

PATTERNS AND PROCESSES OF INVASION OF THE EXOTIC PLANT *MARRUBIUM
VULGARE* (HOREHOUND) IN A MIXED GRASS PRAIRIE

by

ELIZABETH ANN GASTINEAU

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Major Professor
David C. Hartnett

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Abstract

Invasive plants pose a global threat by changing natural communities and ecosystems in ways that may be irreversible. *Marrubium vulgare* L. (horehound), native to Eurasia, is an invasive exotic plant found throughout the United States. Little is known about *M. vulgare* in the U.S. and this study aimed to understand the basic biology, habitat, and population dynamics of *M. vulgare* in its invasive habitat as well as the role of disturbance in the invasions. Wind Cave National Park (WCNP), an area comprising ponderosa pine and mixed grass prairie vegetation types, was used as the site for this study. In a GPS and GIS mapping study, *M. vulgare* was found to be significantly associated with prairie dog towns, an *Aristida purpurea* - *Dyssodia papposa* (threeawn and fetid marigold) vegetation community (a vegetation type found exclusively on prairie dog towns), and certain types of loamy soils. *M. vulgare* was rarely found off of prairie dog towns and then only in other disturbed areas such as bison trails or tree falls. Population studies showed *M. vulgare* populations were mostly stable or slightly decreasing in density (though not significantly) from 2010 to 2011; however, a few of the populations did increase dramatically in density from 2010 to 2011. *M. vulgare* populations existed in high densities (78.3-322.9 ramets/m²) and in low densities (0.1-2.2 genets/m²) throughout WCNP. Disturbances including prairie dog burrows, bison trails, prairie dog and bison presence, mowing, and percent cover of bare ground were measured in relation to population dynamics. While *M. vulgare* populations were disturbance dependent, there was no clear relationship between disturbances and population dynamics. Examination of *M. vulgare* life history traits found that while *M. vulgare* had relatively low biomass allocation to reproduction as compared to native perennial prairie species, *M. vulgare* produced an extremely high number of small seeds (estimated 1487/plant). Seedling establishment rates were also high. While not quantified, *M. vulgare* appears to be effectively dispersed through bison epizoochory. These results help to inform management of *M. vulgare* populations: minimizing disturbance, decreasing propagule supply, and minimizing dispersal may help to reduce *M. vulgare* invasions.

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Chapter 1 - Basic biology and population dynamics of the invasive plant *Marrubium vulgare* (horehound) in a mixed grass prairie

Abstract

Exotic invasive plants threaten natural communities in ways such as impairing ecosystem function or displacing native plants and changing plant community structure and composition. This study focuses on *Marrubium vulgare* (horehound), an invasive plant from Eurasia, found in the Black Hills of South Dakota. Reproductive life history traits and population densities were examined through two growing seasons in 2010 and 2011. Disturbance factors were also quantified to understand relationships with population dynamics. *M. vulgare* traits and populations were compared with other populations from the literature. *M. vulgare* has a relatively low allocation to reproduction as compared to other native prairie forbs; however, *M. vulgare* produces a very large number of small seeds (estimated 1487/plant). Seedling establishment rates are also very high (189-1980/m²) and seedling densities mostly increased from 2010 to 2011. Further, *M. vulgare* appears to be efficiently dispersed through epizoochory by bison. *M. vulgare* population densities were mostly stable or slightly decreasing from 2010 to 2011. However, two sites increased dramatically in ramet or genet number from 2010 to 2011. Site disturbances included prairie dog activity, bison activity, and mowing. *M. vulgare* populations are disturbance dependent, however these disturbances were difficult to measure in relation to changes in population dynamics. *M. vulgare* plant cover shows a negative relationship with native plant cover. *M. vulgare* plants throughout WCNP ranged in age from 1-5 years with

an average of 2.23 years. These results help to inform management of *M. vulgare* populations: minimizing disturbance, decreasing propagule supply, and minimizing dispersal may help to reduce *M. vulgare* invasions.

Introduction

Background on plant invasions

Exotic invasive plants are nonnative plants that are able to successfully establish and reproduce in a natural community or ecosystem (Richardson et al. 2000). Plant and other biological invasions have been cited as one of the major components of global environmental change caused by humans (Vitousek et al. 1997). Yearly estimated costs of environmental damage due to invasive plant species are around \$36 billion (Pimentel et al. 2000, Pimentel et al. 2005).

Invasive plants pose a global threat by changing natural communities and ecosystems in ways that may be irreversible (Mack et al. 2000). Once established, exotic invasive plant species may displace native plants, changing the structure of the native plant community. These changes then have the potential to impair basic ecosystem function. For example, *Bromus tectorum* is an invasive annual grass that has changed the fire regime in the shrub-steppes of the western United States by increasing the horizontal continuity of fuel in the system, which leads to increased fire frequency and extent (Brooks et al. 2004). This in turn harms animals, such as sage grouse (*Centrocercus urophasianus*), that use this habitat (Brooks et al. 2004, Knick et al. 2003, Whisenant 1990). Biodiversity is also affected by plant invasions. While introducing a new species may increase biodiversity at a local scale, on larger scales these invasive species can

result in biodiversity loss (Davis 2003). As plant species become more widespread, they decrease the amount of habitat and resources available for other species, sometimes leading to the decline (and sometimes extinction) of other species (Davis 2003). The tree mallow (*Lavatera arborea*) is an example of an invasive plant causing biodiversity loss (van der Wal et al. 2008). On a small island in Scotland, *L. arborea* has caused a severe decrease in populations of seabirds including puffins (*Fractercula arctica*) and eider ducks (*Somateria mollissima*). Further, where *L. arborea* has invaded on the island, perennial grasses (*Festuca rubra* and *Holcus lanatus*) are less abundant than in areas where *L. arborea* has not invaded (van der Wal et al. 2008). Plant invasions not only can change habitats and contribute to habitat loss, but can also cause changes in trophic interactions (Davis 2003).

There are many barriers exotic species must overcome to become invasive (Blackburn et al. 2011, Richardson et al. 2000). The species must first cross geographic barriers to arrive to a new location outside its native range. Once there, the species must be able to establish, reproduce and survive in the novel habitat. Finally, to become invasive, the species must be able to establish new populations through dispersal and inhabit a broader range of environmental conditions. In rare cases, the invasive may become an ecological transformer (Blackburn et al. 2011, Richardson et al. 2000). The grass *B. tectorum* mentioned above is an ecological transformer because it fundamentally changes the fire regime in the shrub-steppe system it has invaded (Brooks et al. 2004). While avoiding the establishment of an invasive plant species is the easiest way to protect an ecosystem, in many cases invasive species are already established. Understanding the basic biology, life history traits, and population dynamics of invasive plants helps us to develop management tools to diminish the environmental effects of invasions and consequently protect and restore natural communities and ecosystems.

Background on Marrubium vulgare

Marrubium vulgare L. (common horehound) is an exotic invasive perennial herb in the family Lamiaceae (Mint) in the United States (see Figure 1.1). The plant has erect stems with short, stout rhizomes and stands about 30-70 centimeters tall. Leaves are opposite, gray-green, serrate, and tomentose (Brooks 1986). A fruit with hooked spines encases the nutlets or seeds of *M. vulgare*. These hooked spines are bur-like and easily catch in animal fur, thus leading to easy dispersal of the plant by epizoochory (Young and Evans 1986). The plant has a bitter taste, and most livestock and wildlife avoid grazing on *M. vulgare* (Weiss et al. 2000). *M. vulgare* is cultivated for medicinal purposes and likely was introduced in the U.S. for this reason.

Originating from Eurasia, *M. vulgare* is now found in 46 of the 50 states (USDA Plants Database). A variety of agencies and areas identify *M. vulgare* as problematic. For example, *M. vulgare* is naturalized throughout the Great Basin area in arid and semiarid grasslands (Young and Evans 1986) and has been identified and mapped in numerous National Parks in Arizona (Halvorson and Guertin 2003, Mau-Crimmins et al. 2004). This species is also known to be invasive in other areas of the world. In Australia, *M. vulgare* is a huge problem and has been extensively studied as an invasive plant (Lippai et al. 1996, Weiss and Sagliocco 2000, Weiss et al. 2000). There, *M. vulgare* has infested over 26 million ha and decreases the availability of palatable vegetation in grazing lands (Weiss et al. 2000). Further, *M. vulgare* invasions threaten at least two rare native Australian plant species (Weiss et al. 2000).

Study rationale and objectives

Recently, *M. vulgare* has become problematic in the southern Black Hills of South Dakota. Starting in the early 2000s, *M. vulgare* was noticed forming large monotypic populations in the mixed-grass prairies on prairie dog towns within Wind Cave National Park (Beth

Burkhart, *pers. comm.*). This poses problems not only for the native vegetation, but also for the wildlife such as the black-tailed prairie dog (*Cynomys ludovicianus*), bison (*Bison bison*), and the endangered black-footed ferret (*Mustela nigripes*) that depend upon the mixed grass prairie for food and habitat.

Invasive plant species theory offers multiple and sometimes conflicting ideas for why invasive plant species are so successful and what life history traits may confer “invasiveness” (Rejmanek and Richardson 1996). Theory predicts colonizing traits such as an increase in reproductive effort and fecundity provide means for successful invasive qualities. For example, propagule pressure has been cited as an indicator of invasive potential (Colautti et al. 2006). Others predict superior competitive abilities, phenotypic plasticity, or the evolution of traits in a new environment as traits that confer “invasiveness” (Bakker and Wilson 2001, Blossey and Notzold 1995). Understanding these life history traits that may contribute to the invasiveness of *M. vulgare* in non-native habitats is imperative to inform management practices.

Studying the population dynamics of *M. vulgare* further informs management as it indicates whether a population is growing, declining, or stabilizing. Relating these dynamics with the influence of disturbance on *M. vulgare* success can also inform management practices. If disturbance plays a large role in *M. vulgare* success, targeting highly disturbed areas for *M. vulgare* removal or trying to minimize disturbance in certain areas to discourage *M. vulgare* is important.

This study has two main objectives: 1) to investigate life history strategies including fecundity and reproductive effort of *M. vulgare* in its invaded environment and 2) to quantify density and dynamics of *M. vulgare* populations in relation to disturbance. To pursue these objectives, we asked these questions: 1) Is *M. vulgare* successfully reproducing by seed? 2) Do

the patterns of reproduction vary between new foci of invasion and established stands of *M. vulgare*? 3) How do patterns of biomass allocation and reproduction in *M. vulgare* vary with population densities? 4) How does reproductive effort of *M. vulgare* compare to native perennial forbs in these invaded grasslands? 5) How do population densities and reproductive capabilities of *M. vulgare* in WCNP compare to those in native habitats and other non-native habitats (such as in Australia)? 6) Where do *M. vulgare* populations occur in WCNP? 7) Are populations increasing in WCNP, and, if so, at what rates? 8) Is *M. vulgare* a disturbance dependent species? 9) How does disturbance influence population density and growth? and 10) What age are the various populations in WCNP? Answers to these questions will help to understand the invasion of *M. vulgare* and provide insight into possible best management practices.

Methods

Study System

Northern mixed grass prairie

The northern mixed grass prairie extends from northern Nebraska through the Dakotas and north into Canada. The mixed grass prairie represents an ecotone between the shortgrass and tallgrass prairies and includes plant species from both types of prairies (Clements 1920).

Common grass species of the mixed grass prairie include big bluestem (*Andropogon gerardii*), little bluestem (*Schizachyrium scoparium*), western wheatgrass (*Pascopyrum smithii*), blue grama (*Bouteloua gracilis*), sideoats grama (*Bouteloua curtipendula*), and needlegrasses (*Stipa* sp.). Common forb species include fringed sage (*Artemisia frigida*), scarlet globe mallow (*Sphaeralcea coccinea*), and prairie coneflower (*Ratibida columnifera*). The mixed grass prairie

also supports a wide variety of animals including the black-tailed prairie dog (*Cynomys ludovicianus*), bison (*Bison bison*), pronghorn antelope (*Antilocapra americana*) and the endangered black-footed ferret (*Mustela nigripes*).

Wind Cave National Park

Wind Cave National Park (WCNP) is located within the southern Black Hills region of South Dakota (Figure 1.2). WCNP encompasses 28,295 acres of land about six miles north of Hot Springs, SD and has recently acquired an additional 5,555 acres. WCNP is known mainly for an extensive and complex limestone cave system, but is also home to ponderosa pine forest and mixed grass prairie vegetation. Fauna of WCNP comprise the animals mentioned above, including a local population of the endangered black-footed ferret (*M. nigripes*).

Invasion of *M. vulgare* in WCNP was first noticed in the early 2000s (Beth Burkhart, *pers. comm.*). Large monotypic stands of *M. vulgare* were seen forming on prairie dog towns at this time. The earliest known collected specimen of *M. vulgare* within WCNP was on June 20, 1993. The specimen was collected near a dam on Highway 87 (T5S, R5E, Sec 26, Custer County, South Dakota) in an area previously home to headquarters' buildings and roads (Wind Cave National Park Museum Collections/Herbarium). For this study, an *M. vulgare* voucher specimen was collected for the Kansas State University Herbarium (KSC).

M. vulgare life history trait measurements

Reproductive efforts of M. vulgare

M. vulgare aboveground biomass was collected along randomly placed transects within two sites in June 2010 in WCNP. Plants were collected in an area of high density *M. vulgare* on the Norbeck prairie dog town and in an area of low density *M. vulgare* adjacent to the Norbeck

prairie dog town (some older prairie dog burrows were present at this site) (n=30 plants/site). Reproductive and vegetative structures were separated and dried in an oven at 60°C for at least 48 hours. Reproductive biomass included flowers and reproductive structures at the nodes. Vegetative biomass included all the stems and leaves. After drying, total plant aboveground biomass, reproductive biomass, and vegetative biomass was weighed (g). Proportions of biomass allocated to reproduction and vegetative growth were determined. Data distributions were determined using “proc Genmod” in SAS 9.2.1. Data did not follow a normal distribution, so a gamma distribution was used when running analyses. An ANOVA was used in “proc Glimmix” in SAS 9.2.1 to compare differences in reproductive biomass allocation between the two densities.

A literature search was conducted to obtain proportions of aboveground biomass allocated to reproductive effort for other perennial prairie forbs. The reproductive effort proportions gathered from the literature search were measured in a manner similar to this study. *M. vulgare* reproductive effort was compared to the reproductive effort of these other tallgrass native perennial forbs.

M. vulgare fecundity in WCNP and other habitats

M. vulgare plants were collected in July 2010 at peak flowering time and again in late August 2010 after seed set (n=60/collection). Total number of stems was counted for each plant and the number of flowering and non-flowering stems was recorded. The number of clusters of reproductive structures at each node on each stem was also counted. One cluster of reproductive structures occurred at each node. The number of flowers was counted on a sub-sample of clusters and stems (n=139 and n=30 respectively). After seed set, the number of seeds per cluster was counted on a sub-sample of clusters and stems (n=37 and n=10 respectively). The averages,

ranges, and standard deviations of these fecundity measurements were determined in R 2.12.1 (The R Development Team 2010).

Weiss and Sagliocco (2000) also conducted a study of *M. vulgare* plants that measured fecundity and other plant traits. This study examined *M. vulgare* plants in their native range of Cournonterral and La Crau, France and in two non-native habitats, Swifts Creek and Wyperfeld National Park, in Victoria, Australia. Weiss and Sagliocco (2000) measured plant density, mean height (cm), mean stem number, mean seed number/plant, mean number seeds/stem, and mean number of seedlings (m^2). *M. vulgare* measurements from WCNP were compared to these measurements in other habitats.

M. vulgare populations and disturbance

M. vulgare population density and dynamics

M. vulgare population densities were measured over two years (2010 and 2011) during the month of June. In high density, established populations of *M. vulgare*, where the plant community was strongly dominated by *M. vulgare* (hereafter referred to as “high density populations”), ramets were counted in randomly placed $1m^2$ quadrats ($n=15/site$). Seedlings were also counted in $\frac{1}{4} m^2$ quadrats ($n=15/site$) within the larger $1m^2$ quadrats. Four high density populations of *M. vulgare* were counted in four different sites. Each site represented a different prairie dog town within WCNP: East Bison Flats, Norbeck, Research Reserve, and Sanctuary (Figure 1.3). Ramet densities instead of genet densities were used due to the difficulty in distinguishing between individual *M. vulgare* genets in areas of high density. Other common plant species found within the populations of *M. vulgare* were also recorded. WCNP staff unexpectedly mowed the Norbeck study site in August 2010.

In more recently invaded areas of low *M. vulgare* density where the plant community was dominated by native species with *M. vulgare* plants interspersed throughout the native matrix (hereafter referred to as “low density populations”), the point quarter distance measurement method (Cottam and Curtis 1956) was used. Points were randomly selected by throwing a frisbee into a designated area. From the random point, four quadrants to the NW, NE, SW, and SE were determined using a compass and measuring tape. In each of the quadrants, the distance from the random point to the nearest *M. vulgare* plant was measured. The four distances were averaged for each random point. The following equation was used to determine the density of individual plants per square meter (n=20 random points/site):

$$\text{Density} = \frac{1}{(\text{mean point to plant distance})^2}$$

Densities were recorded for three separate sites representing distinct prairie dog towns: East Bison Flats, Research Reserve, and Sanctuary. Other plants nearest the *M. vulgare* plants were also recorded.

Because density data were not normally distributed, data distributions were determined using “proc Genmod” in SAS 9.2.1. Data for the high density populations fit a gamma distribution and data for the low density populations fit a negative binomial distribution, so these distributions were used when running analyses. A fixed effect model and Bonferroni t-tests were used in “proc Glimmix” in SAS 9.2.1 to compare either stem densities and seedling numbers between sites and years or genet densities between sites and years. Further, the correlation

between ramet numbers and seedling numbers was determined using “cor.test” and the Pearson method in R 2.12.1 (The R Development Team 2010).

Estimation of disturbance intensity

On each site for each population, disturbance measurements were also collected since disturbance is a factor cited in invasive spread (Mack et al. 2000). A transect was placed randomly through each site and a $\frac{1}{4}$ m² quadrat (n=10/site/year) was placed every five meters. The quadrats were used to determine percent cover of *M. vulgare*, other non-native plants, native plants, bare areas, and rocky areas. The lack of native plants, presence of non-native plants, and presence of bare areas can be signs of disturbance. Further, I recorded the presence and absence of prairie dogs, bison, prairie dog burrows, and bison trails at each site. Mowing was added as an additional disturbance after the 2010 mowing of the Norbeck site. Data distributions were determined using “proc Genmod” in SAS 9.2.1. Data did not follow a normal distribution, so a gamma or negative binomial distribution was used when running analyses. An ANOVA was used in “proc Glimmix” in SAS 9.2.1 to compare differences in horehound cover, other non-native plant cover, native plant cover, and bare ground cover in both the low and high density populations. Finally, the correlation between native cover and horehound cover was determined using “cor.test” and the Spearman method in R 2.12.1 (The R Development Team 2010).

M. vulgare herbchronology

M. vulgare plants were collected in April 2011 for herbchronology analysis in order to age various *M. vulgare* populations within WCNP (n=163). Herbchronology, the measuring of annual rings in roots of perennial forbs, has been used in other studies to understand population age structure and plant invasion ecology (Dietz and Ullmann 1998, Perkins et al. 2006).

Assuming the largest plants would also be the oldest plants, the five largest plants were collected on the following prairie dog towns in WCNP: Research Reserve, Norbeck, North Boundary, East Bison Flats, Sanctuary, Southeast, and Pringle. Also, transects were randomly placed on the high density populations of Sanctuary, Norbeck, Research Reserve, and East Bison Flats, and the first 30 plants encountered on each transect were collected.

A number of methods were tried to slice and process roots for ring analysis. *M. vulgare* roots proved to be very woody and difficult to slice, so the best method found for *M. vulgare* ring analysis is as follows. Roots were stored at 9°C until processed. Sections of roots were cut using a floral shears or scissors. Roots were examined when dry, after rehydration, and after staining with toluidine blue 0.05%. Depending on the root, some combination of the three methods worked best. Roots were examined under a dissecting scope at varying magnifications. Some roots had obvious rings while other rings were less clear. Rings for each root were counted and recorded; conservative numbers were used for roots with less clear rings.

Results

M. vulgare life history traits

Reproductive effort and comparison to native forbs

Total aboveground biomass allocated to reproduction was 15%. Allocation to vegetative structures was 85%. A comparison of reproductive efforts of *M. vulgare* to other native prairie forbs shows *M. vulgare* generally allocates a lower amount of resources to reproductive efforts than do other native prairie plants (Table 1.1).

Reproductive effort at low and high density

Biomass allocation to reproduction was significantly different between high and low density populations ($F=7.81$, $P=0.007$, Figure 1.4). In areas of high density *M. vulgare*, the average proportion of aboveground biomass allocated to reproductive efforts was greater than that for low density populations (Figure 1.4).

Fecundity and comparison to other habitats

See Table 1.2 for a summary of flowers, seeds, reproductive clusters, and stems per plant as well as plant height. Using these summary statistics, the number of flowers per plant and seeds per plant can be calculated: on average, there were 693.6 flowers/plant and 1487.2 seeds/plant. Table 1.3 shows comparisons of *M. vulgare* fecundity and other measurements between *M. vulgare* in WCNP and France and Australia. Generally *M. vulgare* plants from WCNP produce more seeds and seedlings and were taller than plants from other locations.

Seedling establishment

There were differences in seedling densities among sites and between years (Figure 1.5). Both year and site were significant effects for seedlings numbers ($F=30.37$, $P<0.001$ and $F=18.04$, $P<0.001$ respectively). There was also a significant effect of time x site interaction ($F=10.20$, $P<0.001$). Seedling populations generally increased except for on the Norbeck site. Population growth rates (λ) for seedlings were 0.84 on Norbeck, 1.50 on Sanctuary, 2.25 on Research Reserve and 5.60 on East Bison Flats.

M. vulgare population dynamics and disturbance

High density population measurements

There were differences in ramet density among sites and between years (Figure 1.6). Site effect was significant for ramet numbers ($F=12.93$, $P<0.001$); however, year was not a significant effect ($F=0.20$, $P=0.658$). There was also a significant effect of time x site interaction ($F=12.41$, $P<0.001$). Ramet populations generally decreased except for on the Norbeck site. Ramet population growth rates (λ) for East Bison Flats was 0.62, for Norbeck was 2.64, for Research Reserve was 0.69, and for Sanctuary was 0.75.

Plants found on one or more sites in association with *M. vulgare* included *Rosa arkansana* (rose), *Artemisia frigida* (prairie sagewort), *Verbena bracteata* (bigbract verbena), *Lappula* sp. (stickseed), *Pascopyrum smithii* (western wheatgrass), *Hedeoma hispida* (rough false pennyroyal), *Aristida purpurea* (purple threeawn), *Descurainia sophia* (herb sophia), and *Tradescantia* sp. (spiderwort).

There was no significant correlation between ramet and seedling densities among sites ($R^2=0.01$, $P=0.792$). There is, however, a trend between ramet and seedling densities. On Norbeck, when ramets increased from one year to the next, seedlings decreased. On all other sites, when ramet densities decreased, seedling densities increased (Figure 1.5 and Figure 1.6).

Low density population measurements

There were some differences in genet numbers between sites and between years (Figure 1.7). There was a significant site effect for genet densities ($F=4.33$, $P=0.015$); however, there was not a significant year effect ($F=1.35$, $P=0.247$). There was also a significant year x site interaction ($F=4.21$, $P=0.017$). Genet populations generally declined except for on the East Bison

Flats site. Genet population growth rate was 0.67 for both Research Reserve and Sanctuary and 17.05 for East Bison Flats.

Common plants found on one or more sites included *Rosa arkansana* (rose), *Artemisia frigida* (prairie sagewort), *Lappula* sp. (stickseed), *Pascopyrum smithii* (western wheatgrass), *Stipa* sp. (needlegrass), *Dyssodia papposa* (fetid marigold), *Oxalis stricta* (common yellow oxalis), *Aristida purpurea* (purple threeawn), *Artemisia ludoviciana* (white sagebrush), *Hedeoma hispida* (rough false pennyroyal), *Bouteloua gracilis* (blue grama), *Asclepias verticillata* (whorled milkweed), and *Sphaeralcea coccinea* (scarlet globemallow).

Disturbance measurements and relationships with population dynamics

Cover of horehound, non-native plant cover, bare ground, and native plants differed between sites and years. The average percentage of horehound cover, non-native plant cover, bare ground, and native plant cover are summarized in Table 1.4. There were no significant differences in bare ground cover between sites for high density sites ($F=0.24$, $P=0.867$). There was a significant difference in horehound cover between high density sites ($F=5.45$, $P=0.002$). Sanctuary had significantly lower horehound cover than both Norbeck and East Bison Flats ($P=0.012$ and $P=0.009$ respectively). There was a significant difference in native cover between high density sites ($F=10.40$, $P<0.001$). Sanctuary and Research Reserve had significantly higher amounts of native cover than Norbeck and East Bison Flats (all $P<0.030$). Non-native cover was not significantly different between sites ($F=1.54$, $P=0.212$). For low density populations, there were no significant differences in horehound cover ($P=1.000$). There was a significant difference between sites for native cover ($F=12.70$, $P<0.001$), non-native cover ($F=8.19$, $P=0.002$), and bare ground ($F=14.71$, $P<0.001$). East Bison Flats had significantly higher bare cover than Sanctuary and Research Reserve (all $P<0.001$). Research Reserve had significantly higher cover of native

plants than did East Bison Flats and Sanctuary (all $P < 0.003$). Further, there was a significant correlation between native cover and horehound cover at the site level (Figure 1.8, $R^2 = 0.85$, $P < 0.001$).

The presence and absence of prairie dogs, bison, prairie dog physical disturbance, bison physical disturbance, and mowing are summarized in Table 1.5 along with percent bare ground cover as these variables are all indicators of disturbance. The East Bison Flats high density plots were on inactive prairie dog burrows and had high traffic levels of bison. The East Bison Flats low density plots were on active prairie dog towns and bison were never seen on the plots, although bison were seen nearby. The Norbeck high density plots were on inactive prairie dog burrows and bison were occasionally seen grazing in the area. This site was also mowed. The Research Reserve high density plots were on inactive prairie dog burrows and no bison were ever observed in the area, however there were bison trails running through the plots. The Research Reserve low density plots were on inactive prairie dog burrows with no bison observed in the area. The Sanctuary high density plots were on active prairie dog burrows with bison seen near the area and the Sanctuary low density plots were on active prairie dog burrows with bison seen passing to the west of the plots.

Table 1.5 shows that the East Bison Flats and Norbeck high density populations had the most disturbances with three out of the five disturbance factors. Further, the Norbeck town had a high intensity recent disturbance of mowing. The Research Reserve low density population and had the least amount of disturbance with one of the five factors. All other sites had two of the five factors. This scale is subjective, but illustrates some differences in disturbance between sites. For example, while all of the sites were on prairie dog towns, some of these towns were still active whereas others did not currently house prairie dogs.

Using both Table 1.4 and Table 1.5, populations were ranked according to disturbance. Populations with more disturbances in the presence/absence matrix and higher covers of horehound, bare ground, or non-native plant cover or lower amounts of native plants were ranked above those with less physical disturbance and more native plant cover. Norbeck and East Bison Flats both ranked highly, however, due to the recent mowing of Norbeck, Norbeck was ranked as the most disturbed. One is the most disturbed, seven is the least disturbed:

- 1 (most disturbed): Norbeck high density
- 2 (more disturbed): East Bison Flats high density
- 3 (moderately disturbed): Sanctuary high density
- 3 (moderately disturbed): Research Reserve high density
- 5 (less disturbed): Sanctuary low density
- 5 (less disturbed): East Bison Flats low density
- 7 (least disturbed): Research Reserve low density

***M. vulgare* population age structure**

The age distribution of *M. vulgare* plants in WCNP is found in Figure 1.9. Ages of *M. vulgare* plants varied from 1-5 years. The oldest *M. vulgare* plants were found on the East Bison Flats population and the North Boundary population. All prairie dog towns had *M. vulgare* plants that were at least 3 years old and the average age for *M. vulgare* in the high density populations was 2.23 years.

Discussion

The examined traits and population dynamics of *M. vulgare* in this study provides insight into the invasiveness of *M. vulgare*. *M. vulgare* produces a large amount of seeds, despite a lower allocation to reproductive effort as compared to other native prairie forbs. Most populations of *M. vulgare* are stable or slightly declining, while a few are increasing in density. Importantly, *M. vulgare* is dependent upon disturbance.

Reproductive strategies and life history traits of M. vulgare

Allocation to reproductive effort

Invasive plant theory suggests colonizing ability of invasive plants may be greater than that of other native plants (Colautti et al. 2006). If *M. vulgare* uses a colonizer strategy to be a successful invader, one would expect that a greater proportion of biomass would be allocated to reproductive effort as more allocation to reproduction suggests an ability to colonize better than other prairie plants (Harper 1967, Crawley 1997, Grimes 2001). Overall, *M. vulgare* afforded a proportion of 0.15 to reproductive structures. For other native perennial prairie forb species, the reproductive effort proportion ranges from 0.10 for *Solidago canadensis* to 0.36 for *Ratibida columnifera* (see Table 1.1, Hartnett 1990, Hartnett 1991). *M. vulgare* is on the low end of this spectrum, showing it allocates less to reproduction than many other prairie forb species (Table 1.1). Given that *M. vulgare* is invasive, this lack of allocation to reproduction is interesting since it suggests *M. vulgare* may not be a good colonizer.

Plant life history theory predicts that sexual reproductive effort (SRE) increases with increasing density, allowing for a plant to have a greater ability to disperse into another habitat (Abrahamson 1975). In the case of *M. vulgare*, patterns of reproductive effort confirm

predictions from life history theory. SRE is increasing with increasing plant density. Plant life history theory also predicts that the sexual reproductive effort to vegetative reproductive effort ratio (SRE/VRE) would increase at high density (Abrahamson 1975, Loehle 1987), which is consistent with the patterns we observed for *M. vulgare*. Again, as plant density increases, plants will shift to more sexual reproductive effort for long-distance dispersal.

Seed production

Propagule pressure is one hypothesis for explaining plant invasions (Coulatti et al. 2006, Lockwood et al. 2005). The more seeds produced, the higher the probability for seedling establishment and potential for invasion. While *M. vulgare* does not allocate as much biomass to reproduction, *M. vulgare* produces a large number of seeds per plant. These seeds, however, are small, which likely contributes to the smaller proportion of biomass allocated to reproductive effort. While the low biomass allocation to reproduction may not suggest good colonizing ability, the high number of seeds produced per plant does suggest *M. vulgare* has good colonizing ability. Also, this suggests that *M. vulgare* is efficient at reproduction since it produces a large number of seeds, but uses less biomass to produce these seeds.

Seedlings

The presence of seedlings in plant populations informs the viability of these populations. If seedlings are present, especially in large numbers, the population is reproducing and has the ability to sustain as a population. On most of the high density prairie dog sites, seedlings increased from 2010 to 2011. The increase was especially high on East Bison Flats. On average, seedling establishment was 611 seedlings/m² in high density populations. Thus, the *M. vulgare* populations are continuing to reproduce and self-sustain as populations in WCNP. Increases in seedling numbers could indicate a growth in population if many of these seedlings survive into

the next year. However, data from Table 1.3 suggests only a 3.4% survival rate of seedlings. In the future, direct measurement of seedling survival and mortality would help understand how many seedlings actually survive and become reproductive plants. The increase in seedlings could be due to a number of reasons including environmental factors or the measured disturbance of bison that may act as dispersal vectors. Further, the high density sites had, on average, 20% bare ground. These bare ground areas are available space and potential resources for seedlings to recruit. Although there was not a significant correlation between seedling and ramet numbers, generally, as ramet numbers went down, seedling numbers went up. Resources that were previously used by the ramets may have been available for seedlings to use. Also, the density of ramets for all species in the area (and not just *M. vulgare* species) may also have decreased, freeing up more space and resources for new seedlings to establish.

Comparison to M. vulgare life history traits in other populations

When compared to *M. vulgare* populations in their native habitat in France, *M. vulgare* plants in WCNP generally produce more seeds and seedlings, are taller in height, and denser in number (Weiss and Sagliocco 2000, Table 1.3). This is consistent with many studies that have found invasive plant species to have higher reproductive output, grow denser, and form larger populations in their exotic range than in their native range (Hinz and Schwarzlaender 2004). Additionally, while *M. vulgare* plants found in WCNP were more similar to plants found in *M. vulgare* populations in Australia where *M. vulgare* is also invasive, there are important differences. In WCNP, the mean seed production, and adult plant and seedlings density, was high relative to *M. vulgare* populations in Australia (see Table 1.3, Weiss and Sagliocco 2000). The large number of seeds is important in understanding *M. vulgare* invasion and persistence. Propagule pressure has been found to be a significant predictor of invasiveness (Colautti et al.

2006), and the large numbers of *M. vulgare* seeds indicate a large propagule supply. This seed supply likely helps to sustain populations of *M. vulgare* and likely contributes to the spread of *M. vulgare* throughout WCNP.

Effective epizoochory

M. vulgare is considered to be a good disperser (Young and Evans 1986), which may be a quality that lends it to being invasive. The hooked spines on the fruit of *M. vulgare* catch easily on bison fur and the bison may be the perfect vector to disperse the *M. vulgare* seeds in WCNP. Many exotic plants are adapted for transport by ungulates and vertebrates are found to be good dispersers of invasive plants in other systems (Calvino-Cancela 2011, Constible et al. 2005, Kulbaba et al. 2009, Vavra et al. 2007). Bison have been shown to disperse a wide variety of seeds with different diaspore morphologies (Kulbaba et al. 2009), and, in particular, are a known vector of dispersal for non-native plants on Santa Catalina Island off the coast of California (Constible et al. 2005).

Patterns of *M. vulgare* populations and disturbance

M. vulgare populations and dynamics

Measuring plant population densities across years can indicate the growth, contraction or stability of the population. Understanding these plant population dynamics can inform whether a plant invasion may become worse or may have already reached a peak. In this study, ramet populations on most of the prairie dog towns (Research Reserve, East Bison Flats, and Sanctuary) were similar across years. Ramet populations were generally stable or slightly decreasing, though not significantly. These populations may have reached equilibrium density, and may be less likely to increase in the future. However, as noted above, these populations are

still providing a huge propagule supply for continued invasion and sustainment of populations in WCNP. Also, the ramet densities on the Norbeck prairie dog town were significantly lower than at all other sites in 2010 and then increased to levels similar to the other high density populations in 2011. Plant populations usually increase in density until an equilibrium density has been reached for that specific population (Watkinson 1997). Thus, Norbeck may be a newer population that was increasing from 2010 to 2011 and may now be at equilibrium since it is similar in density to other high density populations. Further, the August 2010 mowing of the Norbeck population may have facilitated ramet population growth by possibly stimulating vegetative growth and encouraging ramet production or by creating a good environment for seedlings and ramets to grow.

Some of the genet populations were also stable and decreasing, although not significantly. For management purposes, these populations should be monitored for a marked increase in genet densities; however, other areas of *M. vulgare* invasion may be of higher priority until these areas show signs of growing populations. On the contrary, the East Bison Flats area had a seemingly very high increase in the number of genets (a 17-fold increase). This suggests that the *M. vulgare* population here has a potential for increasing greatly under current conditions and becoming a problem. This area should be targeted for management (i.e. removal of *M. vulgare* plants) before *M. vulgare* becomes a large, dense population. Further, as individuals within *M. vulgare* populations increase, the plants clump together, and the point quarter distance measurement method is not always the best method for populations that clump (Cottam and Curtis 1956). This may help explain the very marked increase in *M. vulgare* populations, despite the appearance on the ground that there was not a large increase in *M. vulgare* plants.

Finally, a comparison of ramets between the high and low density populations shows 100-fold more ramets in some high density sites compared to low density sites (Figure 1.10). Ramet number was estimated for the low density populations using averages of ramets/genet for all the populations in 2010.

Disturbance dependence

This study shows that *M. vulgare* is a disturbance dependent species. Large, dense, populations of *M. vulgare* were found only on prairie dog sites (see Chapter 2). Populations with higher densities of *M. vulgare* were more disturbed than populations with low densities. High density populations also had less native cover and more signs of disturbance from prairie dogs and bison than the low density populations. This suggests that disturbance does in some way contribute to *M. vulgare* density.

While *M. vulgare* is disturbance dependent at a large scale, we were not able to tell at the local scale what might be influencing *M. vulgare* density as no clear measurement of disturbance emerged in this study. Both disturbance and plant populations are very dynamic and while disturbance obviously has a role in *M. vulgare* population dynamics, it's difficult to pinpoint the precise disturbance and the precise role of disturbance on plant population dynamics. For example, current populations of *M. vulgare* may be legacies of past disturbance. A disturbance may have occurred on the prairie in the past that allowed *M. vulgare* to establish and since the disturbance, *M. vulgare* populations have been able to persist. Also, there may be disturbances that are interacting with each other that may create an ideal environment for *M. vulgare* invasion (Hobbs and Huenneke 1992).

Further, there was no clear difference in ramet and seedling densities according to disturbance rank. The most disturbed sites did not necessarily have the highest densities of *M.*

vulgare and vice versa, the lowest disturbed sites did not necessarily have the lowest density of *M. vulgare*. This holds true for both the high and low density sites. For low density sites, perhaps some of the populations exist as sink populations. Two of the three low density populations are located directly next to high density populations and may be able to maintain themselves due to inputs of seeds from neighboring high density populations and not due to their own reproductive capabilities.

Native plant cover and M. vulgare cover

As one might expect, native plant percent cover and *M. vulgare* percent cover were negatively correlated at the site level. A major effect of invasive plants on communities is displacing native plants and thus contributing to a decline in biodiversity (Davis 2003). This study shows that *M. vulgare* populations are indeed reducing the abundance of native plant species where *M. vulgare* has invaded. Further, there appears a possible threshold for *M. vulgare* invasion. When native plant cover is greater than about 45%, *M. vulgare* is not present; however, when native cover is less than 45%, *M. vulgare* cover is 30% or greater (Figure 1.8).

M. vulgare population age structure

Ages of *M. vulgare* plants were similar across populations on different prairie dog towns. The average age of *M. vulgare* plants in high density populations was 2.23 years, suggesting that *M. vulgare* plants live about 2-3 years. Plants older than five years were not found within any of the populations, even in populations known to exist for longer than five years. The ability to infer an invasion timeline and spatial patterning of invasion in WCNP appears difficult with *M. vulgare* since plants are relatively short-lived. Some populations are at least ten years old and the lack of plants older than five years makes it difficult to infer population age.

Summary and management implications

This study resulted in new information about *M. vulgare* as an invasive plant in the U.S. We found that *M. vulgare* is a disturbance dependent species, though there is not an apparent relationship between disturbance and *M. vulgare* population dynamics. While very small populations of *M. vulgare* exist off prairie dog towns (see Chapter 2), large populations only exist on both active and non-active prairie dog towns in WCNP. Further, while there is no clear pattern linking disturbance and population dynamics for *M. vulgare* at WCNP, larger, denser populations are in areas with more disturbance factors. These results suggest that minimizing disturbance is important for managing populations of *M. vulgare*. Management practices such as the physical removal of plants or mowing may actually encourage population growth instead of the intended desire to decrease populations. Also, since disturbances on plant species can have both negative and positive effects and the effects differ for differing species (Hobbs and Huenneke 1992), some disturbances may encourage *M. vulgare* population growth whereas other disturbances may not encourage growth. For example, while one season of mowing may have encouraged *M. vulgare* population growth, multiple seasons of mowing may actually have the desired effects of reducing seed numbers. Further, focusing management on prairie dog towns should be an effective management tool as *M. vulgare* rarely occurs off prairie dog towns.

Most *M. vulgare* populations in WCNP were found to be stable, and five of the seven populations studied slightly decreased, although not significantly, in density from 2010 to 2011. However, a few of the populations did increase significantly from 2010 to 2011. Seedling densities also increased, indicating that *M. vulgare* is still reproducing and creating sustaining populations. These results further indicate that *M. vulgare* populations are continuing to thrive and will continue to be a problem from WCNP.

Two of the attributes that appear to make *M. vulgare* a successful invader are its ability to produce large numbers of seeds and seedlings and its ability as a good disperser (Young and Evans 1986). The seed rain is estimated to be around 1,500 seeds/plant and more than 30,000 seeds/m² in high density areas. Seedling establishment rates are estimated around 600 seedlings/m² for high density populations. Limiting seed production and seed rain may help to decrease *M. vulgare* populations and help prevent dispersal of *M. vulgare* into new sites.

As a disperser, *M. vulgare* appears to have found a good dispersal agent in bison. Bison are good dispersers of non-native plants in other systems (Constible et al. 2005, Kulbaba et el. 2009) and a further study on dispersal of *M. vulgare* by bison would add greatly to this research. If bison were found to indeed be dispersing large amounts of *M. vulgare* seed, limiting bison movement in certain areas may help reduce the threat of *M. vulgare* invasion. Coutts et al. (2011), in their paper identifying key drivers of invasive plant spread, also suggest that managing dispersal is one of the most important factors in effectively managing invasive plant populations. Further, in their study in a National Battlefield in Maryland, Minor and Gardner (2011) suggest that for invasive plant species that frequently and randomly disperse seeds over long distances, targeting large patches of the invasive is important to decrease the number of long distance dispersal events. Finally, WCNP recently acquired new land to include within the park boundary. A fence currently exists between the park and the new land addition and before removing the fence and adding bison into this new area, the impact of *M. vulgare* dispersal by bison should be considered. Fence boundaries around protected areas, such as National Parks, have been shown to be effective in filtering out invasive species (Foxcroft et al. 2010). While the opposite seems to be occurring in WCNP – the fence seems to be holding in the invasive plant species – this is

something to consider when removing the fence. Fence removal with the addition of bison will likely increase the potential for this new area to be invaded by *M. vulgare*.

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Figures and Tables



Figure 1.1. Picture of flowering *Marrubium vulgare* L. plant. Photograph taken in WCNP.

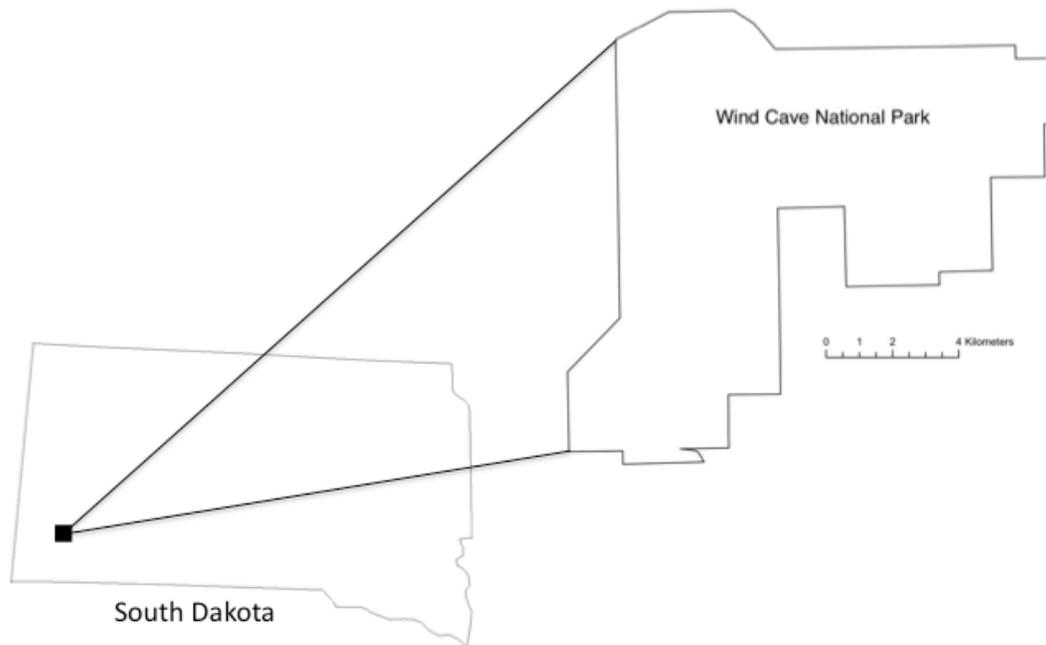


Figure 1.2. Location of Wind Cave National Park (WCNP). WCNP is located in the southern Black Hills of South Dakota.

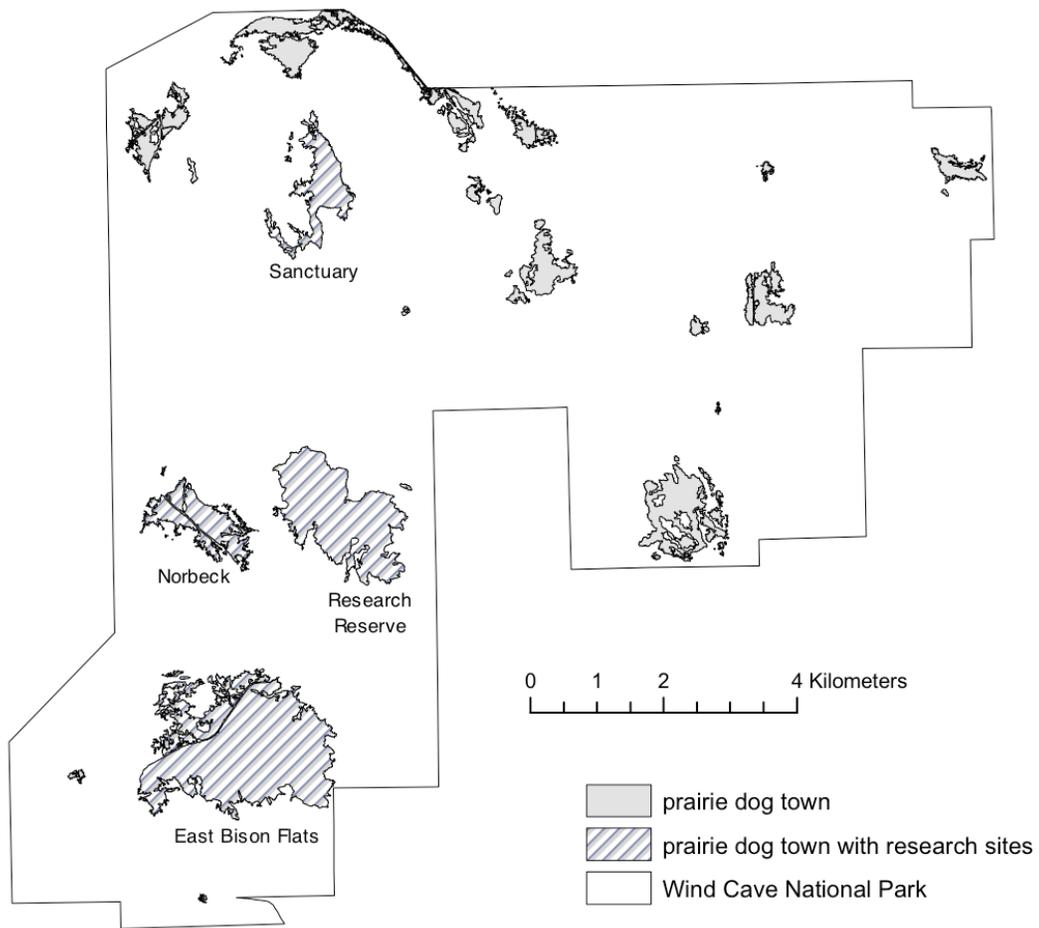


Figure 1.3. Map of prairie dog towns within WCNP. Prairie dog towns labeled with names have research sites (Sanctuary, Norbeck, Research Reserve, and East Bison Flats).

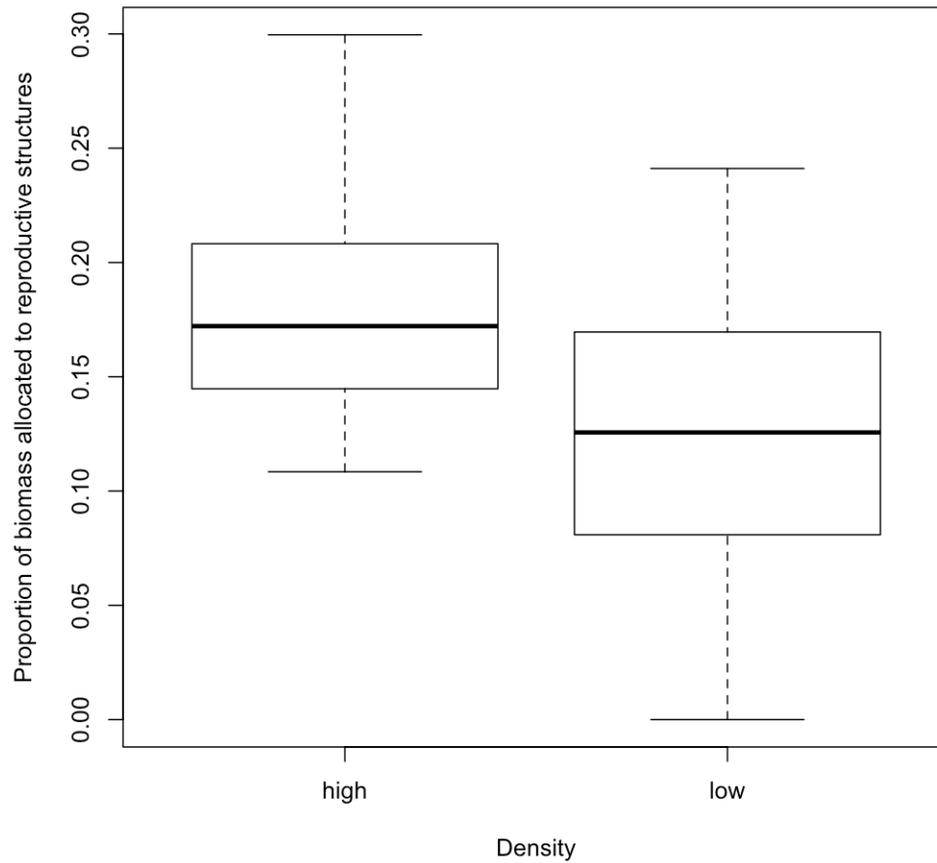


Figure 1.4. Proportion of biomass allocated to reproduction in areas of high density *M. vulgare* and low density *M. vulgare*. The proportions between sites were significantly different (P=0.007).

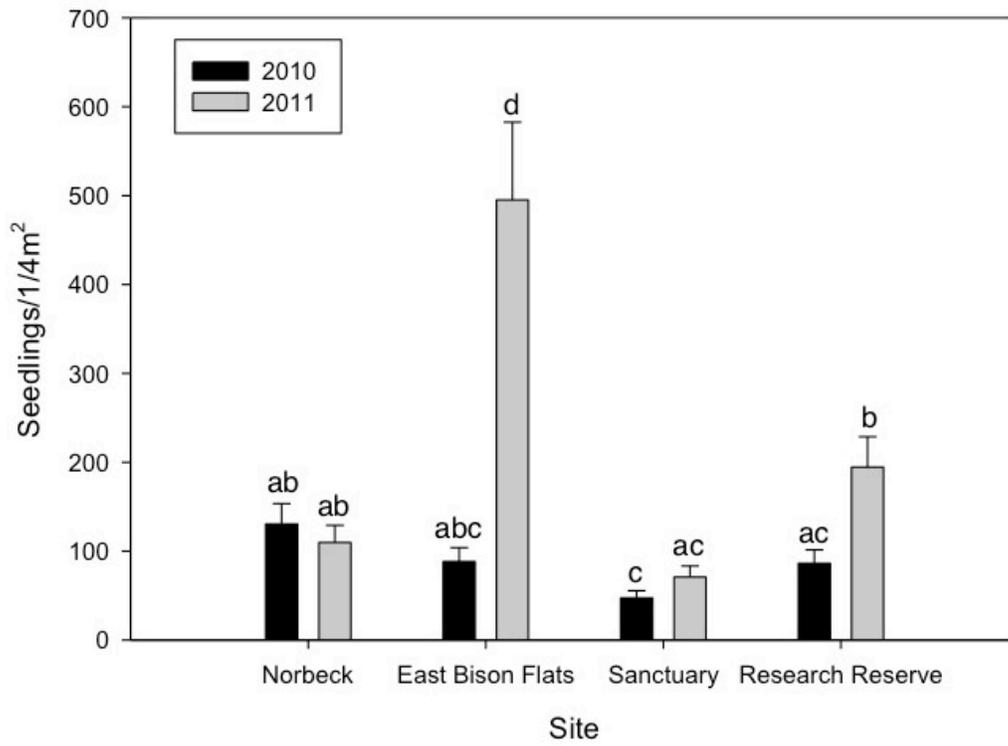


Figure 1.5. Seedling densities on high density populations in both 2010 and 2011. Error bars represent +/-SE. Significant differences ($P<0.05$) denoted by letters. Sites are in order from most disturbed to least disturbed.

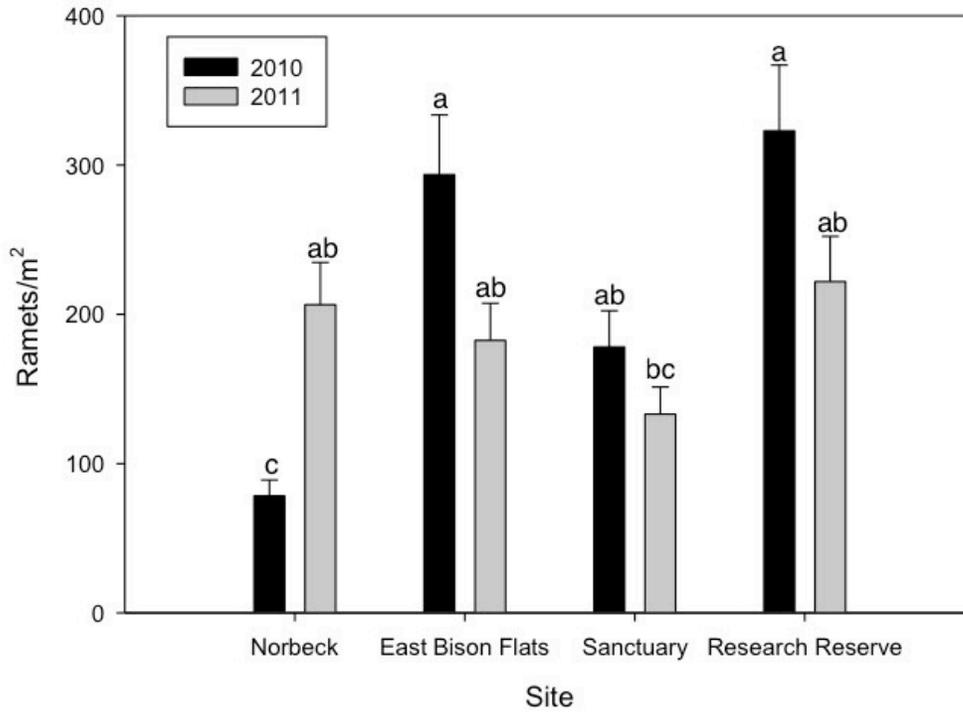


Figure 1.6. Ramet densities on high density populations in both 2010 and 2011. Error bars represent +/-SE. Significant differences ($P < 0.05$) denoted by letters. Sites are in order from most disturbed to least disturbed.

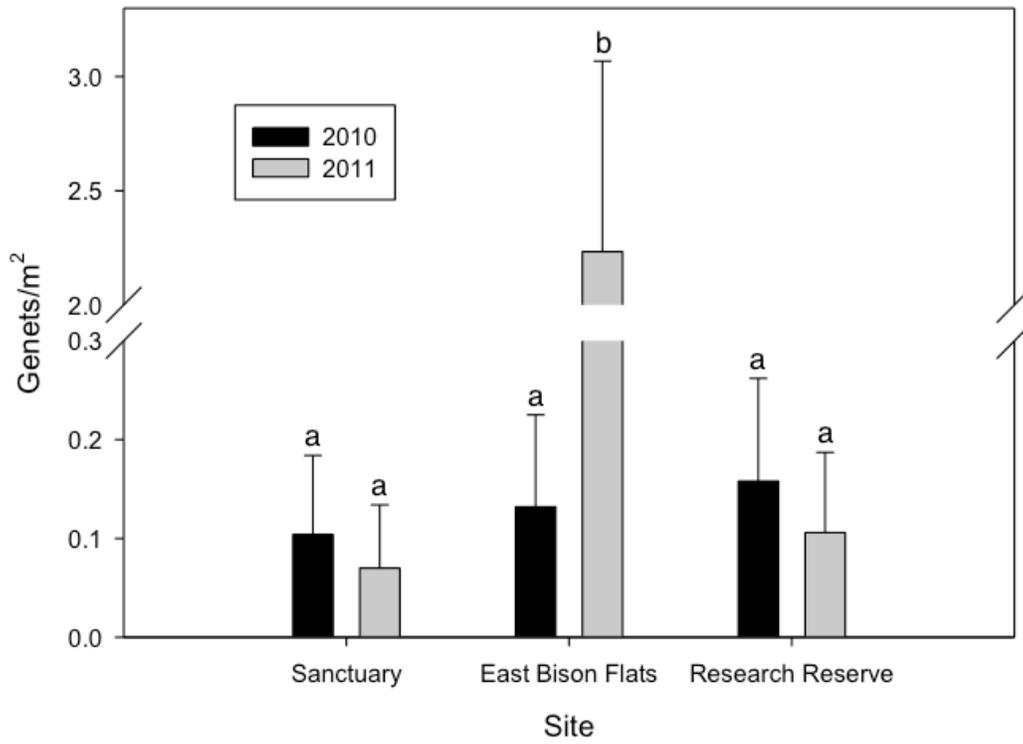


Figure 1.7. Genet densities on low density populations in both 2010 and 2011. Error bars represent +/-SE. Significant differences ($P < 0.05$) denoted by letters. Sites are in order from most disturbed to least disturbed.

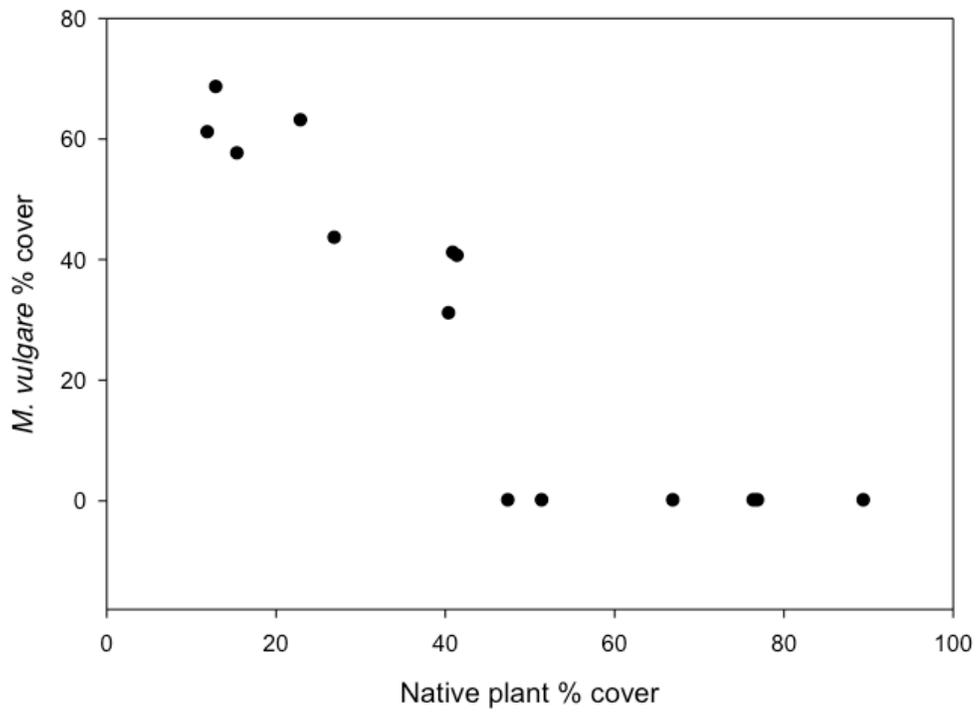


Figure 1.8. Spearman correlation between *M. vulgare* percent cover and native plant percent cover at the site level ($R^2=0.85$, $P<0.001$).

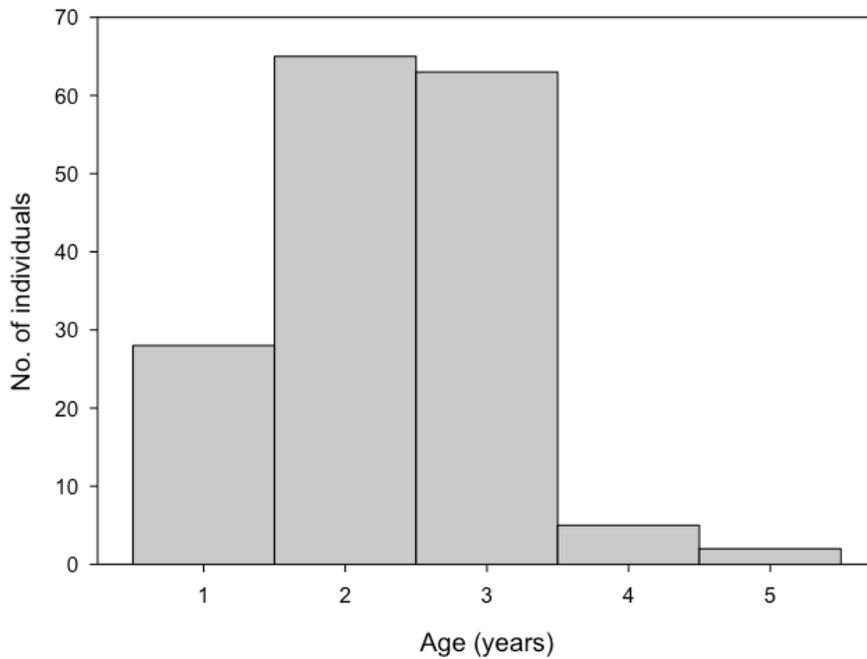


Figure 1.9. Ages distribution of *M. vulgare* plants in WCNP.

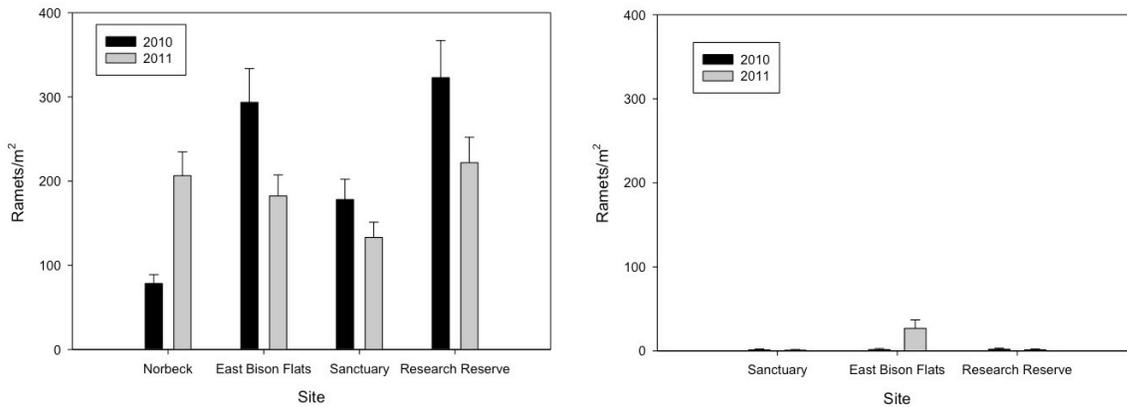


Figure 1.10. Ramet densities from both high and low density populations in 2010 and 2011.

High densities are depicted on the left graph and low densities on the right graph. Error bars represent +/-SE. Ramet/m² for low density is an estimate based on the genets/m² and average number of ramets per genet in 2010 in the low density areas. Sites are in order from most disturbed to least disturbed.

Plant species	Average proportion of aboveground biomass allocated to reproduction	Citation
<i>Ratibida columnifera</i>	0.36	Hartnett 1991
<i>Ruellia humilis</i>	0.30	Hickman & Hartnett 2002
<i>Amorpha canescens</i>	0.28	Hickman & Hartnett 2002
<i>Oenothera speciosa</i>	0.23	Damhoureyeh & Hartnett 1997
<i>Vernonia baldwinii</i>	0.19	Hartnett 1990
<i>Aster ericoides</i>	0.16	Hickman & Hartnett 2002
<i>Marrubium vulgare</i>	0.15	----
<i>Solidago missouriensis</i>	0.15	Damhoureyeh & Hartnett 1997
<i>Solidago canadensis</i>	0.10	Hartnett 1990

Table 1.1. Comparison of proportion of aboveground biomass allocated to reproductive efforts between *M. vulgare* and other prairie forbs. Data taken from noted citations.

	Mean	Range	Standard Deviation
Flowers per reproductive cluster	11.32	0 - 28	8.89
Seeds per reproductive cluster	24.27	0 - 79	20.01
Reproductive cluster per stem	6.14	0 - 31	6.67
Stems per plant	9.98	2 - 39	8.93
Flowering stems per plant	7.5	0 - 30	6.97
Plant height	42.9 cm	10 – 108 cm	16.7

Table 1.2. Summary statistics for reproductive and vegetative traits of *M. vulgare* plants.

	Cournonterral, France	La Crau, France	Swifts Creek, Victoria, Australia	Wyperfeld NP, Victoria, Australia	WCNP, South Dakota, United States
Density of plants/m ²	0.4	0.2	6.9	9.9	20.7
Mean height plant (cm)	14.6	9.6	36.1	27.1	42.9
Mean number of stems	6.3	6.8	35.2	18.9	10.0
Mean number of seeds/plant	878	174	1746	498	1487
Mean number of seeds/stem	139.4	25.6	49.6	26.4	149.0
Mean number of seedlings/m ²	0.1	0.3	69.5	196.3	611.2

Table 1.3. Comparison of *M. vulgare* plants and populations in native (France) and non-native habitats (Australia and United States). France and Australia data taken from Weiss and Sagliocco (2000).

Site	<i>M. vulgare</i> % cover	Non-native plant % cover	Bare ground % cover	Native plant % cover
Norbeck (High density)	62.0	4.4	18.9	18.6
East Bison Flats (High density)	62.8	6.1	20.1	15.8
Sanctuary (High density)	35.7	4.2	21.1	40.7
Research Reserve (High density)	42.0	2.4	22.9	33.5
Sanctuary (Low density)	0	21.0	13.6	62.8
East Bison Flats (Low density)	0	2.5	39.3	56.4
Research Reserve (Low density)	0	0.5	14.1	83.0

Table 1.4. Combined 2010 and 2011 average percent cover of *M. vulgare*, non-native plants, bare ground, and native plants on both high density and low density populations.

Site	Prairie Dogs?	Bison?	Prairie dog burrows?	Bison trails?	Mowing?	Bare ground % cover
Norbeck (High density)	No	Yes	Yes	No	Yes	15-30%
East Bison Flats (High density)	No	Yes	Yes	Yes	No	15-30%
Sanctuary (High density)	Yes	No	Yes	No	No	15-30%
Research Reserve (High density)	No	No	Yes	Yes	No	15-30%
Sanctuary (Low density)	Yes	No	Yes	No	No	<15%
East Bison Flats (Low density)	Yes	No	Yes	No	No	>30%
Research Reserve (Low density)	No	No	Yes	No	No	<15%

Table 1.5. The presence and absence of prairie dogs, bison, prairie dog burrows, bison trails, and mowing on both high density and low density populations. This table also includes bare ground percent cover, as bare ground can be an indicator for disturbance.

Chapter 2 - GPS mapping and GIS analysis of the invasive plant

Marrubium vulgare (horehound) in a mixed grass prairie

Abstract

Exotic invasive plant species pose a threat to ecosystems. Understanding the distributions of invasive plants has practical applications of informing management practices to control invasive species. Geographic Information Systems (GIS) is a valuable tool for studying and quantifying invasive plant patterns, distributions, and spread. *Marrubium vulgare* (horehound) is an invasive plant in the United States that poses a threat to the mixed grass prairie system. *M. vulgare* was mapped in Wind Cave National Park (WCNP) using a handheld Global Positioning System (GPS) device. GIS was used to analyze the associations between *M. vulgare* presence and absence and environmental factors including vegetation and soil type and prairie dog disturbance. This study confirmed that *M. vulgare* was primarily dependent upon disturbance and was significantly associated with prairie dog towns. *M. vulgare* was also found to be significantly associated with a particular vegetation type, the *Aristida purpurea* – *Dyssodia papposa* (threeawn and fetid marigold) type. This vegetation community is described as being exclusive to prairie dog towns. Further, *M. vulgare* was associated with certain types of loam soils. *M. vulgare* was documented as a locally dominant species in a 1999 vegetation survey and has since rapidly expanded into large monotypic stands in some areas. The information gathered from this study can be used to predict future spread of *M. vulgare*. Remote sensing is a potential tool that would aid in monitoring *M. vulgare* invasion.

Introduction

Exotic invasive plant species continue to pose a threat to ecosystems worldwide (Mack et al. 2000). These invasive plants cause declines in biodiversity and interrupt ecosystem processes (Brooks et al. 2004, Davis et al. 2003). More recently, Geographic Information Systems (GIS) and remote sensing have been applied to the study of invasive species spread and dynamics (Hestir et al. 2008, Huang and Asner 2009, Hunt et al. 2010, Madden 2004). For example, Hunt et al. (2010) used GIS and hyperspectral sensor data, along with field data, to increase the accuracy of a model to predict areas susceptible to the invasive *Euphorbia esula* (leafy spurge).

Understanding the current and future distribution of an invasive plant species has practical applications. Mapping (and further monitoring) of the distribution of invasive plant species can help inform management practices. Distribution maps serve as a record of current distribution that can be used in subsequent years to determine the spread or contraction of invasive species populations. Maps can also be used to examine associations between plant distributions and environmental factors such as soil types, elevation, precipitation, or native vegetation types. Further, once associations are understood, the information can be used to create a map of potential distribution of the invasive plant species for use in risk analysis and prevention. Managers can use this information to closely monitor areas where a plant is predicted to become invasive and eradicate the invasive before it becomes a widespread problem.

GIS can be used to understand associations between plant distributions and environmental or habitat factors such as vegetation communities and soil types (Remillard and Welch 1993). The distribution of an invasive species can be combined in GIS with other categorical information (i.e. vegetation and soil types) and a chi-squared test can be used to test the significance of this relationship (Remillard and Welch 1993). Correlation trees and/or

biogeoclimate modeling can also be used to examine the role of different quantitative variables regulating invasive spread. If there are relationships between invasive species presence and other environmental variables and vegetation communities, this information can be used to develop models of further distribution and spread (Andrew and Ustin 2009, Elmendorf and Moore 2008, Tsutsumi 2011).

Marrubium vulgare (common horehound) is an exotic invasive perennial forb in the United States. *M. vulgare* (Lamiaceae), originally from Eurasia, is now found in 46 of the 50 states (USDA Plants Database) and is identified as a problem in areas such as the Great Basin and in the southwestern states such as Arizona (Halvorson and Guertin 2003, Mau-Crimmins et al. 2004, Young and Evans 1986). This species is also known to be invasive in other areas of the world. In Australia, *M. vulgare* has infested over 26 million ha and decreases the availability of palatable vegetation in grazing lands (Weiss et al. 2000). Fruits of *M. vulgare* are bur-like and disperse by epizoochory (Young and Evans 1986). Most livestock and wildlife avoid grazing on *M. vulgare* because it is bitter (Weiss et al. 2000).

Recently, *M. vulgare* has become a problematic invader in Wind Cave National Park (WCNP) in the southern Black Hills of South Dakota. Within the last ten years, large monotypic populations of *M. vulgare* have been observed in the mixed-grass prairie, primarily on prairie dog towns within the park (Beth Burkhart, *pers. comm.*). This poses problems not only for the native vegetation, but also for the wildlife such as the black-tailed prairie dog (*Cynomys ludovicianus*), bison (*Bison bison*), and the endangered black-footed ferret (*Mustela nigripes*) that depend upon the mixed grass prairie for food and habitat.

One cited characteristic for exotic invasive plants success is their ability to be habitat generalists (Fenesi et al. 2011, Fumanal et al. 2008, Marvier et al. 2004). As habitat generalists,

invasive plants have more flexibility in their ability to invade a new habitat since they have wide ecological amplitude and are able to thrive under a variety of local environmental conditions. For example, in North America, *Bromus tectorum* has shown the ability to survive and thrive in a variety of habitats from semi-natural to very degraded habitats and in France, and *Ambrosia artemisiifolia* has shown a wide ecological tolerance in inhabiting several different disturbed habitats with a variety of vegetation cover and soil types (Fenesi et al. 2011, Fumanal et al. 2008). However, there are exceptions to this rule, and some invasive plant species are habitat specialists. For example, *Tamarix chinensis* is an invasive species only found in riparian areas, usually on saline soils (Di Tomaso 1998, Evangelista et al. 2008). Using GIS analyses can help inform whether or not *M. vulgare* is a habitat generalist or specialist species, whether it is disturbance-dependent, and what habitat factors may regulate its distribution and rate of spread.

This study had two main objectives: 1) to survey *M. vulgare* and quantify its current distribution within WCNP and 2) to elucidate associations between the distribution of *M. vulgare* in WCNP and environmental variables including soil type, vegetation community type, and the distribution of prairie dog towns or other disturbances. The information collected in this study will be provided to managers of WCNP in order to help inform management strategies. Since *M. vulgare* seems to be disturbance dependent (Chapter 1), we hypothesized that *M. vulgare* would generally be restricted in its distribution to prairie dog towns and that these areas may have certain associated vegetation and soil types.

Methods

Study system

Wind Cave National Park (WCNP) is located within the southern Black Hills region of South Dakota about six miles north of Hot Springs, SD. WCNP encompasses 28,295 acres of land and has recently acquired an additional 5,555 acres. Known mainly for an extensive and complex limestone cave system, WCNP is also home to ponderosa pine and mixed grass prairie vegetation types. Common grass species of the mixed grass prairie include big bluestem (*Andropogon gerardii*), Indian grass (*Sorghastrum nutans*), little bluestem (*Schizachyrium scoparium*), western wheatgrass (*Pascopyrum smithii*), blue grama (*Bouteloua gracilis*), sideoats grama (*Bouteloua curtipendula*), Junegrass (*Koeleria macrantha*), and needlegrasses (*Stipa* sp.). Common forb species include fringed sage (*Artemisia frigida*), scarlet globe mallow (*Sphaeralcea coccinea*), and prairie coneflower (*Ratibida columnifera*). The mixed grass prairie also supports a wide variety of animals including the black-tailed prairie dog (*Cynomys ludovicianus*), bison (*Bison bison*), and the endangered black-footed ferret (*Mustela nigripes*).

GPS data acquisition

Areas within WCNP were systematically walked to collect *M. vulgare* presence/absence data. While areas with prairie dog towns were the focus, areas without prairie dog towns were also surveyed. A handheld Archer Hemisphere Global Positioning Systems (GPS) XF101 receiver with computer and ArcPad 8.0 and 10.0 software was used to collect point information on *M. vulgare* presence. Areas of large *M. vulgare* infestations were mapped as polygons using the perimeter of the infestation. Observed populations of *M. vulgare* varied from dense monotypic stands to moderate and low-density populations where *M. vulgare* plants were as

many as 20-30 m apart. Another 50-100 meters was surveyed beyond the perimeters of each encountered population to make sure perimeters were accurate. In areas with light infestations (without areas of dense *M. vulgare* infestations) each *M. vulgare* plant or small group of plants (2-15) was recorded with a point. Data were collected in both 2010 and 2011. Areas of focus included two prairie dog towns: Research Reserve and Norbeck. Parts of other prairie dog towns and areas adjacent to towns were also surveyed (see Figure 2.1). Areas without *M. vulgare* were recorded using GPS points, roads, trails, and other geographic features as boundaries and were digitized in ArcMap 9.3. Data were collected in the World Geodetic System (WGS 1984) datum and then transformed into the North American Datum of 1983 (NAD83). Further, evidence or lack of evidence of *M. vulgare* was noted in other areas hiked or driven in the park, although these areas were not systematically walked.

GIS data acquisition

A number of GIS data were acquired from WCNP personnel (Beth Burkhart, *pers. comm.*). These included shapefiles of both prairie dog towns and previous estimates of *M. vulgare* infestations. Perimeters of prairie dog towns were mapped in 2009 and 2010. Estimates of *M. vulgare* infestations were from early 2010. Vegetation information and soils information was also acquired via WCNP personnel. The vegetation information and community classification information is from the NPS-USGS Vegetation Mapping Program (see Cogan et. al 1999, data available at <http://biology.usgs.gov/npsveg/ftp/vegmapping/wica/wica.zip>). See Table 2.1 for a complete listing of vegetation classes and Figure 2.2 for a map of WCNP vegetation. Soil class information is from soil surveys of Custer and Pennington counties in 1990 and 1996 (Ensz 1990, Neilsen 1996). The soil surveys were completed for the National Cooperative Soil Survey and were a cooperative effort between groups such as Soil Conservation Service (now

known as the Natural Resources Conservation Service (NRCS)) and U.S. Forest Service. See Table 2.2 for a complete listing of soil classes and Figure 2.3 for a map of soil types in WCNP. All acquired data was in the NAD83 datum.

Vegetation and soil classifications

Plant communities were merged to make five vegetation classes, so individual vegetation classes contained sufficient data for categorical data analyses: Trees, Shrubs, LittleBlue, Threeawn, and WesternWheat. The “Trees” category combined all forested and woodland areas. These areas consisted mostly of *Pinus ponderosa* community types: *P. ponderosa* (ponderosa pine) Woodland Complex, *P. ponderosa/Schizachyrium scoparium* (ponderosa pine/little bluestem) Woodland, *P. ponderosa/Prunus virginiana* (ponderosa pine/chokecherry) Forest, and *Acer negundo/P. virginiana* (boxelder/chokecherry) Forest. The “shrubs” category consisted of shrublands including *Amorpha canescens* (leadplant), *P. virginiana* (chokecherry), *Salix bebbiana* (beaked willow), and *Symphoricarpos occidentalis* (western snowberry) shrublands. Three subsequent categories were formed in the grasslands communities types: “Threeawn”, “WesternWheat”, and “LittleBlue”. The “Threeawn” category consisted of the *Aristida purpurea* (purple three-awn) - *Dyssodia papposa* (fetid marigold) Herbaceous Vegetation class, also called the Prairie Dog Town Grassland Complex. The “WesternWheat” category consisted of the *Pascopyrum smithii* (western wheatgrass) - *Poa pratensis* (Kentucky bluegrass) Grassland Complex and the “LittleBlue” category consisted of the *S. scoparium* (little bluestem) – *Bouteloua (curtipendula and gracilis)* (Sideoats and Blue grama) - *Carex filifolia* (threadleaf sedge) Herbaceous Vegetation class.

Soil data were also merged to make seven classes of soil textures: silt loam, loam complex (includes a variety of loamy soils), calcareous loam, loam, channery loam, cobbly loam,

and loam clay complex (includes both loamy and clay soils). The silt loam class included the following soils: BrA, BrB, SxaE, and TfB. The loam complex included the following soils: BeB, BwE, CxC, GuC, GvD, HtG, SrE, VcE, and VoG. The calcareous loam includes the CcE soils. The loams include CoA and CvB soils. The channery loam includes HeE and SwE. The cobbly loams include HgB, HgD, and WtB. The loam clay complex soils include HmE, MnC, PbD, PcD, and ZnD.

GIS methods

Prairie dog town data, vegetation data, soil data, and surveyed areas with and without *M. vulgare* were combined in ArcMap 9.3 and 10.1 using the data management intersect function and editing tools. This created combined information for the presence/absence of *M. vulgare*, presence/absence of prairie dog towns, soil type, and vegetation type. Random points were determined from polygons of surveyed areas within WCNP generated in GIS. For each random point (n=1233), *M. vulgare* presence/absence, prairie dog town presence/absence, soil type and vegetation type were determined.

Statistical methods

Generalized linear models were used to test for associations between *M. vulgare* presences and prairie dog towns, vegetation type, and soil type using “Proc Genmod” in SAS 9.2.1 with a binomial distribution and logit link. This procedure yields log odds ratio statistics, which were exponentiated to provide odds ratios comparing odds of *M. vulgare* presence between environmental variable categories. Associations between prairie dog town presence and vegetation and soil type were also tested using the same method.

Results

M. vulgare was distributed almost exclusively on prairie dog towns (Figure 2.1). A few plants (1-3) or small populations of plants (15-20) were found on human or bison trails in the park. Often these plants were found under *P. ponderosa* trees where signs of bison were present. Further, *M. vulgare* plants or small populations were found on prairie dog towns not known previously (i.e. NPS 5 town, Red Valley, and Apple Orchard towns). *M. vulgare* is relatively much more likely to be found on prairie dog towns than off prairie dog towns (Odds Ratio = 18.52, $\chi^2=486.33$, $P<0.001$).

There was a significant effect of vegetation type on *M. vulgare* presence ($\chi^2=482.86$, $P<0.001$). *M. vulgare* is relatively more likely to be found in some vegetation types than in other vegetation types (Table 2.3). When examining specific vegetation types as laid out in Table 2.1, and not lumping vegetation classes together, *M. vulgare* was found on six different vegetation types: the *Aristida purpurea* (purple three-awn) - *Dyssodia papposa* (fetid marigold) Herbaceous Vegetation class, the *Pascopyrum smithii* (western wheatgrass) - *Poa pratensis* (Kentucky bluegrass) Grassland Complex, the *S. scoparium* (little bluestem)– *Bouteloua (curtipendula gracilis)* (Blue grama) - *Carex filifolia* (threadleaf sedge) Herbaceous Vegetation class, the *P. ponderosa* Woodland Complex, the *S. occidentalis* Shrubland and the *A. canescens* Shrubland.

There was a significant effect of soil type on *M. vulgare* presence ($\chi^2=214.82$, $P<0.001$). *M. vulgare* is relatively more likely to be found on some soil textures than other soil textures (Table 2.4). *M. vulgare* was found on all seven different soil textures classes: loam clay complex, calcareous loam, channery loam, loam complex, silt loam, loam, and cobbly loam. *M. vulgare* was found on the following specific soil types as laid out in Table 2.2: BrA, BrB, CcE, CvB, GvD, HgB, HgD, HmE, MnC, NnE, PbD, PcD, RfE, SpE, SxaE, TfB, VcE, VoG, and WtB.

Associations between prairie dog town presence and vegetation type and soil texture were similar to associations between *M. vulgare* presence and vegetation and soil types. There was a significant effect of vegetation type on prairie dog town presence ($\chi^2=524.65$, $P<0.001$) and a significant effect of soil texture on prairie dog town presence ($\chi^2=213.46$, $P<0.001$). Prairie dog towns are relatively more likely to be found on certain vegetation types and soil textures than on other vegetation types and soil textures (Tables 2.5 and 2.6). Prairie dog towns were associated with the “Threeawn” vegetation type and loam complex, silt loam, and loam clay complex soils.

Discussion

M. vulgare plants were found to have associations with certain habitat and environmental factors. Almost all *M. vulgare* plants were found on prairie dog towns and many plants were found in the “Threeawn” vegetation type. Further, *M. vulgare*, while appearing on many soil types, was associated more strongly with certain soil textures.

M. vulgare plants were strongly associated with prairie dog towns, with only a few *M. vulgare* plants outside prairie dog towns. This is consistent with the stated hypothesis that *M. vulgare* is disturbance-dependent and is restricted primarily to prairie dog towns. This suggests that *M. vulgare* is a habitat specialist associated with disturbance and that there is a relatively low likelihood of *M. vulgare* becoming established and invasive in mixed-grass prairies subject to fewer disturbances. This information is valuable for managers in that focusing *M. vulgare* management on the prairie dog towns should be a priority and that limiting the spread of prairie dog towns in the grasslands may help to limit the invasion of *M. vulgare*.

M. vulgare is strongly associated with the “Threeawn” vegetation class, also known as the Prairie Dog Town Grassland Complex. Since *M. vulgare* is strongly associated with prairie

dog towns, it is not surprising that *M. vulgare* is strongly associated with a type of vegetation that is specifically found on prairie dog towns. Analyses confirm that prairie dog towns are also strongly associated with the “Threeawn” vegetation type. This “Threeawn” community is described as being found on highly disturbed prairie dog town soils, further emphasizing the role of disturbance in *M. vulgare* distribution (Cogan et al. 1999). Dominant species in this “Threeawn” vegetation type are patchy and vary with locality. Other common species include *Conyza ramosissima*, *Cirsium arvense*, and *Verbena bracteata* (Cogan et al. 1999). These species are known to be weedy or in some cases, also invasive. For example, *C. arvense* is an invasive plant species (USDA Plants Database), and *M. vulgare* appears to be dependent on similar conditions in WCNP as this invasive. *M. vulgare* is also mentioned as a local dominant, although *M. vulgare* is not included in the species list at the end of the vegetation mapping report (Colgan et al. 1999). This “Threeawn” plant community is also a new vegetation type first described in this survey (Colgan et al. 1999). Focusing efforts on monitoring and managing the “Threeawn” vegetation type should be a priority for stopping and reducing *M. vulgare* invasions. Further, *M. vulgare* presence is negatively associated with the “Trees” category, indicating the *M. vulgare* is primarily found in grassland vegetation and not in woody areas. Consistent with these results, *M. vulgare* is also more associated with other grassland vegetation types (the “WesternWheat” and “LittleBlue”) than with trees and in some cases, shrublands (Table 2.3).

Interestingly, the plant community data were collected in WCNP around the same time *M. vulgare* was thought to start increasing in the park. The vegetation survey acknowledges that *M. vulgare* was locally dominant in the *A. purpurea* – *D. papposa* community (Cogan et al. 1999). While local populations of *M. vulgare* were present in the late 1990s, some factor caused these populations to subsequently increase significantly and become more dominant on the

prairie dog towns. One possible factor is that in the early 2000s, WCNP experienced severe drought. This drought may have led to a decrease in the abundance and competitive effects of other native plant species on the prairie dog towns that allowed for *M. vulgare* to increase in population size and extent. Other invasive species have shown to be more drought tolerant than co-occurring native species. For example, the invasive *Tamarix ramosissima* is more drought tolerant than the natives *Pluchea sericea*, *Prosopis pubescens*, and *Salix exigua* in the Mojave Desert (Cleverly et al. 1997). In Yucatan, Mexico, seedlings of the invasive plant *Ruellia nudiflora* were more drought tolerant than seedlings of the native congeneric *Ruellia pereducta* (Cervera and Parra-Tabla 2009). Further, *M. vulgare* is found as an invasive in other arid and semi-arid environments (Young and Evans 1986, Halvorson and Guertin 2003, Mau-Crimmins et al. 2004) and in WCNP, *M. vulgare* may be more tolerant of drier conditions than other native plants. A second possible factor causing the increase of *M. vulgare* throughout WCNP is the removal of another invasive species, *C. arvensis* (Canada thistle) (Beth Burkhart, *pers. comm.*). *C. arvensis* was removed from some prairie dog towns and the removal likely caused disturbance. This novel disturbance may have aided *M. vulgare* invasion either by the physical disturbance itself or the increase in availability of resources for *M. vulgare*.

Although *M. vulgare* is found almost exclusively on prairie dog towns, *M. vulgare* does have the ability to inhabit other disturbed habitats, as evidenced by plants and small populations found along trails. While this still indicates that *M. vulgare* is a disturbance dependent species, *M. vulgare* is found in vegetation along the trails that differs from the “Threeawn” vegetation type. Many of these *M. vulgare* plants along trails were found in stands of *P. ponderosa* trees, sometimes around tree falls, and often near trees with signs of bison. As mentioned in Chapter 1, bison may contribute to the dispersal of *M. vulgare*.

All of the *M. vulgare* plants were found on loamy soil types, although there was a significant effect of soils on the local distribution of *M. vulgare*. *M. vulgare* plants were more likely to occur on silt loams, loam clay complexes, and cobbly loams. *M. vulgare* was less likely to occur on calcareous loams, loams, and channery loams. Prairie dog towns were similarly associated and were more likely to be found on silt loams, and loam clay complexes than on loam complexes. There is evidence that invasive plants are able to inhabit a number of soil textures, although are more successful on certain soil textures. For example, the invasive plant species *Acroptilon repens* was found to be most successful on clay and clay loam soils, but was also found on loam and loamy sand soils in Colorado (Goslee et al. 2006). Further, seedlings of *Schinus molle*, an invasive plant in southern Africa, were able to establish in both clay and sandy soils, although seedlings did better in fine-textured soils (Iponga et al. 2009). The invasive *Rubus armeniacus* in the Pacific Northwest is also tolerant of a wide range of soils (Caplan and Yeakley 2006).

M. vulgare has a mix of generalist and specialist habitat characteristics. *M. vulgare* appears to be restricted to disturbed areas and is found mostly in the “Threeawn” vegetation type. However, “Threeawn” is a specific vegetation type that is only associated with disturbed areas and there is evidence *M. vulgare* is able to exist in other vegetations such as the “WesternWheat” vegetation type. *M. vulgare* seems to favor some loamy soils such as silt loam, loam clay complexes and cobbly loams. However, all of the soils used in analysis were classified as loamy soils. Very sandy and clay soils were not present in the surveyed area. Further, while *M. vulgare* was found in some other vegetation and soil types, this may be more due to metapopulation dynamics and *M. vulgare* may be existing as sink populations and only surviving due to the “rescue effect” associated with regular epizoochorous dispersal by bison into these other areas.

This association data can be used to create a potential distribution map for *M. vulgare* within WCNP. In recent years, creating potential distribution maps for various invasive species has become common. The potential distribution for *M. vulgare* can help managers prioritize and target certain areas in the park. For example, *M. vulgare* does not seem to be a threat off of prairie dog towns, so focusing on prairie dog towns for *M. vulgare* management would be effective. Further, *M. vulgare* may be a threat to other very disturbed areas. Marvier et al. (2004) modeled invasive plant species spread and found that short-term disturbance promote invasions by habitat generalists. Minimizing disturbances within WCNP would not only help decrease the invasion potential of *M. vulgare*, but also of other invasive plant species.

Finally, the large established populations and multiple nascent foci of *M. vulgare* invasions throughout WCNP made mapping *M. vulgare* populations time-consuming. Using remote sensing data to map the distribution of *M. vulgare* in WCNP may be more practical. *M. vulgare* has the potential to be easily distinguished in remote sensing imagery for two reasons: 1) it is found almost exclusively in grassland areas and thus will not be disguised by tree cover and 2) *M. vulgare* senesces much later in the season than other prairie plants and breaks dormancy before most associated vegetation in the spring, which should yield spectral reflectance signals of *M. vulgare* patches that are distinct from those of surrounding vegetation near the beginning and end of the growing season.

Summary

This study confirmed that *M. vulgare* is a disturbance-dependent species and is primarily associated with prairie dog towns within WCNP. *M. vulgare* also proved to be significantly associated with certain native plant community types (the grassland “Threeawn” community) and soil textures (various loamy soils). These environmental factors co-vary, however, so it is

not possible to separate causal influence of disturbance, edaphic factors, and vegetation type. While *M. vulgare* was locally dominant in the late 1990s, *M. vulgare* rapidly expanded in the early 2000s and now forms monotypic stands in some areas.

This study has shown GIS is a valuable tool for quantifying patterns of invasive spread and determining environmental factors that best explain and constrain patterns of plant invasions. GIS can further be used to examine rates of invasive spread and in developing biogeoclimatic models for predicting future expansion of exotic species distributions. Also, as mentioned above, remote sensing may be a potential tool for monitoring the rate and patterns of *M. vulgare* invasion as *M. vulgare* has spectral properties early and late in the season that allow it to be easily distinguished from the surrounding native plant community.

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Figures and Tables

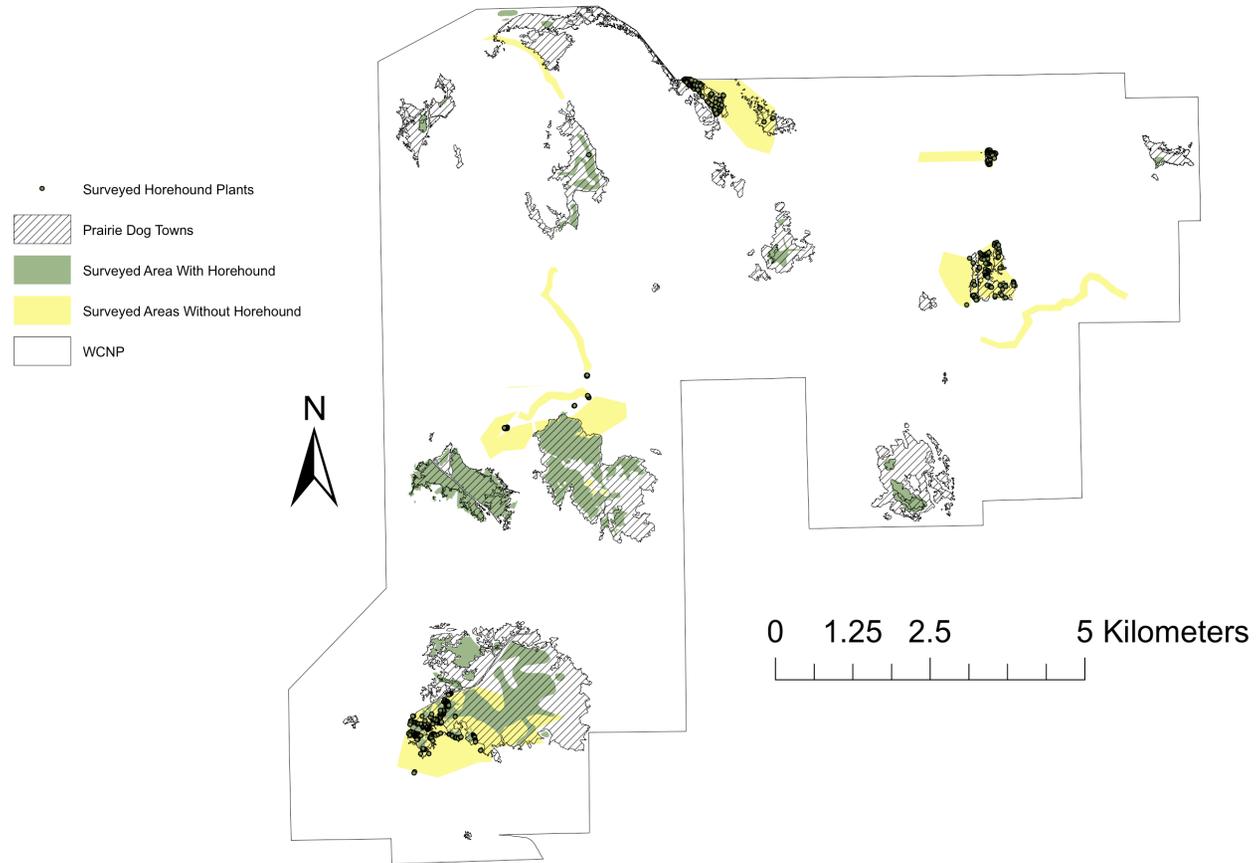


Figure 2.1. Areas surveyed for *M. vulgare* and *M. vulgare* presence.

Vegetation Class/Land Use

-  Prairie Dog Town
-  Purple Three-awn - Fetid Marigold
-  Ponderosa Pine Limestone Cliff Sparse Vegetation
-  Redbeds Sparse Vegetation
-  Black Hills Rock Outcrop Sparse Vegetation
-  White Sedimentary Rock Outcrop
-  Bison Wallows
-  Little Bluestem - Grama Grass - Threadleaf Sedge (with burned ponderosa pine)
-  Chokecherry Shrubland (with burned ponderosa pine)
-  Western Wheatgrass - Kentucky Bluegrass (with burned ponderosa pine)
-  Emergent Wetland Herbaceous Complex
-  Little Bluestem - Grama Grass - Threadleaf Sedge Herbaceous Vegetation
-  Western Wheatgrass - Kentucky Bluegrass Grassland Complex
-  Introduced Weedy Graminoid Herbaceous Vegetation
-  Needle-and-thread - Blue Grama - Threadleaf Sedge Herbaceous Vegetation
-  Mountain Mahogany/Sideoats Grama Shrubland
-  Mountain Mahogany/Sideoats Grama Dense Shrubland
-  Lead Plant Shrubland
-  Chokecherry Shrubland
-  Western Snowberry Shrubland
-  Creeping Juniper/Little Bluestem Shrubland
-  Plains Cottonwood/Western Snowberry Forest
-  Boxelder/Chokecherry Forest
-  Bur Oak Stand
-  Birch-Aspen Stand
-  Ponderosa Pine Woodland Complex I
-  Ponderosa Pine/Little Bluestem Woodland
-  Ponderosa Pine/Chokecherry Forest
-  Ponderosa Pine Woodland Complex II
-  Young Ponderosa Pine Dense Cover Complex
-  Transportation, Communications, Utilities
-  Mixed Urban or Built-up Land
-  Croplands and Pastures
-  Open Water

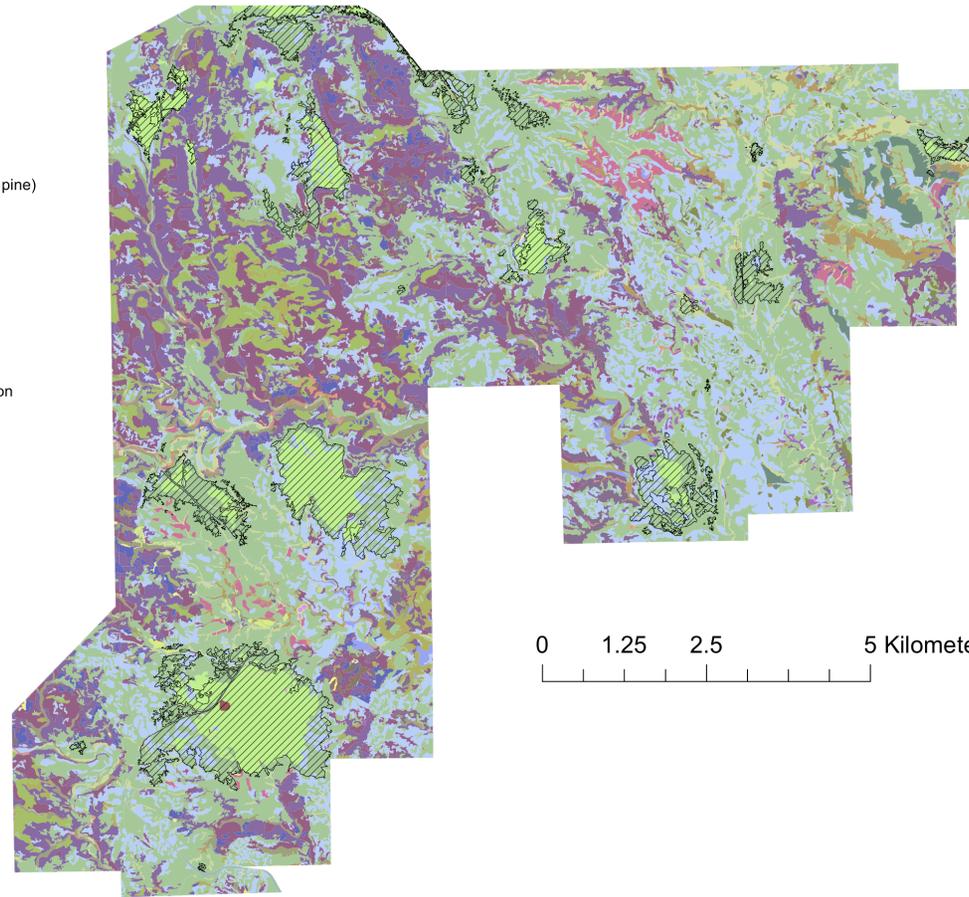


Figure 2.2. Vegetation map of WCNP. Prairie dog towns are overlaid on top of vegetation classes. Data from Cogan et al. (1999) and WCNP personnel.

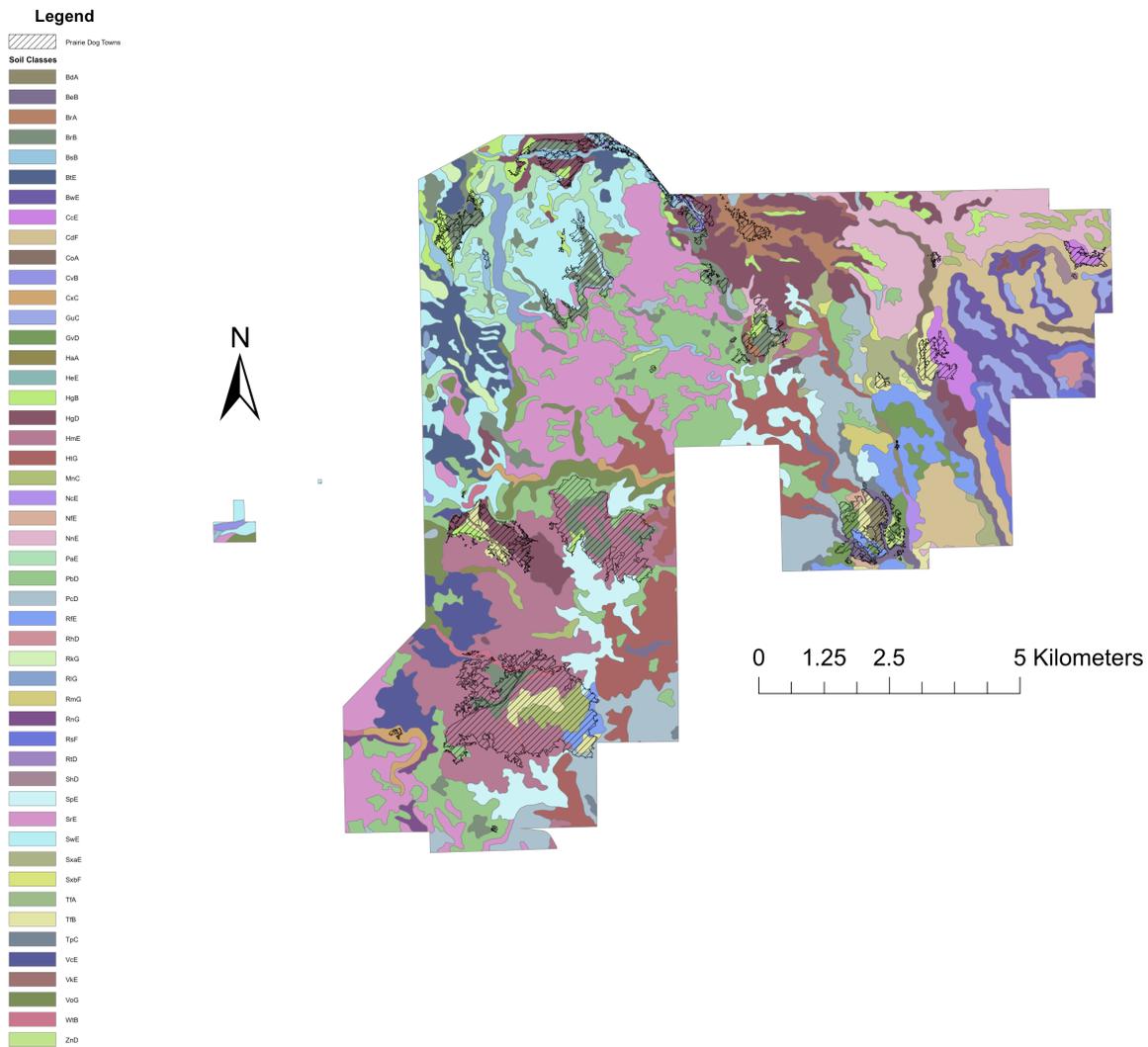


Figure 2.3. Map of soils within WCNP. Prairie dog towns are overlaid on soil types. See Table 2.2 for descriptions of soils. Data acquired from WCNP personnel, Ensz (1990), and Nielson (1996).

National Vegetation Classification System (NVCS) Association	Common Name
Hardwood Forests and Woodlands	
<i>Acer negundo</i> / <i>Prunus virginiana</i> Forest	BOX ELDER/CHOCHECHERRY FOREST
<i>Fraxinus pennsylvanica</i> - <i>Ulmus americana</i> / <i>Symphoricarpos occidentalis</i> Forest	ASH - ELM/WOLFBERRY FOREST
<i>Populus deltoides</i> / <i>Symphoricarpos occidentalis</i> Woodland	COTTONWOOD/WOLFBERRY - WESTERN ROSE FLOODPLAIN
Coniferous Forests and Woodlands	
<i>Pinus ponderosa</i> / <i>Carex inops</i> ssp. <i>Heliophila</i> Woodland	PONDEROSA PINE/SEDGE WOODLAND
<i>Pinus ponderosa</i> / <i>Pascopyrum smithii</i> Woodland	PONDEROSA PINE/WESTERN WHEATGRASS WOODLAND
<i>Pinus ponderosa</i> / <i>Schizachyrium scoparium</i> Woodland	PONDEROSA PINE/LITTLE BLUESTEM WOODLAND
<i>Pinus ponderosa</i> / <i>Juniperus communis</i> Woodland	PONDEROSA PINE/COMMON JUNIPER WOODLAND
<i>Pinus ponderosa</i> / <i>Prunus virginiana</i> Forest	PONDEROSA PINE/CHOCHECHERRY FOREST
Shrublands	
<i>Cercocarpus montanus</i> / <i>Bouteloua curtipendula</i> Shrubland	MOUNTAIN MAHOGANY/SIDE-OATS GRAMA SHRUBLAND
<i>Juniperus horizontalis</i> / <i>Schizachyrium scoparium</i> Dwarf-shrubland	CREEPING JUNIPER/LITTLE BLUESTEM DWARF- SHRUBLAND
<i>Prunus virginiana</i> Shrubland	CHOCHECHERRY SHRUBLAND
<i>Symphoricarpos occidentalis</i> Shrubland [Provisional]	WOLFBERRY SHRUBLAND
<i>Salix bebbiana</i> Shrubland	BEAKED WILLOW SCRUB

<i>Herbaceous Vegetation, Upland</i>	
<i>Schizachyrium scoparium</i> – <i>Bouteloua (curtipendula gracilis)</i> - <i>Carex filifolia</i> Herbaceous Vegetation	NORTHERN GREAT PLAINS LITTLE BLUESTEM PRAIRIE
<i>Stipa comata</i> - <i>Bouteloua gracilis</i> - <i>Carex filifolia</i> Herbaceous Vegetation	NEEDLE-AND-THREAD - BLUE GRAMA MIXEDGRASS PRAIRIE
<i>Pascopyrum smithii</i> - <i>Nassella viridula</i> Herbaceous Vegetation	WESTERN WHEATGRASS - GREEN NEEDLEGRASS MIXEDGRASS PRAIRIE
<i>Andropogon gerardii</i> - <i>Schizachyrium scoparium</i> Northern Plains Hillslope Herbaceous Vegetation	NORTHERN PLAINS BIG BLUESTEM PRAIRIE
<i>Poa pratensis</i> Herbaceous Vegetation	KENTUCKY BLUEGRASS HERBACEOUS VEGETATION
<i>Aristida purpurea</i> – <i>Dyssodia papposa</i> Herbaceous Vegetation	Purple Three-awn - Fetid Marigold Herbaceous Vegetation PRAIRIE DOG TOWN GRASSLAND COMPLEX
Introduced Weedy Graminoid Herbaceous Vegetation	
<i>Herbaceous Vegetation, riparian/wet meadow</i>	
<i>Eleocharis palustris</i> Herbaceous Vegetation	CREEPING SPIKERUSH WET MEADOW
<i>Spartina pectinata</i> - <i>Carex</i> spp. Herbaceous Vegetation	PRAIRIE CORDGRASS - SEDGE WET MEADOW
Western Great Plains Streamside Vegetation	WESTERN GREAT PLAINS STREAMSIDE VEGETATION
<i>Sparse Vegetation</i>	
<i>Pinus ponderosa</i> Limestone Cliff Sparse Vegetation	PONDEROSA PINE LIMESTONE CLIFF
Black Hills Rock Outcrop Sparse Vegetation	BLACK HILLS ROCK OUTCROP
Shale Barren Slope Sparse Vegetation	SHALE BARREN SLOPES
Redbeds (Silt/sandstone) Sparse Vegetation	REDBEDS

Table 2.1. Vegetation classifications within WCNP. Table adapted from Cogan et al. (1999).

Soil Code	Soil Name	Soil Description	Soil texture classes	Associated Vegetation
BeB	Barnum-Winetti	complex	loam complex	native grasses, thin stands of <i>Pipo</i>
BdA	Barnum	very fine sandy loam	----	native grasses
BrA	Bullfat	silt loam	silt loam	native grasses
BrB	Bullfat	silt loam	silt loam	native grasses
BsB	Bullfat-Cordeston	silt loam	----	native grasses and limited trees
BtE	Buska-Mocmount-Rock outcrop	complex	----	<i>Pipo</i>
BuE	Buska-Rock outcrop	complex	----	<i>Pipo</i> , <i>Scsc</i> , <i>Rhtr</i>
BvC	Buska-Virkula	loam	----	<i>Pipo</i> , native grasses
BwE	Butche-Rock Outcrop	complex	loam complex	<i>Pipo</i>
CcE	Canyon-Bridget	complex	calcareous loam	native grasses
CdF	Canyon-Rock outcrop	complex	----	native grasses
CoA	Colombo loam	loam	loam	?
CxC	Cordeston-Winetti	complex	loam complex	native grasses and clusters of trees
CvB	Cordeston	loam	loam	native grasses (hardwoods)
CwB	Cordeston-Marshbrook	loams	----	native grasses (wetlands)
GuC	Gurney-Butche	complex	loam complex	native grasses
GvD	Gypnevee-Rekop-Rock outcrop	complex	loam complex	native grasses with sparse <i>Pipo</i>
HeE	Heely	channery loam	channery loam	native grasses
HfC	Heely-Cordeston	complex	----	native grasses
HgB	Hilger	cobbly loam	cobbly loam	native grasses, encroached by <i>Pipo</i>
HgD	Hilger	cobbly loam	cobbly loam	native grasses, encroached by <i>Pipo</i>
HmE	Hilger-Metre	complex	loam clay complex	Native grasses and scattered <i>Pipo</i>
HtG	Hopdraw-Sawdust-Rock outcrop	complex	loam complex	<i>Pipo</i> , tall shrubs, <i>Jusc</i>
MhA	Marshbrook	loam	----	native grasses (wetlands)
MnC	Meter-Norrest	complex	loam clay complex	native grasses
MtE	Mocmont-Rock outcrop	complex	----	<i>Pipo</i>
NaC	Navee	channery loam	----	native grasses
NcE	Navee-Gullised land	complex	----	native grasses
NfE	Nihill-Zigweid	complex	----	native grasses and limited <i>Pipo</i>
NnE	Norrest-Fairburn-Metre	complex	loam clay complex	native grasses and limited <i>Pipo</i>
PaE	Pactola-Virkula-Rock outcrop	complex	----	<i>Pipo</i> and other trees

PbD	Paunsaugunt-Gurney	complex	----	native grasses and <i>Rhtr-Cemo</i>
PcD	Paunsaugunt-Rock outcrop	complex	loam clay complex	<i>Pipo</i>
RhD	Rock outcrop – Butche	complex	----	<i>Pipo</i>
RfE	Rekop-Gypnevee-Rock outcrop	complex	----	native grasses and sparse <i>Pipo</i>
RiG	Rock outcrop – Pactola	complex	----	<i>Pipo</i>
RkG	Rock outcrop – Mocomont	complex	----	<i>Pipo</i>
RmG	Rock outcrop – Rekop	complex	----	native grasses
RnG	Rock outcrop – Sawdust	complex	----	<i>Pipo</i>
RsF	Rockoa – Rock outcrop	complex	----	<i>Pipo</i>
ShD	Satanta-Canyon	loams	----	native grasses
SpE	Sawdust-Hopdraw-Paunsaugunt	complex	----	<i>Pipo</i>
SrE	Sawdust-Vanocker-Paunsaugunt	complex	loam complex	<i>Pipo</i>
SwE	Shirttail	channery loam	channery loam	native grasses and thin <i>Pipo</i>
SxaE	Spearfish-Nevee	silt loam	silt loam	native grasses
SxbF	Spearfish-Rock outcrop	complex	----	native grasses and scattered <i>Pipo</i>
TfB	Tilford	silt loam	----	native grasses
TfC	Tilford	silt loam	silt loam	native grasses
TpC	Tilford-Paunsaugunt	complex	----	native grasses and some <i>Pipo</i>
VcE	Vanocker-Citadel	complex	loam complex	<i>Pipo</i>
VkE	Vancoker-Lakoa	complex	----	<i>Pipo</i>
VoG	Vanocker-Sawdust-Rock outcrop	complex	loam complex	<i>Pipo</i>
WtB	Winetti	cobbly loam	cobbly loam	native grasses and thin <i>Pipo</i>
ZnD	Zigweid-Nihill	complex	loam clay complex	native grasses and sparse <i>Pipo</i>

Table 2.2. Soil classifications within WCNP. Table adapted from Cogan et al. (1999). Data also from Ensz (1990) and Nielson (1996). “Soil texture classes” refer to the classes used for analyses. “----” indicates soils not used in analyses. “Pipo” = *Pinus ponderosa*, “Sesc” = *Schizachyrium scoparium*, “Rhtr” = *Rhus trilobata*, “Cemo” = *Cercocarpus montanus*, “Jusc” = *Juniperus scopulorum*.

Vegetation Type	LittleBlue	Shrub	Threeawn	Trees	WesternWheat
LittleBlue	—	1.739 1.74	0.026* 133.73	12.862* 21.85	0.714 2.71
Shrub	0.575 1.74	—	0.016* 83.88	7.456* 9.87	0.411* 5.32
Threeawn	36.914* 131.10	64.200* 83.88	—	474.803* 115.47	26.364* 148.53
Trees	0.078* 21.85	0.135* 9.87	0.002* 115.47	—	0.056* 30.80
WesternWheat	1.400 2.71	2.435* 5.32	0.037* 151.02	18.010* 30.80	—

Table 2.3. Odds ratio, χ^2 , and significance values for presence of *M. vulgare* in different vegetation types. Odds ratio of the likelihood of *M. vulgare* appearing on the indicated vegetation type. Odds ratio numbers are represented in the top of each box, corresponding χ^2 values are represented in the bottom of each box. The vegetation types across the top represent the reference vegetations. “*” denotes significant odds ratios (P<0.05). For example, when using the “Shrub” category from the top and “LittleBlue” category from the side, the odds of *M. vulgare* being present in LittleBlue instead of Shrub is 1.739, though this is not significant.

Soil Texture	Loam complex	Calcareous loam	Channery loam	Cobbly loam	Loam	Loam clay complex	Silt loam
Loam complex	—	1.800 1.27	0.304 2.86	0.109* 70.33	0.851 0.04	0.092* 102.80	0.10* 84.05
Calcareous loam	0.556 1.27	—	0.169* 4.67	0.061* 31.34	0.473 0.64	0.051* 37.43	0.06* 34.06
Channery loam	3.289 2.86	5.920* 4.67	—	0.359 2.22	2.800 0.97	0.302 3.12	0.33 2.60
Cobbly loam	9.166* 70.33	16.500* 31.34	2.787 2.22	—	7.803* 6.33	0.842 0.89	0.92 0.15
Loam	1.175 0.04	2.114 0.64	0.357 0.97	0.128* 6.33	—	0.108* 7.60	0.12* 6.89
Loam clay complex	10.879* 102.80	19.582* 37.43	3.308 3.12	1.187 0.89	9.262* 7.60	—	1.10 0.35
Silt loam	9.896* 84.05	17.812* 34.06	3.009 2.60	1.080 0.15	8.424* 6.89	0.910 0.35	—

Table 2.4. Odds ratio, χ^2 , and significance values for presence of *M. vulgare* in different soil textures. Odds ratio of the likelihood of *M. vulgare* appearing on the indicated soil texture. Odds ratio numbers are represented in the top of each box, corresponding χ^2 values are represented in the bottom of each box. The soil textures across the top represent the reference soil texture for analyses. “*” denotes significant odds ratios (P<0.05). For example, when using the “Calcareous loam” category from the top and “Loam complex” category from the side, the odds of *M. vulgare* being present in Loam complex instead of Calcareous loam is 1.800, though this is not significant.

Vegetation Type	LittleBlue	Shrub	Threeawn	Trees	WesternWheat
LittleBlue	—	1.607 1.02	0.022* 166.08	Not enough data	0.420* 15.80
Shrub	0.622 1.02	—	0.014* 81.34	Not enough data	0.261* 9.63
Threeawn	46.035* 166.08	73.988* 81.34	—	Not enough data	19.321* 159.23
Trees	Not enough data	Not enough data	Not enough data	—	Not enough data
WesternWheat	2.383* 16.80	3.829* 9.63	0.052* 9.63	Not enough data	—

Table 2.5. Odds ratio, χ^2 , and significance values for presence of prairie dog towns in different vegetation types. Odds ratio of the likelihood of prairie dog towns appearing on the indicated vegetation type. Odds ratio numbers are represented in the top of each box, corresponding χ^2 values are represented in the bottom of each box. The vegetation types across the top represent the reference vegetations. “*” denotes significant odds ratios ($P < 0.05$).

Soil Texture	Loam complex	Calcareous loam	Channery loam	Cobbly loam	Loam	Loam clay complex	Silt loam
Loam complex	—	0.079* 33.26	0.173* 5.13	0.064* 62.94	0.108* 9.01	0.037* 101.16	0.034* 98.51
Calcareous loam	12.700* 33.26	—	2.200 1.04	0.818 0.35	1.375 0.19	0.468* 5.52	0.435* 6.18
Channery loam	5.773* 5.13	0.455 1.04	—	0.372 1.88	0.625 0.23	0.213* 4.71	0.198* 5.09
Cobbly loam	15.532* 62.94	1.223 0.35	2.690 1.88	—	1.682 0.57	0.572* 10.49	0.532* 10.62
Loam	9.246* 9.01	0.727 0.19	1.600 0.23	0.595 0.57	—	0.340 2.53	0.316* 2.84
Loam clay complex	27.132* 101.16	2.136* 5.52	4.700* 4.71	1.747* 10.49	2.938 2.53	—	0.929 0.21
Silt loam	29.213* 98.51	2.300* 6.18	5.060* 5.09	1.881* 10.62	3.163 2.84	1.077 0.21	—

Table 2.6. Odds ratio, χ^2 , and significance values for presence of prairie dog towns in different soil textures. Odds ratio of the likelihood of prairie dog towns appearing on the indicated soil texture. Odds ratio numbers are represented in the top of each box, corresponding χ^2 values are represented in the bottom of each box. The soil textures across the top represent the reference soil texture for analyses. “*” denotes significant odds ratios (P<0.05).