency was found with two very different statistical methods (mean crowding vs. Mantel's *r*), although the difference in statistical significance between the two methods emphasizes the need for caution in interpreting statistics on aggregation. However, in general, it appears that aggregation was reduced by herbicide treatment, primarily by lowering the variation in stem density among occupied quadrats. The net, qualitative result is that while quadrats with similar densities maintained a close association across space under natural conditions, this relationship appeared to break down when herbicide was applied.

PREDICTING LOCAL OCCUPANCY AND DENSITY OF EXOTIC PLANTS

Despite the attention that *L. cuneata* has recently received as an invasive species, only 17 out of 70 studies conducted on it in the last decade address either its spread or its impact on native communities (search of *Lespedeza cuneata* in BioAbstracts, January 1997 - December 2007. Of these 17 studies, only six included spatially explicit data, and only one was conducted with local scale resolution (≤1 m). My high resolution, spatially-explicit data set thus offers a unique opportunity to address two key questions pertaining to predictions of occupancy and density of *L. cuneata* under managed and unmanaged conditions: 1) what are the relative values of different data structures in making predictions, and 2) to what degree can local neighborhood information affect predictions? Addressing these questions is an important step towards the design of *L. cuneata* monitoring and management programs, but it also suggests a way to examine spatially explicit data for invasive species in general.

Natural Conditions (Unsprayed)

Under natural conditions, two results were common to both the PA- and density-based models predicting the local occupancy of *L. cuneata*. First, the odds of colonization are low relative to the probability of persistence. Second, the probability of local occupancy significantly increases with presence and/or abundance of *L. cuneata* in neighboring quadrats. Further, it is noteworthy that the range of colonization probabilities for the PA- and density-based models (Figures 2.4a & c, broken lines) were similar, and colonization was consistently influenced by the state of *L. cuneata* abundance in neighboring quadrats (occupancy in the PA-based model and the total number of stems in the density-based model). Though the range of persistence probabilities under natural conditions were also comparable for both models (Figures2.4a &c, solid lines), a closer inspection of the probability distributions reveals important differences. When *L. cuneata* is absent in neighboring quadrats (i.e., occupied neighbors in 2002 = 0), the selected PA-based model gives a single persistence probability of 57% (Figure 2.4a), but the probability of persistence is variable when density is used as a predictor (Figure 2.4c). For example, the selected density-based model predicted that 5-25% of quadrats with relatively low densities (1-4 stems m^{-2}) would persist when neighboring quadrats were empty; but more than half of the quadrats ≥6 stems m^{-2} were predicted to persist (Figure 2.4c).

In models where stem density was the predicted response, nearly every quadrat experienced an increase in local density under natural conditions (Figure 2.5a). The minor density dependence indicated by the model did not lead to any predicted decreases in local density. In fact, the significance of the quadratic term disappeared when the two quadrats with the highest stem densities in 2002 were dropped from the analyses (data not shown). In order to more rigorously test for density dependence, future research needs to include a wide range of local densities that are well represented across the study area.

Taken together, this approach for predicting *L. cuneata* occupancy and density under natural conditions could allow managers to assess the risk of spread if a population is left untreated. However, if my results are typical of *L. cuneata* infestations, the low resolution of PA data could cause problems. For example, if management plans for a field with even moderate levels of infestation (i.e., scattered areas of 4-6 stems m^{-2}) are based on PA data then persistence will likely be grossly underestimated. Conversely, PA data will likely overestimate persistence in areas with local densities of 1-3 stems m^{-2}. Thus, the materials budgeted to control the projected populations would fall short of what would be needed, highlighting the importance of basing even short term decisions on quantitative data.

Managed Conditions (Spot sprayed)

Models for predicting *L. cuneata* occupancy under managed conditions (i.e., spot spraying) retained fewer terms than the corresponding models of *L. cuneata* occupancy in unsprayed quadrats. The only terms that were retained were local occupancy in the PA-based model and local density in the density-based model. Similarly, in the model where stem density was the predicted response, only terms describing local density remained in the model. The poor model fits for predictions of both occupancy and density (indicated by consistently low R^2 values) suggest that the effectiveness of spot spraying essentially negates the predictive value of variables describing the previous year's pre-treatment patterns in population occupancy and density.

Perhaps the most curious result is the small but significant quadratic term selected in the model for predicting stem density in sprayed quadrats (Figure 2.5b). Though a large proportion of quadrats with at least six stems m^{-2} experienced reductions in stem density, these decreases were greatest in plots with the highest stem density in 2002. It is also noteworthy that the only quadrats to experience increases in stem density between 2002 and 2003 were those that had six or fewer stems in 2002. At least two explanations could account for this pattern. The first is simply numerical; that large reductions in density can only occur where large numbers occur in the first place. The second explanation highlights a key potential problem: management practices are only as effective as the ability of workers to detect and treat areas of infestation. This issue of "detectability" is an important reason why eradication is so difficult, particularly when applying control treatment to individual plants. One might expect, for example, that areas of high stem density are likely to receive greater attention and effort than patches with only a few, scattered stems. In my field work (Chapter 1), I attempted to find and treat all plants equally regardless of their location in the field. It is conceivable, however, that some plants located in quadrats with low densities were not found and treated (and thus persisted) while all plants found in high density quadrats were treated (and either died or experienced a reduction in stem number). More controlled experiments will need to be conducted in order to determine the effectiveness of spot spraying in known patches with a range of densities. Another approach would be to use simulations to test how detectability could influence the longer-term control on *L. cuneata*. The highlighting of potential detectability problems, as well as the analysis of predictive models and the tests of potential density-dependence, illustrate the value of multi-year spatially explicit data sets in studies of the ecology and management of exotic plants.

Table 2.1. Changes in *L. cuneata* following one year of spraying. Observed change represents the average difference in plot level occupancy and two measures of aggregation (mean crowding, and autocorrelation) between the 2002 and 2003 censuses. Simulated change represents the average difference between 1000 Monte Carlo simulations of paired data. Census data for 2002 and 2003 were paired according to plot and were randomly categorized as initial or final census during each simulation. For both the observed and simulated data a positive change indicates an increase in the response while a negative change indicates a decrease. The one-tailed alternative hypothesis (H_A) is given for each response. The p-values represent the proportion of simulations that fit the null hypothesis for each test.

		Observed Change		**Simulated Change**			
	n	**Mean**	**s.d.**	**Mean**	**s.d.**	**H_A**	**p**
Occupancy							
Unsprayed	18	0.0429	0.0608	-0.0006	0.0172	OBS ≥ SIM	0.002
Sprayed	18	-0.0909	0.1180	0.0006	0.0350	OBS ≤ SIM	0.000
Mean Crowding							
Unsprayed	18	7.0001	9.8926	0.0873	2.8018	OBS ≥ SIM	0.000
Sprayed	15	-10.1314	18.3521	0.1887	5.3565	OBS ≤ SIM	0.009
Autocorrelation (Mantel's *r*)							
Unsprayed	18	0.0007	0.0437	0.0003	0.0101	OBS ≥ SIM	0.468
Sprayed	15	-0.0353	0.1043	-0.0007	0.0277	OBS ≤ SIM	0.119

Table 2.2. Results for the selected logistic regression models of *Lespedeza cuneata* occupancy based on either presence/absence data or abundance data from 2002. The response in each model is the probability that a quadrat is occupied in 2003. This response is based on the parameters that describe that quadrat in 2002. Parameters are described further in Equations 2.1 and 2.2 as well as in the accompanying text.

Occupancy Prediction Models

Presence/Absence Data	**Coeff**	**SE**	**p**	**Odds Ratio**
Unsprayed				
Constant	-3.0218	0.4611	≤ 0.0001	
*Local Occupancy**	3.3138	0.7602	≤ 0.01	10.5
Occupied Neighbors†	0.8977	0.2390	≤ 0.0001	2.4
$G = 84.109$	$R^2 = 57.9\%$			
Sprayed				
Constant	-3.3142	0.5090	≤ 0.0001	
*Local Occupancy**	2.6210	0.6396	≤ 0.0001	13.8
$G = 19.006$	$R^2 = 16.7\%$			

Density Data	**Coeff**	**SE**	**p**	**Odds Ratio**
Unsprayed				
Constant	-2.6978	0.3856	≤ 0.0001	
*Local Density***	0.6087	0.1895	≤ 0.001	1.84
Neighbor Abundance‡	0.1450	0.0389	≤ 0.0001	1.16
$G = 86.877$	$R^2 = 59.9\%$			
Sprayed				
Constant	-2.4243	0.3085	≤ 0.0001	
*Local Density***	0.0398	0.0175	≤ 0.05	1.04
$G = 5.474$	$R^2 = 6.1\%$			

* Presence of absence of *L. cuneata* in a quadrat.
† The number of neighboring quadrat with at least one *L. cuneata* stem.
** The number of stems present in a quadrat.
‡ The total number of stems in neighboring quadrats.

Table 2.3. Results for the selected linear regression models for prediciting 2003 *Lespedez cuneata* density based on density data from 2002. The response in each model is the 2003 quadrat stem density; predictor variables relate quadrat parameters in the 2002. Parameters are described further in Equation 2.3 and the accompanying text.

Density Prediction Models

	Coeff	SE	T	p
Unsprayed				
Constant	-0.4630	0.6397	-0.72	n.s.
Local Density	1.6924	0.0988	17.13	≤ 0.0001
(*Local Density*)^2	-0.0066	0.0010	-6.75	≤ 0.0001
Neighbor Abundance	0.7523	0.3010	2.50	≤ 0.05
$F_{3, 140} = 445.19$**** $R^2 = 90.3\%$				
Sprayed				
Constant	0.2969	0.1880	1.58	n.s.
Local Density	0.1744	0.0467	3.74	≤ 0.0001
(*Local Density*)^2	-0.0019	0.0006	-3.09	≤ 0.01
$F_{2, 141} = 7.78$**** $R^2 = 8.7\%$				

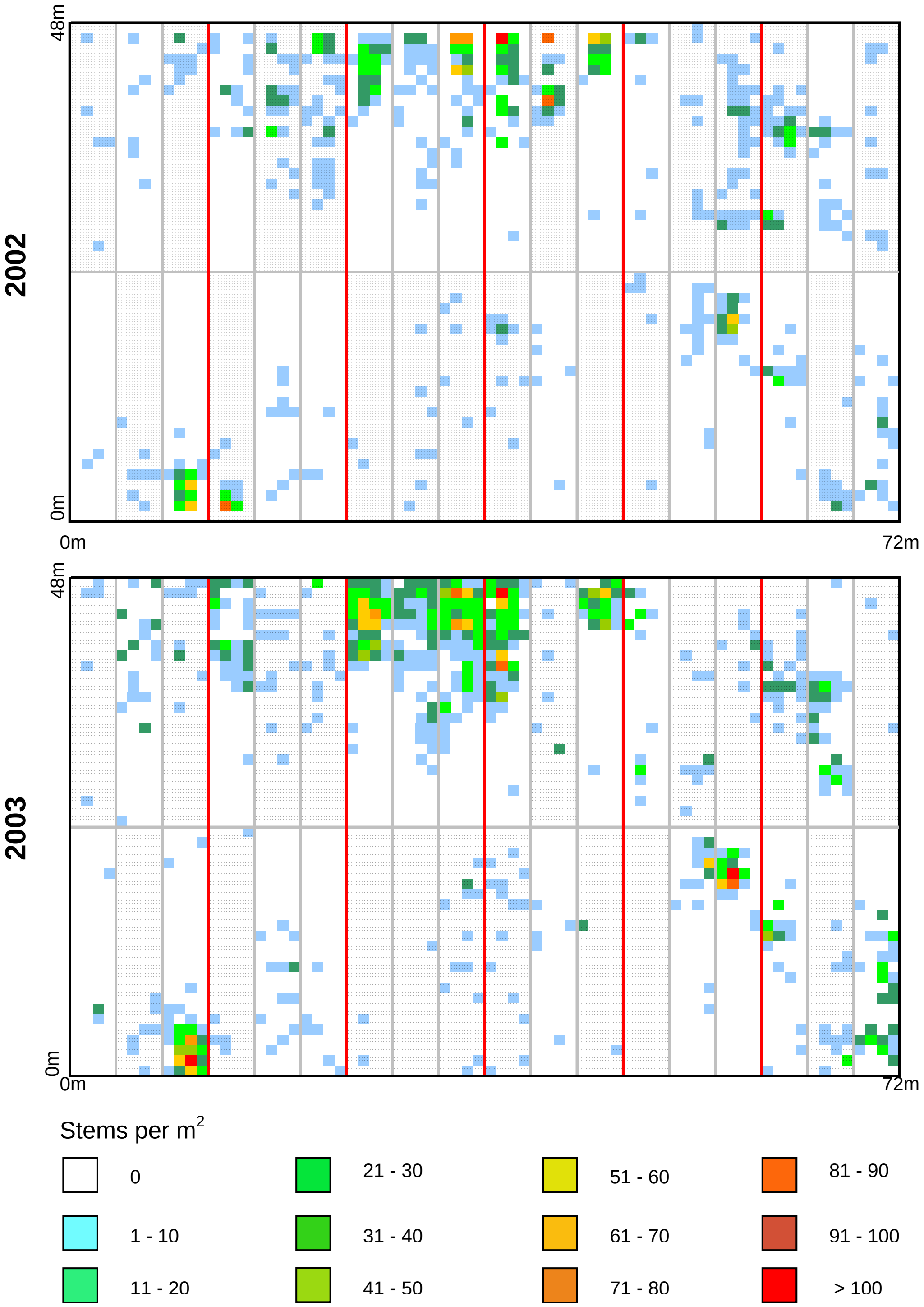

Figure 2.1 Density map of adult *Lespedeza cuneata* stems in the plots. Stippled areas represent plots where *L. cuneata* was spot sprayed in 2002 and 2003. Small squares within each plot are 1-m^2 quadrats and are color coded according to density. The red lines in each map denote boundaries between the experimental blocks.

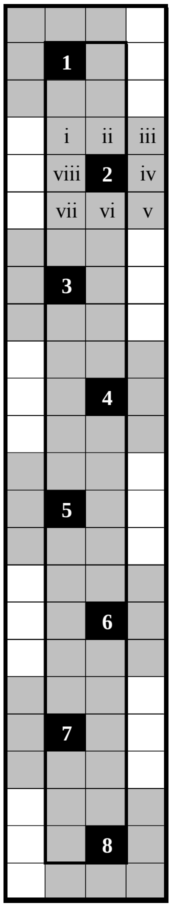

Figure 2.2. Sampling scheme for collecting the data used in the logistic and linear regressions that modeled *Lespedeza cuneata* presence/absence or density in a quadrat based on its initial state and the initial state of its neighboring quadrats. The figure depicts one of the 96-m^2 plots (out of a total of 36 plots, 18 of which were sprayed and 18 unsprayed). The black quadrats (1-8) represent the individual quadrats for which presence/absence was predicted in the models. The shaded quadrats (i-viii) are the neighboring quadrats from which data were collected. Note that no neighbors were shared between quadrats and that all quadrats within a plot were subjected to the same herbicide treatment.

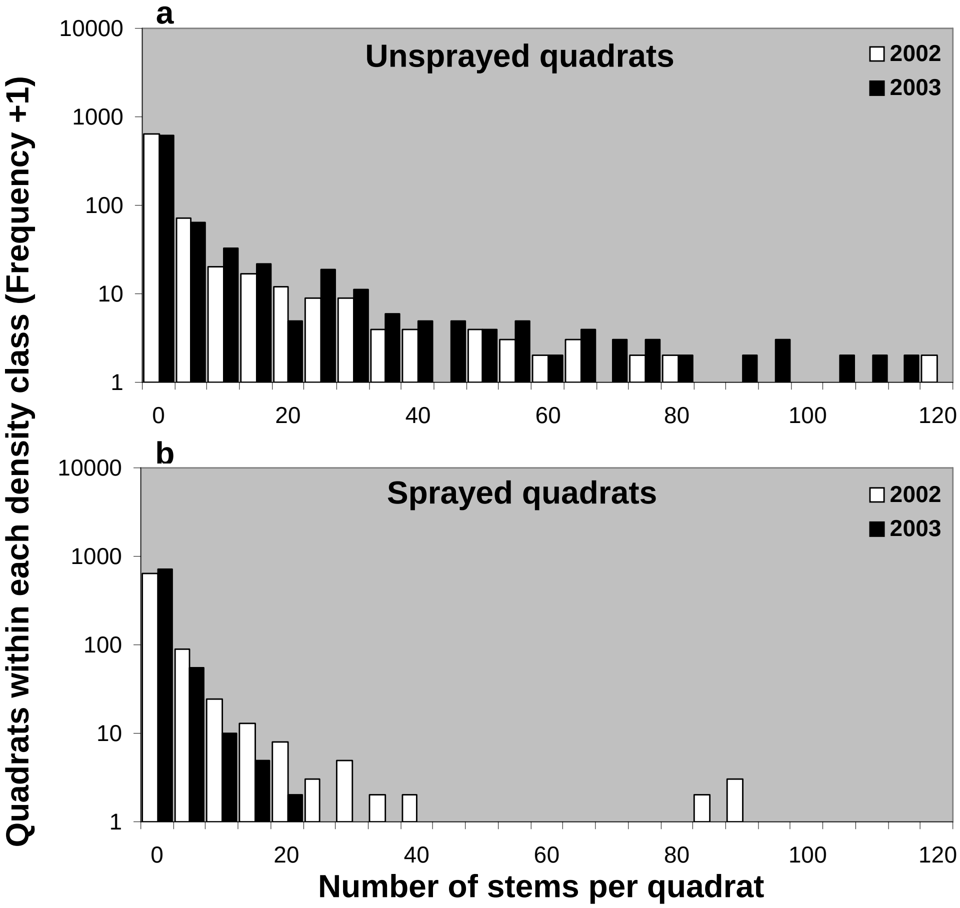

Figure 2.3. Frequency distributions of *Lespedeza cuneata* stem density within quadrats in 2002 and 2003. Unsprayed quadrats (a) were located in plots that were kept under natural conditions. Sprayed quadrats (b) were located in plots in which any existing *L. cuneata* plants were spot sprayed. In each figure, white bars represent pre-treatment conditions; black bars represent the population after one year of treatment. Density classes are 0, 1-5, 6-10, 11-15…116-120). Note that frequency is presented along a logarithmic scale due to the large number of unoccupied quadrats.

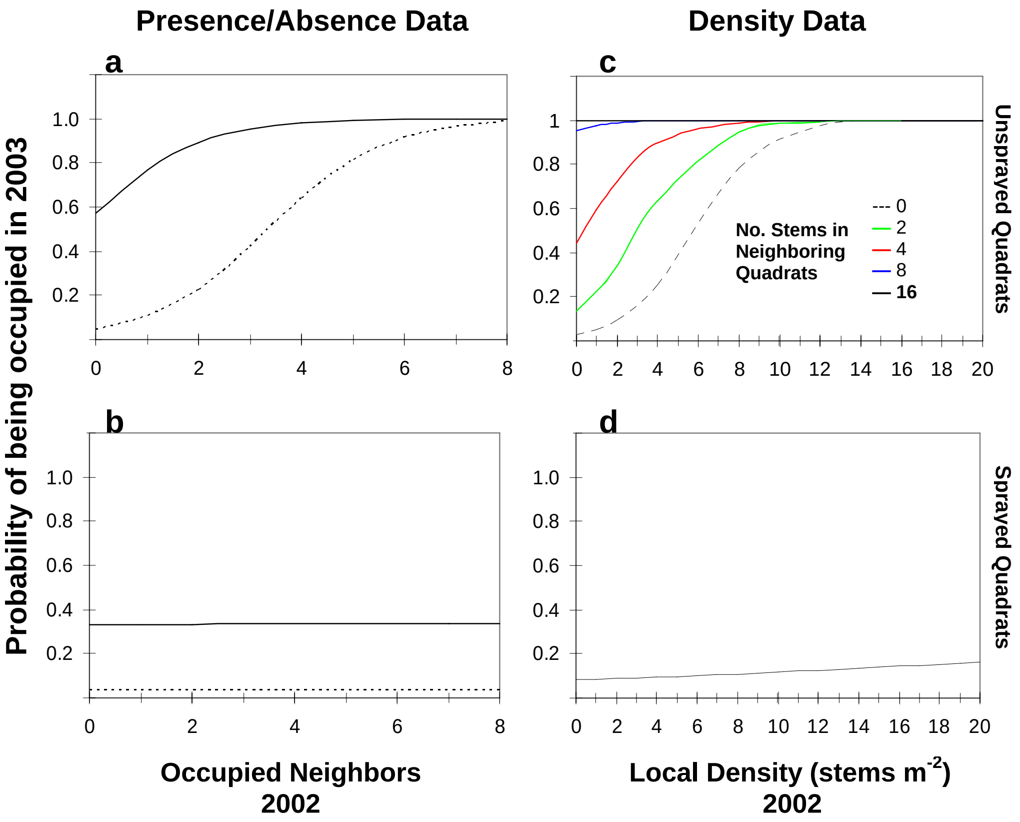

Figure 2.4. Fitted probability distributions for the logistic regression based on the models in table 2.2. Graphs on the left (a & b) represent models derived using presence/absence data (i.e., binary data); graphs on the right (c & d) represent models derived using density data. The upper and lower graphs show the fate of quadrats in which *Lespedeza cuneata* was either unsprayed vs. sprayed respectively. The lines in each graph represent the probability predicted by equation 2.1 that a quadrat is occupied by *L. cuneata* in the second year (X_{t+1}) based on both its own conditions and the condition of its neighboring quadrats in the first year (X_t and Y_t respectively). In presence/absence graphs (a & b), solid lines (—) represent model predictions for when *L. cuneata* was present in 2002 (persistence, $X_t \geq 1$) while dashed lines (---) lines represent model predictions for previously unoccupied quadrats (colonization, $X_t=0$). In the density-based models (c & d), the y-intercept (local density [X_t] = 0) represents the probability of colonization: and the probability of persistence is depicted by points along the curves where local density in 2002 is greater than zero($X_t > 0$). Note that in the density-based models, the 2003 occupancy of unsprayed quadrats (c) was determined by neighbor abundance as well as by local density while the 2003 occupancy of sprayed quadrats (d) was only influenced by local density.

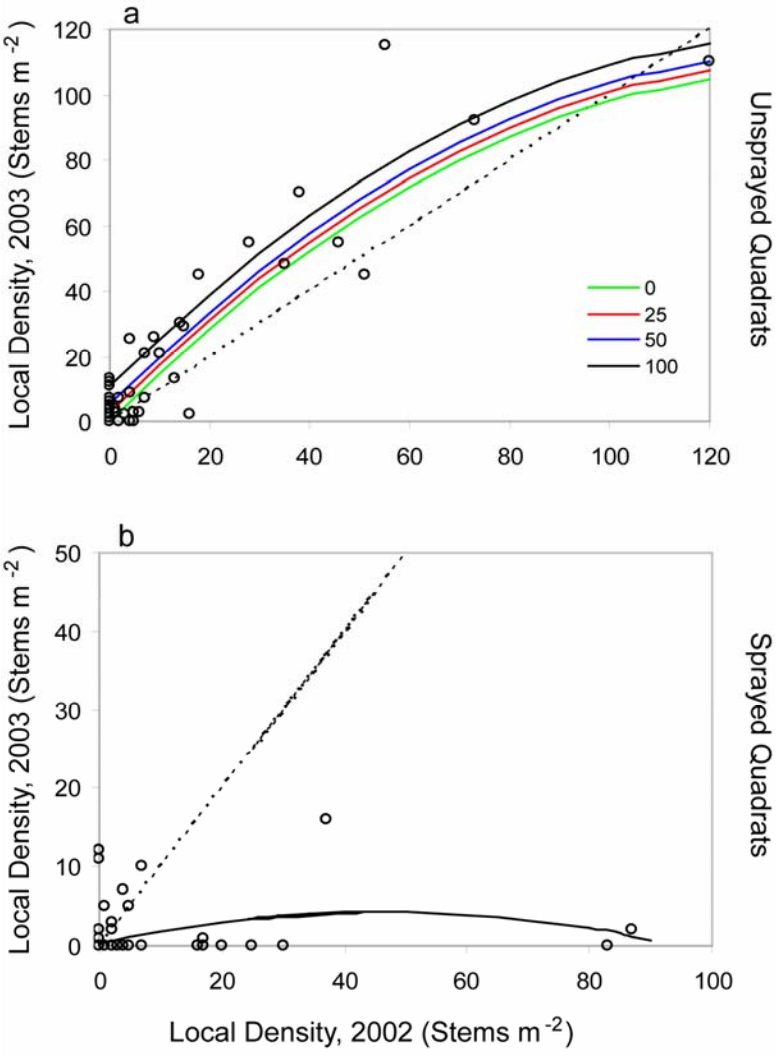

Figure 2.5. Observed data and fitted polynomial regressions for reduced models of *Lespedeza cuneata* stem densities presented in table 2.3. The data points (○) in each graph represent the observed density values for individual quadrats. In both graphs the solid lines represent predicted *L. cuneata* density for 2003 based on 2002 density. Note that total stem abundance in neighboring quadrats was also included as a model term in predicting stem density in unsprayed quadrats (a). In both graphs, the dashed line represents the one to one relationship of initial and final density. Points above the dashed line represent quadrats where density increased from one census to another while points lying below the line represent quadrats where density decreased.

Chapter 3

Modeling the local spread of invasive plants: importance of including spatial distribution and detectability in management plans

CHAPTER SUMMARY

The success with which locally applied treatments control exotic weeds depends on workers' abilities to find and treat all plants within infested sites; detectability, in turn, is likely to depend on the spatial distribution of plants. Using the exotic legume *Lespedeza cuneata* as a model, I developed a simulation program to examine how treatment intensity, local spatial distribution, and detectability of stems within a field could influence the overall effectiveness of control efforts. When left untreated, occupancy and abundance were higher in fields with randomly distributed infestations than fields with patchily distributed populations. Control treatments slowed these increases, but only the most intense treatments actually reduced both occupancy and abundance. Detectability had the greatest influence on the overall effectiveness when treatment intensity was low; indicating that intensive control could maintain populations even if workers fail to find and treat all patches in a single year. In actual infestations, however, changes in annual budgets may lead to variable treatment intensities, and reduce the overall effectiveness of control. In these situations, managers should consider utilizing multiple observer surveys to quantify the probability of detection of individual plants by field workers, and develop maps of plant locations to maximize detection from year to year.

INTRODUCTION

Exotic plants that have invaded native communities are a major ecological and economic concern. They have been shown to outcompete native plant species (Brandon et al. 2004), alter nutrient cycling (Ehrenfeld 2003), and influence burn intensity (Prater et al. 2006). These effects in turn lead to declines in the diversity of indigenous plants in natural habitats (Price and Weltzin 2003) and reductions in forage quality in rangeland habitats as well as in native hay meadows (Masters and Sheley 2001). Effective control strategies must therefore be developed to manage populations of particularly problematic species before they negatively impact native plant communities. At least three issues need to be considered in any management program: 1) the effectiveness of the treatment in controlling the target species (= treatment intensity), 2) the spatial distribution of the population to be treated, and 3) how easily the target species can be found (= detectability) and treated.

A typical management treatment is designed to reduce the population density of an exotic plant by lowering the reproduction and/or survival of individuals (Sheley et al. 1999, Masters and Sheley 2001, Kluth et al. 2003, Barney et al. 2005). The first consideration in management is, therefore, to determine how effective a given treatment is at reducing plant density in the area to which it is applied. Treatment measures can be applied to an entire site as is the case with burning, mowing, and broadcast herbicide applications. More localized management practices such as spot spraying and hand pulling, however, treat exotic plants but leave the rest of the habitat untreated. Both approaches are likely to meet with varying levels of success depending on the effectiveness of the treatment itself. For ecological and economic reasons, management treatments that target only the exotic plants are preferable in cases where the invading population has not become completely dominant (Humston et al. 2005, Shaw 2005)

The spatial distribution of the exotic plant in the invaded habitat also has important effects on management. Habitat heterogeneity across space and limited dispersal distances mean that most plant populations have locally patchy spatial distributions (Shaw 2005, Lawes et al. 2006). Populations with true random dispersion are rare in nature, but some populations' distributions may be indistinguishable from random (Grieg-Smith 1979). Such a distribution could occur for exotic plants if, for example, seed from invasive species occur as contaminants in seed mixes. Random spatial distributions also serve as a null model for comparison to patchy and even distributions (Dale 1999). Numerous studies have documented the importance of spatial distribution in determining the dynamics of population growth and persistence. For example, small patches commonly found in randomly distributed populations can confer a high potential for growth and spread (Moody and Mack 1988) but may also be more susceptible to stochastic events that increase the probability of local extinction (Lawes and Grice 2007). In patchy populations, propagules can disperse between areas within a single patch or between closely spaced patches, thereby reducing the chance that a stochastic event will result in local extinction (Humston et al. 2005, Jäkäläniemi et al. 2005). Finally, while patchily distributed populations are amenable to targeted treatment applications such as hand pulling and spot spraying, random or uniform distributions may be more efficiently managed with broad-scale treatment options such as mowing or broadcast spraying.

If individual exotic plants are the focus of management (as opposed to broadcast treatments applied to whole fields), the ability of field workers to literally "find" the problem species is a third consideration in management planning. Since plants are sessile, researchers often assume all plants can be detected. However, the combination of cryptic or small plants and dense vegetation structure may make it difficult to detect and treat all invasive plants at a site. Rates of detection of individual plants can be less than 1 due to observer error, dormancy, or herbivory (Shefferson et al. 2001). Such incomplete detection can lead to biases in estimation of population size, vital rates, or rates of population extinction (Alexander et al. 1997, Kéry and Gregg 2003, Kéry 2004, Kéry et al. 2005, Shefferson 2006). Several factors could determine whether or not an exotic plant or patch is detected. The most obvious of these are species-specific characteristics of the plants themselves such as size, distinctive features, and color. Further, the size and density of plant patches are also likely to be important, with plants in large and/or dense patches having a higher likelihood of detection than plants in small patches (Williams and Hunt 2002, Kéry 2004, Brown and Noble 2005, Casady et al. 2005). The spatial distribution of plants is thus crucial in determining the success with which exotic plants are detected and treated.

It would be difficult to develop experimental approaches to jointly explore how treatment effectiveness, spatial distribution, and detectability influence exotic weed management. However, these factors can be incorporated into simulation models. Several workers have used simulation models to develop targeted control strategies that reduce the persistence and spread of an exotic plant species (Wadsworth et al. 2000, Buckley et al. 2004, Grevstad 2005, Cacho et al. 2006, Provencher et al. 2007). Although theoretical (Moody and Mack 1988, Higgins and Richardson 1996) and empirical (Humston et al. 2005) work have addressed how the spatial distributions of weed populations can influence their persistence and spread, few workers have incorporated this concept into either field experiments or models of exotic plant management/control (but see Wadsworth et al. 2000 and Grevstad 2005). Further, to my knowledge, models of exotic plant management assume that all plants in the population are easily seen and thus treated. If only a portion of the plants in a population are detected when control strategies are implemented, however, then the potential for the population's persistence and spread is obviously greater than when all existing patches are found and treated.

The goal of this study was to use a simulation model to examine how treatment effectiveness interacts with the initial spatial distribution of a population and the detectability of individual plants to determine the abundance and spatial extent of an invasive plant. My model focuses on locally applied treatments (for example, mechanical removal of plants or spot-spraying with a short lasting herbicide), since detection is not an issue with broadcast treatments. Although the questions I address are general in nature, I based the model on the biology of an actual exotic plant to ensure that the initial populations would have realistic levels of local density and spatial distributions. I thus took a two step procedure. First, I developed a simulation model based on census data for an important exotic plant of North American grasslands (*Lespedeza cuneata* (Dumont) G. Don. (Fabaceae)) and verified that model was predictive of spread over a three year period at a Kansas, USA field site. I then used this model to develop a more general computer simulation that allowed different a) control levels, b) initial spatial distributions of patches (either patchily distributed as in the original field, or the same amount of plants randomly distributed across the site), and c) levels of detectability. I explored the effects of these factors on occupancy, abundance, local density, and patch size after five years of population spread. In particular, I determined under what combination(s) of treatment intensity and spatial distribution the detectability of plants is a factor in the overall effectiveness of control.

METHODS

INITIAL MODEL – SPREAD OF *LESPEDEZA CUNEATA*

I created a grid-based, cellular automaton (CA) model in Visual Basic for Applications (VBA Excel®) to simulate the spread of an invasive plant species. The model was parameterized using three years of spatially explicit census data from a population of *L. cuneata* growing in an old field (see Chapter 2 for details). The study area was 48 x 72 m and was divided into 36 plots (4 x 24 m). Half of the plots were randomly assigned to a herbicide treatment in which all *L. cuneata* stems present in the plots were spot sprayed with a 0.26 g L^{-1} solution of metsulfuron methyl (Escort®, DuPont™ Industries) until all leaf and stem surfaces were coated (as per label instructions for spot spraying). Any *L. cuneata* in the remaining plots were left unsprayed. The number of stems in each 1 m^2 cell of the entire site was counted in mid-June 2002 (prior to treatment), 2003, and 2004.

In order to match the field population, simulated fields had a 48 x 72 m inner grid and a boundary area that extended three meters from each edge of the inner grid. All grid cells (each 1 m^2) were considered to be suitable habitat and were therefore treated as reflecting, as would be expected for a species which exhibits spatial autocorrelation at the scale of the one meter (Chapter 2). Both the spread and the changes in local stem density were dependent on three factors: 1) the stem density within a cell in the previous year, 2) the occupancy of neighboring cells during the previous year, and 3) the total number of stems in the neighboring cells during the previous year.

In the initial model every field had the same starting population and was identical to the 2002 stem population observed in the field. For each subsequent year in a simulation, I first used logistic regression to determine the probability that a grid cell would be occupied given the local and neighborhood conditions in the previous year. For example, to predict occupancy in year$_{t+1}$, I used the following equation:

$$p(X_{t+1} > 0 | X_t, Y_t) = \frac{e^{\beta_0 + \beta_1 X_t + \beta_2 Y_t}}{1 + e^{\beta_0 + \beta_1 X_t + \beta_2 Y_t}} \qquad \textbf{\textit{Equation 3.1}}$$

where X_t and X_{t+1} represent local density within a grid cell in the first and second year of an annual transition, respectively. The variable Y_t represents the total number of stems in the neighboring cells in the first year. In this and subsequent equations, I estimated parameters using only the unsprayed plots in the original study, with the goal of simulating natural persistence and spread of the exotic plant.

Once the occupancy of a grid cell was determined I used linear regression to estimate how local stem density (including a quadratic term) and neighborhood stem abundance in the previous year affected local stem density (i.e., within an occupied grid cell) in the current year:

$$X_{t+1} = \beta_0 + \beta_1 X_t + \beta_2 X_t^2 + \beta_3 Y_t + \varepsilon \qquad \textbf{\textit{Equation 3.2}}$$

I then used coefficient estimates from Equation 3.2 to create Poisson distributions from which to draw density values for each occupied grid cell. The probability of a given density within a grid cell is given by Equation 3.3.

$$\Pr\left[X_{t+1} | \beta_0, X_t, Y_t\right] = \frac{e^{-\left(\beta_0 + \beta_1 X_t + \beta_2 X_t^2 + \beta_3 Y_t\right)} \times \left(\beta_0 + \beta_1 X_t + \beta_2 X_t^2 + \beta_3 Y_t\right)^{X_{t+1}}}{\left(X_{t+1}\right)!}$$

Equation 3.3

The variables X_{t+1}, X_t, and Y_t in Equations 3.1, 3.2, and 3.3 are identical. Values for the coefficients β_0, β_1, β_2, and β_3 are the same in equations 3.2 and 3.3 but differ from those in 3.1 (Tables 3.1, 3.2). Although the quadratic term in equations 3.2 and 3.3 incorporated density-dependence in the model equation, I also placed a cap of 120 stems per grid cell in order to ensure that local density remained within a realistic range. This was the highest local density observed during any census over the course of the field study (Chapter 2). In cases where a previously unoccupied cell was colonized, cell density was drawn from a distribution defined by the power function in Equation 3.4.

$$Freq[X_{t+1}] = 0.2134(X_{t+1})^{-0.7201} \qquad \textbf{\textit{Equation 3.4}}$$

The flowchart in Figure 3.1 describes the order in which density changes were applied to each grid cell during a single annual transition, and illustrates how stochasticity was incorporated into the simulations.

Separate models were parameterized for each annual transition (i.e. 2002-3, 2003-4). Reduced models were fitted in cases where one or several variables had low explanatory value (see Chapter 2 for a complete description of the model selection procedure). The final fitted values for each model are listed in Tables 3.1 and 3.2.

VALIDATION

To ensure that the models produced realistic patterns of spread and abundance, I compared the results of 1000 simulations to those observed in the original empirical study. The model was set up to mimic the field experiment (i.e. the initial distribution of stems was identical to the *L. cuneata* stem population observed in 2002, the location of unsprayed plots within the simulated field matched that of the original field, and parameters for the first and second transitions were based on the changes observed between 2002-3 and 2003-4 respectively (see Chapters 1 and 2 for details).

Three responses were used to compare simulated and observed results: 1) the proportion of occupied grid cells in a plot, 2) the total abundance of stems within a plot, and 3) the mean stem density of occupied cells within a plot. If the mean simulated response fell within the 95% confidence interval of the observed response for each year then the model was considered to be a reasonable fit. Following a small adjustment to the quadratic term (original $\varepsilon = -0.006$, adjusted $\varepsilon = -0.015$), the unsprayed model met my validation criteria for all responses.

GENERAL MODEL DEVELOPMENT

In the general model, I maintained the basic structure of the *Lespedeza* simulation, but made three major changes. The first change to the *Lespedeza* model was the incorporation of four levels of treatment effectiveness into the simulations. The first level was a control treatment in which changes in the local occupancy and stem density were modeled by the same parameters that were used in the initial model of *L. cuneata* spread in untreated plots. For the three levels where management treatments were applied, my goal was to simulate a situation where adult over-winter and early-season survival and seed germination and seedling survival took place before treatments (i.e. herbicide or local pulling of plants) were applied. Thus in the model, I first allowed the annual changes in occupancy and density to proceed as they did under the untreated conditions. I then reduced stem density by 25%, 50%, or 75% within each occupied grid cell. Local extinction occurred when the reduced stem density fell below one stem. A second change was that the simulated fields had either patchily or randomly distributed populations of *L. cuneata*. In this study, occupied cells were considered to be members of the same patch if they were either cardinal or diagonal neighbors. All fields were based on the 2002 stem population; they thus had identical starting values for occupancy, total stem abundance, and mean number of stems per occupied cell. While the "patchy" fields had the same number and size of patches as the 2002 stem population, cells within the "random" fields were populated with stem densities without regard to patch membership (see flowchart in Figure 3.2 for details). Thus the number and size of patches in the starting populations were strongly influenced by field type, with random fields having more than twice as many patches as patchy fields (Figure 3.3). Specifically, both field types had a high frequency of patches composed of 1-3 occupied cells, but the patchy fields had a broader range of patch sizes including patches made up of more than 30 cells (Figure 3.3a, b).

Finally, the general model included six levels of detectability. Since the original field study did not include data on individual stems I could not explicitly estimate detectability. I therefore approximated the detectability levels based on my experience in searching for stems in dense vegetation. The levels ranged from "very low" with a constant detection probability of 50% to "full detection" where every occupied cell within a field is detected. The low baseline of detectability (50%) of stems in the model closely matches initial detectability estimates of a threatened milkweed in a similar habitat (Alexander et al. unpublished data). The probabilities of detection in the intermediate levels of detectability are based on logistic models (Figure 3.4). With “low” detectability, the probability of detection increases with the number of neighbors in adjacent cells but is not affected by local density. When detectability is “moderate” to “very high”, increases in both local density and neighbor abundance result in an increased probability of detection.

GENERAL MODEL RUNS

The model was run to include all combinations of initial distribution, treatment intensity, and detectability (thirty-six runs total). Each run simulated the spread of *L. cuneata* in 500 replicate fields over five years under both sprayed and unsprayed conditions. The five-year period was chosen because it was a reasonable span of time for extrapolation and was a relevant time frame for management. At the end of each run the data for all simulations were compiled. Occupancy represented the proportion of grid cells with at least one *L. cuneata* stem and provided an indication of the population’s spatial extent. Abundance was defined as the total number of stems in the field and represented the overall population size and the local density was the average number of stems within occupied grid cells. Finally, the number and size of patches in a field allowed me to gauge the spatial distribution of density and occupancy in the field.

RESULTS

Occupancy in random fields was, on average, 1.3 times higher than in fields with an initially patchy distribution when no treatments were applied (Figures 3.5a, b; 3.7a, b; 3.8a, b). The pattern of higher occupancy in the random fields held across all levels of treatment intensity for the three lowest levels of detectability, where small patches can avoid detection and treatment. In contrast, the proportion of occupied cells was slightly higher in the patchy fields at higher levels of detectability (Figures 3.5a, b; 3.7e, f).

Abundance was nearly 1.2 times higher in the random compared to patchy fields if the populations were left untreated (Figures 3.5c, d). When populations were subjected to control treatments, however, abundance was higher in the patchy fields across all levels of detectability. As expected, both random and patchy fields had a greater number of stems with less intensive management (25% vs. 50% or 75% reduction in stems) (Figures 3.5c, d). The difference between field types was most pronounced at the lowest intensity of management (25%) (Figures 3.7e, f; 3.8e, f).

On average, occupied cells in patchy fields had nearly five more stems than those in the random fields (44.8 vs. 40.1 stems/m^2) when no treatments were applied (Figures 3.5e, f). With treatment, local density was always highest in the patchy fields, although differences between field types decreased at higher control intensity and increased detectability. Local density was highest at the extremes of detectability (i.e., 50% or 100% of occupied cells detected and treated) for the 25% stem reduction for both field types (Figures 3.5e, f).

Initially, random fields had many more patches than patchy fields (Figures 3.3a, b; 3.6a, b). However, patch convergence occurred when fields were left untreated with the net result being that patchy fields ended up with >3.5 times more patches than random fields (Figures 3.6a, b). The application of management treatments to both field types prevented patches from expanding and merging, particularly at higher treatment intensity and increased detectability (Figures 3.7c-f, 3.8c-f). In patchy fields, management treatments disrupted the growth of large and/or expanding patches and resulted in an increase in the number of patches (Figures 3.6b; 3.7d, f; 3.8d, f).

DISCUSSION

As is well known, the highest likelihood of successful control of exotic species occurs when populations in the earliest stages of invasion and establishment are found and treated (Simberloff 2003, Dewey and Anderson 2004, Arriaga et al. 2005). By implementing control programs at these early stages we can employ cost-effective local treatment applications. Local treatments also reduce the extent of environmental harm that management could have within the native community (Shaw 2005). Unfortunately, populations in the early stages of invasion often have few individuals, making their detection difficult. Although the issue of detectability is not new to invasion biology, most attention has occurred at the landscape and regional scale (i.e. remote sensing of invasions; addressing whether exotic species have been introduced into nations, states, or counties) (Shuster et al. 2005). In contrast, few if any studies have directly tested how the spatial distribution of the exotic species influences detectability and the implications this can have for management. This gap in research seems important since workers have implied that detectability at the local scale could affect the success of control efforts (Shaw 2005).

EFFECT OF TREATMENT INTENSITY, SPATIAL DISTRIBUTION, AND DETECTABILITY

Simulations with the general model illustrate three key points regarding the effect of spatial distribution and detectability on the effectiveness of locally applied management treatments. First, the potential for spread and increased overall abundance are greater when invading populations are randomly distributed within a field compared to when populations are more patchily distributed. This finding falls in line with the predictions of Moody and Mack's (1988) model as well as with simulation studies involving weed spread in both agricultural fields (Blumenthal and Jordan 2001) and in native marsh (Grevstad 2005). In comparison to the patchy fields, the random fields were characterized by a large number of small patches, creating multiple foci for spread. In actual infestations, random distributions of exotic plants are rare since invasions often occur along roads or waterways in areas where human-meditated disturbance has created patchy or linear invasion fronts (Wadsworth et al 2000). A possible exception to this would be cases in which introduction at an infestation site resulted from the presence of seeds in a seed mix that is randomly sown at a site either for restoration or to establish Conservation Reserve Program (CRP) acreage.

Second, the application of a local treatment slowed increases in the number and spatial extent of stems in the field, but only the most effective treatments actually reduced both occupancy and stem abundance. In fields where 25% of the stems were removed each year, local density (i.e., the average number of stems in occupied grid cells) increased after five years in both field types and at every level of detectability (Figures 3.5e, f). In fact, local density within the patchy fields slightly increased even when 50% of the stems were removed each year. The fact that these increases were greater in the patchy fields suggests that recruitment from neighboring cells plays an important role. In contrast, cells in random fields with relatively few stems were more likely to experience local extinction because rescue effects (Brown and Kodric-Brown 1977, Drake and Lodge 2006) were less likely since neighbors of these cells were also frequently unoccupied. Further evidence of the importance of recruitment in increasing the probability of persistence can be seen in the simulations of the highest detectability levels (Figures 3.5a, b; High, Very High and Full). As more occupied cells are found and treated, only those cells with high densities to begin with are likely to persist into the next year (also see Figures 3.7e, f).

With no treatment, the numerous small patches present at the start of the simulations merged over time for both field types (Figures 3.7a, b; Figures 3.8a, b). This meant that the average number of patches per field dropped from 245 to 15 in random fields and from 105 to 53 in patchy fields after only five years of uncontrolled spread (Figures 3.6a, b). Decreases in the number of patches per field under treated conditions might be thought to result from local extinction rather than patch convergence. However, when 25% of stems were removed, the only instance where patch loss in the random fields resulted from local extinction was when the probability of detection was equal to one (100% detectability). Local extinction played a stronger role when the annual stem removal rates were 50% or 75%, but this still only occurred in simulations of the three highest detectability levels. The patchy fields provide a more realistic example of the distribution of stems. In patchy fields, the increase in the number of patches following treatment appeared to result from the break up of existing patches as well a reduction in patch convergence (Figures 3.7d, f; 3.8d, f). The resulting patches were smaller than the original patches and thus should have experienced higher local extinctions among their member cells. Nevertheless, the 75% stem removal rate was the only control treatment that decreased the overall occupancy, and the decreases only occurred at the three highest levels of detectability (Figure3.5b).

Finally, the influence of detectability on the overall effectiveness of the treatments also differed between the field types. At the three lowest levels of detectability, control efforts were generally more effective at reducing spread (i.e., minimizing occupancy increases) in patchy fields; but greater reductions in occupancy occurred in the random fields at higher detectability levels while higher detectability levels led to greater occupancy decreases in the random fields (Figures 3.5a, b; bar height relative to the initial occupancy). One of most obvious indications of spread in the untreated fields is the merging of existing patches. Starting populations in both field types had a large number of small patches (1-3 m^2), but the patchy fields had a greater number of larger patches. These larger patches would be less likely to escape detection and treatment even at low detectability levels. With higher detectability, however, the numerous small patches in the random fields were more likely to be detected and treated. Since many neighboring cells of these small patches were unoccupied, the chance of immigration from nearby cells was low, and the probability of local extinction increased. In contrast, to occupancy, both abundance and local density were higher in patchy fields across all detectability levels (Figures 3.5c-f), suggesting that the presence of larger patches has a greater impact on persistence and population growth than on spread at the one meter scale. Further, the most intensive management treatment in the model (75% annual stem removal) had similar effects in both field types and at all detectability levels (citing Fig. 3.8c-f).

This indicates that high treatment intensity could outweigh the influence that occupied neighboring cells have on persistence. It also suggests that intensively treated infestations can be effectively managed even if detectability is imperfect because patches undetected in one year will likely be found and treated in another year. However, treatment intensities can vary from year to year (Chapter 1) both due to changes in annual budgets that restrict the amount of effort directed toward management as well as the challenge of timing control treatments to coincide with seasons when plants are most vulnerable. If control is inconsistent, detectability becomes a more important consideration for land managers.

The results of the simulations presented in this study were based on an initial occupancy of 12%. This level of occupancy was chosen so that the model was parameterized using spatially explicit field data on an exotic plant. Lower levels of initial occupancy could lead to higher rates of increases in occupancy than were observed in this study, unless all stems occurred in a few easily detectable patches. Conversely, if initial occupancy was higher or the population was widely spread over the entire site, whole-field, broadcast treatment applications may be more efficient. If local treatments are still desirable, the best strategy would most likely be to treat the outer patches first and then work towards the center of the infestation (Moody and Mack 1988, Blumenthal and Jordan, 2001, Grevstad 2005).

Another assumption of the model is that detection of a single occupied cell is independent from year to year. However, the probability of finding a patch or an individual plant is typically greater once it has already been marked (Alexander et al.

1997, Kéry and Gregg 2003). Managers could therefore increase their chances of finding and treating all stems by maintaining weed maps that document the location of weed patches within the site. If these maps included density data they could prove even more useful in predicting future weed presence (Chapter 2). The model is also restricted to the detectability of adult stems, but the detectability of juveniles and seedlings is undoubtedly much lower. If the survival rate of the younger life stages is high or if the seed bank is well developed, then the likelihood of control is not going to be as high as would be expected from the model results.

IMPORTANCE OF DETECTABILITY IN EXOTIC PLANT MANAGEMENT

The model presented here allowed simultaneous manipulation of the spatial distribution of the invading population, the intensity of treatment used to manage the population, and the detectability of occupied areas within a field. In areas invaded by exotic plants, the spatial distribution of the infestation will most likely be unique to the species and the site. Further, although one can control the treatment intensity, it is reasonable to assume that most managers will try to implement treatments that have the greatest impact on individual mortality and reproductive success while still being cost effective. The extent to which managers need to focus on detectability is, however, more open to interpretation. In the case of large, obvious exotic plants such as Chinese tallow trees (*Triadica sebifera*) in southeastern U.S.A. coastal plains; detectability may be a “non issue”. However, given the large areas often treated for exotics, the limited number of field workers and their time, and the cryptic nature and small size of some exotic plants and life stages, the ability to find either patches or individual plants may be crucial to successful control.

Given the results of the model, managers would be advised to estimate the percentage of plants detected in typical treatment programs; and if detectability is not 100%, explore whether detectability is dependent on local patch density or size. A typical approach would be to have two observers independently survey a site, noting the location of the exotic plants they see. This approach generates “capture histories” of individual plants, and allows one to distinguish how many plants were observed by only observer 1, only observer 2, or both observers (Nichols 1992, Shefferson et al. 2001, Kéry and Gregg 2003, Lesica and Crone 2007). These data can then be used to estimate population size and probabilities of detection using capture-recapture (CR) models. If data are also recorded on the size of patches in which the plants occur and the local density of areas where the plants occur, more complicated models could be used to explore the effect of these factors on the probability of detection (Amstrup et al. 2003). CR statistics have been increasingly utilized in plant ecology as a method of assessing detectability and its influence on demographic estimates (Shefferson et al. 2001, Kéry and Gregg 2003, Slade et al. 2003). For example, Kéry and Gregg (2003) found biases in detectability of individual plants based on plant size and tagging history. In a simulation study by Kéry (2004) CR modeling also correctly determined that habitat type (open vs. closed) and population size influenced detectability of populations while conventional analyses using logistic regression falsely indicated that habitat type and population size influenced extinction rates.

Though these studies were primarily directed at estimating population size, survival rates and population extinction rates for rare or threatened plants, it is clear that detectability could be important in population studies of exotic weeds as well.

Table 3.1. Coefficient values for the logistic models predicting *Lespedeza cuneata* presence within a grid cell. See chapter 2 for a complete description of the model selection procedure.

		Annual Transition	
Parameter	Coefficient	2002 to 2003	2003 to 2004
Constant	β_0	-2.69775	-2.38782
Local Density	β_1	0.60865	0.34446
Neighbor Abundance	β_2	0.14499	0.07028

Table 3.2. Coefficient values for the linear models predicting *Lespedeza cuneata* stem density within a grid cell. Values were used to construct Poisson distributions from which density was drawn. Reduced models were fitted in cases (2003 to 2004 transition). See Chapter 2 for a complete description of the model selection procedure.

		Annual Transition	
Parameter	Coefficient	2002 to 2003	2003 to 2004
Constant	β_0	0.0543	0.6621
Local Density	β_1	1.5209	1.3532
Local Density^2	β_2	-0.0054	-0.015
Neighbor Abundance	β_3	0.1075	---------

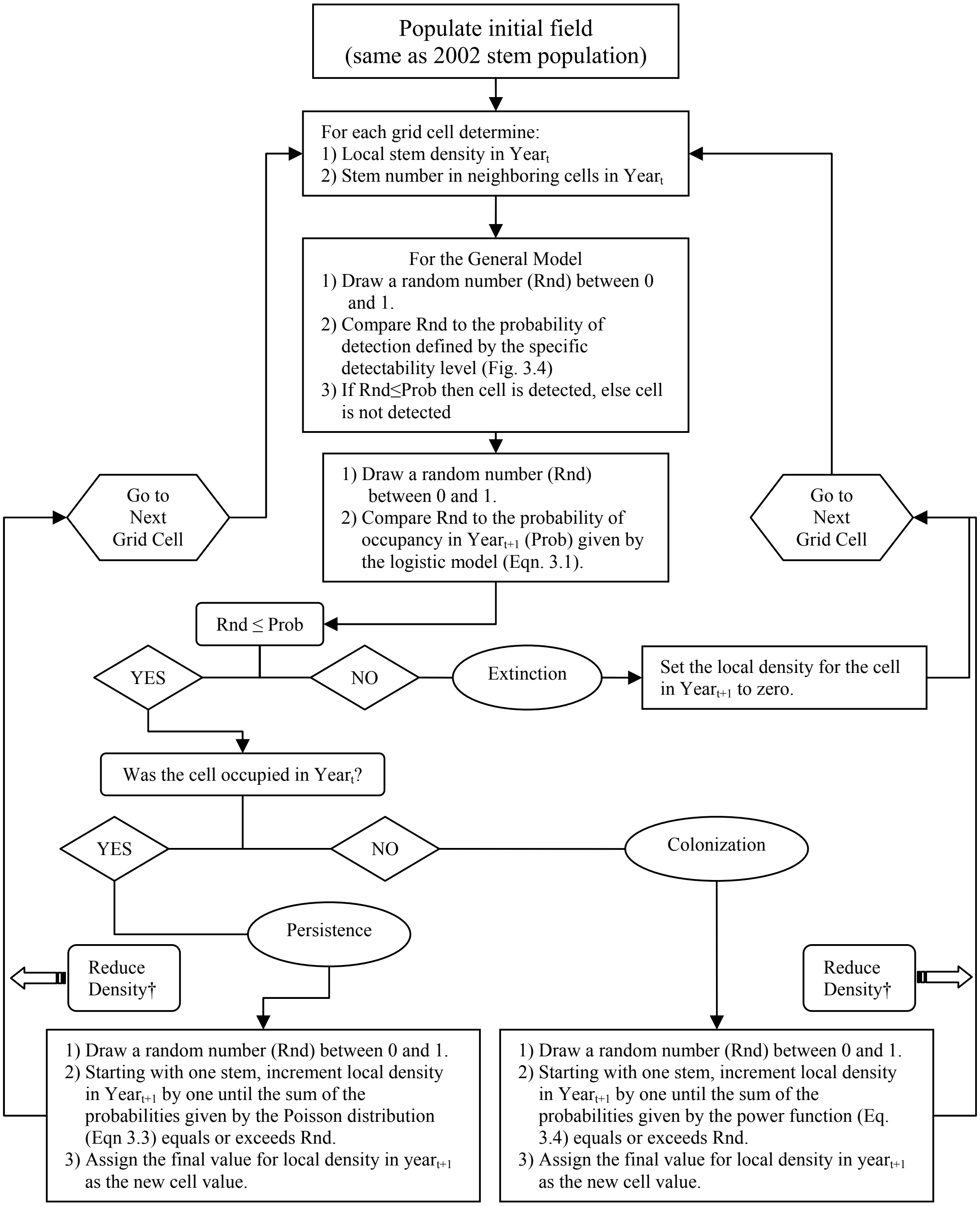

Figure 3.1. Flowchart for determining the changes that occur within a single annual transition during each simulation run. †Density reductions are applied only under managed conditions within the general model and only to grid cells that are detected and treated.

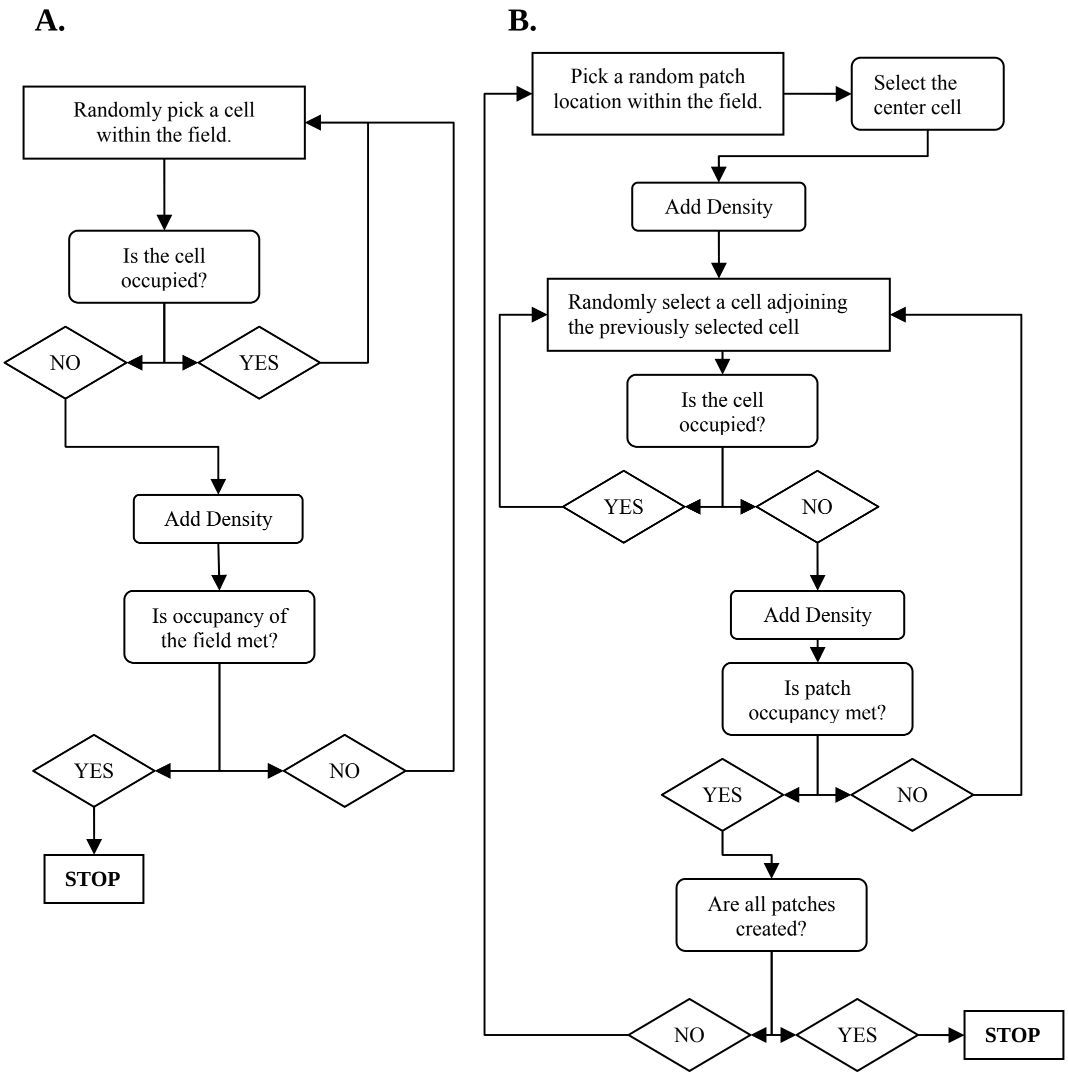

Figure 3.2. Flow charts describing the algorithms used to create the initial field in each simulation. A) Generates randomly distributed fields by drawing without replacement cell densities from a distribution based on the 2002 stem population of entire field. B) Generates patchily distributed fields by identifying the patches in the 2002 stem population and creating cell density distributions for each patch. Density is added to each cell within the recreated patch by drawing without replacement cell densities from the distribution of the patch.

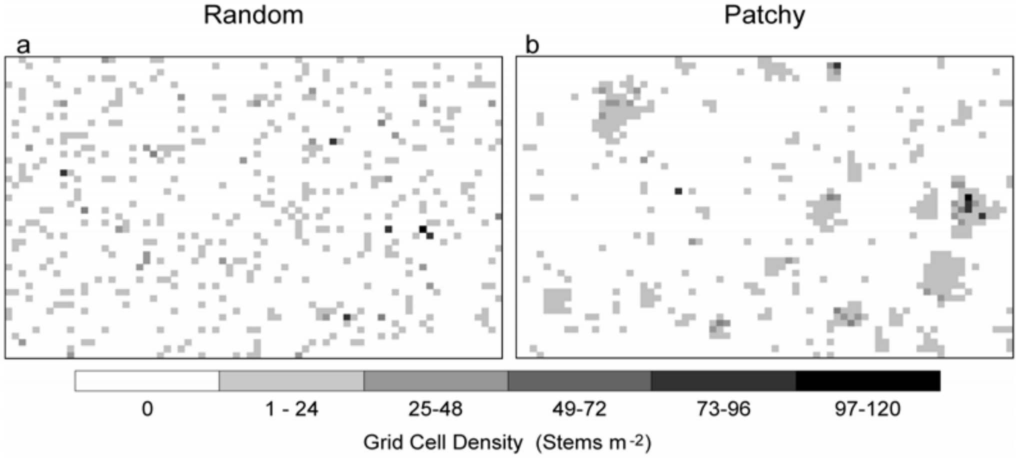

Figure 3.3. Sample maps of starting populations in simulated fields with either (a) random or (b) patchy spatial distributions. In both maps each shaded cell represents a 1-m^2 grid cell. Occupied cells were members of the same patch if they were either cardinal or diagonal neighbors.

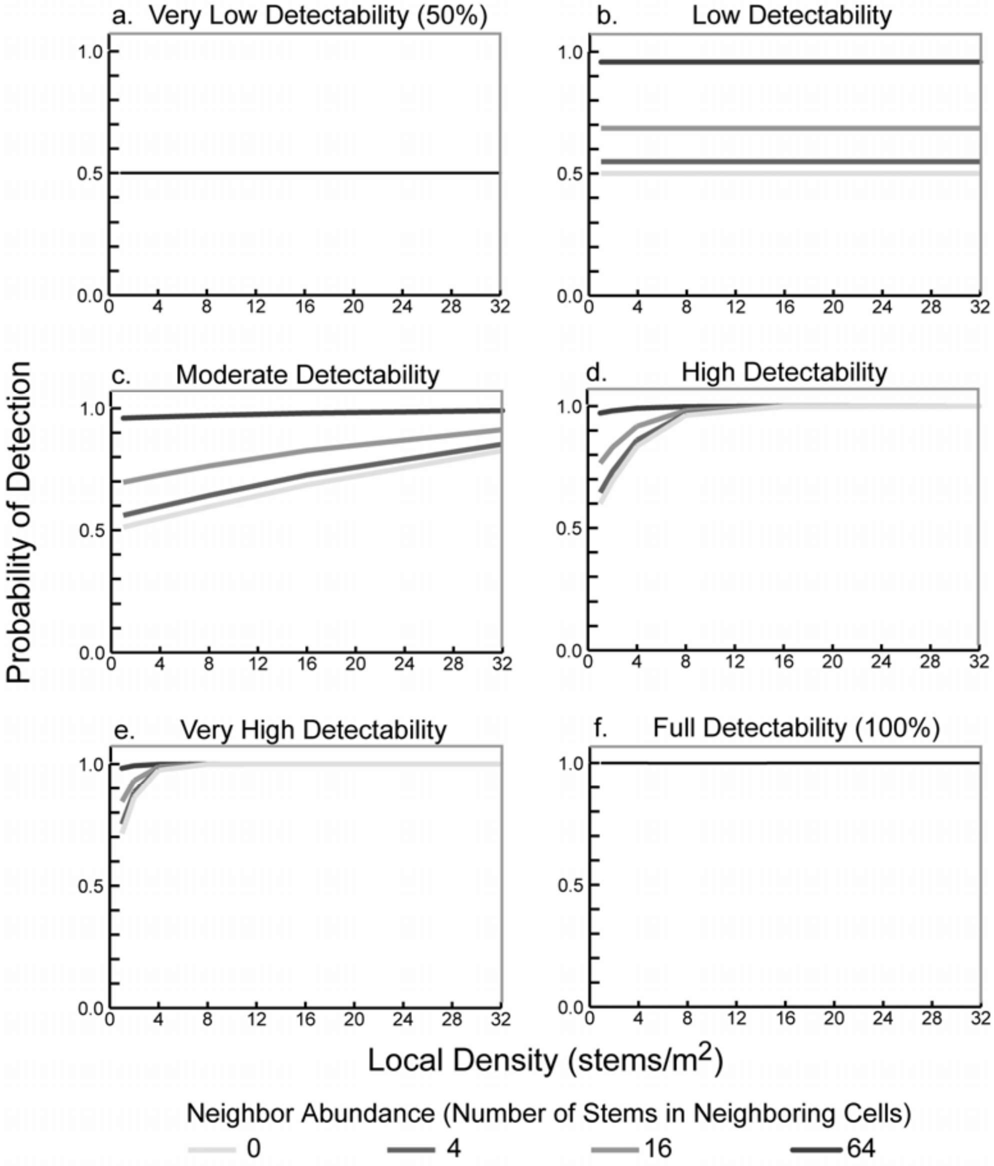

Figure 3.4. Sample probability distributions for each level of detectability. In each graph local stem density represents the number of stems in a grid cell. Individual lines in graphs b-e represent the probability distributions for different levels of neighbor abundance (the number of stems present in the eight adjoining cells [Chapter2, Figure 2.2]). Lines in graphs a and f show the two detectability levels used in simulations where the probability of detection was constant.

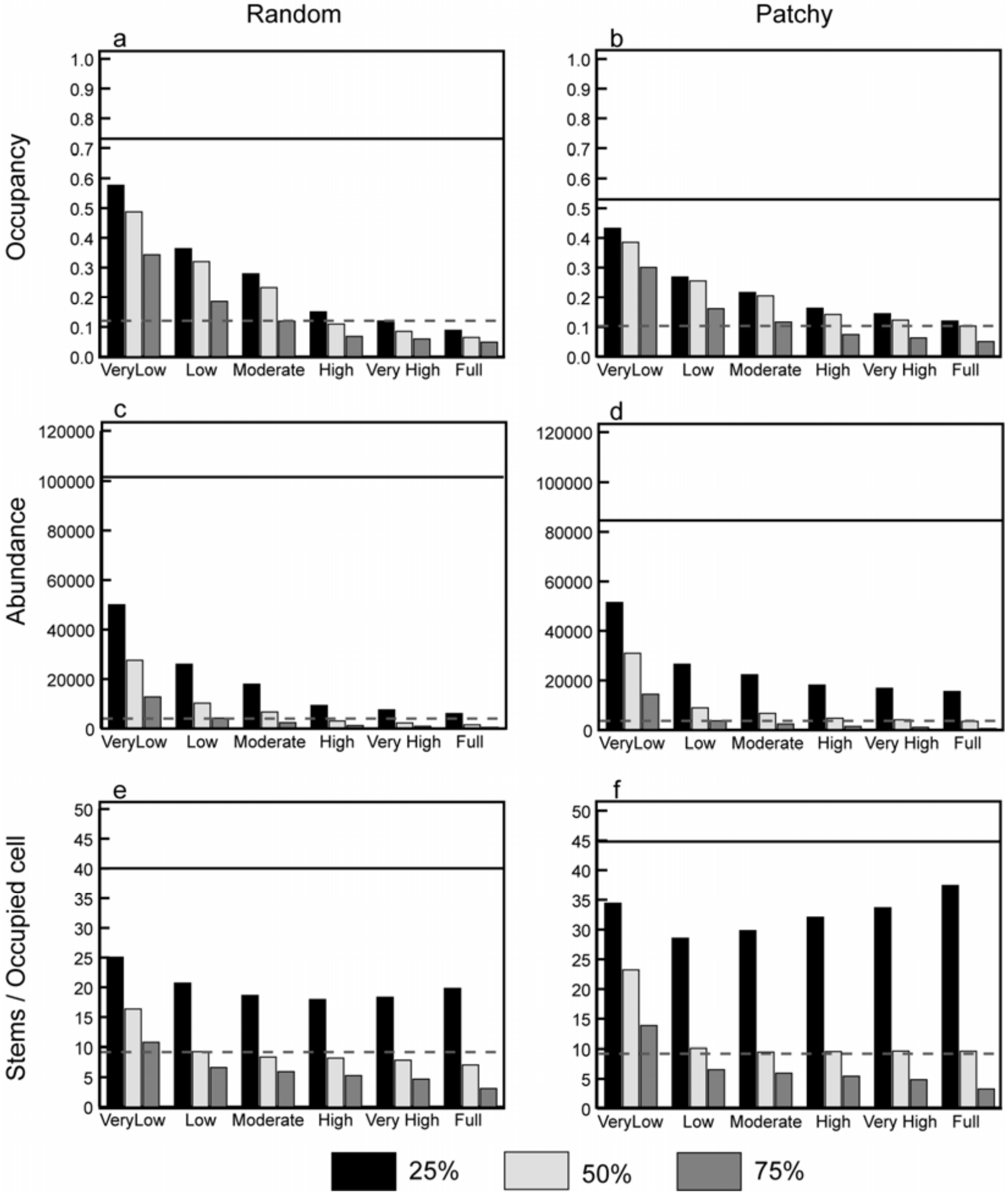

Figure 3.5. Simulation results for occupancy, abundance and density following five years of treatment. Graphs on the left represent fields that had starting populations that were randomly distributed while graphs on the right represent fields with patchily distributed starting populations. In all graphs the dashed lines represents the initial value of the response, and the solid line represents the average response of unsprayed fields at the end of five years. Different colored bars represent the levels of treatment intensity (25%, 50% or 75% density reductions each year).

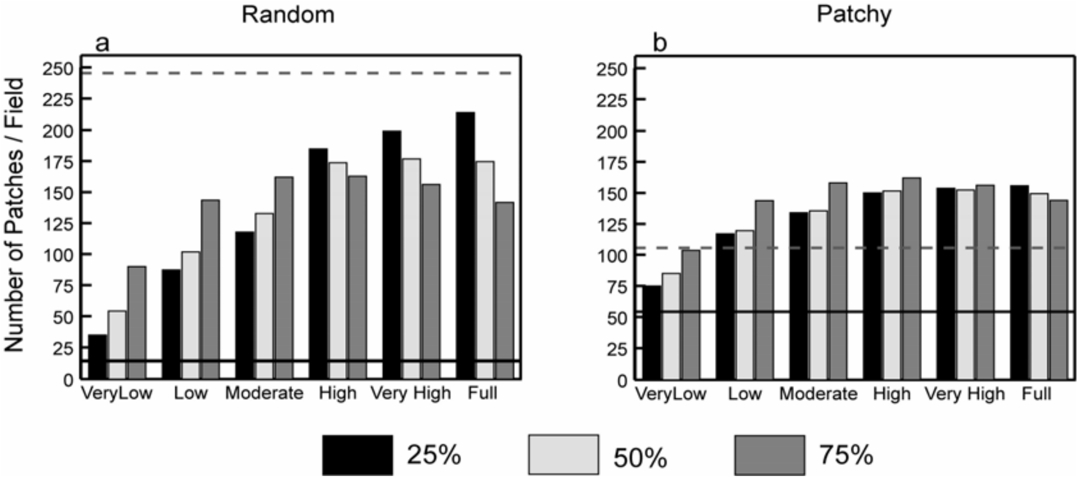

Figure 3.6. Number of patches occurring in simulated fields following five years of treatment. The graph on the left represents fields that had starting populations that were randomly distributed while the graph on the right represents fields with patchily distributed starting populations. In both graphs, the dashed line (- - -) represents the number of patches initially present in each simulated field, and solid the line (—) represents the average number of patches present in unsprayed fields at the end of five years. Different colored bars represent the levels of treatment intensity (25%, 50%, or 75% reductions in stem density/year/treated cell).

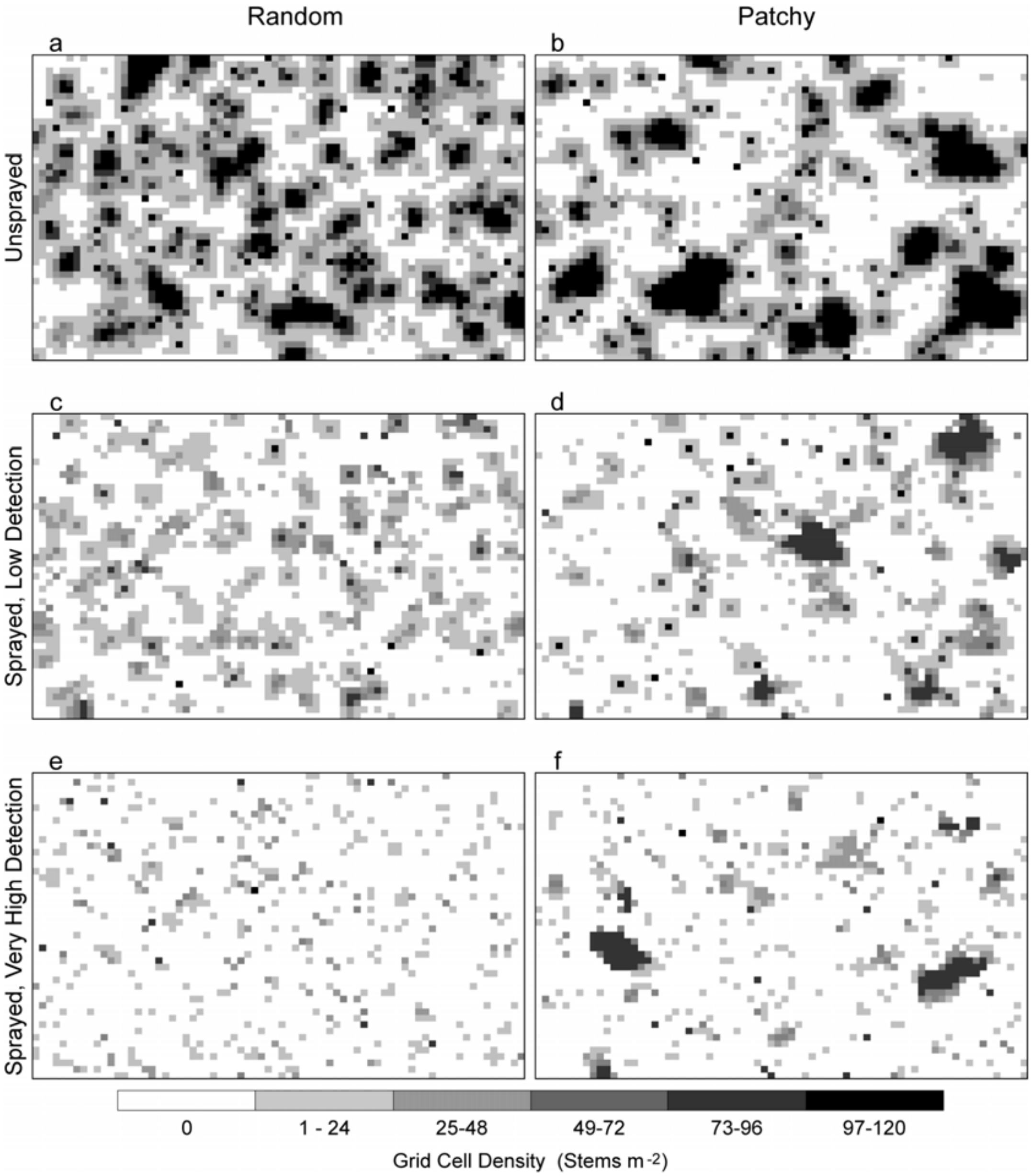

Figure 3.7. *L. cuneata* stem density following five years of spread in fields that were either (a, b) left untreated or (c-f) subjected to a treatment that reduced stem density by 25% just before reproduction each year. Each shaded cell represents a 1-m^2 grid cell. Occupied cells were members of the same patch if they were either cardinal or diagonal neighbors. Maps on the left represent fields that started with random spatial distributions; those on the right represent fields that started with patchy spatial distributions. The topmost maps (a and b) show populations that were left untreated while the remaining maps (c-f) depict populations in which occupied cells were treated if detected. The middle and bottom maps represent fields in which the probability of detecting and treating an occupied cell is “Low” or “Very High” respectively.

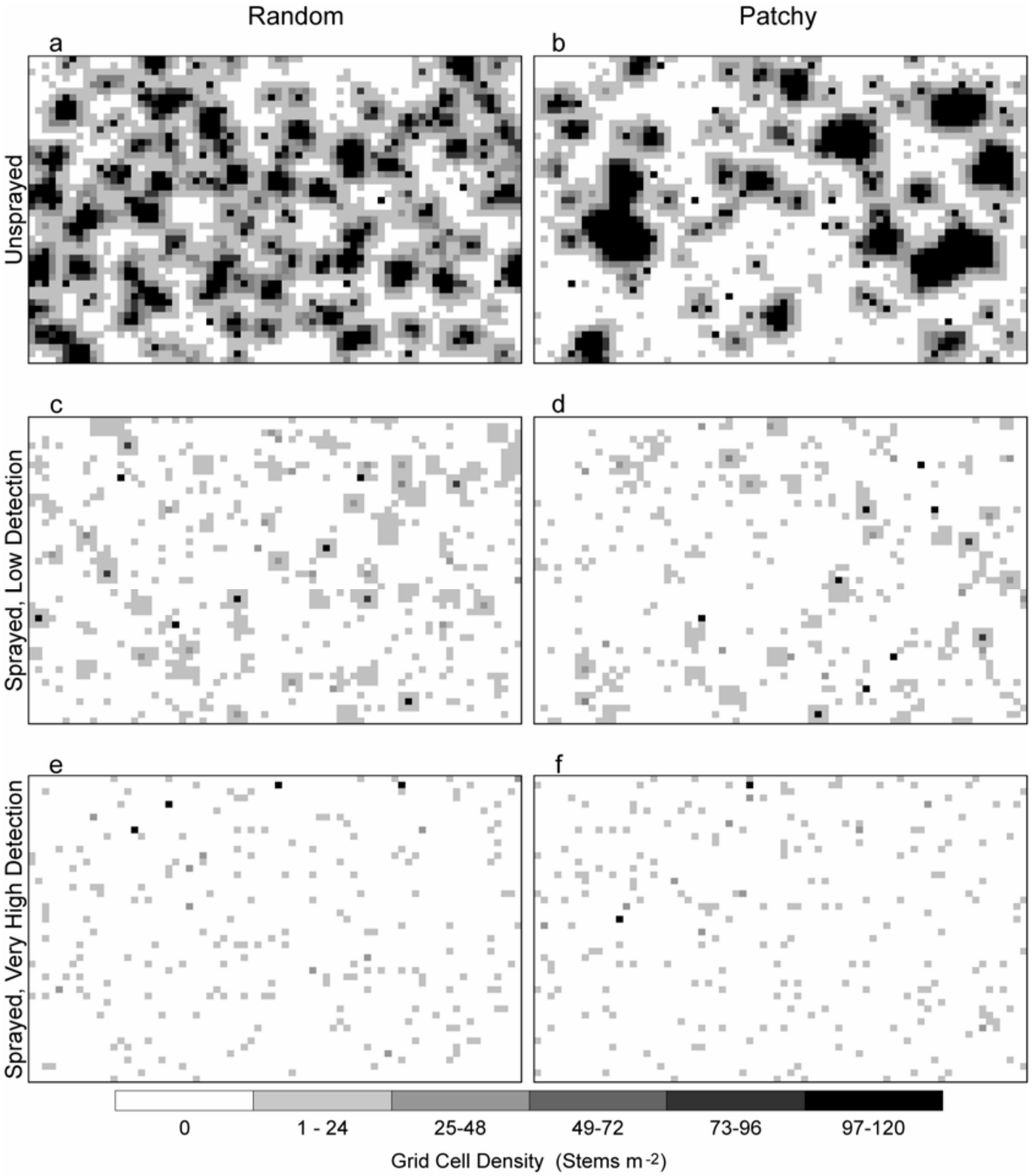

Figure 3.8. *L. cuneata* stem density following five years of spread in fields that were either (a, b) left untreated or (c-f) subjected to a treatment that reduced stem density by 75% just before reproduction each year. Each shaded cell represents a 1-m^2 grid cell. Occupied cells were members of the same patch if they were either cardinal or diagonal neighbors. Maps on the left represent fields that started with random spatial distributions; those on the right represent fields that started with patchy spatial distributions. The topmost maps (a and b) show populations that were left untreated while the remaining maps (c-f) depict populations in which occupied cells were treated if detected. The middle and bottom maps represent fields in which the probability of detecting and treating an occupied cell is "Low" or "Very High" respectively.

CONCLUSIONS

In this dissertation, I explored the population ecology of *Lespedeza cuneata* (sericea lespedeza), a perennial legume that has become invasive in much of the Great Plains of North America. In the context of a field experiment on population ecology and management, I found that herbicide application had the most dramatic effects on abundance and occupancy (Chapter 1) and this treatment became the focus for further investigation (Chapters 2 and 3). Despite the effectiveness of herbicide, the large differential between treatments was due mostly to dramatic increases in untreated plots rather than large decreases in treated plots. This result suggests that control efforts should be repeated over multiple years if established populations are to be eradicated.

In the first chapter I monitored adult and juvenile populations in 44-m^2 plots to investigate how plants in different life stages respond to management treatments commonly used in natural areas, pastures, and rangeland settings. Both life stages experienced increases in both occupancy and total abundance in the plots where sericea was left unsprayed. In the absence of soil disturbance, seed bank recruitment appeared to be minimal, making annual seed input necessary for population growth and spread at the site. This conclusion is further substantiated by the positive correlation between juvenile and adult presence among quadrats within a plot. In the absence of any soil disturbance, a *L. cuneata* seed bank could thus slow eradication at a site, but it may not intensify the infestation without additional seed input from the current year.

In Chapter 2, I used a fine-scale, spatially explicit data set (1 m resolution) to determine how the spatial autocorrelation of local stem density within a field could impact the efficacy of control. I also explored how different data structures (presence/absence vs. stem density) and the inclusion of simple spatial information about plants in neighboring quadrats could influence the prediction of local population changes between survey years. I found that even though stems exhibited significant spatial autocorrelation, this did not alter the conclusion that the herbicide was effective in reducing local stem density. All models predicted that the odds of colonizing an empty quadrat were low but increased in quadrats with occupied neighboring quadrats, particularly in unsprayed plots. This likely resulted from the presence or absence of seed input from plants within unsprayed and sprayed quadrats respectively (Chapter 1). The probability of persistence was consistently high but varied with both local density and neighbor abundance under unmanaged conditions. Accurate predictions of occupancy and density under unmanaged conditions allow managers to assess the potential risk posed by a population. Although collecting spatially explicit data on stem density requires substantial effort, it provides better estimates of local population growth and spread than presence/absence data with no spatial context. These results, although specific to this study, outline a simple approach for incorporating spatially explicit data into monitoring and management programs.

Finally, in Chapter 3, I used a simulation model to investigate the joint influences of treatment intensity, initial spatial distribution of plants, and detectability of plants by workers applying control treatments on the persistence and spread of an invasive plant. After five years of uncontrolled spread, populations that had initially random spatial distributions had higher abundance and occupancy than in initially patchy populations. Although control treatment slowed these increases, only the most intensive treatments actually reduced both occupancy and abundance. Intensive control efforts can also prevent rapid spread even if imperfect detectability prevents workers from treating all patches in a single year. These results do however indicate that detectability should not be overlooked. In order to address the detectability issue I recommend that managers maintain weed maps to better track areas of local infestation. By including abundance data on these maps, they may further refine their ability to predict the level of infestation from one year to the next.

Potential Future Research

The results of the first chapter were based on census data from multiple years. In order to determine if the observed changes on the abundance and size of adults represent mortality or shifts in age structure of the population one needs more detailed demographic studies that track the fate of individual plants. Since surviving *L. cuneata* individuals grow from existing crown roots each year, it is realistic to tag individual plants. During each census workers could then note changes in the number of stems, estimate seed production, and determine mortality rates under a variety of treatment conditions. If the censused individuals occur in patches with a range of local densities then the potential impact of density dependence on demography could also be more directly determined.

The speculation that *L. cuneata* (Ohlenbusch and Bidwell 2001) forms a seed bank points to another goal for future work. In this study, soil disturbance was absent. However, such disturbance is frequently required to initiate recruitment from the seed bank (Meyer and Schmid 1999b, Grigulis et al. 2001, Moody-Weis and Alexander 2007). Therefore, we should pursue more rigorous studies to determine seed longevity under field conditions and the influence of disturbance in germination. A simple method to test for the presence of a seed bank would be to collect soil samples from beneath existing patches, spread them in shallow trays in a greenhouse, and identify the emerging seedlings. This approach however, does not provide information about how long the germinated seeds have been in the soil. Alexander and Schrag (2003) performed a field experiment in which they buried sunflower seeds in mesh bags and monitored seedling emergence, By retrieving a subset of bags each year of the study and counting the number of viable seeds remaining they could estimate the recruitment potential of seeds of various ages. This type of study would be well suited to *L. cuneata* since it would allow workers to determine the population dynamics of seed population without the risk of establishing new populations.

In Chapter 2, I found that the predictive value of local and neighborhood abundance were all but negated when herbicide was applied to quadrats. A curious result led me to pursue the simulations in Chapter 3; namely, that increases in local density only occurred in herbicide-treated quadrats with the lowest density. This suggested that small numbers of plants may not be detected by workers applying herbicides, and this lack of detectability could influence the persistence of localized patches. The simulation results indicated that low detectability had the greatest impact when treatment intensity was low. Although managers tend to apply the most intensive treatments, yearly variation in effectiveness due to timing or budget constraints may not lead to consistent density declines. Thus, detectability should be addressed in future work. In order to refine the detectability estimates I would use capture-recapture methods that have increasingly been applied to population studies of rare and cryptic plants (Alexander et al. 1997, Kéry 2004). The methodology of these studies is akin to the mark-recapture methods that were devised to estimate survivorship and population size in animal populations (Amstrup et al. 2003). In capture-recapture studies, the record of whether an individual is either found or not found is generated by multiple surveys and/or multiple observers. Such capture histories can then be used to estimate the probability that an individual is detected and can provide better estimates of the number of individuals in the population. By including factors such as plant size, patch size, local density, and habitat type in more complex analyses, estimates for detectability could be determined for populations in a variety of settings; thus providing greater insight on the management of invasive plant populations.

LITERATURE CITED

Ahrens, W.H. 1994. Relative costs of a weed-activated versus conventional sprayer in northern great-plains fallow. *Weed Technol.* 8(2): 50-57.

Alexander, H.M. and A.M. Schrag. 2003. Role of soil seed banks and newly dispersed seeds in population dynamics of the annual sunflower, *Helianthus annuus. J. Ecol.* 91: 987-998.

Alexander, H.M., N.A. Slade and W.D. Kettle. 1997. Application of mark-recapture models to estimation of the population size of plants. Ecology. 78: 1230-1237.

Alexander, H.M., N.A. Slade, W.D. Kettle, G.L.Pittman. In press. Detection, survival rates, and dynamics of a cryptic plant, *Asclepias meadii*: applications of mark-recapture models to long-term monitoring studies. *J. Appl. Ecol.*

Amstrup, S.C., T.L. McDonald and B.F.J. Manly. 2003. *Handbook of Capture-Recapture Analysis*. Princeton University Press. Princeton.

Altom, J.V. J.F. Stritzke and D.L. Weeks. 1992. Sericea lespedeza (*Lespedeza cuneata*) control with selected potemergence herbicides. *Weed Technol*. 6: 573-576.

Arim, M, S.R. Abades, P.E. Neill, M. Lima and P.A. Marquet. 2006. Spread dynamics of invasive species. *Proceedings of the National Academy of Sciences of the United States of America* 103(2): 374-378.

Arriaga, L., A.E. Castellanos V., E. Moreno, and J. Alarcón. 2005. Potential ecological distribution of alien invasive species and risk assessment: a case study of buffel grass in arid regions of Mexico, *Cons. Biol.* 18: 1504-1514.

Barney, J.N. 2006. North American history of two invasive plant species: phytogeographic distribution, dispersal vectors, and multiple introductions. Biol.Invasions 8: 703-717.

Blair, E.C. 1933. Lespedeza in North Carolina. North Carolina Agri. Coll. Ext. Cir. 195, (Revised 1937), 8 pages.

Blocksome, C.E.B., 2006. Sericea Lespedeza (Lespedeza cuneata): Seed Dispersal, Monitoring, and Effects on Species Richness. Doctoral Dissertation. Kansas State University. Manhattan.

Blumenthal, D. and N. Jordan. 2001. Weeds in field margins: a spatially explicit simulation analysis of Canada thistle population dynamics. *Weed Science* 49: 509-519.

Bossard, C.C. and M. Rejmánek. 1994. Herbivory, growth, seed production, and resprouting of an exotic invasive shrub *Cytisus scoparius*. *Biol. Cons*. 67: 193-200.

Brandon, A.L., D.J. Gibson, and B.A. Middleton. 2004. Mechanisms for dominance in an early successional old field by the invasive non-native *Lespedeza cuneata* (Dum. Cours.) G. Don. *Biol Invasions* 6: 483-493.

Brown, R.B. and S.D. Noble. 2005. Site-specific weed management: sensing requirements- what do we need to see? *Weed Sci*. 53: 252-258.

Brown, J. H., and A. Kodric-Brown. 1977. Turnover rates in insular biogeography: effect of immigration on extinction. *Ecology* 58:445-449.

Buckley, Y.M., M. Rees, Q. Paynter, M. Lonsdale. 2004. Modelling integrated weed management of an invasive shrub in tropical Australia. *J. Appl. Ecol*. 41: 547-560.

Bussan, A.J. and W.E. Dyer. 1999. Herbicides and rangeland. Pages 116-132 *in* R.L. Sheley and J.K. Petroff, eds. Biology and Management of Noxious Rangeland Weeds. Corvallis OR: Oregon State University Press.

Cacho, O.J., D. Spring, P. Pheloung, S. Hester. 2006. Evaluating the feasibility of eradicating an invasion. *Biol Inv*. 8: 903-917.

Casady, G.M., R.S. Hanley, and S.K. Seelan. 2005. Detection of leafy spurge (*Euphorbia esula*) using multidate high-resolution satellite imagery. *Weed Tech*. 19: 462-467.

Clark, D.L. and M.V. Wilson. 2001. Fire, mowing and hand-removal of woody species in restoring a native wetland prairie in the Willamette Valley of Oregon. *Wetlands.* 21(1): 135-144.

Cook, A., G. Marion, A. Butler, and C. Gibson. 2008. Bayesian inference for the spatio-temporal invasion of alien species. *Bull. Math. Biol.* 69(1): 2005-2025.

Crawley, M.J. 1986. The population biology of invaders. *Philos. Trans. R. Soc. London Ser. B* 314: 711-731.

Dale, M.R.T. 1999. Spatial Pattern Analysis in Plant Ecology. Cambridge University Press, Boston.

Dewey, S.A. and K.A. Anderson. 2004. Strategies for early detection – using the wildfire model. *Weed Tech.* 18(Suppl): 1396-1399.

Dieleman, J.A. and D.A. Mortensen. Chararterising the spatial pattern of *Abutilon theophrasti* seedling patches. *Weed Research* 39: 455-467.

DiTomasso, J.M. 2000. Invasive weeds in rangelands: species, impacts, and management. *Weed Science* 48: 255-265.

Donnelly, E. D. 1979. Selection for chasmogamy in sericea lespedeza. *Crop Sci.* 19:528-531.

Drake, J.M. and D.M. Lodge. 2006. Allee effects, propagule pressure and the probability of establishment: Risk analysis for biological invasions. *Biol. Invasions* 8(2): 365-375.

Duncan, C.A., J. J. Jachetta, M.L. Brown, V.F. Carrithers, J.K. Clark, J.M. DiTomaso, R.G. Lym, K.C. McDaniel, M.J. Renz, and P.M. Rice. 2004. Assessing the economic, environmental, and societal losses from invasive plants on rangeland and wildlands'. *Weed Tech.* 18, Invasive Weed Symposium, 1411-1416.

Dunkerley, DL. 1997. Banded vegetation: development under uniform rainfall from a simple cellular automaton model. *Plant Ecol.* 129: 103-111.

Eddy, T.A. and C.M. Moore. 1998. Effects of sericea lespedeza (*Lespedeza cunetea* (Dumont) G. Don) invasion on oak savannas in Kansas. *Wisconsin Acad. Sci. Arts Lett.* 86: 57-62.

Ehrenfeld, J.G. 2003. Effects of exotic plant invasions on soil nutrient cycling processes. *Ecosystems*. 6: 503-523.

Elton, C.S. 1958. The ecology of invasion by animals and plants. Methuen: London.

Fechter, R. 2003. Sericea lespedeza: economics of control. Kansas State Univ. Agric Exp. Sta. And Coop. Ext. Serv., Manhattan.

Fick, W.H. and G.L. Kilgore. 2000. Herbicides and related control: a review. *In* Sericea lesdeza and the future of invasive species: a symposium with a look to the future. MF-2453. Kanas State Univ. Agricultural Experimental Station and Cooperative Extension Service.

Fortin, M. and J Gurevitch, 2001. Mantel Tests: Spatial structure in field experiments IN Design and Analysis of Ecological Experiments, Second Edition. Eds, S. Scheiner and J Gurevitch. Oxford University Press, New York.

Global Invasive Species Database. 2005. *Lespedeza cuneata*. Available from: http://www.issg.org/database/species/ecology.asp?si=270. [Accessed 31 March 2008].

Gordon, K. 2003. Weed Eaters. Hay and Forage Grower. Retrieved June 20, 2006 from <http://www.lexisnexis/>

Gotelli, N.J. and A.M Ellison. 2004. *A Primer of Ecological Statisitcs.* Sinauer Associates, Inc., Sutherland, Massachussetts.

Greig-Smith, P. 1979. Pattern in vegetation. *J. Ecol*. 67: 755-779.

Grekul, C.W., D.E. Cole, and E.W. Bork. 2005. Canada thistle (*Cirsium arvense*) and pasture forage responses to wiping with various herbicides. *Weed Tech*. 19(2): 298-306.

Grevstad, F.S. 2005. Simulating control strategies for a spatially structured weed invasion: *Spartina alterniflora* (Loisel) in Pacific Coast estuaries. *Biol. Invasions*. 7: 665-677.

Grigulis, K., Sheppard, A.W., Ash, J.E., & Groves, R.H. 2001. The comparative demography of the pasture weed *Echium plantagineum* between its native and invaded ranges. *J. Appl. Ecol.* 38: 281-290.

Harrison, S., J.B. Grace, K.F. Davies, H.D. Safford, and J.H. Viers. 2006. Invasion in a diversity hotspot: exotic cover and native richness in the Californian serpentine flora. *Ecology.* 87(3): 695-703

Heisel, T.C.S. and A.M. Walter. 1999. Whole-field experiments with site-specific weed management. *In:* Proceedings Precision Agriculture 1999 Conference (ed. J.V. Stafford), Odense, Denmark. 759-768.

Higgins, S.I., D.M. Richardson and R.M. Cowling. 2001. J. Appl. Ecol. 38: 571-584.

Hooftman, D.A.P., J.G.B. Oostermeijer, and J.C.M. den Nijs. 2006. Invasive behavior of Lactuca serriola (Asteracea) in the Netherland: Spatial distribution and ecological amplitude. *Basic Appl. Ecol.* 7(6): 507-519.

Hoveland, C.S. and E.D. Donnelly. 1985. The Lespedezas. Pages 128-135 *in* M.E. Heath, R.F. Barnes, and D.S. Metcalfe, eds. Forages: The Science of Grassland Agriculture. Ames, IA: Iowa State University Press.

Huenneke, L.F. and P.M. Vitousek. 1990. Seedling and clonal recruitment of the invasive tree *Psidium cattleianum*: implications for the management of native Hawaiian forests. *Biol. Cons*. 53: 199-211.

Humston, R., D.A. Mortensen, and O.N. Bjornstad. 2005. Anthropogenic forcing on the spatial dynamics of an agricultural weed: the case of the common sunflower. *J. Appl. Ecol*. 42: 863-872.

Jäkäläniemi, A, J. Tuomi, P. Siikamäki and A Kilpiä. 2005. Colonization-extinction and patch dynamics of the perennial riparian plant, *Silene tatarica*. *J. Ecol*. 93: 670-680.

Jordan, M. and B. Jacobs. 2002. Monitoring effects of Roundup application for control of cypress spurge (*Euphorbia cyparissias*) and Chinese lespedeza (*Lespedeza cuneata*) on Long Island, NewYork. The Nature Conservancy's

Wildland Invasive Species Team. University of California, Davis, California. Retrieved from http://tncweeds.ucdavis.edu/moredocs/eucyp01.hmtl on 15 November 2005.

Jordan, M.J., B. Lund and W.A . Jacobs. 2002. Effects of mowing, herbicide, and fire on *Artemisia vulgaris*, *Lespedeza cuneata*, and *Euphorbia cyparissias* at the Hempstead Plains Grassland, Long Island, New York. The Nature Conservancy's Wildland Invasive Species Team. University of California, Davis, California. Retrieved from http://tncweeds.ucdavis.edu/esadocs/lespcune.hmtl on 15 November 2005.

Kansas Department of Agriculture Plant Protection and Weed Control Program. 2004. Sericea lespedeza (*Lespedeza cuneata*) Official Control Program. Retrieved from http://www.accesskansas.org/ on 15 November 2005.

Kapustka, L.A. 2005. Assessing ecological risksat the landscape scale: opportunies and technical limitations. Ecology and Society 10(2): 11. [online] URL: http://www.ecologyandsociety.org/vol10/iss2/art11/

Kéry, M. 2004. Extinction rate estimates for plant populations in revisitation studies: importance of detectability. *Cons. Biol*. 18: 570-574.

Kéry, M. and K.B. Gregg. 2003. Effects of life-state on detectability in a demographic study of the terrestrial orchid *Cleistesbifaria*. J. Ecol. 91: 265-273.

Kéry, M. K.B. Gregg and M. Schaub. 2005. Demographic estimation methods for plants with unobservable life-states. *Oikos*. 108: 307-320.

Kleijn, D. and G.I.J. Snoeijing. 1997. Field boundary vegetation and the effects of agrochemical drift: botanical change caused by low levels of herbicide and fertilizer. *J. Appl. Ecol.* 34: 1413-1425.

Kluth, S., A. Kruess, and T. Tscharntke. 2003. Influence of mechanical cutting and and pathogen application on the performance and nutrient storage of *Cirsium arvense. J. Appl. Ecol*. 40: 334-343.

Koger, C.H., J.F. Stritzke and D.C. Cummings. 2002. Control of sericea lespedeza (*Lespedeza cuneata*) with triclopyr, fluroxypyr, and metsulfuron. *Weed Technol.* 16: 893-900.

Lawes, R.A., H.T. Murphy, A.C. Grice. 2006. Comparing agglomerative clustering and three weed classification frameworks to assess the invasiveness of alien species across spatial scales. *Div. and Distrib.* 12: 633-644.

Lehtila, K. and K. Syrjanen. 1995. Compensatory responses of 2 *Melampyrum* species after damage. Functional Ecol. 9: 511-517.

Lennartsson, T. and J.G.B. Oostermeijer. 2001. Demographic variation and populations viability in *Gentianella campestris*: effects of grassland management and environmental stochasticity. *J. Ecol.* 89(3): 451-463.

Lesica, P. and E.E. Crone. 2007. Causes and consequences of prolonged dormancy for and iteroparous geophyte, *Silene spaldingii*. J. Ecol. 95: 1360-1369.

Lesica, P. and S. Miles. 2001. Tamarisk growth at the northern margin of its naturalized range in Montana, USA. *Wetlands* 21: 240-246.

Lodge, D.M., S. Williams, H.J. MacIsaac, K.R. Hayes, B. Leung, S. Reichard, R.N. Mack, P.B.Moyle, M. Smith, D.A. Andow, J.T. Carlton, and A. McMichael. 2006. Biological invasions: recommendation for U.S. policy and management. *Ecol. Appl.* 16(6): 2035-2054.

Logan, R.H., C.S. Hoveland, and E.D. Donnelly. 1969. A germination inhibitor in the seedcoat of sericea (*Lespedeza cuneata* (Dumont) G. Don). *Agron. J.* 61: 265-266.

Lloyd, M. 1967. Mean Crowding. *J.Animal Ecol*. 36: 1-30.

MacDougall, A.S. and R. Turkington. 2004a. Relative importance of suppression-based and tolerance-based competition in an invaded oak savanna. *J. Ecol.* 92: 422-434.

MacDougall, A.S. and R. Turkington. 2004b. Are invasive species the drivers or the passengers of changes in degraded ecosystems? *Ecology.* 86(1): 42-55.

Magadlela, A.M., M.E. Dabaan, W.B. Bryan, E.C. Prigg, J.G. Skousen, G.E. Dsouza, B.L. Arbogast and G. Flores. 1995. Brush clearing on hill and pasture with sheep and goats. *J. Agron. And Crop Sci.* 174(1): 1-8.

Marrs, R.H. and A.J. Frost. 1997. A microcosm approach to the detection of the effects of herbicide spray drift in plant communities. *J. Envir. Manage.* 50(4): 369-388.

Marshall, E.J.P. 1988. Field-scale estimates of grass weed populations in arable land. *Weed Research* 28(3): 191-198.

Masters, R.A. and R.L. Sheley. 2001. Invited synthesis paper: principles and practices for managing raneland invasive plants. *J. Range Manage.* 54: 502-517.

Masters, R.A. and R.L. Sheley. 2001. Invited synthesis paper: principles and practices for managing raneland invasive plants. *J. Range Manage.* 54: 502-517.

May, G. and R. Jones. 2000. Sericea lespedeza invasion and control: a preliminary economic impact estimate. *In* Sericea lesdeza and the future of invasive species: a symposium with a look to the future. MF-2453. Kanas State Univ. Agricultural Experimental Station and Cooperative Extension Service.

Melgoza, G., R.S. Nowak, and R.J. Tausch. 1990. Soil water exploitation after fire: competition between *Bromus tectorum* (cheatgrass) and two native species. *Oecologia* 83: 7-13.

Meyer, A.H. and B Scmid. 1999a. Experimental demography of the old-field perennial *Solidago altissima*: the dynamics of the shoot population. *J. Ecol.* 87: 17-27.

Meyer, A.H. and B. Schmid. 1999b. Seed dynamics and seedling establishment in the invading perennial *Solidago altissima* under different experimental treatments. *J. Ecol.* 87(28-41).

Minchinton, T.E., J.C. Simpson and M.D. Bertness. 2006. Mechanisms of exclusion of native coastal marsh plants by an invasive grass. *J. Ecol*. 94: 342-354.

Moody, EM and RN Mack. 1988. Controlling the spread of plant invasions: the importance of nascent foci. *J. Appl Ecol.* 25: 1009-1021.

Moody-Weis, J. and H.M. Alexander. 2007. The mechanisms and consequences of seed bank formation in wild sunflowers (*Helianthus annuus*). *J. Ecol.* 95(4): 851-864.

Moog, D., P. Poschold, S. Kahmen, and K.-F. Schreiber. 2002. Comparison of species composition between different grassland management treatments after 25 years. *Appl. Veg. Sci.* 5: 99-106.

Mooney, H.A. and R.J. Hobbs, ed. 2005. Invasive species in a changing world: the interaction between global change and invasives. *in* H.A. Mooney, R.N. Mack, J.A. McNeely, L.E. Neville, P.J. Schei and J.K. Waage eds. Invasive Alien Species: a New Synthesis. Washington, DC: Island Press.

Mosjidis, J.A. 1990. Daylength and temperature effects on emergence and early growth of sericea lespedeza. *Agron J.* 82: 923-926.

Munger, Gregory T. 2004. Lespedeza cuneata. In: Fire Effects Information System, [Online]. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (Producer). Available: http://www.fs.fed.us/database/feis/ [Accessed 31 March 2008].

National Research Council. 2000. Incorporating science, economics, and sociology in developing sanitary and phytosanitary standards in international trade. National Academy Press, Washington D.C.

Nichols, J.D. 1992. Capture-recapture models: Using marked animals to study population dynamics. *BioScience*. 42: 94-102.

Obermeyer, B., J. Davidson and G. Kilgore. 2001. Sericea lespedeza and herbicides: cost effective controls. MF-2531. Kansas State University Agricultural Experimental Station and Cooperative Extension Service.

Ohlenbusch, P.D. and T. Bidwell. 2001. Sericea lespedeza: history, characteristics, and identification. MF-2408. Kanas State University. Agricultural Experimental Station and Cooperative Extension Service.

Olden, J.D., N.L.Poff, M.R. Douglas, M.E. Douglas and K.D. Fausch. 2004. Ecological and evolutionary consequences of biotic homogenization. *TREE*. 19(1): 18-24.

Pande, A., C.L. Williams, C.L. Lant and D.J. Gibson. 2007. Using map algebra to determine the mesoscale distribution of invasive plants: the case of *Celastrus orbiculatus* in Southern Illinois, USA. *Biol. Invasions* 9(4): 419-431.

Panetta, F.D. and R.P. Randall. 1993. Herbicide performance and the control of *Emex australis* in an annual pasture. *Weed Research*. 33: 345-353.

Parker, I.M., D. Simberloff, W.M. Lonsdale, K Goodell, M. Wonham, et al. 1999. Imapct: Toward a framework for understanding the ecological effects of invaders. *Biol. Invasions* 1:3-19.

Pauchard, A, P. Alaback, and E. Edlund. 2003. Plant invasions in protected areas at multiple sacels: *Linaria vulgaris* (Scrophulariaceae) in the West Yellowstone area. *West. N. Am. Nat.* 63: 416-428.

Peterson, AT, M. Papas, and DA Kluza. 2003. Predicting the potential invasive distributions of four alien plant species in North America. *Weed Science* 51(6): 863-868.

Petersen, J.C. and N.S. Hill. 1991. Crop quality and utilization. *Crop Sci*. 31: 827-832.

Pieters, A.J. 1950. Sericea and other perennial lespedezas for forage and soil conservation. U.S. Dept. Agric.Circ. 863.

Pimentel, D., R. Zuniga, and D. Morrison. 2005. Update on the environmental and economic costs associated with alien-invasive species in the United States. *Ecol Econ.* 52: 273-288.

Prater, M.R. D. Obrist, J.A. Arnone and E.H. DeLucia. 2006. Net carbon exchange and evapotranspiration in postfire and intact sagebrush communities in the Great Basin. *Oecologia* 146: 595-607.

Price, C.A. and J.F. Weltzin. 2003. Managing non-native pant populations through intensive community restoration in Cades Coves, Great Smoky Mountains National Park, U.S.A. *Restor. Ecol.* 11(3): 351-358.

Provencher, L, T.A. Forbis, L. Frid, G. Medlyn. 2007. Comparing alternative management strategies of fire, grazing, and weed control using spatial modeling. *Ecol. Mod.* 209: 249-263.

Purves, D.W. and R. Law. 2002. Fine-scale spatial structure in a grassland community: quantifying the plant's-eye view. *J. Ecology* 90: 121-129.

Puth, L.M. and D.M Post. 2005. Studying invasions: have we missed the boat? *Ecol. Letters* 8: 715-721.

Pyšek, P., V. Jarošík, J. Müllerová, J. Pergl and J. Wild. 2008. Comparing the rate of invasion by *Heracleum mantegazzianum* at continental, regional and local scales. *Diversity Distrib.*14: 355-363.

Quinn, G. and M. Keough, 2002. Experimental design and data analysis for biologists. Cambridge University Press.

R Development Core Team, 2006. R: A Language and Environment for Statistical Computing. http://www.R-project.org. R Foundation for Statistical Computing. Vienna, Austria.

Rew, L.J. and R.D. Cousens. 2001. Spatial distribution of weeds in arable crops: are current sampling and analytical methods appropriate? *Weed Research* 41: 1-18.

Rice, P.M., J.C Toney, D.J. Bedunah, and C.E. Carlson. 1997.Plant community diversity and growth form responses to herbicide application for control of *Centaurea maculosa*. *J. Appl. Ecol*. 34: 1397-1412.

Rinella, M.J., J.S. Jacobs, R.L. Sheley and J.J. Borkowski. 2001. Spotted knapweed response to season and frequency of mowing. *J. Range Manage.* 54: 52-56.

Sakai, A. K, F.W. Allendorf, J.S. Holt, D.M. Lodge, J. Molofsky, K.A. With, S. Baughman, R.J. Cabin, J.E. Cohen, N.C. Ellstrand, D.E. McCauley, P. O'Neil, I.M. Parker, J.N. Thompson, and S.G. Weller. 2001. The population biology of invasive species. *Annu. Rev. Ecol. Syst*. 32: 305-332.

Sala, O.E., F.S. Chapin III, J.J. Armesto, E. Berlow, J. Bloomfield, R. Dirzo, E. Huber-Sanwald, L.F. Huenneke, R.B. Jackson, A. Kinzig, R. Leemans, D.M. Lodge, H.A. Mooney, M. Oesterheld, N.L. Poff, M.T. Sykes, B.H. Walker, M. Walker, and D.H. Wall. 2000. Global biodiversity scenarios for the year 2100. *Science* 287: 1770-1774.

Sanchez-Flores, E. 2007. GARP Modelling of natural and human factors affecting the potential distribution of the invasives *Schismus arabicus* and *Brassica toumefortii* in El Pinacate y Gran Desierto de Altar Biosphere Reserve. *Ecol. Mod.* 204 (3-4): 457-474.

Schott G.W. and S.P Hamburg. 1997. The seed rain and seed bank of an adjacent native tallgrass prairie and old field. *Can J. Bot*. 75:1-7.

Shaw, D.R. 2005. Translation of remote sensing data into weed management decisions. *Weed Science*: 53:264-273.

Shefferson, R.P. 2006. Survival costs of adult dormancy and the confounding influence of size in lady's slipper orchids, genus *Cypripedium*. *Oikos*. 115: 253-262.

Shefferson, R.P., B.K Sandercock, J. Propoer, and S.R. Beissinger. 2001. Estimating dormancy and survival of a rare herbaceous perennial using mark-recapture models. Ecology 82: 145-156.

Sheley, R.L., J.S. Jacobs and M.F. Carpinelli. 1998. Distribution, biology, and management of diffuse knapweed (*Centaurea diffusa*). *Weed Technol*. 12: 353-362.

Sheley, R.L., S. Kedzie-Webb, and B.D. Maxwell. 1999. Integrated weed management on rangeland. Pages 57-68 *in* R.L. Sheley and J.K. Petroff, eds. *Biology and Management of Noxious Rangeland Weeds*. Oregon State University Press. Corvallis.

Shinn, S.L. and D.C. Thill. 2002. The response of yellow starthistle (*Centaurea solstitialis*), annual grasses, and smooth brome (*Bromus inermis*) to imazapic and picloram. *Weed Tech*. 16(2): 366-370.

Shuster, W.D., C.P. Herms, M.N. Frey, D.J. Doohan, and J. Cardina. 2005. Comparison of survey methods for an invasive plant at the subwatershed level. *Biol.Invasions*: 7(3): 393-403.

Silliman, S., and A.D. Maccarone. 2005. Distribution, infestation, and habits of serecia lespedeza (*Lespedeza cuneata*) in Cowley County, Kansas. *Transactions of the Kansas Academy of Science:* 108(3/4): p. 83-92.

Simberloff, D. 2003. How much information on population biology is needed to manage introduced species? *Cons. Biol.* 17(1): 83-92.

Slade, N.A., H.M. Alexander, and W.D. Kettle. 2003. Estimation of populations size and probabilities of survival and detection in Mead's milkweed. Ecology 84: 791-797.

Smous, P.E., J.C. Long, R.R. Sokal. 1986. Multiple regression and correlation extensions of the Mantel test of matrix correspondence. *System. Zool.* 35: 627-632.

Stevens, S. 2002. Element Stewardship Abstract for *Lespedeza cuneata* (Dumont-Cours.) G. Don Sericea Lespedeza, Chinese Bush Clover. The Nature Conservancy's Wildland Invasive Species Team. University of California, Davis, California. Retrieved from http://tncweeds.ucdavis.edu/esadocs/documnts/lespcun.pdf on March 30 2008.

The Nature Conservancy. 2001. Sericea lespedeza. *In* Plains Keeper newsletter, Fall/Winter 2001. The Nature Conservancy, Kansas Chapter, Topeka.

Theoharides, A., and J.S. Dukes. 2007. Plant invasion across space and time: factors affecting nonindigenous species success during four stages of invasion. *New Phytol.* 176: 256-273.

Thompson, M.J. 1996. Winter foraging response of elk to spotted knapweed removal. *Northwest Sci.*70: 10-19.

Turkington, R., and J.L. Harper. 1979. The growth, distribution, and neighbor relationships of *Trifolium repens* in permanent pastures, IV. Fine scale biotic differentiation. *J. Ecol.* 67: 244-254.

Turnbull, LA, DA Coomes, DW Purves, and M Rees. 2007. How spatial structure alters population and community dynamics in a natural plant community. *J. Ecology* 95: 79-89.

United States Fish and Wildlife Service. 2004. Invasive species control activities: Mountain-Prairie Region Partners for Wildlife. Retrieved June 21, 2006 from http://www.invasives.fws.gov/

USDA, NRCS. 2005. *The PLANTS Database*, Version 3.5. Data compiled from various sources by Mark W. Skinner. National Plant Data Center, Baton Rouge, LA 70874-4490 USA. Retrieved March 1, 2008 from http://plants.usda.gov

Valverde, T. and J. Silvertown. 1997. A metapopulation model for *Primula vulgaris*, a temperate forest understory herb. *J.Ecol*. 85: 193-210.

Verrier, F.J. and J.B. Kirkpatrick. 2005. Frequent mowing is better than grazing for the conservation value of lowland tussock grasssland [sic.] at Pontville, Tasmania. *Austral Ecol.* 30: 74-78.

Vitousek, P.M. and L.R. Walker. 1989. Biological invasion by *Myrica faya* in Hawai'i: plant demography, nitrogen fixation, ecosystem effects. *Ecol. Monogr*. 59(3): 247-265.

Vitousek, P.M., C.M. D'Antonio, L.L. Loope, and R. Westerbrooks. 1996. Biological invasions as global environmental change. *Amer Sci*. 84: 468-478.

Wadsworth, R.A., Y.C. Collingham, S.G. Willis, B. Huntly, and P.E. Hulme. 2000. Simulating the spread and management of alien riparian weeds: are they out of control? *J. Appl. Ecol*. 37 (Suppl. 1) 28-38.

Wallace, A., R.A. Lancaster, and N.L. Hill, 1998. Application of non-selective herbicides during flowering of pasture legumes can reduce seed yield and alter seed characteristics. *Aust J. Exp. Agric*. 38(6): 583-594.

Wilcove, D.S., D. Rothstein, J. Dubow, A. Phillips, and E. Losos. 1998. Quantifying threats to imperiled species in the United States. *BioScience* 48: 607-615.

Williams, A.P. and E.R. Hunt, Jr. 2002. Estimation of leafy spurge cover from hyperspectral imagery using mixture tuned matched filtering. *Remote Sens. Environ*. 82: 466-456.

Williamson. 1996. *Biological Invasions*. Chapman and Hall, London.

Wilson, M.V. and D.L. Clark. 2001. Controlling invasive *Arrhenatherum elatius* and promoting native prairie grasses through mowing. *Appl. Veg. Sci.* 4(1): 129-138.

Zamora, D.L. and D.C. Thill. 1999. Early detection and eradication of new weed infestations. Pages 73-84 *in* R.L. Sheley and J.K. Petroff, eds. Biology and Management of Noxious Rangeland Weeds. Corvallis OR: Oregon State University Press.

Zhu, L., O.J Sun, W.G. Sang, Z.Y. Li, and K.P. Ma. 2007. Predicting the spatial distribution of an invasive plant species (*Eupatorium adenophorum*) in China. *Land. Ecol.* 22(8): 1143-1154.

APPENDIX

LLOYD’S MEAN CROWDING [Adapted from Lloyd (1967)]

This index quantifies the mean neighborhood density (across individuals within a quadrat) relative to the overall density of the species. Standard statistics are used to calculate the sum (*N*), sum of squares (*SS*), mean density (*m*) and variance (σ^2) for the stems or individuals within all the quadrats (j=1,2,…,Q) in the field.

$$N = \sum_{j=1}^{Q} x_j \qquad (1) \qquad\qquad SS = \sum_{j=1}^{Q} x_j^2 \qquad (2)$$

$$m = \sum_{j=1}^{Q} x_j \Big/ Q = \frac{N}{Q} \qquad (3) \qquad\qquad \sigma^2 = \frac{\sum_{j=1}^{Q} x_j^2 - \left(\sum_{j=1}^{Q} x_j\right)^2 \Big/ Q}{Q} \qquad (4)$$

Lloyd (1967) referred to the average neighborhood density experienced by individuals ($\overset{*}{m}$) as ‘mean crowding’ and calculated its value using the equation:

$$\overset{*}{m} = \frac{\sum_{J=1}^{Q} x_j^2}{\sum_{j=1} x_j} - 1 \qquad (5).$$

Substituting equations (1) an (2) into equation (5) more clearly illustrates the relationship between $\overset{*}{m}$ and *m*.

$$\overset{*}{m} = m + \left(\frac{\sigma^2}{m} - 1\right) \qquad (6)$$

If individuals and/or stems are randomly distributed among the grid cells in the field then the variance and the mean density would be equal, the quantity in the parentheses would disappear, and $\overset{*}{m}$ and m would be equal. Lloyd emphasized the importance of using $\overset{*}{m}$ because its value is not affected by empty quadrats and thus it provides information on individuals.