

Effects of White-tailed Herbivory on a Tallgrass Prairie Remnant

by

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ABSTRACT

Since the 1980s white-tailed deer (*Odocoileus virginianus*) populations have irrupted across southern Manitoba, to include the critically-endangered tallgrass ecosystem of Saint Charles Rifle Range (SCRR). A tallgrass: aspen forest tract embedded within an agro-urban complex, a study was conducted to determine what impact these large ungulates were having on the native flora. Examining soils, agricultural histories, and floristic cover, strong cause and effect relationships were found. Microhistological fecal analysis was employed to determine dietary composition over a 13-month period, both with and without access to row-crops. Using preference indices, white-tailed deer were found to be placing a number of native plant species at risk of extirpation. Measuring woody stem abundance and height along and near the prairie: forest ecotone, deer were restructuring but not directly retarding or promoting woody expansion. Indirectly, using an inverse distance weighted equation and correlating grazing trails to disturbance vegetation, they were found to facilitate woody encroachment and prairie degradation through seed dispersal, nitrogen deposition, gap-dynamics, and trampling. Comparing dietary preferences to August nutritional data (crop/no crop), deer grazed row-crops to maximize fitness, selecting foods high in IVDMD, minimizing energy expenditure, and optimizing CP. Optimizing CP was achieved by intensively grazing targeted native plants. Unlike for many other ungulates and monogastrics, ADF and not AIA was an effective nutritional marker for free ranging deer. If this northern tallgrass prairie remnant is to be preserved, resident deer populations must be dramatically reduced, through culls and by leveraging known animal biology, and active restoration measures employed.

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ABSTRACT

Manitoba's second largest tract of critically endangered northern tallgrass prairie, Saint Charles Rifle Range (SCRR) is an ecosystem under siege. With the ecological disturbance engines that, for millennia, shaped its associated flora and fauna now all but silent, the site currently supports a burgeoning population of exotic white-tailed deer that graze in a manner unlike that of its predecessor large ungulates and modify their environment in distinctly different ways. Embedded within an agro-urban landscape, SCRR has become a terrestrial island within a sea of exotics and row-crops. Subjugated to various forms of anthropological disturbance since the 1880s, organic matter, nitrate, and total nitrogen have all decreased on formerly tilled lands, retarding the proliferation of ruderals. Where nitrogen and calcium are not limiting, aspen encroachment appears to be most vigorous. Indeed, aspen may be facilitating its own spread through $\delta^{15}\text{N}$ enrichment of the soil.

INTRODUCTION

Together, fire and bison grazing are thought to have been the primary disturbances that prevented the establishment of forest in the North American Great Plains. Fires, started either by lightning or deliberately set by Amerindians, would race across the open lands until all available fuel was burned, eliminating woody growth and promoting grasslands in its stead (Howe 1994, Biondini et al. 1999). Bison (*Bison bison*) quickly evolved on the grasslands and were soon ebbing and flowing by the millions across the open spaces, consuming tremendous amounts of plant matter (Knapp et al. 1999, Kline 1997). The

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enormous diversity of plants and the biota these prairies supported evolved in the presence of these disturbances (Fuhlendorf and Engle 2001).

When European settlers first arrived in on the Great Plains the tallgrass prairie standing before them stretched from southern Manitoba to Texas and east to Indiana (Samson and Knopf 1994, Packard 1997). From 1830 to the 1880s these fertile lands were put to the plough or fenced for cattle. Grass fires were actively prevented and the bison were all but exterminated. By 1880 bison are estimated to have numbered in the mere thousands, reduced from the estimated 30-60 million of the preceding century (Knapp et al. 1999). Uncultivated lands whose soil was capable of supporting woody growth quickly transformed into forestlands. Today, less than one percent of North America's, and less than 0.1% of Manitoba's, former tallgrass prairie remains (Samson and Knopf 1994).

Concurrent to the disappearance of free-ranging bison was the extirpation of elk (*Cervus canadensis*) and the reduction of mule deer (*Odocoileus hemionus*) across much of the Canadian Prairies (England and DeVos 1969). This effectively eliminated the last of the large native herbivores from the ecosystem. Another large herbivore, the white-tailed deer (*Odocoileus virginiana*), historically either uncommon or unknown in southern Manitoba, was also on the brink of extinction (McCabe and McCabe 1997, England and DeVos 1969).

Extirpated through large areas of their original range due to over hunting and a loss of habitat, through a combination of active management, the conversion of old-fields back

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to forested lands, and the proliferation of row-crops, white-tailed deer have made a dramatic recovery (Knox 1997). They now exist at record-high densities across much of North America, to now include the northern tallgrass prairies, and are displacing mule deer in some regions (McCabe and McCabe 1997). Although there is considerable overlap between these two species, mule deer have less generalized dietary and habitat requirements (Loveless 1967, Anthony and Smith 1977).

In southern Manitoba, the rapid rise in white-tailed deer populations in the late 1960s and 1970s coincided with the shift from cattle (*Bos taurus*) farming to row cropping (Shoesmith et al 1981, Manitoba Agriculture: Census of Agriculture 1966, 1971, 1976, 1981). Until then, despite cattle and deer having minimal dietary overlap, the two ungulates were unable to co-exist on extensively grazed pastures (Hansen and Reid 1975, Austin and Urness 1986, Loft et al. 1991, Ortega et al. 1997). The switch to row-crops prompted the region's farmers to cut down many of the forest stands occupying marginal lands (Nixon 1970), thereby depriving deer of necessary thermal shelter and browse, but this loss was more than offset by the introduction of nutritionally rich food sources in the form of crops and associated harvest residue. As a result, the white-tailed deer population in the City of Winnipeg and its immediate vicinity has increased from 207 in 1980 to 1,286 in 2006 (Manitoba Conservation, unpublished data).

Immediately west of the City of Winnipeg is Manitoba's second largest remnant northern tallgrass prairie, Saint Charles Rifle Range. How the growing resident white-tailed deer population is impacting the native flora of this critically endangered ecosystem (Samson

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et al. 2003) and the site's aspen forest's ability to encroach upon it is not clear. The following chapters explore these questions by looking at what the deer are eating, how they are affecting the native tallgrass prairie both directly through herbivory (Chapter 2) and indirectly through such mechanisms as fecal deposition, trampling, seed dispersal, and gap dynamics, determine if they are facilitating or retarding aspen encroachment (Chapter 3), and understand why they make the dietary choices they do (Chapter 4). This information is then used to develop a site-specific ecological management framework (Chapter 5).

LITERATURE REVIEW

Intermediate Disturbance Hypothesis

Connell first proposed the Intermediate Disturbance Hypothesis (IDH) in 1978. It postulates that, in order for diversity to be maximized, an intermediate degree of disturbance must be present. This disturbance regime, which could include fire, grazing, trampling, flooding, or other abiotic forces or disruption, will prevent competitively superior species from becoming completely dominant and thereby dramatically reduce or extirpate less competitive species. If the disturbances are too frequent, however, then diversity will be reduced as the affected species are unable to withstand the repeated disturbance.

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This is a conceptual framework in that it does not quantitatively define “intermediate” (Hobbs and Huenneke 1992). For IDH to work, a number of conditions must be met.

First, the disturbance will reduce the dominant species. Second, that there is an ecological trade-off between disturbance-tolerance and competitive ability. Third, a trade-off exists between the ability to colonize and to compete. Fourth, there are at least two successional stages within the community and, lastly, the regional species pool is greater than that of the disturbed site (Collins and Glenn 1997).

IDH is associated with temporal and spatial scales. Once a disturbance occurs, the shift in advantage to the competitively inferior species will allow that species to become fleetingly dominant. As time progresses, unless removed from the site, the competitively superior species will again gain advantage and become dominant, until the next disturbance. Spatially, the use of scale and definition of diversity will influence the final validity of the IDH model. Extremely small patches, as defined by the habitat requirements of the system or species in question, may not be able to withstand disturbance or have the necessary surrounding species to affect colonization, resulting in a decrease in diversity. Studies have revealed that the greatest ecological diversity occurs at the landscape level, with low within-patch diversity and high among-patch diversity (Petraitis et al. 1989). The low within-patch diversity (alpha diversity) allows for sufficient species robustness to withstand intense disturbances and still re-colonize so long as there is a seed source or patches are connected. Across the landscape (beta diversity) the large variety of species permits longer-range re-colonization if necessary, so long as patches are connected (Hobbs and Heunneke 1992).

Patch-level extinctions and colonization have been associated with two classes of ecological state: equilibrium and nonequilibrium. The equilibrium hypothesis model assumes that species composition is naturally at an equilibrium and unchanging. Although there is a cyclical movement from colonizing to successor species, alternately replacing each other, the overall diversity of the biotic assemblage is at equilibrium at intermediate scales (Wiegand et al. 1998). While mortality can in fact be caused by predation, these are not on a large enough scale to destabilize the equilibrium. The nonequilibrium hypothesis model assumes that species composition is rarely at a state of equilibrium, with diversity maximized only when the ecological composition is continually changing (Petraitis et al. 1989). This occurs particularly in the case of mass mortality or catastrophic disturbance. Considering diversity at an intermediate scale is important because asynchronized disturbance across the landscape will create a series of adjacent patches at differing states of post-disturbance recovery, creating further diversity (Collins and Glenn 1997).

Combining equilibrium and nonequilibrium hypothesis, diversity is maximized with short-term, nonequilibrium states at the patch level, allowing a flux of transient biota to establish themselves. At larger temporal and spatial scales, equilibrium is achieved as the sum of beta diversity across all patches remains stable (Wiegand et al. 1998, Petraitis et al. 1989, Glenn et al. 1992).

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For disturbance to be ecologically beneficial, it must be appropriate spatially, temporally, and in nature for the ecosystem in question. Otherwise, the subject species or patch may not be able to withstand the effects of the disturbance or its effects will alter the competitive balance with which the ecosystem has evolved (Roberts and Gillam 1995, Hobbs and Huenneke 1992). Wiens (1976) referred to patchiness as organism-defined, suggesting that small organisms with short life spans are the most sensitive to disturbance whereas large organisms may be “buffered” from the effects of small-scale variation. Given the number of possible organisms that live within a patch or community, there is an infinite number of scales in which an ecosystem may be considered.

In a tallgrass prairie setting, bison were the dominant biotic source of disturbance. As they moved in large herds they consumed primarily the competitively superior C₄ grasses, leaving the smaller forbs (Knapp et al. 1999). This allowed the passed-over forbs to profit from greater sunlight and to propagate into the canopy gaps left by grazing and soil disturbance, generating an increase in plant diversity on a large scale (Hartnett et al. 1996) and a diversity of habitat structures (Tews et al. 2004). In southeastern Manitoba, located at the northeastern extremity of the tallgrass prairie biome, bison are believed to have been present less often than elsewhere, likely not more than 6-7% of the time (Shaw 1998). As such, given their irregular movement patterns, bison likely only denuded the region of vegetation once every 5-8yrs, allowing the favoured grasses to recover.

White-tailed deer exert a very different influence than bison on the remnant tallgrass prairie assemblages. Large generalist herbivores, they preferentially graze those plants

that offer the greatest nutritional advantage at that moment. Partly in response to their smaller stomach cross section size – and therefore reduced ability to fill that stomach with low-nutrition foods, white-tailed deer rarely graze the poorly digestible grasses favoured by bison (Penry 1993, Illius and Gordon 1993). Instead, during the growing season they most often select forbs, when the plants are most vulnerable to the negative effects of herbivory. Because they are easiest to digest and generally highest in digestible energy, the most succulent forbs are usually grazed over those with high C:N and stem:leaf ratios (Olf and Ritchie 1998, Rooney and Waller 2003). Compared to bison, then, white-tailed deer herbivory enhances the inter-specific competitive advantage inherent to late summer grasses, providing an inappropriate disturbance regime that does not destabilize the phyto-successional cycle. Only those forbs that are graze-intolerant due to phenology, toxins, or reproductive strategy increase under deer grazing. While limited deer grazing can increase native plant diversity (Kellogg and Bridgham 2004, Russell et al. 2001), at high densities deer graze in such a manner as to decrease the diversity of native species (Alverson 1988, Anderson et al. 2001, Rooney and Waller 2003).

Optimal Forage Theory

Understanding diet selection for free-ranging large herbivores such as white-tailed deer is a daunting task and theoretical models have only been in extensive development since the 1970s (Robbins 1993). Rooted in Optimal Diet Theories initially developed to model predator-prey relationships (Pulliam 1974), one of the conceptual frameworks put forth in

the 1960s was the Optimal Foraging Model. In his 1974 analysis, Westoby wrote that the strategic objective of dietary selection for a large generalist herbivore is to obtain the best possible mix of nutrients within a given foraging period, and that a learning mechanism must be associated with this process in order to enhance the animal's ability to maximize its foraging performance. For any animal, the amount of food that can be processed is a function of the cross-section area of the stomach (volume) and the metabolic time to digest (processing rate). Because large generalist herbivores eat large amounts of nutritionally low value foods, they tend to keep their stomachs full all of the time. They therefore must select foods that will ensure a balanced diet and that their nutritional needs are met. Under this model, foods will only increase as a component of the total diet if they enhance the overall nutritional value of that diet. Conversely, foods that decrease or do not change the quality of the diet, such as those plants high in poorly digestible fibres and lignin, will not.

Foods were grouped into two categories: those with properties detectible before ingestion and those that are detectible only after ingestion. Because it may take ruminants 18-24hrs to digest a food, the feedback mechanism is inadequate to support the idea of food quality differentiation. Westoby therefore proposed a Reinforcement Differential (RD), whereby positive feedback responses would reinforce the selection of sampled foods.

The limitations of this model were defined as fallibilities, and were described as follows. Some nutrients are not detectible in the food before it is consumed, but a failure to optimize these nutrients could lead to a failure to optimize the diet. Next, some nutrients

can only be detected if there is a significant deficiency, therefore the food may be selected to avoid death, but not at optimal levels. Third, only sodium and sugar have a strong sensory component, likely reinforced through chemostatic responses. There is no natural control on limiting voluntary intake of these compounds so an animal could over consume. Fourth, animals cannot learn from what kills them.

The Optimal Model suggests that so long as a plant species occurs above a minimum threshold, it will be consumed regardless of availability because of the nutritional advantage offered by it. Once below that threshold, greater effort may be required to locate the plant than the nutritional benefit contributed by it. Conversely, the Palatability Model suggests that there is a continuous response; the ratio of the plant consumed is constant, regardless of its abundance (Westoby 1974).

As with all functional models, Optimal Forage Theory describes general population-level dynamics but does not address the precise mechanisms involved in the process (Pyke 1984). It also does not address how herbivores know or learn what they should or should not eat. This knowledge is partly explained by the consumer's post-digestive feedbacks from nutrients and toxins as well as the food's palatability. Palatability is related to the nutritional value of the foods while unpalatability is related, in part, to the toxins within the forage they sample. It is assumed that, with experience, certain individual animals will learn what foods should be avoided. Animals have been found to decrease their intake of foods that contain toxins, presumably because of negative post-digestive

feedbacks, and that they seem to be able to recall which foods to avoid or favour (Provenza and Cincotta 1993).

For large herbivores the question is complex. Not only are the most nutritious foods distributed unevenly across the landscape in differing densities and combinations, the quality of these foods also vary spatially and temporally. Forage Maturation Hypothesis suggests that herbivores actively graze plants as they enter the most nutritious phenological stage, selecting plants with younger growth and present in higher densities (Stewart et al. 2000). Most plants peak in nutritional value as they prepare to flower and seed, thereafter declining. When the plants enter senescence in the fall, nutrients are translocated to the roots, rendering them inaccessible to most herbivores.

While forage theorists generally recognized that the nutritionally ephemeral nature of vegetation was important in influencing actual diet selection, Illius and Gordon (1993) argued that the physiological limitations of the consumer must also be considered. Plants vary in digestibility due to indigestible and poorly digestible components such as lignin, silica, cutin, suberin, cellulose, and hemicellulose (Robbins 1993). Variations in digestibility affect gut retention times and, given that gut sizes are fixed, optimizing intake quality and intake rates is an ongoing challenge. While forbs are roughly 1.6 times more nutritious than grasses, they generally exist at lower biomass densities on the landscape than grasses. The larger stomached bison can extract more nutrition by quickly grazing large amounts of readily-accessible grasses and then maximizing its rumen function than by actively seeking out forbs (Berteaux et al. 1998). Possessing smaller

stomachs and unable to digest grasses as quickly or effectively, white-tailed deer must selectively graze a greater proportion of forbs to optimize their dietary intake (Illius and Gordon 1993).

To obtain at least some insight into current food quality, white-tailed deer have developed a partial selection strategy. As they graze through patches they continuously sample a wide variety of plants. In patches where forage quality is high the deer will remain longer but will not stay until all plants are consumed, always leaving a quantity behind (Focardi et al. 1996, Berteaux et al. 1998). At high deer population densities, selectivity towards the highest quality patches often decreases, possibly reflecting social factors or other dynamics (Wiens 1976). This behaviour may also ensure that all essential nutrients and compounds are consumed by varying diet. It could also be a risk-avoidance mechanism. Regardless, this pattern of partial selection suggests that deer treat movement, patch exploitation, and patch assessment as concurrent activities (Illius and Gordon 1993).

As white-tailed deer densities increase, this partial selection foraging strategy both offsets grazing pressure on favoured plant species and places locally rare, less favoured plants at risk of extirpation. Central place feeders, deer move outwards when foraging and graze most intensively near their thermal shelter (Anderson et al. 2005), grazing along a tortuous path within feeding stations to maximize the encounter and selection of preferred foods (Pyke 1984, Etzenhouser et al. 1998). By partially selecting all possible foods, they reduce the abundance of those species least able to withstand grazing (Coté et al. 2004). At high enough densities deer are mathematically likely to encounter all, or almost all,

plants within their foraging area, potentially placing the most favoured plant's survival at risk.

White-tailed Deer Population Irruptions

The introduction of highly nutritional, highly concentrated foods in the form of intensive row-cropping has been a major contributing factor to the white-tailed deer population irruption in the past thirty to forty years. The concept of population irruption was first put forth by Leopold in 1943 and expanded upon by Caughley (1981). It proposes that when a population-limiting factor such as predation is removed, the population will irrupt, exceeding historical limits until it surpasses the availability of food. The population will then crash, that limiting resource will rebound, and the dynamic will repeat until the limiting factor is either restored or replaced with a surrogate (McCullough 1997). In Caughley's version of the theory, subsequent population densities will oscillate at a level lower than that of the original dynamic state, establishing an alternate equilibrium. All three case histories of white-tailed deer irruptions reviewed by McCullough (1997) failed to demonstrate that alternate steady states would be achieved. Instead, a cycle of population irruptions and crashes of similar amplitude persisted. In these three examples sufficient vegetation survived on the sites to support future growth.

From a system perspective, then, white-tailed deer population irruptions may be considered non-problematic. Caughley (1981) explored the concept of overabundance. He suggested that there are four Classes of overabundance, each replete with human

subjectivity. The first is when animals threaten human life or livelihood. The second is when a particular animal is considered to depress the densities of favoured species, such as elk consuming aspen in Yellowstone National Park, coyotes hunting deer in North America, or lions killing wildebeest. Third is when it is deemed that an animal is too numerous for its own good. He stated that this Class 3 is often used by hunters to justify their actions, possibly stating humanitarian reasons or the need to re-establish a population dynamic. Fourth is the assertion that the plant/animal dynamic is not at equilibrium. Of these four, only the last is truly an ecological reason, but then goes on to speculate that even this Class must be considered carefully.

Population irruptions are not necessarily bad and, referring back to IDH, a healthy ecosystem should experience some rate of local extinctions and immigrations. It is ecologically unsound for an entire landscape to be at equilibrium. Caughley asserts that even the Class 4 irruption of non-native large herbivores in New Zealand has created a Class 2, but not Class 4, irruption. Because many natural cycles or oscillations last many decades or longer, humans need to avoid viewing ecosystems in improper temporal scales for the species or biotic assemblage in question (Debinski and Holt 2000).

This view may be valid at a landscape scale where the overabundant species cannot dominate all niches or areas, allowing those prey species most at risk to persist. Owen – Smith (2004) refers to this as Functional Heterogeneity, where what is important is not the total available food or forage as measured by the observer, but what is known to the species in question. In isolated fragmented landscapes where herbivores can know the

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location of all available favoured forage and where migrations and re-colonization of locally extirpated species cannot occur, the magnitude of disturbances needs to be tempered to ensure that they do not extend across the entire ecosystem.

Immigrations, local extinctions, and specific equilibrium form the basic underpinnings of Island Biogeography (Wu and Vankat 1995). While there is no intent to examine this theory here, it is relevant to ecological islands within larger terrestrial settings. Where native flora and fauna within an island ecosystem become extinct, opportunities exist for immigration by species from the same functional group or invasive to occur (Symstad 2005). Over time, stochastic events, genetic drift, and reduced plant pollination rates can reduce diversity within small remote islands (Simberloff and Gotelli 1984, Menges 1991, Jennersten 1988). Where possible immigrants are non-native species, the eventual pattern will be for a net reduction of native species on that island. Small remnant ecosystems are, by their nature, vulnerable to disturbance and experience abiotic forces possibly very different from those that existed before landscape fragmentation (Saunders et al. 1991).

STUDY AREA

The primary study area is Saint Charles Rifle Range (SCRR), a military rifle range and dismounted training area less than 2km west of Winnipeg, Manitoba, located in the Rural Municipalities of Headingley and Rosser (49° 55' North latitude, 97° 13' West longitude, elevation 238m) (Figure 1.1). It comprises 280ha of remnant northern tallgrass prairie

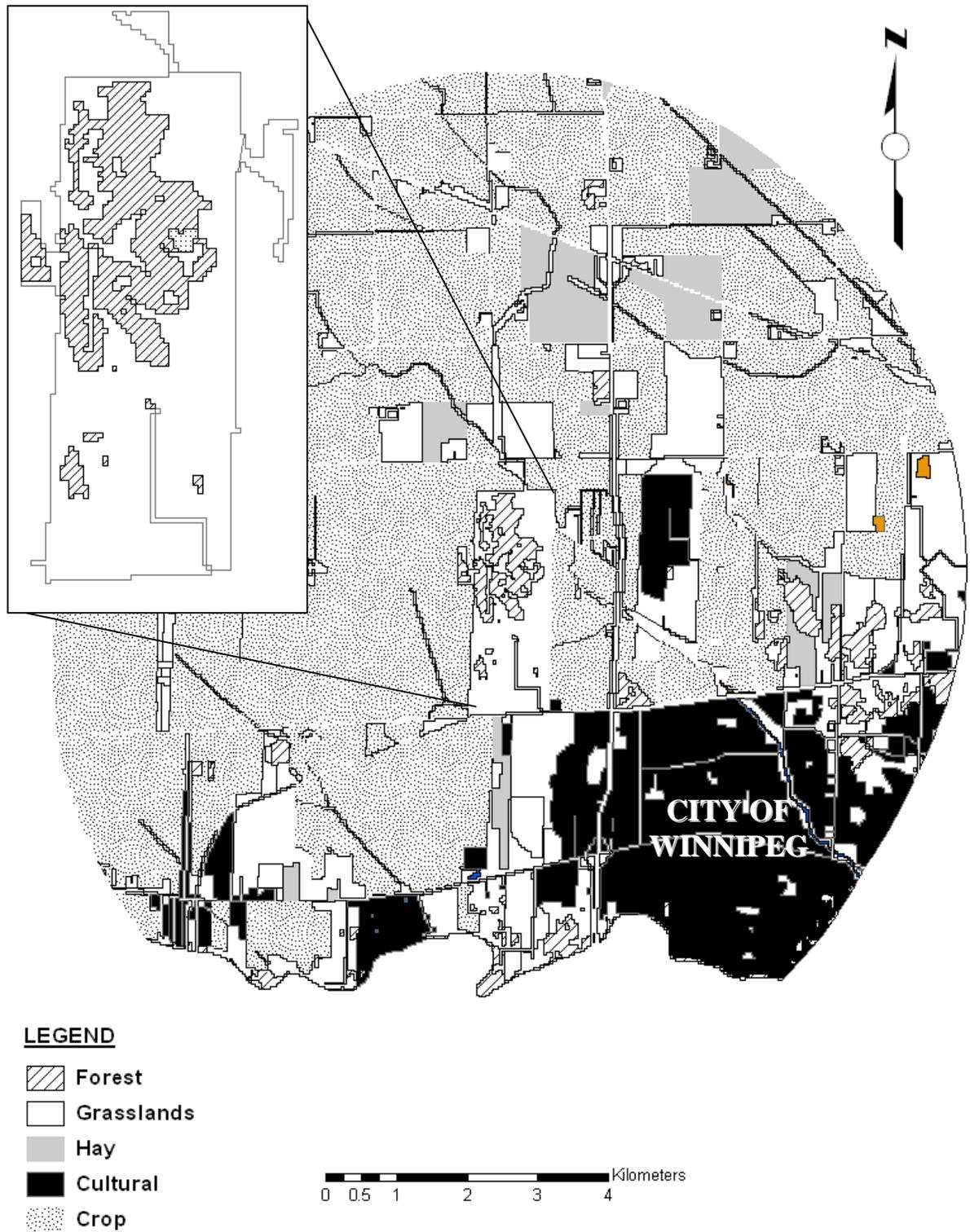


Figure 1.1. Saint Charles Rifle Range. A tallgrass prairie remnant imbedded within an agro-urban setting. The range is located in the centre of this map.

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and 102ha of aspen forest. The site is flat and poorly to imperfectly drained with <2% slope. Soils are classified as Clayey Lacustrine (Gleysols and Black Chernozems) (Land Resource Unit 1999). As a result, it is not uncommon for low-lying areas such as the forest floors to be flooded in spring and during wet summers. Sturgeon Creek cuts the northeast corner of the site, providing a source of drinking water to the resident deer.

The quality of the northern tallgrass prairie varies, partly as a function of site history. Described in the 1880's as open prairie with some burnt brush and willow swales in low lying areas, by 1928 the eastern half of the site had been broken for cultivation while the western half was being hayed (Prairie Habitats 1994). Today, the eastern half is generally characterized as a lower quality native prairie than the west, dominated by *poa pratensis* and *Symphoricarpos occidentalis*, instead of more *Agropyron* spp (wheatgrasses), *Koleria cristata* (June grass), *Andropogon* spp (bluestem), and *Spiraea alba*. During this same period the aspen forest took hold and expanded, now covering over one third of the site. Although aspen encroachment continues, total forest cover has remained relatively stable in recent decades (Walker 2004). Less the grassland openings within the forest, the native prairie has been burned a number of times since 1996, the last being in spring 2005. Much of the southern half of the site is mowed as it supports the rifle ranges, obstacle course, and buildings (Figure 1.2).

Within a 25km radius of the site, land cover consists of 81.5% agriculture, 29.3% grasslands, including urban grasslands, 4.4% forage crops 2.1% forest, and 1.3% cultural. More immediately, the area within 6km of the study site is 52.3% agriculture, 10.4%

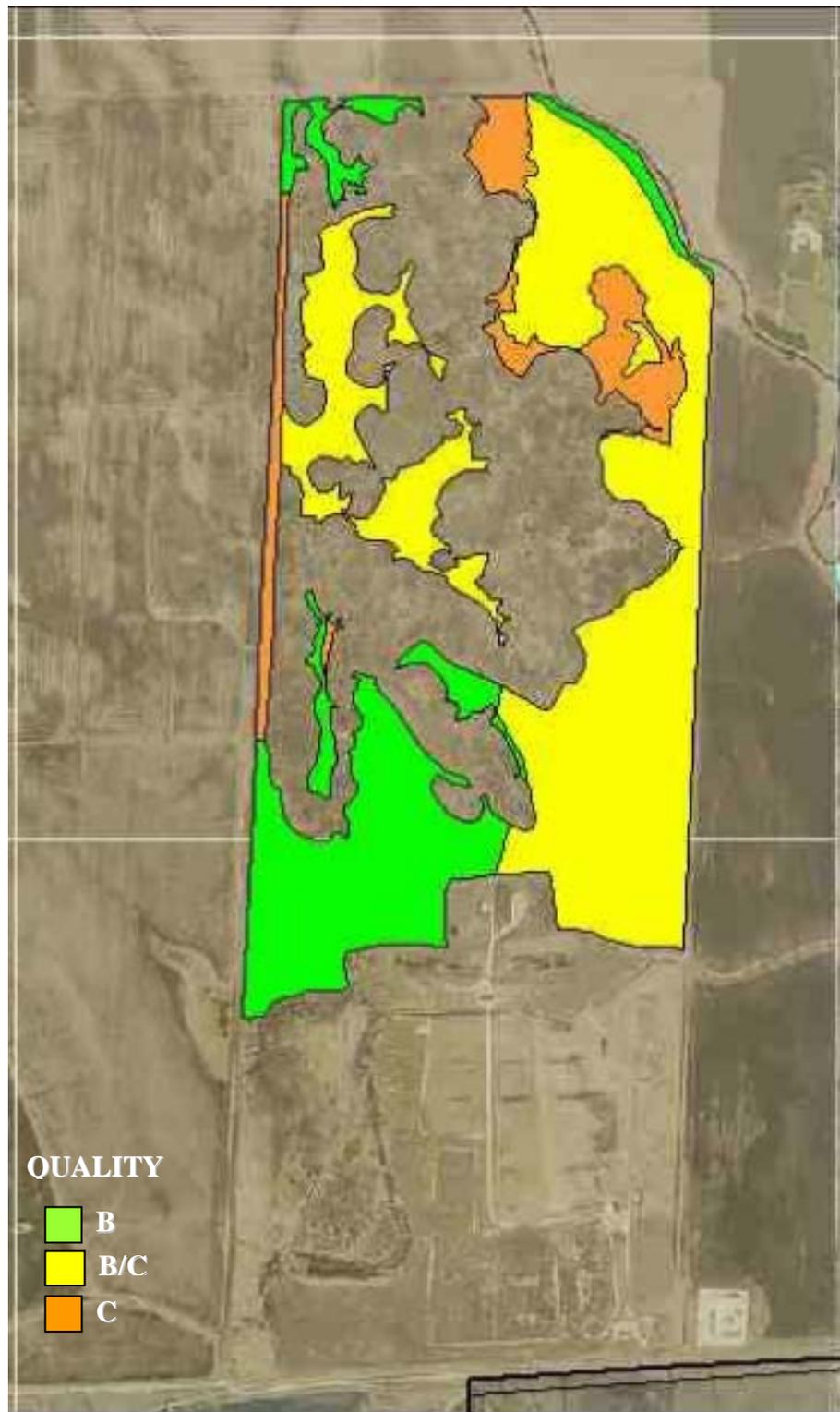


Figure 1.2. Study site and tallgrass prairie grading map. The highest quality prairie flora generally persists where the land was not put to the till (Class B), although the prairie tracts inside the forest have become degraded in more recent times. Highly degraded sites are Class C. This map does not reflect the distribution of invasives or woody encroachment. The southern half of the site is mowed (Used with permission from 17 Wing Winnipeg).

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cultural, 10.0% grasslands, 5.7% forage crops, and 2.8% forest (calculated using the MB Conservation 2004 Land Cover GIS layer). Approximately 4.5km to the south of the main study forest is the Assiniboine River, which flows east/west. Although such water barriers have not been found to be movement barriers, they do serve to restrict free movement of deer, especially where adequate resources exist on both sides of the water obstacle (Coulon et al 2006, Michael 1965, Eberhardt et al 1984). For this reason the land cover of the region to the south of this river was not included in the above figures. The Perimetre Highway, a 4-lane structure <1km to the east, may contribute to deer mortality but likely has little effect on deer movements and home ranges (Etter et al. 2002). Hunting has not been permitted on the range for at least five years although, until 2005, rifle hunting was allowed in adjacent lands. In 2006 provincial regulations were changed to permit bow hunting and shotgun only, although some poaching continues both on-site and in the surrounding area.

The climate is temperate continental, consisting of warm summers and cold winters. The average daily maximum temperature occurs in July (25.8°C, +/- 1.5°C) and the average daily minimum temperature occurs in January (-22.8°C, +/- 3.9°C), based on a 20-year average. Rainfall averages 415.6mm and snowfall is 110.6cm, generating a blanket of at least 20cm for 40.8 days a year. At least 0.2cm of snow falls 54.7 days a year and the average maximum end month snow depth is 24.0cm (Environment Canada).

While distribution fluctuates annually, the region's overall deer population has increased more than six-fold over the last 26years, counting 1,286 in 2006 (MB Conservation, pers comm). At SCRR, the 2006 population was 135. This exceeds the maximum of 6-7 km⁻²

proposed by Anderson et al. (2005) for a tallgrass prairie community, the 10km^{-2} recommended by Healy (1997) for an oak forest, and the maximum of 20km^{-2} densities recommended by Augustine and Jordan (1998) in a forest/agricultural setting.

Summer White-tailed Deer Densities

Just how many deer reside on the study site during the summer is not known. While numerous aerial counts have been conducted over the past three decades, all have been done in February-March using an aerial count methodology. Based on findings in Minnesota, wintering deer consist of 15% non-migratory deer, 35% obligate migrators, and 42.5% facultative migrators (7.5% had inconsistent migratory patterns) (Brinkman et al. 2005). This could mean that just 20 deer reside on the range year-round. This number is likely too low, however, given the overall size of the forest, that the site is most likely a population source for the region, and that it provides a significant fawning ground in the early summer. It provides the largest forest cover in a 25km radius outside of the City of Winnipeg's urban forests in a landscape with <5% forestlands. Furthermore, female dispersion tends to be lowest where there is extensive woody cover and readily available forage (Nixon et al. 1991, Nixon et al. 2006). For a number of reasons, Winnipeg's large urban forests no longer support significant wintering deer populations (34 in 2006).

Lastly, a 1974 white-tailed deer movement study conducted in southern Manitoba revealed that herds residing within aspen forest-grassland settings were relatively stable, possessing small home ranges (Shoesmith and Bidlake 1974). An earlier study in

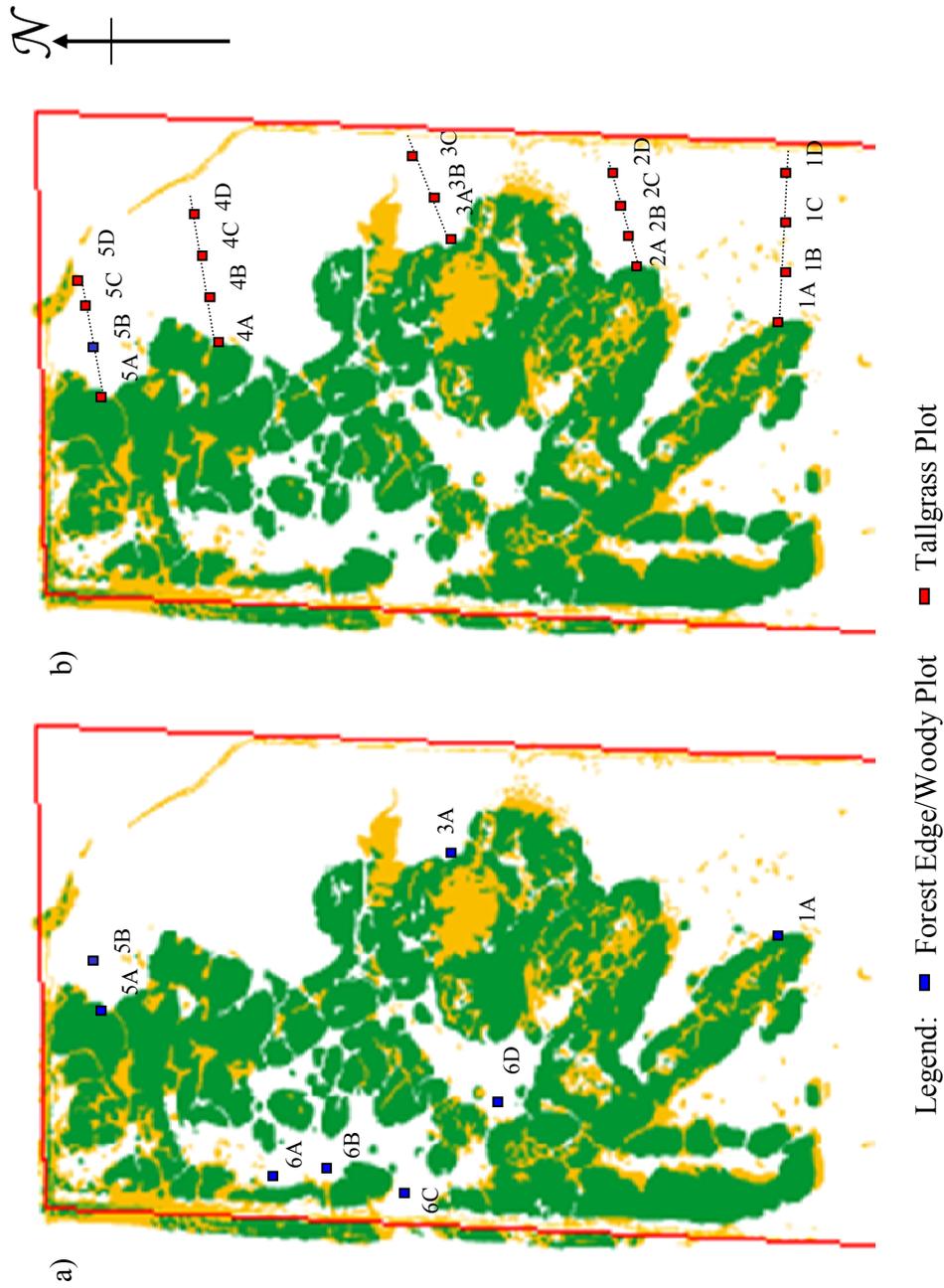


Figure 1.3. Plot locations. a) Plots 1A, 3A, 5A, 5B, and the 6 series were used to assess woody growth. Plot series 6 and plot 5B were also used to examine shrubby growth/degraded prairie. b) All others were used to evaluate tallgrass prairie cover and quality.

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Wisconsin revealed the same results, with deer moving only when necessary resources became depleted (Sparrowe and Springer 1970). It can be assumed that at least 30 deer reside on SCRR in the summer, and likely significantly more; in Illinois a similar-sized refuge in an agricultural setting witnessed just a 60% total summer migration rate (Nixon et al. 1991).

Soil Analysis

To assess if there was a relationship between the flora and the underlying soils, composite soil samples were taken from 53 plots across the site (Figure 1.3). To reduce the incidence of point-specific variations, especially under the forest canopy (Kleb and Wilson 1997), four 15cm holes were dug at each of the four corners of the sample plots. Roots and organic matter were removed to the extent possible and the remaining soil was combined and stored in a plastic bag.

Methods

The soils were evaluated for moisture, organic matter, pH, conductivity, and texture. They were also analyzed for the macronutrients nitrite, nitrate, total nitrogen, phosphorus, magnesium, and calcium. Moisture was assessed by drying samples at 60°C for 24hrs and measuring the difference in weight using an electronic scale. The risk with this process is that it may extract more moisture than is available to the plants (Jones and Reynolds 2005). Organic matter was assessed by crushing the dried soil sample, placing it through a 2mm sieve, and then igniting 5-10g of the sample at 450°C for 3hrs. Including furnace

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heating and cool-down time, soil samples were in the furnace for 7hrs. Samples were then weighed and the difference in mass was calculated. Conductivity and pH were determined using an Accumet AP85 Portable Waterproof pH/Conductivity Metre (Fisher Scientific Ltd., Pittsburgh, PA, USA) calibrated using a single point, with deionised water at 21.6°C. Soil samples were dried, ground, passed through a 2mm sieve, and then approximately 100g were mixed with 50mm of water to ensure a sufficiently slurry solution to enable the probe to take a correct reading. Soil texture was measured using Bouyoucos method, first drying at 60°C for 24hrs, crushing, and passing the samples through a 2mm sieve. Because of the high clay content 40g of soil were placed into a 250ml beaker with 50ml of distilled water and placed on a shaker table for 24hrs (Jones and Reynolds 2005). All macronutrients were measured using the Melich-1 double acid extraction process with a LaMotte Model AST-5 (5410) soil testing kit (LaMotte, Chesterland, MA, USA).

Results

As expected, soil texture ranged from sandy clay loam /sandy clay to clay with a mean clay value of 45.87%% (S.E. 1.11) and sand of 34.81% (S.E. 1.07). Comparing clay content to vegetative cover, the forest plots tended to be on the lighter soils while the tallgrass prairie plots were on the heavier clay soils (Figure 1.4). The internal prairie plots were in between, as were the forest edge plots for series 3, which has a weakly defined forest edge. Reflecting the clay soil and flood conditions of 2005 were the high soil moisture values of 34.03% (S.E. 0.58) with a slightly greater diversity of moisture levels

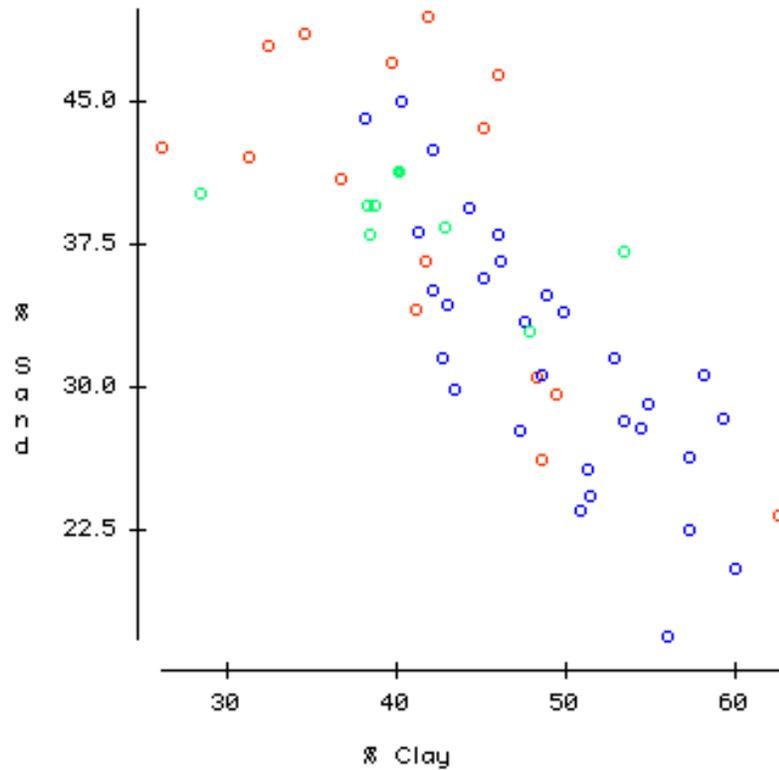


Figure 1.4. Forest and forest edge (red) plots tended to be on the sandier soils whereas the open prairie (blue) was on heavier clay. Internal prairie plots were between the two (green). The forest plots with the heavier clay soil had a poorly defined forest edge (red).

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nearest the forest edge, but both drier and wetter. Organic matter was 16.46% (S.E. 0.30), pH was 6.389 (S.E. 0.05), conductivity was 947 (S.E. 17.18), NO₃ was 30.94 (S.E. 4.57), NO₄ was 25.47 (S.E. 5.83), total N was 56.41 (S.E. 7.70), and phosphorus was 18.33 (S.E. 1.51).

Exploring the values by site grouping, the importance of site agricultural history became apparent. In old-fields 50 yrs may be sufficient time for the effects of cultivation on certain soil nutrients to recover, but not always and organic matter may take longer (Lauenroth and Coffin 1995, Fulendorf et al. 2002). Knops and Tilman (2000) predicted that as many as 180yrs would be required to restore N to pre-agricultural levels. At SCRR, soil moisture, organic matter, pH, conductivity, and total N were significantly different between sites, with non-overlapping 95% Confidence Intervals in all four cases (Figure 1.5). N was also higher inside the forest and crown-zone than the adjacent grasslands ($r^2 = 71.2$, $s = 17.51$ 15df) (Figure 1.6). For the old-field and hayed sites, the mean values were: soil moisture – 32.84% (S.E. 0.54) and 37.04% (S.E. 1.30) (paired t-test: $p = 0.0049$); organic matter – 15.46% (S.E. 0.19) and 18.98% (S.E. 0.62) ($p \leq 0.0001$); pH: 6.48 (S.E. 0.06) and 6.15 (S.E. 0.08) ($p = 0.0003$); conductivity – 906.95 μ S (S.E. 16.24) and 1049 μ S (S.E. 33.95) ($p = 0.0106$), and total N: 37.76ppm (S.E. 3.75) and 103.67ppm (S.E. 22.23) ($p = 0.0080$). Included in the total N values were the nitrite and nitrate values for the old-field and hayfield of 19.47ppm (S.E. 3.44) and 60.00ppm (S.E. 10.91); 4.29ppm (S.E. 3.75) and 43.67ppm (S.E. 20.88). Phosphorus was not significantly different between soil groupings, with old-field and hayfield values of

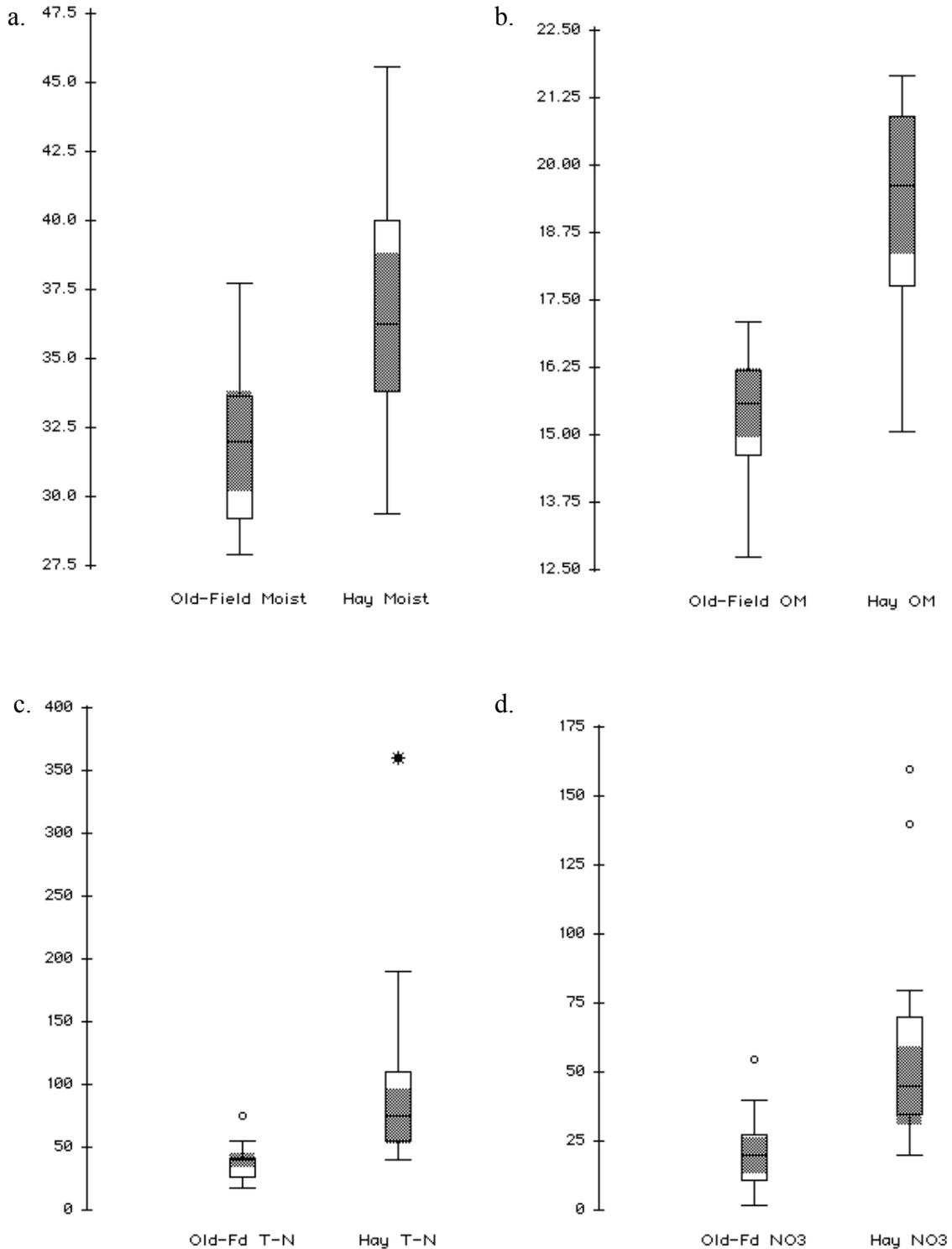


Figure 1.5. Soil values by site history. By grouping principle soil nutritional values by site history (Old-Field (east) and Hay (West)) it becomes evident that site history still has a legacy and will influence the vegetative cover. Figure a) soil moisture, b) organic matter, c) Total nitrogen, and d) nitrite. In most instances the non-overlapping 95% Confidence Intervals underscore the dissimilarity between the two groupings.

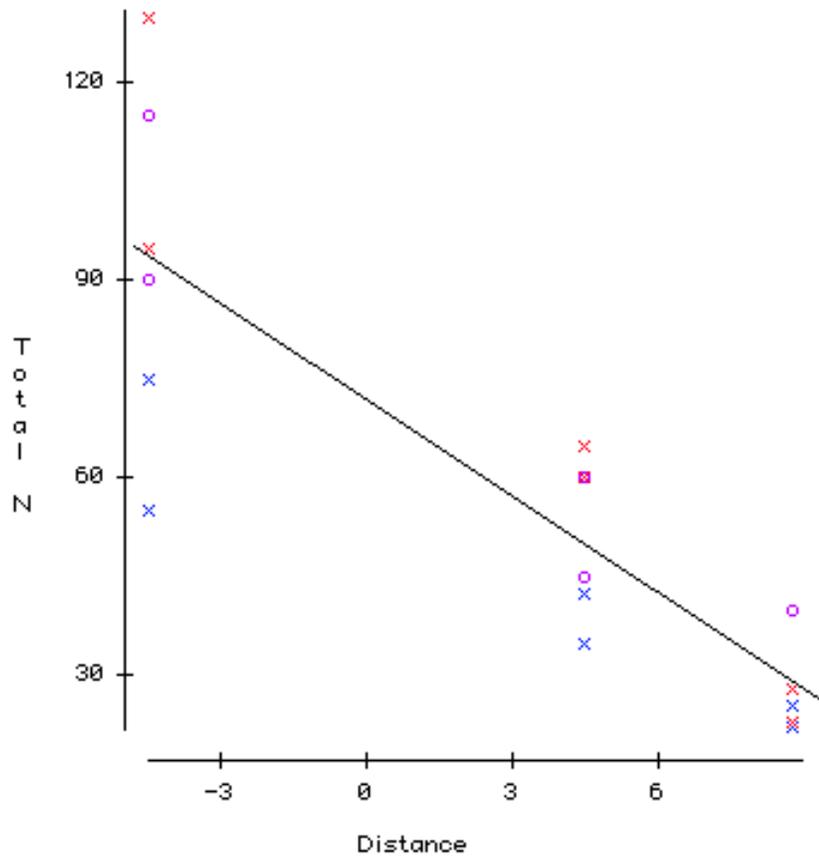


Figure 1.6. N as a function of distance from the forest edge. N levels are highest inside the forest and under the drip zone than on the grasslands, regardless of agricultural history. The purple “o” represents old-field forest edge. $r^2 = 71.2$, $s = 17.51$ 15df.

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19.37ppm (S.E. 1.84) and 15.70ppm (S.E. 2.63) ($p = 0.1453$) respectively. Magnesium and calcium were also not significantly different ($p = 0.5456$ and $p = 0.6647$).

Conducting Principle Component Analysis (PCA) (SYN-TAX 2000) and treating the soil characteristics as variables and the plots as objects, the first two axes cumulatively explain 29.50% and 45.41% of total variance (Figure 1.7). NO_3 , organic matter, and moisture have the greatest effect on the dispersion of the objects along the first axis ($r = 0.789, 0.789, \text{ and } 0.689$). Along the second axis, soil texture (sand, clay) and calcium are important ($r = -0.874, 0.677, \text{ and } -0.703$). The opposing placement of the formerly hayed lands and old-field highlights their persisting differences. Vegetatively, these two areas are dominated by tallgrass prairie and woody growth while the dispersion along the second axis separate those areas that are experiencing active encroachment and those that have a low *Populus tremuloides* (aspen) density along the forest edge. Axis 3 was most correlated with silt and magnesium ($r = 0.874, 0.500$) and axis 4 was correlated with NH_4 and total N ($r = 0.799, 0.428$). Together, the four axes explain 68.06% of the total variance.

Discussion

The preference of forests for the slightly lighter soils on this imperfectly drained site was not expected given that *P. tremuloides* stands are usually found in moist depressions. *P. tremuloides*, however, does not like flooded soils as these suppress recruitment and stress the plant (Archibold and Wilson 1978). It is possible that *P. tremuloides* are encroaching

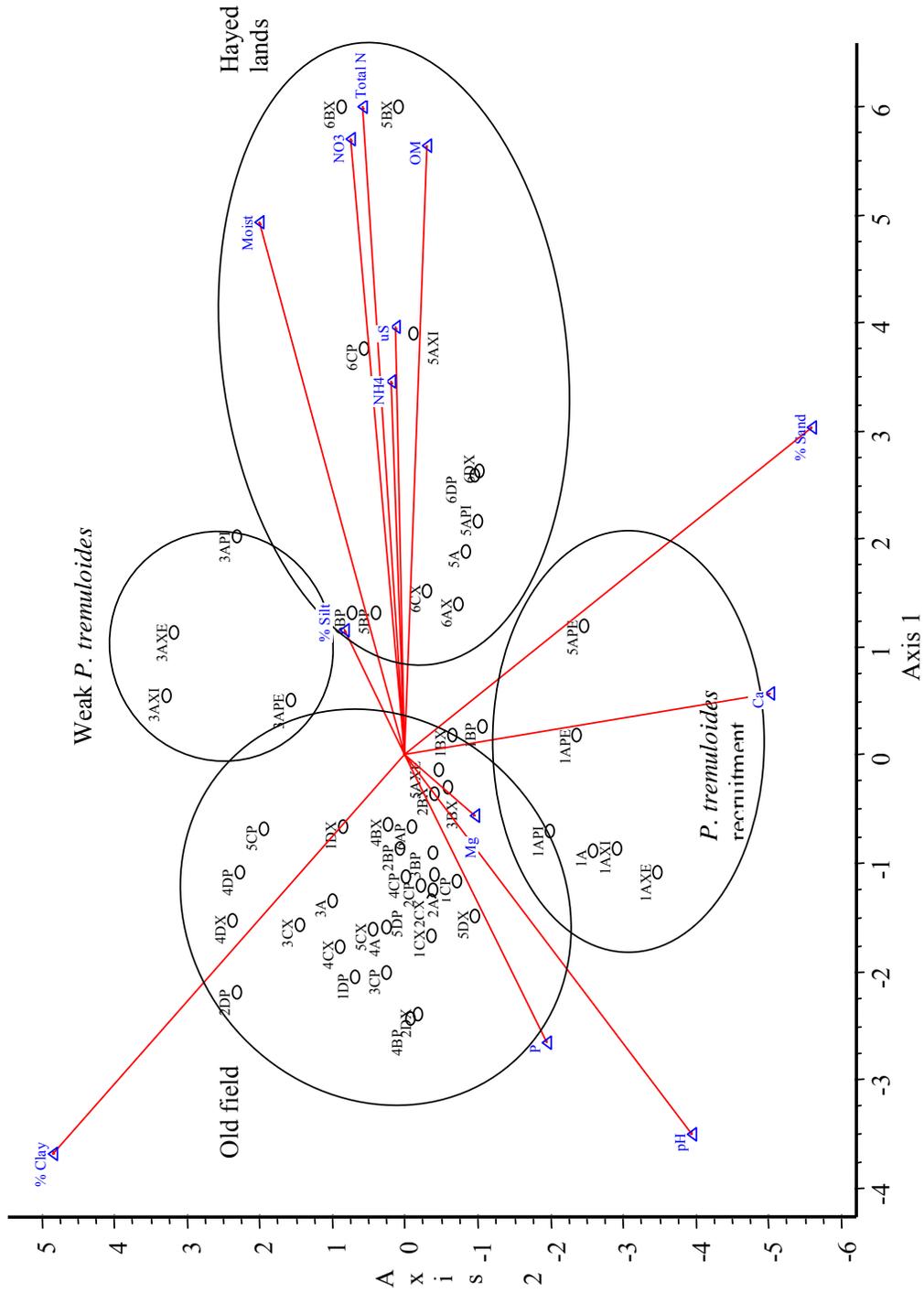


Figure 1.7. PCA of all soil nutrients. The first two axes cumulatively explain 29.50% and 45.41% of total variance. Organic matter, N, and moisture have the greatest effect on the dispersion of the objects along the first axis. Along the second axis, soil texture and calcium are important. The opposing placement of the formerly hayed lands and old-field highlights their persisting differences.

faster onto the better-drained soils because, there, they experience less severe flooding. Normally higher on the prairies (Köchy and Wilson 2000), old-fields often have lower N and organic matter levels. Tilling aerates the soils, accelerating rates of nutrient cycling and plant matter decay (Fuhlendorf et al. 2002). The elevated moisture on the hayed lands is in agreement with the historical accounts that the west side supported willow swales: too wet to plough.

The higher total N values just inside the forest edge and, to a lesser degree, under the crown-zone regardless of agricultural history may be partly a product of N mineralization from leaf deposition (Belsky 1994), but the literature is not clear. Although trees translocate nutrients during senescence, this process is not completely efficient and some N and P remain (Killingbeck 1996). For several hardwood species, Lodhi (1977) found net N to decrease as a function of distance from the tree trunk. For Legare et al. (2005), this distance was greatest just 3 to 7m from the tree. Köchy and Wilson (1997) also found that N accumulation rates were higher in the forest than the prairie, even though mineralization rates were slower. Litter quality was more important than decomposition rates.

Conversely, Pastor and Bockheim (1984) found *P. tremuloides* stands to be nutrient sinks. On lacustrine soils similar to those of the study site, *P. tremuloides* was found to change soil conditions so that they actually decreased net N, Ca, and pH (Ste-Marie and Pare 1999, Pare and Bergeron 1996). These, however, were well-drained soils. On wet soils, denitrification from flooding could be expected to further reduce net N values (Zak

and Grigal 1990). Short-term (2 yrs) nitrogen and carbon mineralization rates on clay soils may be misleading over the long-term due to curvilinear mineralization rates; Giardina et al. (2001) concluded that total mineralization was similar over time, regardless of soil type.

Perhaps the clay soil and leaf deposition are not the primary drivers. Instead, enhanced N accumulation under the forest canopy-zone could be related more to $\delta^{15}\text{N}$ deposition resulting from urban air pollution, whose deposition rate has increased more than ten-fold since the 1950s (Wedin and Tilman 1996). *P. tremuloides* in parkland forests was found to extract this N isotope from the air and translocate it to roots before dropping its leaves, resulting in elevated rates of forest expansion. Elevated $\delta^{15}\text{N}$ was therefore found neither in the leaves nor the litter (Köchy and Wilson 2001). Further, higher N levels under the forest crown-zones could indicate that N is not limiting there but rather that it is on the tallgrass prairie, and hence the competition for it is reduced (Köchy and Wilson 2001, Tilman 1988). Whatever the underlying cause, it would appear that N is not limiting along the ecotone of the *P. tremuloides* forest-tallgrass prairie and that the aspen forest may play a part in preparing the soil for future encroachment. *P. tremuloides* has been found to have greater shoot, root, and leaf mass under higher N and pH conditions (Desrochers et al. 2003), suggesting a facultative interaction

Calcium was found to be limiting for *P. tremuloides*. Stands with low exchangeable Ca were more susceptible to early decline due to its requirement for vigorous plant growth (Frey et al. 2004). This may be why Ca is important in explaining the variance between

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plots and, concurrently, between vegetative cover types. The forest edge plots identified as having a weak aspen edge and poor growth had the lowest Ca values of the study area (3210ppm S.E. 356). Where *P. tremuloides* recruitment is most active the Ca values are the highest (5129ppm, S.E. 236). Although Ca and pH have been found to be positively correlated and lower under older *P. tremuloides* stands (Lohdi 1977, Alban 1982), the trend across soil history (hayfield, old-filed) suggests that the trees may not be the primary cause of distribution variation of Ca, or that the aspen stands are simply not old enough to have impacted the soil to the full extent.

That the separation of the plots by soil characteristics also resulted in the grouping of plots by cover-type indicates the strong influence soil and moisture play in determining plant vegetative cover. The internal prairie plots (6 series) have more in common with some of the plots associated with the forest and shrub cover than the prairie. But soil is not completely deterministic and the current vegetative cover may be shifting relative nutrient values, just as it modifies abiotic characteristics (Saunders et al. 1991). Grass-tree interactions can be both facultative and competitive and are poorly understood (Wilson 1998), but it appears that belowground mechanisms do play an important part in determining which plant and vegetative assemblage grows where.

Conclusion

The distribution of plants on SCRR is indicative of the underlying abiotic conditions and site history. While in recent years the distribution of aspen forest has been relatively

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stable, the process of encroachment persists, especially where the soil, moisture, and nutrient conditions are most conducive. The increase in forested area is resulting in a corresponding decrease in the size of remnant northern tallgrass prairie. Ironically, past agricultural practices reduced soil fertility on the eastern portion of the study site, limiting native tallgrass prairie diversity but also inhibiting the establishment and spread of weedy ruderals and aspen parkland forest. Presently, it is the apparent deposition of $\delta^{15}\text{N}$ produced by urban sprawl that is serving to enrich the grassland soils, facilitating this encroachment and placing the tallgrass prairie at greater risk of extirpation.

LITERATURE CITED

- Alban, D.H. 1982. Effects of nutrient accumulation by aspen, spruce, and pine on soil properties. *Soil Science Society of America Journal* 46:853-861.
- Alverson, W.S., Waller, M.W., and Solheim, S.L. 1988. Forests Too Edge: Edge Effects in Northern Wisconsin. *Conservation Biology*. 2:348-358.
- Anderson, R.C., Corbett, E.A., Anderson, M.C., Corbett, G.A., and Kelley, T.M. 2001. High white-tailed deer density has negative effect on tallgrass prairie forbs. *Journal of the Torrey Botanical Society*. 128:381-392.
- Anderson, R.C., Nelson, D., Anderson, M.A., and Rickey, M.A. 2005. White-tailed deer (*Odocoileus virginianus* Zimmermann) browsing effects in tallgrass prairie forbs: diversity and species abundance. *Natural Areas Journal* 25:19-25.
- Anthony, R.G. and Smith, N.S. 1977. Ecological Relationships Between Mule Deer and White-tailed Deer in Southern Arizona. *Ecological Monographs* 47:255-277.
- Archibold, O.W. and Wilson, M.R. 1978. Spatial Pattern and Population Dynamics of *Populus tremuloides* in a Saskatchewan Aspen Grove. *Canadian Field-Naturalist*. 92:369-374.
- Augustine, D.J. and Jordan, P.A. 1998. Predictors of white-tailed deer grazing intensity in fragmented deciduous forests. *Journal of Wildlife Management*. 62:1076-1085.
- Austin, D.D. and Urness, P.J. 1985. Effects of Cattle Grazing on Mule Deer Diet and Area Selection. *Journal of Range Management* 39:18-21.
- Berteaux, D., Crete, M., Huot, J., Maltais, J, and Ouellet, J-P. 1998. Food choice by white-tailed deer in relation to protein and energy content of the diet: a field experiment. *Oecologia*. 115:84-92.
- Belsky, A.J. 1994. Influences of trees on savanna productivity: tests of shade, nutrients, and tree-grass competition. *Ecology*. 75:922-932.
- Biondini, M.E., Steuter, A.A., and Hamilton, R.G. 1999. Bison use of fire-managed remnant prairies. *Journal of Range Management*. 52:454-461.
- Brinkmann, T.J., Deperno, C.S., Jenks, J.A., Haroldson, B.S., and Osborn, R.G. 2005. Movement of female white-tailed deer: effects of climate and intensive row-crop agriculture. *J. Wildl. Manage.* 69:1099-1111.

Chapter 1: Introduction and study site

- Caughley, G. 1981. Overpopulation. Pages 7-19 in P.A. Jewel and S. Holt, editors. *Problems in Management of Locally Abundant Wild Mammals*. Academic Press, New York, New York, USA.
- Collins, S.L. and Glenn., S.M. 1997. Intermediate disturbance and its relationship to within- and between-patch dynamics. *New Zealand Journal of Ecology*. 21:103-110.
- Côté, S.D., Rooney, T.P., Tremblay, J-P, Dussault, C, and Waller, D. 2004. Ecological Impacts of Deer Overabundance. *Annual Review of Ecology, Evolution, and Systematics* 35:113-47.
- Coulon, A., Guillot, G., Angibault, J.M.A., Aulagnier, S., Cargnelutti, B., Galan, M., and Hewison, J.M. 2006. Genetic structure is influenced by landscape features: empirical evidence from a roe deer population. *Molecular Ecology*. 15:1669-1679.
- Debinski, D.M. and Holt, R.D. 2000. A survey and overview of Habitat Fragmentation experiments. *Conservation Biology*. 14:342-354.
- Desrochers, A., van den Driessche, R., and Thomas, B.R. 2003. Nitrogen fertilization of trembling aspen seedlings grown on soils of different pH. *Canadian Journal of Forestry Resources*. 33:552-560.
- Eberhardt, L.E., Hanson, E.E., and Caldwell, L.L. 1984. Movement and activity patterns of mule deer in the sagebrush-steppe region. *Journal of Mammalogy*. 65:404-409.
- England, R.E. and DeVos, A. 1969. Influence of animals on pristine conditions on the Canadian grasslands. *Canadian Grasslands*. 22:87-94.
- Environment Canada. National Climate Data and Information Archive. Retrieved 20 September 2007.
http://www.climate.weatheroffice.ec.gc.ca/climateData/hourlydata_e.html?timeframe=1&Prov=XX&StationID=47407&Year=2009&Month=3&Day=1
- Etter, D.R., Hollis, K.M., Van Deelan, T.R., Ludwig, D.R., Chelavig, J.E., Anchor, C.L., and Warner, R.E. 2002. Survival and movements of white-tailed deer in suburban Chicago, Illinois. *Journal of Wildlife Management*. 66:500-510.
- Etzenhouser, M.J., Owens, M.K., Spangler, D.E., and Murden, S.B. 1998. Foraging behaviour of browsing ruminants in a heterogeneous landscape. *Landscape Ecology*. 13:55-65.
- Focardi, S., Marcellini, P., and Montrano, P. 1996. Do ungulates exhibit a food density threshold? A field study of optimal foraging and movement patterns. *The Journal of Animal Ecology*. 95:606-620.

Chapter 1: Introduction and study site

- Frey, B.R., Lieffers, V.J., Hogg, E.H., and Landhäusser, S.M. 2004. Predicting landscape patterns of aspen dieback: mechanisms and knowledge gaps. *Canadian Journal of Forest Resources*. 34:1379-1390.
- Fuhlendorf, S.D. and Engle, D.M. 2001. Restoring Heterogeneity on Rangelands: Ecosystem Management Based on Evolutionary Grazing Patterns. *BioScience* 51:625-632.
- Fuhlendorf, S.D., Zhang, H., Tunnell, T.R., Engle, D.M., and Cross, A.F. 2002. Effects of grazing on restoration of southern mixed prairie soil. *Restoration Ecology*. 10:401-407.
- Giardina, C.P., Ryan, M.G., Hubbard, R.M., and Binkley, D. 2001. Tree species and soil textural controls on carbon and nitrogen mineralization rates. *Soil Science Society of America Journal*. 65:1272-1279.
- Glenn, S.M., Collins, S.L., and Gibson, D.J. 1992. Disturbances in tallgrass prairie: local and regional effects on community heterogeneity. *Landscape Ecology*. 7:243-251.
- Hansen, R.M. and Reid, L.D. 1975. Diet overlap of deer, elk, and cattle in southern Colorado. *Journal of Range Management*. 28:43-47.
- Hartnett, D.C., Hickman, K.R., and Fischer Walter, L.E. 1996. Effects of bison grazing, fire, and topography on floristic diversity in tallgrass prairie. *Journal of Range Management* 49:413-420.
- Healy, W.M. 1997. Influence of deer on the structure and composition of oak forests in central Massachusetts. Pages 249-266 in W.J. McShea, H.B. Underwood, and J.H. Rappole, editors. *The Science of Overabundance: deer ecology and population management*. Smithsonian Books, Washington D.C., USA
- Hobbs, R.J. and Huenneke, L.F. 1992. Disturbance, Diversity, and Invasion: Implications for Conservation. *Conservation Biology*. 6: 324-337.
- Howe, H.F. 1994. Managing Species Diversity in Tallgrass Prairie: Assumptions and Implications. *Conservation Biology* 8: 691-704.
- Illius, A.W., and Gordon, I.J. 1993. Diet selection in mammalian herbivores: Constraints and tactics. Pages 157-181 in R.N. Hughes, editor. *Diet Selection: An Interdisciplinary Approach to Foraging Behaviour*. Oxford University Press, Don Mills, ON, Canada
- Jennersten, O. 1988. Pollination in *Dianthus deltoides* (*Caryophyllaceae*): Effects of Habitat Fragmentation on Visitation and Seed Set. *Conservation Biology* 2:359-366.

Chapter 1: Introduction and study site

- Jones, J.C. and Reynolds, J.D. 2005. Environmental variables. Pages 281-318 in W.J. Sutherland, editor. *Ecological Census Techniques: A Handbook*. Cambridge University Press, Cambridge, UK.
- Kellogg, C.H. and Bridgham, S.D. 2004. Disturbance, herbivory, and propagule dispersal control dominance of an invasive grass. *Biological Invasions* 6:319-329.
- Killingbeck, K.T. 1996. Nutrients in senesced leaves: keys to the search for potential resorption and resorption proficiency. *Ecology*. 77:1716-1727.
- Kleb, H.R. and Wilson, S.D. 1997. Vegetation Effects on Soil Resource Heterogeneity in Prairie and Forest. *The American Naturalist*. 150:283-298.
- Köchy, M. and Wilson, S.D. 1997. Litter Decomposition and Nitrogen Dynamics in Aspen Forest and Mixed-grass Prairie. *Ecology*. 78:732-739.
- Köchy, M and Wilson, S.D. 2000. Competitive effects of shrubs and grasses in prairie. *Oikos*. 91:385-395.
- Köchy, M. and Wilson, S.D. 2001. Nitrogen deposition and forest expansion in the northern Great Plains. *Journal of Ecology*. 89:807-817.
- Knapp, A.K., Blair, J.M., Briggs, J.M., Collins, S.L., Hartnett, D.C., Johnson, L.C., and Towne, E.G. 1999. The Keystone Role of Bison in North American Tallgrass Prairie. *Bioscience* 49:39-50.
- Knops, J.M.H. and Tilman, D. 2000. Dynamics of soil nitrogen and carbon accumulation for 61 years after agricultural abandonment. *Ecology*. 81:88-95.
- Knox, W.M. 1997. Historical Changes in the Abundance and Distribution of Deer in Virginia. Pages 27-36 in W.J. McShea, H.B. Underwood, and J.H. Rappole, editors. *The Science of Overabundance: Deer Ecology and Population Management*. Smithsonian Institution Press, Washington, USA.
- Land Resource Unit. 1999. Soils and Terrain. An Introduction to the Land Resource. Rural Municipality of Headingley. Information Bulletin 99-2, Brandon Research Centre, Research Branch, Agriculture and Agri-Food Canada. Brandon, Manitoba, Canada.
- Lauenroth, W.K. and Coffin., C.P. 1995 Semiarid Grasslands: Implications for the Conservation Reserve Program. *Ecological Applications*. 5:793-801.
- Legare, S., Pare, D., and Bergeron, Y. 2005. Influence of aspen on the forest floor properties in black spruce-dominated stands. *Plant and Soil*. 275:207-220.

Chapter 1: Introduction and study site

- Lodhi, M.A.K. 1977. The influence and comparison of individual forest trees on soil properties and possible inhibition of nitrification due to intact vegetation. *American Journal of Botany*. 64:260:264.
- Loft, E.R., Menke, J.W., and Kie, J.G. 1991. Habitat shifts by mule deer: the influence of cattle grazing. *Journal of Wildlife Management*. 55:16-26.
- Loveless, C.M. 1967. Ecological Characteristics of a Mule Deer Wintering range. Colorado Game, Fish, and Parks Department. Technical Publication #20.
- McCabe, T.R. and McCabe, R.E. 1997. Recounting whitetails past. Pages 11-26 *in* W.J. McShea, H.B. Underwood, and J.H. Rappole, editors. *The Science of Overabundance*. Smithsonian Books, Washington D.C., USA.
- McCullough, D.R. 1997. Irruptive behaviours in ungulates. Pages 69-98 *in* W.J. McShea, H.B. Underwood, and J.H. Rappole, editors. *The Science of Overabundance*. Smithsonian Books, Washington D.C., USA.
- Menges, E.S. 1991. Seed Germination Percentage Increases with Population Size in a Fragmented Prairie Species. *Conservation Biology* 5:158-164.
- Michael, E.D. Movements of white-tailed deer on the Welder Wildlife Refuge. *Journal of Wildlife Management*. 29:44-52
- Nixon, C.M., Hansen, L.P., Brewer, P.A., and Chelsvig, J.E. 1991. Ecology of white-tailed deer in an intensively farmed region of Illinois. *Wildlife Monographs* 118.
- Nixon, C.M., Mankin, P.C., Etter, D.R., Hansen, L.P., Brewer, P.A., Chelsvig, J.E., Esker, T.L., and Sullivan, J.B. 2006. White-tailed deer dispersal behaviour in an agricultural environment. *American Midland Naturalist*. 157:212-220.
- Nixon, C.M., McClain, M.W., and Russell, K.R. 1970. Deer Food Habits and Range Characteristics in Ohio. *Journal of Wildlife Management*. 34 :870-886.
- Olf, H. and Ritchie, M. 1998. Effects of herbivores on grassland plant diversity. *TREE*. 13:261-265.
- Ortega, I.M., Soltero-Gardea, S., Drawe, D.L., and Bryant, F.C. 1997. Evaluating grazing strategies for cattle: Nutrition of cattle and deer. *Journal of Range Management*. 50:631-637.
- Packard, S. and Ross, L.M. 1997. Restoring remnants. Pages 63-95 *in* S. Packard and C.F. Mutel, editors. *The Tallgrass Restoration Handbook: for prairies, savannas, and woodlands*. Island Press, Washington, D.C., USA.

Chapter 1: Introduction and study site

- Pare, D. and Bergeron, Y. 1996. Effect of colonizing tree species on soil nutrient availability in a clay soil of the boreal mixedwood. *Canadian Journal of Forest Resources*. 26:1022-1031.
- Pastor, J. and Bockheim, J.G. 1984. Distribution and cycling of nutrients in an aspen-mixed-hardwood-spodosol ecosystem in northern Wisconsin. *Ecology*. 65:339-353.
- Penry, D.L. 1993. Digestive constraints on diet selection. Pages 32-55 *in* R.N. Hughes, editor. *Diet Selection: An Interdisciplinary Approach to Foraging Behaviour*. Oxford University Press, Don Mills, ON, Canada.
- Petraitis, P.S., Latham, R., and Niesenbaum, R. 1989. The maintenance of species diversity by disturbance. *The Quarterly Review of Biology*. 64:393-418.
- Prairie Habitats. 1994. Prototype Vegetation Management Plan: Department of National Defence, Canadian Forces Base Winnipeg, Winnipeg, Manitoba, Canada.
- Provenza F.D. and Cincotta, R.P. 1993. Pages 78-101 *in* R.N. Hughes, editor. *Diet Selection: An Interdisciplinary Approach to Foraging Behaviour*. Oxford University Press, Don Mills, ON, Canada.
- Pulliam, H.R. 1974. On the theory of optimal diets. *The American Naturalist*. 108:59-74.
- Pyke, G.H. 1984. Optimal Foraging Theory: A Critical Review. *Annual Review of Ecological Systematics* 15:523-575.
- Robbins, C.T. 1993. *Wildlife Feeding and Nutrition*, 2nd Edition. Academic Press, Toronto, Ontario, Canada.
- Roberts, M.R. and Gillam, F.S. 1995. Patterns and Mechanisms of Plant Diversity in Forested Ecosystems: Implications for Forest Management. *Ecological Applications*. 5:969-977.
- Rooney, T.P. and Waller, D.M. 2003. Direct and indirect effects of white-tailed deer in forest ecosystems. *Forest Ecology and Management* 181:165-176.
- Russell, F.L., Zippin, D.B., Fowler, N.L. 2001. Effects of White-tailed Deer (*Odocoileus virginianus*) on Plants, Plant Populations and Communities: A Review. *The American Midland Naturalist*. 146:1-26.
- Sainte-Marie, C. and Pare, D. 1999. Soil, pH and N availability effects on net nitrification in the forest floors of a range of boreal forest stands. *Soil Biology and Biochemistry*. 11:1579-1589.

Chapter 1: Introduction and study site

- Samson, F. and Knopf, F. 1994. Prairie Conservation in North America. *Bioscience* 44: 418-421.
- Samson, F.B., Knopf, F.L., McCarthy, C.W., Noon, B.R., Ostlie, W.R., Rinehart, S.M., Larson, S.G., Plumb, G.E., Schenbeck, G.L., Svingen, D.M., and Byer, T.W. 2003. Planning for population viability on Northern Great Plains national grasslands. *Wildlife Society Bulletin*. 31:986-999.
- Saunders, D.A., Hobbs, R.J., and Margules, C.R. 1991. Biological Consequences of Ecosystem Fragmentation: A Review. *Conservation Biology* 5:18-32.
- Shaw, H. 1997. Bison Ecology- What We Do and Do Not Know. Pages 113-120 *in* Irby, L.R. and Knight, J.E., editors. *International Symposium on Bison Ecology and Management in North America*. Montana State University, Bozeman, Montana, USA.
- Shoosmith, M.W. and Bidlake, L.J. 1974. Preliminary results of white-tailed deer movement studies in southwestern Manitoba. Manitoba Department of Mines, Resources, and Environmental Management, Research Branch. MS Report 74-2.
- Simberloff, D., and Gotelli, N. 1984. Effects of Insularisation on Plant Richness in the Prairie-Forest Ecotone. *Biological Conservation*. 29:27-46.
- Sparrowe, R.D. and Springer, P.F. 1970. Seasonal Activity Patterns of White-tailed Deer in Eastern South Dakota. *Journal of Wildlife Management*. 34 :420-431.
- Stewart, K.M., Fulbright, T.E., and Drawe, L.E. 2000. White-tailed deer use of clearings relative to forage availability. *Journal of Wildlife Management*. 64:734-741.
- Symstad, A.J. 2000. A Test of the Effects of Functional Group Richness and Composition on Grassland Invasibility. *Ecology*. 8:99-109.
- Tews, J., Brose, U, Grimm, V., Tielbörger, K., Wichmann, M.C., Schwager, M, and Jeltsch, F. 2004. Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. *Journal of Biogeography*. 331:79-92.
- Tilman, D. 1988. *Plant Strategies and the Dynamics and Structures of Plant Communities*. Princeton University Press, Princeton, New Jersey, USA.
- Walker, D.J. 2004. Development of a Preliminary GIS Database and Vegetation Framework for the St. Charles Rifle Range Tall Grass Prairie: Final Report. Prepared for World Wildlife Fund Canada.
- Wedin, D.A. and Tilman, D. 1996. Influence of nitrogen loading and species composition on the carbon balance of grasslands. *Science*. 274:1720-1723.

Chapter 1: Introduction and study site

- Westoby, M. 1974. An Analysis of Diet Selection by Large Generalist Herbivores. *The American Naturalist*. 108:290-304.
- Wiegand, T., Moloney, K.A., and Milton, S.J. 1998. Population dynamics, disturbance, pattern evolution: identifying the fundamental scales of organization in a model ecosystem. *The American Naturalist*. 152:321-337.
- Wiens, J.A. 1976. Population responses to patchy environments. *Annual Review of Ecological Systems*. 7:81-120.
- Wilson, S.D. 1998. Competition between grasses and woody plants. Pages 231-254 *in* G.P. Cheplick, editor. *Population Biology of Grasses*. Cambridge University Press. Cambridge, U.K.
- Wu, J. and Vankat, J.L. 1995. Island biogeography: theory and applications. Pages 371-379 *in* W.A. Nierenberg, editor. *Encyclopaedia of Environmental Biology*, Vol. 2. Academic Press, San Diego, California, USA.
- Zak, D.R. and Grigal, D.F. 1991. Nitrogen mineralization, nitrification and denitrification in upland and wet ecosystems. *Oecologia*. 88:189-196.

ABSTRACT

When present in high densities, white-tailed deer (*Odocoileus virginianus*) can extirpate favoured plants through intensive herbivory within simple and dual ecosystems. A study was conducted on a northern tallgrass prairie remnant within a forest: agro-urban setting to determine if the native grassland flora were at risk. Diets were determined through microhistological analysis of composite fecal samples collected over a 13-month period. Due to extensive flooding, crops were not available for the first half of the study, allowing corrected August diets with and without row-crops to be compared. Employing metric and non-metric preference indices, row-crops were found to be important dietary components only in April and the fall, reducing mortality and maintaining high fecundity. Several tallgrass species were deemed to be at risk. Ornaments were not consumed as they were located greater than 1.5km away. White-tailed deer population densities need to be dramatically reduced if the ecosystem is to survive.

INTRODUCTION

Since teetering on the brink of extinction at the beginning of the twentieth century, white-tailed deer (*Odocoileus virginianus*) populations have irrupted across and beyond their former range (Caughley 1970). This remarkable recovery has been attributed to a number of anthropologically-induced factors, including the implementation of intensive conservation measures, the elimination of most large predators, the reduction in hunting (Alverson *et al.* 1988, McCabe and McCabe 1984, Rooney 2001), and the spread of intensive agriculture (Coté *et al.* 2004, McCabe and McCabe 1997, McCullough 1997).

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While historical deer densities have been assessed to have been in the range of 3.1-4.2 deer km⁻² (McCabe and McCabe 1997), today, where hunting is restricted, deer densities of 37-74 deer km⁻² are not uncommon (Underwood and Porter 1997). In the American Midwest, fragmented natural habitats embedded among highly nutritious row-crops have encouraged deer densities to increase well above historical levels and ecological carrying capacities (Schmitz and Sinclair 1997, Sinclair 1997). In several regions including portions of the Canadian prairies, white-tailed deer have responded to changes in the landscape by out-competing the native mule deer (*Odocoileus hemionus*) (England and DeVos 1969, Baker 1984).

Another principle cause of this population explosion is the animal's dietary plasticity. For example, within a single study area deer were found to consume at least 614 different plant species (Atwood 1941), with selection varying by season, phenology, and local plant availability (Arnold and Drawe 1979, Krausman et al. 1997). As different groups of plants peak in nutritional value, deer correspondingly shift their dietary selection (Chamrad and Box 1968). Possessing a narrow mouth and dental morphology well suited for high selectivity (Illius and Gordon 1993), they are able to obtain the specific plant and plant structures that best meets their perceived nutritional needs. This grazing behaviour differs from that of many other larger herbivores, such as bison (*Bison bison*) and cattle (*Bos taurus*), which are physiologically better suited to consume a much greater proportion of grasses (Elliott and Barrett 1985, Steuter 1997, Martinez et al. 1997).

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Deer are able to “know” the ever-changing nutritional value of the plants they encounter by employing a partial selection foraging strategy. By continuously sampling small amounts of all plants they encounter, they are somehow able to evaluate relative nutritional values and palatability (Illius and Gordon 1993, Berteaux et al. 1998). The mechanics of this process are not well understood, but the ability is apparently influenced by neither innate nor learned dietary preferences (Robbins 1993). What is known is that white-tailed deer can quickly adapt to a rapidly changing selection of foods, thereby optimizing dietary selection and maximizing fitness (Berteaux 1998). When present at sufficient densities, this preferential selectivity has the potential to affect the floristic community on which they feed (Bowers 1997).

Deer can exert a positive impact on their host ecosystem by imposing an appropriate degree of disturbance, defined as Intermediate Disturbance (Petraitis, et al. 1989, Wiegand et al. 1998). Through such activities as grazing, trampling, and nutrient translocation, large herbivores can shape the vegetative cover upon which they live, maximizing biotic diversity by contributing to a spatially and temporally heterogeneous landscape (Rooney and Waller 2003). When too numerous, however, large herbivores can reduce diversity. Numerous studies have examined the effects of elevated deer populations on native plants within eastern forests (Alverson and Waller 1997, Rooney and Dress 1997, Rooney and Waller 2003) and, more recently, the tallgrass prairie (Anderson et al. 2001, Anderson et al. 2005, Spotswood et al. 2002, Olf and Ritchie 1998). These have all revealed that the preferential nature of white-tailed deer herbivory can result in the extirpation of favoured native forage species, shift floristic cover and

trajectories towards unfavoured and browse-tolerant species (Russell et al. 2001, Noy-Meir 1981, Anderson et al 2005), and prevent forest regeneration after harvest (Tilghman 1989, Atwood 1941). Within complex landscapes, the effects of elevated white-tailed deer herbivory are less well understood.

It is not clear if row-crops offset the effects of elevated deer populations on the local ecosystem. Examining forest fragments within an agricultural-urban setting, Augustine and Jordan (1998) found that grazing intensity of native forbs was influenced by forb abundance, crop availability, and deer density. Where winter deer densities remained $<20\text{km}^{-2}$, early-summer and late-summer forb consumption was much lower when alfalfa or row-crops were available within a 1.5km radius. At greater deer densities the presence of row crops did not offset grazing pressure of native forest forbs. Hansen et al. (1997) recorded similar results, finding that crops buffered native flora from the effects of deer herbivory except when at high deer densities. A Japanese study of Sika deer found that, even at high densities, deer herbivory did not alter the host forest forb community composition when agricultural fields were located adjacent to the forest (Takada et al. 2004). Conversely, a Texas study found that when white-tailed deer frequented warm-season food plots up to 1km away, the percent of native forbs found in the feces did not decrease, suggesting that grazing pressure on these favoured species was not reduced in the presence of supplemental feeding (Hehman and Fulbright 1997). It was hypothesized that food plots could artificially increase deer populations and increase the absolute consumption of native forbs.

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Studies examining the effects of white-tailed deer herbivory within more complex landscapes have not been completed. Despite the afore mentioned findings, caution is required when extrapolating the results to other settings due to the temporal, spatial, and floristic variances between different ecosystems (Russell et al. 2001). Saint Charles Rifle Range (SCRR) is Manitoba's second largest remnant northern tallgrass prairie/aspen forest complex. It is embedded within an agricultural-urban landscape, offering its resident deer every possible type of forage choice: tallgrass prairie, aspen forest, row-crops, tame forage, and ornamentals. Previous southern Manitoba studies found that the region's deer consume very few forbs, focussing instead on grasses, crops, and browse (Howe et al. 1974, Garrod et al. 1981). Thus the effect of white-tailed deer herbivory on the site's native tallgrass prairie flora is unclear.

In 2005 excessive moisture precluded the sowing of row-crops in many parts of southeastern Manitoba. The following year drought set the stage for a favourable harvest as the heavy Red River clay soils acted as a moisture reservoir. These conditions provided the unique opportunity to examine white-tailed deer dietary selection within a northern tallgrass prairie/aspen forest/agricultural complex with crops both unavailable and then available. The objectives of the study were to determine the seasonal and annual white-tailed deer dietary preferences with and without row-crops in order (1) to evaluate if the presence of row-crops mitigated the potentially deleterious effects of intensive white-tailed herbivory on the native northern tallgrass prairie, and (2) to ascertain which tallgrass species, if any, were being placed at risk of extirpation from elevated deer densities.

STUDY AREA

The primary study area is SCRR, a military rifle range and dismounted training area less than 2km west of Winnipeg, Manitoba, located in the Rural Municipalities of Headingley and Rosser (49° 55' North latitude, 97° 13' West longitude, elevation 238m). It comprises 280ha of remnant northern tallgrass prairie and 102ha of aspen forest. The site is flat and poorly to imperfectly drained with <2% slope. Soils are classified as Clayey Lacustrine (Gleysols and Black Chernozems) (Land Resource Unit 1999). As a result, it is not uncommon for low-lying areas such as the forest floors to be flooded in spring and during wet summers.

Today, the eastern half is generally characterized as a lower quality native prairie than the west, dominated by *Poa pratensis* and *Symphoricarpos occidentalis* instead of more *Agropyron* spp (wheatgrasses), *Koeleria cristata* (June grass), *Andropogon* spp (bluestem), and *Spiraea alba*. Since 1880 an aspen forest has become established on the site, now covering over one third of the range. Although aspen encroachment continues locally, forest cover has remained relatively stable (Walker 2004). Less the grassy openings within the forest, the native prairie has been burned a number of times since 1996, the last being in spring 2005. Much of the southern half of the site is mowed as it supports the rifle ranges, obstacle course, and buildings.

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Within a 25km radius of the site, land cover consists of 81.5% agriculture, 29.3% grasslands, including urban grasslands, 4.4% forage crops 2.1% forest, and 1.3% cultural. More immediately, the area within 6km of the study site is 52.3% agriculture, 10.4% cultural, 10.0% grasslands, 5.7% forage crops, and 2.8% forest (calculated using the MB Conservation 2004 Land Cover GIS layer). Approximately 4.5km to the south of the main study forest is the Assiniboine River, which flows east/west. Although such water barriers have not been found to be movement barriers, they do serve to restrict free movement of deer, especially where adequate resources exist on both sides of the water obstacle (Coulon et al 2006, Michael 1965, Eberhardt et al 1984). The land cover of the region to the south of this river was therefore not included in the above figures. Additional details are found in Chapter 1.

METHODS

A common method employed to assess the magnitude and nature of the effects of herbivory on a particular vegetative assemblage is to establish an exclosure study (Anderson et al. 2001, Bowers 1997, Healy 1997). By measuring differences in species abundance, structure, and composition over time conclusions can be drawn and estimates made regarding site-specific, ecologically sound herbivore population densities. Typically, however, it takes 3-4 years before significant differences emerge (Anderson et al. 2005), longer than the two growing seasons available for this study. While an exclosure methodology was nevertheless employed, the accidental destruction of the second year's plant biomass eliminated the possibility of exploring apparent emerging

patterns and extrapolating diverging trajectories. In response, it was decided to evaluate white-tailed dietary selection against the tallgrass prairie plant biomass abundance data, developing preference indices for each of the species grazed. Rare plants consumed in high proportions could be considered to be at greater risk of extirpation than more common species occasionally consumed or rare species not selected.

Fecal Collection and Analysis

In order to determine dietary composition, composite deer fecal samples of at least 30 deposits were collected from across the study area during the middle of each month, from August 2005 to August 2006. Fewer samples were collected in August 2005 simply because more could not be located. Only fresh pellets were collected to minimize plant epidermal decay and enhance dietary fidelity (Leitte and Stuth 1994). During the winter this was not an issue because pellets were quickly frozen and, by only gathering those pellets lying on top of the snow, their age could be fairly accurately assessed. April was the most difficult month because melting snow immersed most of the pellets in water, making it difficult to determine their age. Because deer tend to forage linearly outwards from their shelter (Alverson et al. 1988), by collecting fecal matter from all areas of the site the resultant samples should reflect all foods consumed by the deer. Further, because deer consume different combinations of foods during non-discrete “meals”, employing instead a “batch” digestive process, the animal’s stomach contents typically represents a cross section of about 2 days’ intake (Robbins 1993).

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Once collected, pellets were placed into individual plastic bags and frozen at -4°C (Hodgman et al. 1996). After no more than three months two pellets from each sample were assembled to form a composite fecal sample. Monthly samples were then grouped based on food availability and phenology. During the growing months (May, June, July, and August) individual monthly samples were collated. The September-October sample represented senescence before the first major snowstorm. Thereafter, the deer yarded but during the months of November and December the snow was not so deep as to prevent them from grazing along the forest edge and into the prairie. During January-February-March deer browsed within the aspen forest and internal grassy clearings only. Just after the last fecal samples were collected in March the snows began to rapidly melt, releasing the deer to find other food sources. April was therefore analyzed on its own.

These composite fecal samples were sent to the Wildlife Habitat Nutritional Laboratory at Washington State University for Microhistological Analysis, using frequency-density conversion sampling procedures of Sparks and Malehek (1968), Flinders and Hansen (1972), Holchek and Vavra (1981), and Holechek and Gross (1982). The greatest single source of error during microhistological analysis is the technician's ability to properly identify the remaining epidermal fragments in the feces (Bartolome et al. 1995); by using the Washington State University laboratory this source of error was minimized. Relative cover (Davitt 1979) of plant cuticle and epidermal fragments were quantified for 25 randomly located microscope views on each of eight slides, for a total of 200 views. A 10 x 10 square grid mounted in the eyepiece of the microscope was used to measure the area covered by each positively identified fragment observed at 100x magnification. Larger

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magnification (200x to 450x) was used to aid in identification of discernable fragments (Holechek and Valdez 1985). Measurements of the area covered were recorded by species. Percent diet composition was calculated by dividing cover of each plant by the total cover observed for all species, then multiplied by 100.

Fecal analysis is the only means of measuring dietary intake of free roaming wild herbivores without sacrificing the animal (Saunders et al. 1980, Holechek et al. 1982). The principle difficulty of this approach over rumen and oesophageal fistula analysis is that not all plant epidermal material survives the digestive process, resulting in under-reporting of easily digested plants. Forbs are the class most affected by this problem, and grasses, the least (Holechek, Vavra and Piper 1982, Bartolome et al. 1995). To partially address this problem correction factors for the August 2005 and 2006 diets were calculated. This was done by recreating the measured diet using plant material harvested from the study site and then digesting that diet *in vitro* for 48hrs using steer inoculum. Microhistological analysis was then repeated on this digested sample and, using multiple regression, correction factors by species were derived (Leslie et al. 1983).

The more difficult problem arises for those plants that completely disappear or cannot be positively identified by species using fecal analysis due to their fragile epidermal cells. This occurs among some annual forbs (Free et al. 1970, Bartolomé et al. 1995). For the purposes of this study the unidentified forb component, listed as “Other forbs” in both 2005 and 2006, was reconstituted using equal amounts of *Viola pedatidia* (Early prairie violet), *Ratibida pinnata* (Grey-headed coneflower), *Epilobium grandulosium* (Purple-

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leaved willow herb), and *Crepis tectorum* (Narrow-leaved Hawk's beard). None of these species were identified during fecal analysis and were locally rare (*Viola* spp and *C. tectorum*) or sparse (*E. grandulosium*). This latter species showed evidence of browsing while other studies have found that *Viola* spp are favoured by deer (Nixon et al. 1970).

For the August 2006 corrected forb diets, domestic sunflower was assumed to be consumed instead of the native *Helianthus* spp. Sunflowers were grown adjacent to the study site and deer were observed to intensively graze those plants. "Other shrubs" were assigned as *Spiraea alba*, common and heavily browsed on site. "Other grasses" were assigned to be *Phleum pratensis* (Timothy) and *Agrostis scabra* (Rough hair grass).

Plants not provided for the correction factor determination but found during fecal analysis were: *Astragalus agretis*, *Agoseris glauca*, *Gallardia aristata*, *Penstemon glacilis*, *Psorela* spp, *Lonicera dioica* and *Stipa comata*, totaling 7.4% and 2.9% of the 2005 and 2006 diets respectively. These plants were generally rare on the site and, although small numbers of certain plants were found earlier in the year, they could not be located in the fall for harvest. The analyses were therefore conducted without these species.

Local Movement Patterns

Unless present in such high densities as to force the animals to consume all available phytomass, large herbivore grazing pressure is temporally and spatially heterogeneous, varying as a function of their distribution. To understand where the white-tailed deer were residing, moving and browsing on site, monthly (fall and winter) and weekly (spring and summer) observations were made concerning the location of deer beds and areas of high trail and fecal concentrations. In addition, in the summer of 2006 two wildlife movement monitors were placed at a series of locations and rotated weekly, when their batteries were changed. One was a digital surveillance still camera (PBox D-435) using an Olympus D-435, set to high sensitivity with a 30 second delay and a 15m range. The second was a game monitor that simply recorded movement events, time, and direction of movement. Set to a sensitivity of 7, it had a detection range of 22.7m (Vigil 650X). Both monitors operated using a passive infrared motion detector that sensed heat-in-motion within a conical beam (Cirtronique Estrie Inc, Rock Forest, Quebec). Initially, the monitors were rotated according to a strict schedule, but once it was observed that the deer were routinely changing their movement and grazing patterns in response to shifting dietary preferences, the devices were relocated as required to suspected high use areas. These areas were determined by observing animal activity, new bedding sites, and fresh fecal deposits. To maximize cover, the two monitors were normally placed at opposite points of the compass: either north and south or east and west. The disadvantage of the game monitor was that it could not be verified if counted events were either white-tailed

deer or some other form of movement. Secondly, groups of travelling deer could not be differentiated from a single deer.

Tallgrass Composition

Vegetative composition on the tallgrass prairie was measured using the clip and weigh method. A total of 23 exclosures and paired plots were established on the prairie. Four 5m x 5m paired plots were located in clearings within the aspen forest while three 10m x 10m paired plots were established along the forest/tallgrass prairie ecotone. An additional sixteen 5m x 5m plots were erected along five transects emanating from the forest edge at 100m intervals (Figure 1.3). For biomass, a 1m x 1m quadrat was placed 2m from the northwest corner of each plot in early September 2005 and the plant matter was clipped to within 2-5cm of the soil, bagged, and frozen at -4°C. The harvested biomass was then sorted by species, dried at 60°C for four days in a cabinet oven, and then weighed using a digital scale. The advantage of this procedure is that small and rare plants can be captured, identified, and included in the survey, especially spring and early summer plants. The disadvantage is that the clipping of the vegetation alters floristic composition and biomass in subsequent years as soil moisture and nutrients decrease, and soil temperature and sunlight increase (Bullock 2004). Further, the removal of woody species directly alters plant composition. Quadrats dominated by woody species were therefore not sampled using this method ($n = 12$). These consisted of all quadrats in the internal prairie, those along the forest edge, and one 100m from the forest edge along the northern-most transect. To offset this reduction, five unprotected clipping quadrats were

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established along the transects 12m from the forest edge, and another adjacent to the northern plot. In total, 32 quadrats were clipped.

The vegetative values above were assumed to be representative of the study site's tallgrass prairie and from them total biomass, by species, was derived. Given the heterogenous nature of the site's soil type, moisture, history, and thus vegetation, the resultant values do not precisely reflect the true floristic composition of the total site, especially for habitat specialists and rare plants. A much more rigorous sampling and mapping regime would have been necessary to enhance accuracy but, for the purposes of this study, the extrapolated values should suffice as general indicators of grazing intensity.

Preference Indices

Because of the difficulties inherent in accurately determining range composition for free roaming ungulates, developing accurate preference indices is problematic. Even if the site's vegetative composition were completely known, fine-scale foraging behaviour is a function of landscape perception (Etzenhouser et al. 1998), forage distribution and density (Focardi et al. 1996), individual animal preferences (Arnold and Drawe 1979), movement barriers and accessibility (Loehle and Rittenhouse 1982), sex and weather (Bergman 2001, Weckerly 1993), snow depth (Dumont et al. 2000), and predation (Pierce 2004). All of these factors influence where individual animals live, move, and forage on the landscape, independent of pure "preference" (Loehle and Rittenhouse 1982). Further,

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the consumption of reproductive structures may be more impacting on plant survival than the grazing of larger biomasses of those plant parts less important to its survival and reproduction. These differences are obscured when comparing only biomass values. For example, twenty-four dried flowers from the thin leaved sunflower, the portion of the plant most often consumed, weighed a mere 6.4gr while nine flowers from five wild bergamot plants weighed only 1 gr, far less than a complete single plant. Recognizing these limitations, preference indices were nevertheless calculated by extrapolating the biomass of the tallgrass species encountered within the quadrats over the entire tallgrass prairie region using a modified log transformed forage ratio equation:

$$\ln P_i = \ln \left[\frac{D_i + 0.001}{\sum RA_{ik} + 0.001} \right]$$

Where P_i is the Preference Index of species i , D_i is the percent of species i in the diet, and RA_{ik} is the percent of species i in the herbage of quadrat k . To establish a positive and negative preference scale results were log transformed. The addition of 0.001 avoids the problem of taking a log of either zero or infinity values (Loehle and Rittenhouse 1982). Species selected over the relative proportion of overall biomass have positive values whereas those selected less often have negative values.

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Plant species found in the diet but not encountered in the quadrats were treated separately. For these, the frequency of their presence was categorized non-metrically as Very Rare, Rare, Uncommon, and Common. By comparing dietary component to presence frequency categories based on site knowledge, threat survival values were developed for each of these plant species.

Data Analysis

Dietary composition was first compared using Principle Component Analysis (PCA) (SYN-TAX 2000) in order to observe similarities by month and season. Dietary similarities by sampling period were then determined by calculating the Pearson Product Moment correlation by species and then by class. Months with high scores were then plotted against one another on a scatter plot in order to assess overlap. PCA was also conducted on the summer forb component of the 2006 diet to assess the effect of flowering period on dietary selection. The categories of flowering period were deemed to be Spring (May), Early Summer (June), Summer (July), and Late Summer (August) as described in Vance et al. (1999) and Ladd (1995).

RESULTS

Dietary Composition

A total of 74 different plant species, major plant groupings, and plant structures (leaf, stem) were identified in the white-tailed deer fecal matter collected at SCRR from August 2005 to August 2006 (Table 2.1, Figure 2.1). When available and in line with other studies, forbs were the most often selected plant class, followed by shrubs, grasses, *Carex/Juncus*, and Other (thorns, flowers, mosses, and other accidental and minor components) (Nixon et al. 1970, Hakim 1998, Arnold and Drawe 1979, Drawe 1968). Crops were actively selected immediately after snowmelt when the nutritional level of surrounding native vegetation was extremely low and again in the fall when row-crops were high in digestible nutrients. They were not present in the fecal analysis during most of the active growing season (May –July). The proportion of each plant class varied with time in accordance with the plants' nutritional value and availability, supporting the forage maturation hypothesis (Hakim 1998, Etter et al. 2002, Stewart et al. 2000).

Analyzing the diets with PCA, the relative importance of individual principle species is illustrated (Figure 2.2). Most similar were the May, June, and July diets, dominated as they were by new forb growth (60.1-64.0%). Thirty-one forb species were identified in the deer feces, with an unidentified forb component comprising of 7.8, 4.2, 4.2, and 4.1% from May until August. Interestingly, the maximization of variance displayed by the biplot places the July diet between May and June, likely because of the presence of the

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Table 2.1.a. Grasses, Crops, and *Carex/Juncus* spp dietary content. Uncorrected values.

	Aug 05	Sep- Oct	Nov- Dec	Jan – Mar	Apr	May	Jun	Jul	Aug 06
<i>Agropyron</i> spp	18.9	3.2	6.1	0.6	3.6	1.3	0.4	1.6	18.7
<i>Andropogon</i> spp	2.1	2.0	1.4	0.4	0.8			0.5	0.4
<i>Bechmannia syzigachne</i>					0.3				
<i>Bromus inermis</i>	4.7	2.7	8.9	2.4	4.0	1.6	1.7	2.1	0.6
<i>Hierchloa odorata</i>				0.2					
<i>Hordeum</i> spp.	1.0	1.2	0.8						0.9
<i>Koeleria cristata</i>					0.1				
<i>Poa</i> spp	2.8	1.5	2.6	6.3	5.3	3.5	4.7	1.6	0.4
<i>Sporobolus heterolepis</i>	2.1				0.6				
<i>Stipa comata</i>		0.5	0.4	1.2	4.0	1.9	0.4		1.7
Other Grasses	2.4	1.0	1.0	1.4	1.4	1.1	0.2	1.6	1.1
Total Grasses	34.1	12.1	21.2	12.5	20.1	9.4	7.4	7.4	23.8
Barley					1.8				
Oats					4.5	1.3			
Soybean					0.3	4.8	0.6	5.8	24.1
Wheat					22.8	0.8			0.6
Total Crops					29.4	6.9	0.6	5.8	24.7
<i>Carex</i> spp	1.2		0.8		38.1	2.7	5.3	1.3	0.4
<i>Eleocharis</i> spp		0.7							
<i>Juncus balticus</i>		0.5							
Total <i>Carex/Juncus</i>	1.2	1.2	0.8		38.1	2.7	5.3	1.3	0.4

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Table 2.1.b. Forbs dietary content. Uncorrected values.

	Aug 05	Sep- Oct	Nov- Dec	Jan – Mar	Apr	May	Jun	Jul	Aug 06
<i>Achillea</i>									
<i>millifolium</i>	1.3	1.0	1.6		0.1	0.7	4.7	1.7	0.8
<i>Agoseris glauca</i>		0.3				0.3	0.2		0.1
<i>Alisma plantago</i>	0.5	0.7							
<i>Amorpha nana</i>	1.0				0.3	9.3	1.7	2.0	0.4
<i>Aster spp</i>						1.1	0.4	0.4	0.6
<i>Astragalus</i>									
<i>agretis</i>	1.2	0.3					1.5	1.9	
<i>Campanula</i>									
<i>rotundifolia</i>			0.6						
<i>Cirsium spp</i>	2.8	0.3	7.5		2.7		0.2	0.5	1.5
<i>Erigeron spp</i>	2.0	3.2	2.1	0.8		6.0	0.3	1.5	2.3
<i>Fragaria</i>									
<i>virginiana</i>	1.9	3.1	0.4			1.3	2.7	2.1	
<i>Gaillardia</i>									
<i>aristata</i>							5.1	0.3	0.9
<i>Galium boreale</i>	3.6	0.5	0.8	0.2		14.6	1.9	1.1	1.9
<i>Geum triflorum</i>	2.7					7.1	3.5	4.0	0.4
<i>Helianthus spp</i>	0.1		0.2		0.3	0.8		1.9	2.2
<i>Lactuca</i>									
<i>pulchella</i>		1.0	0.2	1.7		1.3		0.8	
<i>Lathyrus spp.</i>	2.8	0.4	0.8			3.8	1.8	2.6	1.7
<i>Lithospermum</i>									
<i>canescens</i>	2.1	3.5	6.8			1.4	0.8		
<i>Monarda</i>									
<i>fistulosa</i>	1.2	0.5				0.5	0.6	4.8	6.7
<i>Oenothera</i>									
<i>biennis</i>	0.5						4.2	0.4	0.1
<i>Penstemon</i>									
<i>gracilis</i>	4.5	5.5	1.6				2.7	2.9	
<i>Petasites</i>									
<i>sagittatus</i>		1.1	1.3						
<i>Plantago major</i>	0.5	0.1	0.6	0.6	0.1	0.7	1.3	0.8	0.4
<i>Potentilla spp</i>									
<i>leaf</i>	1.8	0.5		0.2			2.3		0.4
<i>Psoralea spp</i>			0.9				1.3	0.5	0.2
<i>Rumex spp</i>		0.3	1.6		0.6	0.3	0.6	0.5	0.6
<i>Solidago spp</i>	1.8	2.5	0.2			0.5	3.0	0.5	1.9
<i>Stachys palustris</i>	2.0		0.2			2.3	0.5		
<i>Taraxacum</i>									
<i>officinale</i>							0.6	4.8	
<i>Thalictrum spp</i>							1.3		
<i>Trifolium/Medic</i>									
<i>ago/Melilotus</i>	0.5	3.5					12.8	20.3	1.6
<i>Vicia spp</i>	0.5	0.7	0.4			0.3	3.8	3.2	2.4
Other Forbs	3.8	4.2	2.2	0.2	1.1	7.8	4.2	4.2	4.1
Total Forbs	38.9	33.2	30.0	3.7	5.2	60.1	64.0	63.7	31.2

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Table 2.1.c. Shrub and Other dietary content. Uncorrected values.

	Aug 05	Sep- Oct	Nov- Dec	Jan – Mar	Apr	May	Jun	Jul	Aug 06
<i>Amelanchier alnifolia</i> leaf	2.4	1.5	1.2					1.1	
<i>Amelanchier alnifolia</i> stem				5.0					0.9
<i>Artemisia</i> <i>ludoviciana</i>	1.3	0.1	2.9	0.1		2.6	1.3	0.1	0.4
<i>Elaeagnus</i> <i>commutata</i>				0.6					
<i>Lonicera dioica</i> leaf	1.7	2.2	1.0						
<i>Populus</i> spp leaf	2.6	6.4	6.7				4.0		2.2
<i>Populus</i> spp stem	0.7	1.7		11.1	0.6	0.5	3.4	4.0	
<i>Rosa</i> spp leaf			0.6					4.8	0.9
<i>Rosa</i> spp stem	1.4			6.1	0.4	1.1	0.4		
<i>Rubus pubescens</i> leaf		1.2	0.4					2.9	2.8
<i>Rubus pubescens</i> stem						0.8			
<i>Salix</i> spp leaf	11.4	3.0	3.5				3.2	0.5	5.4
<i>Salix</i> spp stem	1.4	4.2	1.4	57.5	3.5	8.3	8.5	5.0	6.0
<i>Symphoricarpos</i> leaf	2.1	18.8	8.1			1.3	1.1		
<i>Symphoricarpos</i> stem		4.0	0.8	0.4		1.3			
<i>Other Shrub</i> leaf	1.0	0.3		0.4			0.6	0.8	
<i>Other Shrub</i> stem		1.5	0.8			0.5			
Total Shrub	25.9	44.9	27.4	81.2	4.5	16.4	22.5	19.2	18.6
Composite hair		0.5	0.9			0.0			
Composite flower			0.9			4.2			
Lichens			0.8	0.2					
Mosses			0.6	2.4	0.8			0.8	0.2
Flower		2.2	2.9				0.2	0.5	
Thorn		4.7	11.5		1.4			0.8	1.1
Seed/Nut		1.2	3.9		0.5				
Insect						0.3		0.5	
Total “Other”		8.6	21.5	2.6	2.7	4.5	0.2	2.6	1.3

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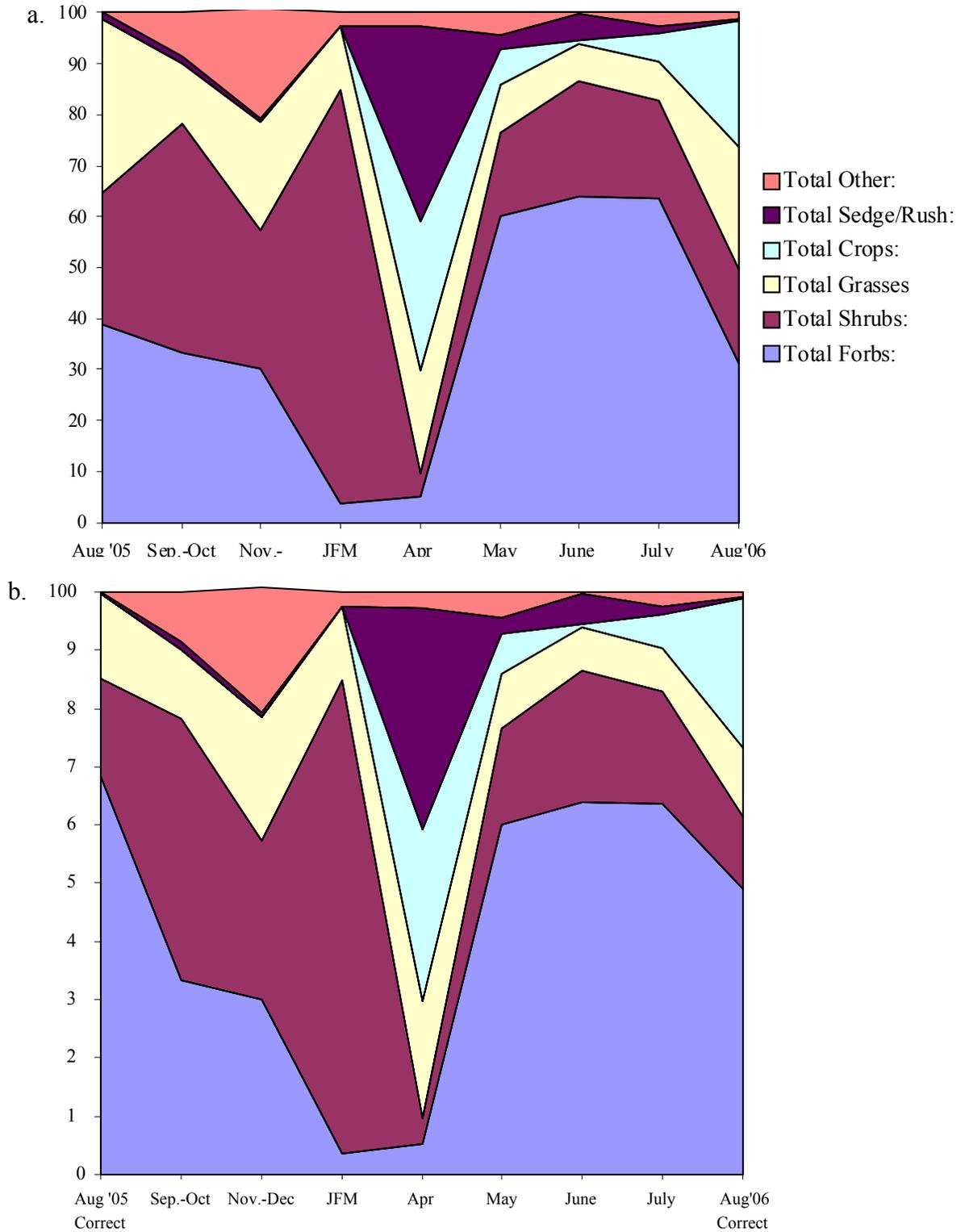


Figure 2.1 . Dietary Composition. When available, Forbs make up the greatest proportion of the diet. (a) In 2005, without access to crops, deer met their nutritional needs by relying entirely on native species. Figure (b) includes the August corrected values, increasing Forbs and decreasing Shrubs and Grasses. Crops remain stable.

row-crop soybean and *G. triflorium*, a common perennial forb more abundant in the May diet. August 2005 (no crop) is positioned to reflect the importance of *Agropyron* spp (18.8%), along with the other grasses (15.2%) and *Salix* leaf (11.4%) more closely associated with late winter. September to December was marked by their high woody species leaf content. In September-October this was primarily *S. occidentalis* (18.8%) with *Populus* spp representing an important secondary element (6.4%). Even after leaf drop and the first snows in November, woody leaves persisted in the diet. Leaf litter within hardwood forests have been found to be a major potential source of nutrition for deer, especially from younger trees typically found along the forest edge. *Populus* spp leaf in particular is higher in Crude Protein, calcium, and magnesium than most other forages beginning in September (Ditchkoff and Servello 1998, Tew 1970).

The prominence of thorn in the September-December diets underscores the importance of *C. arvensis* to white-tailed deer but also the high digestibility of the invasive forb. The digestibility of *C. arvensis* is on par with that of wheat and sunflower (Chapter 4). Interestingly, the thorn component of the diet (4.7, 11.5%) outweighed that of the parent plant (0.3, 7.5%), possibly an artefact of the manner in which deer graze the plant. Deer were observed to consume the outer layers of the tillers much like a person would eat corn off the cob, concurrently ingesting large amounts of thorn. Correcting for relative digestibility the reported thorn component would certainly decrease, but the *C. arvensis* dietary representation would also increase.

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With snow depths increasing beyond the 30cm threshold by end December 2005, deer were forced to remain yarded. As snow continued to accumulate, seeking thermal cover became more important than maximizing dietary selection in order to maintain a favourable net nutritional balance (Dumont et al. 2000, Pauly et al. 1993). With deeper snows making most litter, grasses, and forbs inaccessible (Carpenter et al. 1979), deer gradually changed their foraging strategy, become less specialized (Brown and Doucet 1991). They resorted to consuming large amounts of shrub stem (*Salix* spp 57.5%, *Populus* spp 11.1%, *Rosa* spp 6.1%, *Amelanchier anifolia* 5.0%, and *S. occidentalis* 0.4%). The animals were also found to dig in the snow for food, typically at the base of *Populus* spp. trees, consuming increased amounts of mosses and lichens (2.4%, 0.2%). The placement of mosses opposite to the January-March diet was an artefact of maximizing dispersion on the Axes rather than of dietary selection.

Efforts to forage beyond the central yarding area exposed the deer to increased predation from the three resident coyotes, further restricting choice (Patterson and Messier 2000). Nevertheless, as the quality of available browse decreased during the winter the need for nutrition outweighed the importance of thermal cover. Browse alone does not provide sufficient energy for maintenance (Gray and Servello 1995). Deer then accepted the risk of predation and the greater energy expenditure of moving through the deeper snow, pushing into the edges of the forest where the trail network was sparse and the ability to flee reduced (Pauly et al. 1993, Dumont et al. 1998, Pierce et al. 2004). Seven of the eight deer killed during the January to March period died while foraging just inside the eastern edge of the forest, outside of the established deer yard.

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By end March the local food supply was exhausted and the deer were extremely lethargic, unwilling to flee unless absolutely necessary. In the final days of that month the snows finally melted and the resident deer were free to forage off-site. With no fresh native growth available, the deer began to travel to outlying foraging stations, primarily to consume winter wheat (22.8%) in a field located 2km to the west along with volunteer crop stems (oats: 4.5%, barley: 1.8%, and soybean: 0.3%). Also consumed were large amounts of *Carex* (38.1%) and a variety of grasses (20.1%). Despite this, the deer remained weakened from the winter and seven more fell to predation before the end of the April.

The portions of each plant class identified as “Other” represents those plants whose epidermal cells could not be identified because of damage due to digestion or because, by species, the plants represented <0.1%. Among the classes, Forbs consistently had the highest portion classified as “Other”. Within the class, the “Other” category decreased from a high of 7.8% in May to 4.1% in August. This reflects the relative decreasing digestibility of forbs over the growing season. What cannot be known is how many forbs were consumed in spring and early summer and completely digested, rendering their identification impossible and, thus, the herbivorous pressure being placed upon them unknown.

Examining dietary selection in August 2005 (no crops) and August 2006 (crops), the two corrected diets were not found to be significantly different between treatments (Total

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Diet, $p = 0.9805$) or classes (Grasses, $p = 0.3858$; Forbs: $p = 0.3171$; Shrubs: $p = 0.4724$). Crops were absent in 2005 but comprised 25.4% of the corrected diet in 2006. Offsetting the consumption of crops, the intake of Grasses, *Carex* spp, Forbs, and Shrubs declined by 2.8%, 0.2%, 19.3%, 4.2%, while Mosses and Thorns increased by 1.5% of the total diet. By principle dietary component (>5%) (Chamrad and Box 1968), the composition of the two corrected months were marginally dissimilar ($F_{1,6} = 161.85$, $p = 0.0499$). The addition of crops eliminated the consumption of *Penstemon gracilis* and *Stachys palustris* while reducing the intake of *Galium boreale* (6.5, 2.6%), Other forbs (7.0, 5.6%), and *Salix* spp leaf (7.2, 4.9%). Increasingly selected were *Monarda fistulosa* (2.2, 15.4%) and soybean (0.0, 25.4%). *Agropyron* spp. consumption remained relatively stable (8.1, 9.5%).

No Crops vs Crops

Comparing the exact composition of the total August 2005 and August 2006 diets, to include the quantities consumed by species, the diets were very poorly correlated ($r = 0.149$). This was due to a small number of species that were consumed in very different proportions between years. Of the 54 plant species and components identified over the two years, 28 appeared in both 2005 and 2006. Thirteen appeared only in 2005 while another 13 appeared only in 2006. On a crop presence/absence basis, the addition of crops created the greatest difference among Shrubs, Forbs, and then Grasses. Mosses and Thorns were not present in 2005, but these classes were likely only coincidental dietary constituents as they have little or no nutritional value. Why Thorns did not appear in the

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2005 diet despite *Cirsium* spp being present in the diet in larger quantities than in 2006 is unclear, perhaps reflecting the higher moisture levels. The addition of crops therefore reduced the total number of component species by just two in the overall diet, although the volumes of many native species did decrease. With soybean and *M. fistulosa* removed from the data set, correlation between years increased to 0.580. Grasses were highly correlated, Shrubs less so ($r = 0.618$), and Forbs very poorly ($r = 0.137$). This was reflective of the general decrease in the consumption of forbs in the presence of crops. Sunflower was not found during the fecal analysis despite its proximity to the site, being closer than soybean and situated between the forest edge and wheat, which was selected in small amounts

Forage Maturation Theory

Considering all species, the diets correlated poorly between adjacent months as various species peaked in nutritional value. Only the June and July as well as the two August diets were strongly correlated ($r = 0.721$, $r = 0.835$). Other diets that had a correlation, such as January to March and July, were the product of similar minor crop classes or because of the presence of a few common larger species such as *Solidago*, *C. arvense*, and *Helianthus* spp that persisted into the winter. Otherwise, the deer continually shifted their grazing efforts to different species as they peaked in nutritional value. For example, all visible patches of *Andropogon* were observed to be aggressively grazed in the first week of August 2006. Before then, they were relatively untouched.

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Conducting PCA on the May to August 2006 diet, 51.25% and 81.95% of the variance among the months were explained on the two axes (Figure 2.3). Colour coding the dietary constituents by when they flower and, thus, are at their highest nutritional value (Bruinenberg et al. 2001), the monthly diets were highly differentiated. The co-location of objects (monthly diets) with the principal species that comprised those diets (variables) supports the notion of preferential selection when food quality is maximized. The overlap of spring and early summer forbs means that those species (i.e. *F. virginianus*, *Vicia* spp) were consumed during most if not all of the growing season. Also consumed out of season were a number of perennial species such as *Stachys palustris*, *Galium boreale*, and *Erigeron* spp. Eaten in May, they possibly provided at least some nutrition until greater new growth appeared. The overlap of certain plant species was expected, as plants do not tidily enter flower within specific months. Additionally, once they have flowered smaller forbs such as *Lithospermum canescens* and *Trifolium/Medicago/Meililotus* (*TMM*) remain readily digestible and therefore continued to be grazed, albeit often at a reduced rate.

The July diet was placed directly between August and June in PCA and was not strongly associated with any single species except *Taraxacum officinale*; July is the month with the greatest amount of flowering overlap. Many June forbs continue to flower into early July while late July flowering plants persist into August, such as *Lactuca pulchella*, *Solidago* spp, *Stachys palustris*, and *Astragalus agretis*. In the spring, the deer consumed both new growth as well as standing perennial tillers from the previous fall, such as *Galium boreale*, *Helianthus*, *Cirsium* spp, *Aster* spp, and *Erigeron* spp. In this manner the

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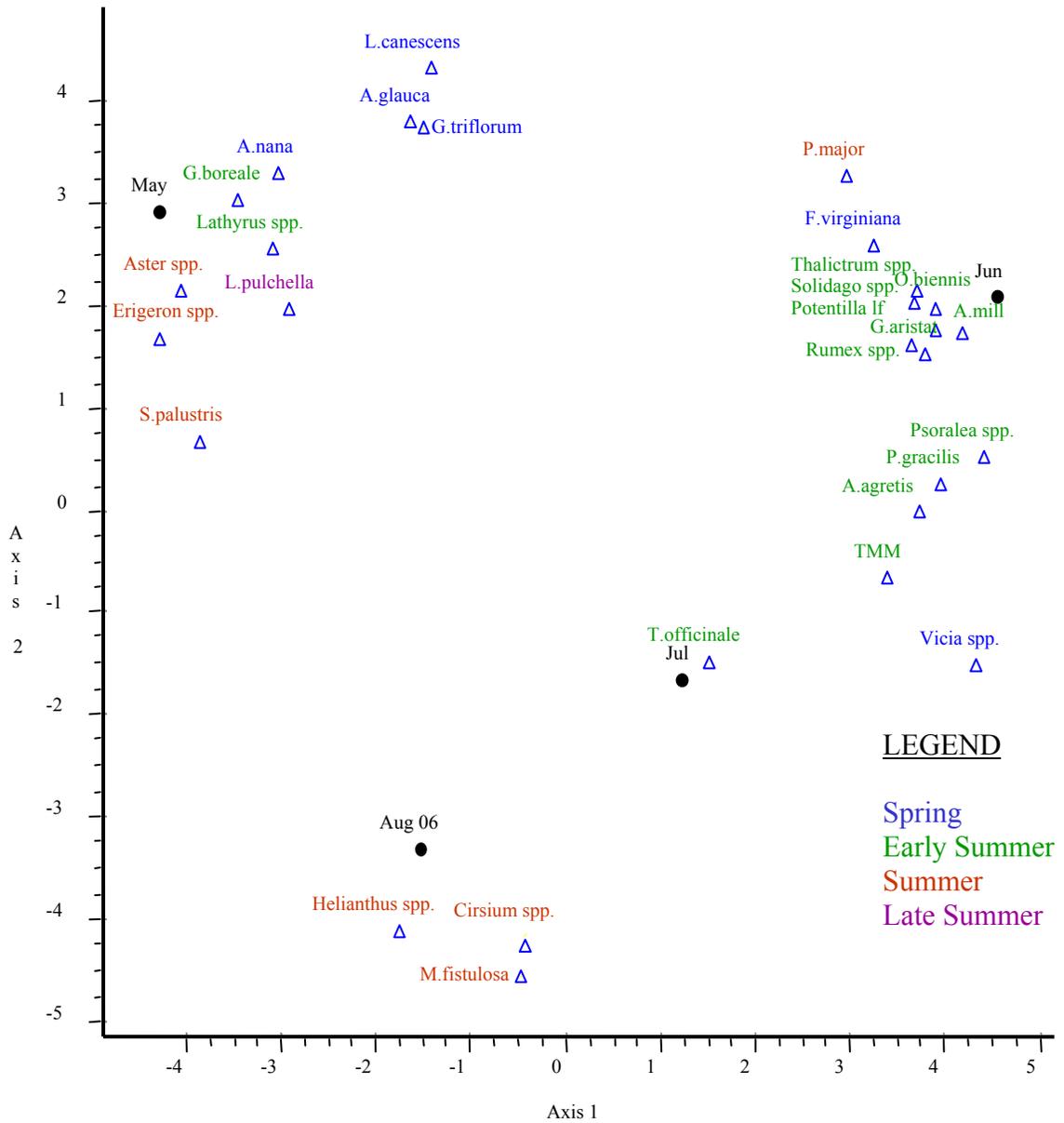


Figure 2.3. PCA of summer 2006 forb diet. Eigenvalues are 51.25% (Axis 1) and 31.7 (Axis 2). While deer did consume spring flowering plants in May, they also consumed perennial tillers from the previous year. Most summer forbs flower July and August, placing the July diet between the early summer and late summer plants.

May, and especially April, diets have more in common with the fall forb diet than any other period.

Corrected Diets

Examining the corrected dietary intake for the months of August 2005 and 2006, the relative digestibilities of each plant class were revealed. Grasses, with their large surface area, parallel arrangement of vascular bundles, and greater poorly-digestible structural compounds (Bruinenberg et al. 2001, Robbins 1993), had a mean correction factor of 0.43 ($s = 0.13$), meaning that they were overstated in the fecal analysis; actual consumption by the resident white-tailed deer was about half of what was reported (Table 2.2). Actual and measured crop intake remained essentially unchanged after applying correction factors, although wheat inflorescence correction values were more similar to those of the native grasses (0.50). At the other end of the spectrum were the forbs, with a total correction factor of 1.75 in 2005 and 1.57 in 2006 ($s = 0.13$), indicating that true dietary values were under reported. There were, however, a few notable exceptions. In 2005 *G. triflorium* was a low of 0.67 while *Stachyus palustrum* was 3.25. In 2006 *M. fistulosa*, *Cirsium* spp, and *TMM* all surpassed 2.00. Closer to grasses were the shrubs (0.65, 0.68, $s = 0.20$). Notable exceptions were *Rosa* spp stems in 2005 (1.14) and *A. ludoviciana* (0.31, 0.50). Mosses (0.0, 0.50) and Thorns (0.0, 0.64) were also similar to the grasses.

Table 2.2.a. Grasses, Crops, and *Carex/Juncus* corrected diets and correction factors.

Plant Species	Uncorrected Diets (%)		Corrected Diets (%)		Correction Factor	
	Aug 05	Aug 06	Aug 05	Aug 06	Aug 05	Aug 06
<i>Agropyron</i> spp.	18.9	18.7	8.1	9.5	0.43	0.51
<i>Andropogon</i> spp.	2.1	0.4	1.0	0.2	0.48	0.50
<i>Bromus inermis</i>	4.7	0.6	1.8	0.3	0.38	0.50
<i>Hordeum</i> spp.	1.0	0.9	0.3	0.4	0.30	0.44
<i>Poa</i> spp.	2.8	0.4	0.7	0.2	0.25	0.50
<i>Sporobolus heterolepsis</i>	2.1		1.8		0.86	
<i>Stipa comata</i>		1.7		0.7		0.41
Other					0.38	0.45
Grasses	2.4	1.1	0.9	0.5		
Total Grasses	34.1	23.8	14.6	11.8	0.43	0.43
					(s = 0.13)	
Soybean		24.1		25.4		1.05
Wheat		0.6		0.3		0.50
Total Crops:	0.0	24.7	0.0	25.7		1.04
<i>Carex</i> spp.	1.2	0.4	0.4	0.2	0.33	0.50
Total <i>Carex/Juncus</i>	1.2	0.4	0.4	0.2	0.33	0.50
					(s = 0.12)	

Table 2.2.b. Forb corrected diets and correction factors.

Plant Species	Uncorrected Diets		Corrected Diets		Correction Factors	
	Aug 05	Aug 06	Aug 05	Aug 06	Aug 05	Aug 06
<i>Achillea millifolium</i>	1.3	0.8	2.3	1.1	1.77	1.38
<i>Agoseris glauca</i>		0.1		0.1		1.00
<i>Alisma plantago</i>	0.5		0.9		1.80	
<i>Amorpha nana</i>	1.0	0.4	1.7	0.5	1.70	1.25
<i>Aster spp.</i>		0.6		0.8		1.33
<i>Astragalus agretis</i>	1.2		2.2		1.83	
<i>Cirsium spp.</i>	2.8	1.5	4.2	3.9	1.50	2.60
<i>Erigeron spp.</i>	2.0	2.3	3.7	3.0	1.85	1.30
<i>Fragaria virginiana</i>	1.9		2.3		1.21	
<i>Gaillardia aristata</i>		0.9		1.2		1.33
<i>Galium boreale</i>	3.6	1.9	6.5	2.6	1.81	1.37
<i>Geum triflorum</i>	2.7	0.4	1.8	0.5	0.67	1.25
<i>Helianthus spp.</i>	0.1	2.2	0.2	1.8	2.00	0.82
<i>Lathyrus spp.</i>	2.8	1.7	5.2	2.3	1.86	1.35
<i>Lithospermum canescens</i>	2.1		3.0		1.43	
<i>Monarda fistulosa</i>	1.2	6.7	2.2	15.4	1.83	2.30
<i>Oenothera biennis</i>	0.5	0.1	0.9	0.1	1.80	1.00
<i>Penstemon gracilis</i>	4.5		8.3		1.84	
<i>Plantago major</i>	0.5	0.4	0.9	0.5	1.80	1.25
<i>Potentilla spp. leaf</i>	1.8	0.4	3.3	0.5	1.83	1.25
<i>Psoralea spp.</i>		0.2		0.3		1.50
<i>Rumex sp.</i>		0.6		0.4		0.67
<i>Solidago spp.</i>	1.8	1.9	3.3	2.6	1.83	1.37
<i>Stachys palustris</i>	2.0		6.5		3.25	
<i>Trifolium/Medicago/ Melilotus</i>	0.5	1.6	0.9	3.5	1.80	2.19
<i>Vicia spp.</i>	0.5	2.4	0.9	2.2	1.80	0.92
Other Forbs	3.8	4.1	7.0	5.6	1.84	1.37
Total Forbs:	38.9%	31.2%	68.2%	48.9%	1.75	1.57
					(s = 0.13)	

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Table 2.2.c. Shrubs and “Other” corrected diets and correction factors.

Plant Species	Uncorrected Diets		Corrected Diets		Correction Factors	
	Aug 05	Aug 06	Aug 05	Aug 06		
<i>Amelanchier alnifolia</i> leaf	2.4		2.1		0.88	
<i>Amelanchier alnifolia</i> stem		0.9		0.6		0.67
<i>Artemisia ludoviciana</i>	1.3	0.4	0.4	0.2	0.31	0.50
<i>Lonicera dioica</i> leaf	1.7		0.9		0.53	
<i>Populus</i> spp. leaf	2.6	2.2	1.4	1.0	0.54	0.45
<i>Populus</i> spp. stem	0.7		0.5		0.71	
<i>Rosa</i> spp. leaf		0.9		0.3		0.33
<i>Rosa</i> spp. stem	1.4		1.6		1.14	
<i>Rubus pubescens</i> leaf		2.8		1.3		0.46
<i>Salix</i> spp. leaf	11.4	5.4	7.2	4.9	0.63	0.91
<i>Salix</i> spp. stem	1.4	6.0	0.7	4.3	0.50	0.72
<i>Symphoricarpos</i> leaf	2.1		1.4		0.67	
Other Shrub leaf	1.0		0.6		0.60	
Total Shrubs:	25.9	18.6	16.8	12.6	0.65	0.68
					(s = 0.20)	
Mosses:		0.2		0.1		0.50
Thorn:		1.1		0.7		0.64
Total Other:	0.0	1.3	0.0	0.8		0.62

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As hinted above, correction factors varied in magnitude by year within species and among plant classes (Figure 2.4). Although species values generally correlated with those of their parent class, especially among the forbs, there were a few species that were significantly different. Grasses tended to have lower digestibility in 2006, as did forbs, but to a lesser degree. Shrubs were more consistent as a class, but even thorns had lower correction values in 2005 than 2006. It is possible that the higher correction values were caused by the flood conditions of 2005; higher available moisture would have enhanced the fragility of the plant cellular walls (Wilshurst et al. 1995). An increase in fragility would have led to a corresponding increase in digestibility of plant cuticle and epidermal cells, reducing their survivability of these indicator cells during the animal's digestive process. This is the very same process that leads to an over-reporting of grasses and shrubs and an under-reporting of forbs.

Exceptions to this trend toward reduced digestibility in 2006 were *Cirsium* spp, *M. fistulosa*, *TMM*, and *G. triflorum*, all of which are late summer forbs, have higher correction values, and thus have higher digestibility, but represent both tall and short plants. Taller plants are generally less digestible due to the fibre and silica required to provide structural rigidity. Conversely, *Oenothera biennis*, *Vicia* spp, and *Helianthus* spp were all much less digestible in 2006. Often co-located on the study site, this may underscore some environmental condition particular to those plots, such as soil drainage or moisture.

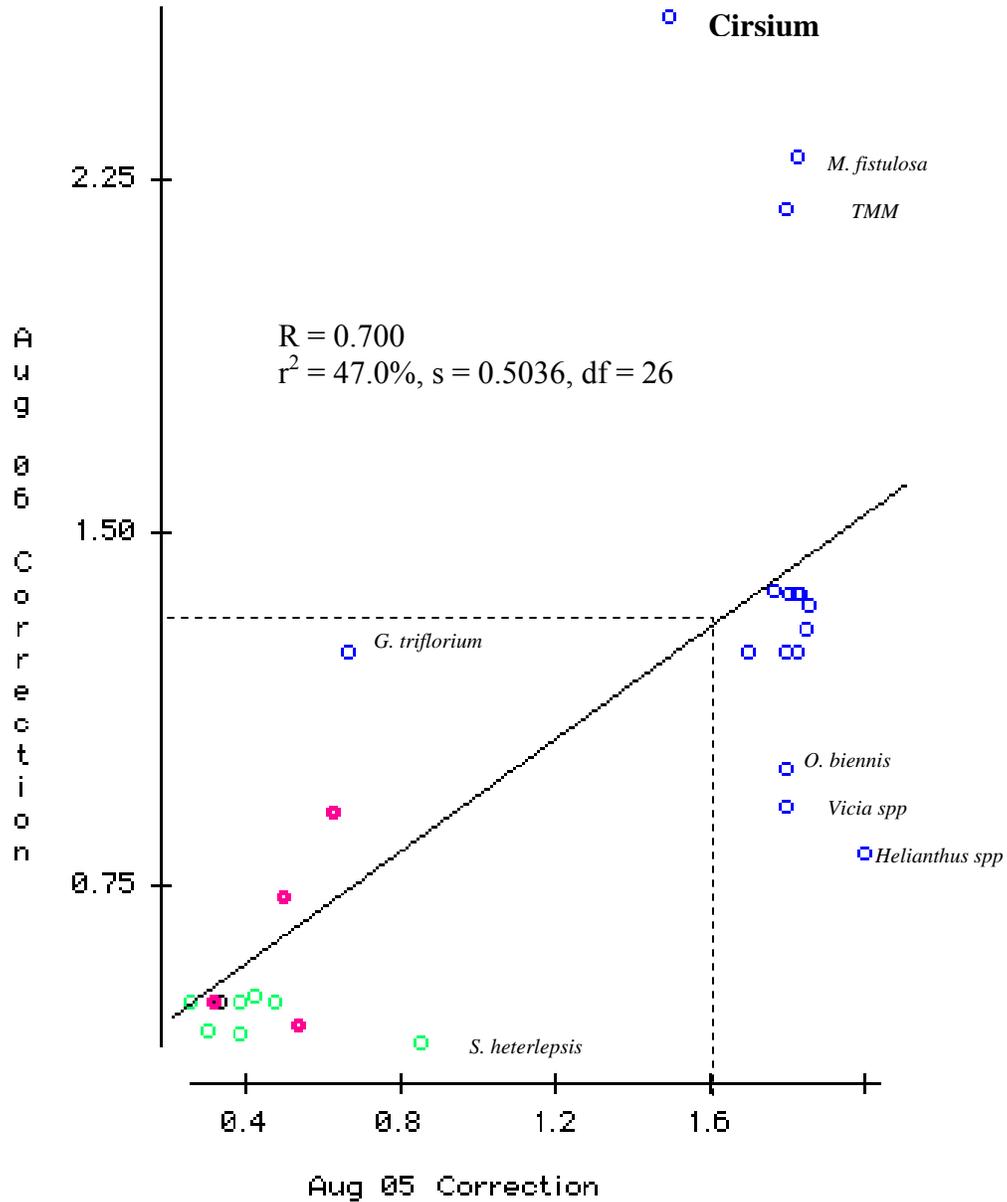


Figure 2.4. Correction Factors 2005 vs 2006. The correction factors for the majority of species was greater in 2005 than 2006, especially for the Forbs (blue). Grasses (green) were also relatively constant except for *S. heterolepsis* (0.86, not present in 2006). Shrubs (red) were similar both years. This suggests a higher possible digestibility for most plants in 2005 due to the elevated moisture.

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Monthly, correction values also varied. Applying mean correction values to the entire data set, total dietary intake figures decreased below 100% in January to April and then increased above 100% from May to July (Figure 2.5). This suggests that correction values for winter foods such as shrubs increase closer to 1.0 while correction values for forbs and possibly crops decrease in the summer. This reflects variances in relative digestibility of the diet's constituent plants during the year. Dietary correction values therefore can not be extrapolated beyond the month for which they are calculated.

Fine Scale Movement Patterns

Similar to observations made by Arnolde and Drawe (1979), Murphy et al. (1985), and Nixon et al. (1970), the spatial distribution of white-tailed deer was in a state of constant flux in response to thermal requirements and food distribution. With the forest floor flooded in the summer and fall of 2005, deer were found to concentrate on the tallgrass prairie edges and internal fields, which remained dry (Figure 2.6). This distribution was likely reinforced by the associated very high mosquito densities (Coleman et al. 2003), peaking at 20,196 in the New Jersey Light Trap on 13 July 2005 (25W bulb), versus 528 in June 2006 (Taz Stuart, pers comm 2006). By mid-November there was approximately 10-20cm of snow on the ground and the deer had stopped crossing the tallgrass prairie. While they continued to reside principally within the internal prairie fields they were also commonly found sheltering along the forest edge and in protected bays on the east side of the wood line, often laying so that they could bask in the sun. These deer beds were

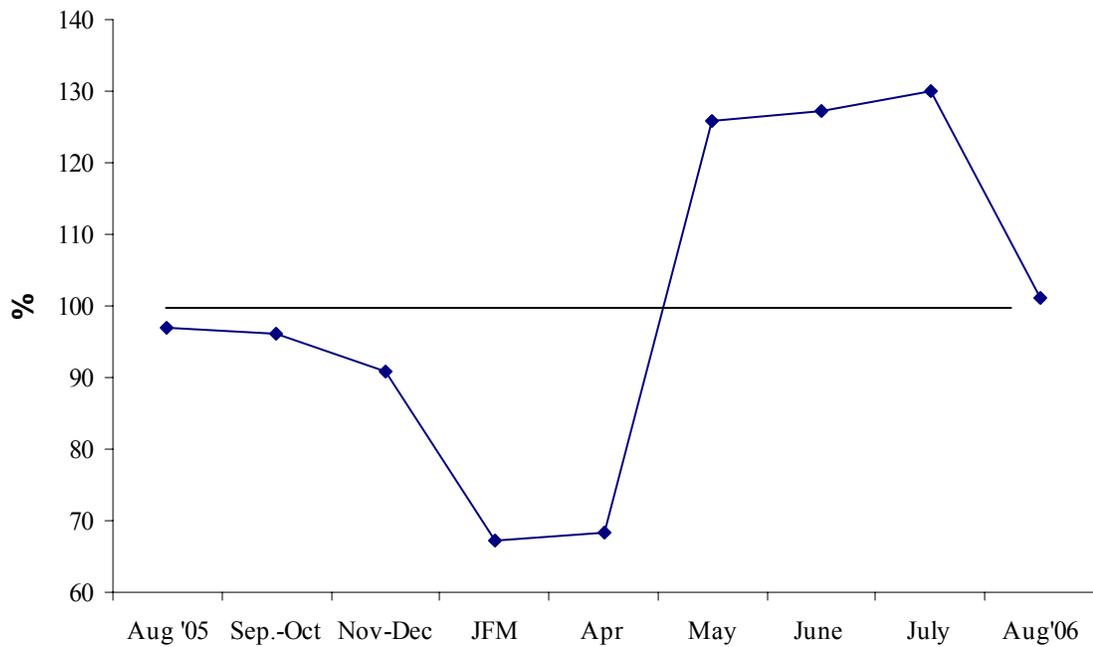


Figure 2.5. Monthly variations in correction values. Using mean correction values from 2005 and 2006, all dietary intake data was adjusted. The result was an over reporting in the summer, when plants are more digestible, and an under reporting for the remainder of the year.

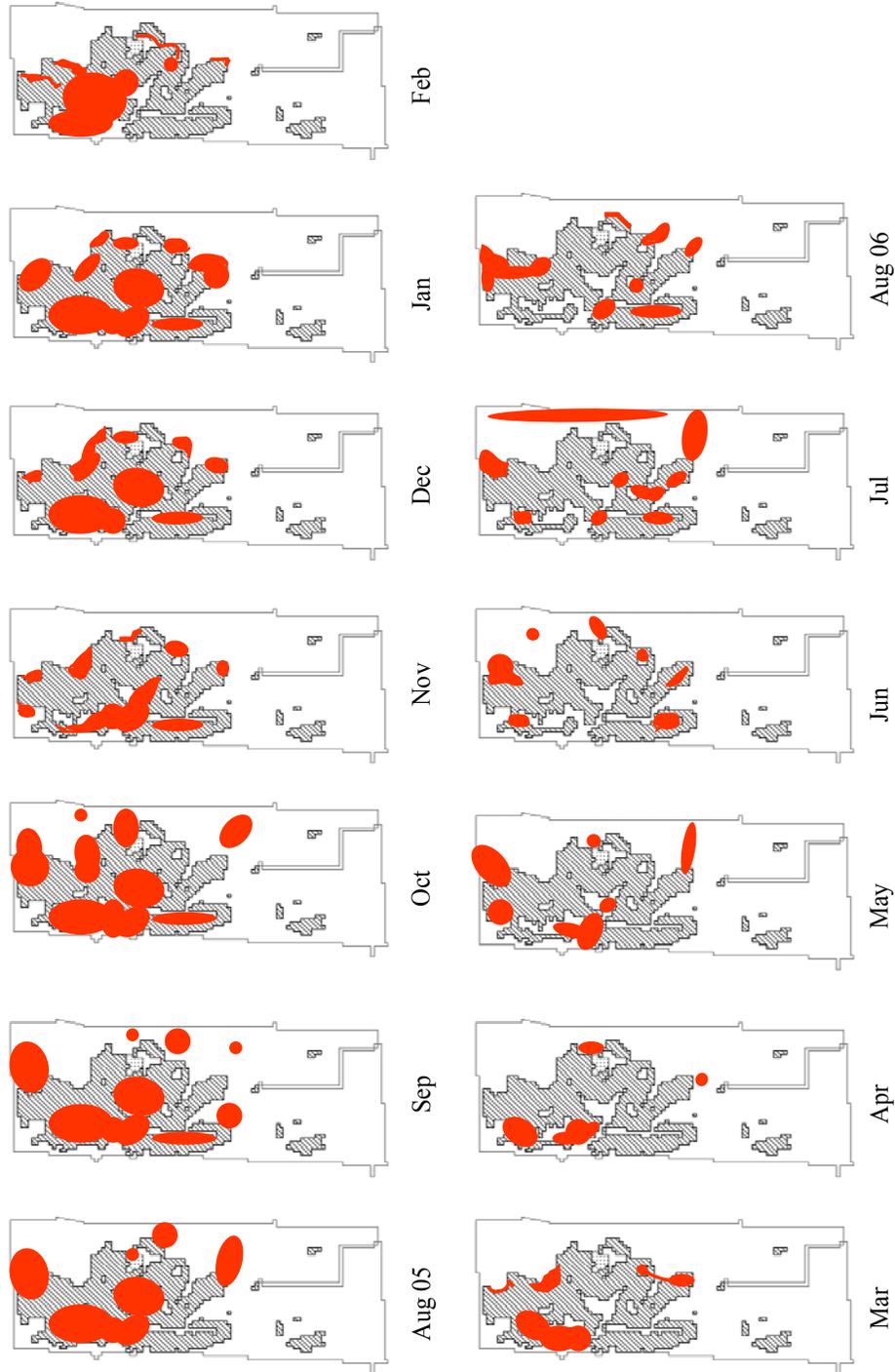


Figure 2.6. White-tailed deer habitat and foraging areas. Forced to obtain almost all nutritional intake on site in the fall and winter 2005, their grazing pressure would have been greater than in the presence of crops the following year. Deer still tended to congregate and move about the site as a function of food availability. Where they congregated the effects of herbivory and secondary impacts would have been greatest.

typically situated among taller tillers of *C. arvensis* and *Solidago* spp. There they foraged and rested in the same location, conserving significant energy (Parker et al. 1984).

As snows deepened in December and the coyotes appeared to consume most available jackrabbits (*Lepus spp*), deer generally withdrew further into the forest interior, yet continued to visit a small number of favoured grazing sites. By late January 2006 deer began to be killed, first along the eastern edges but then increasingly into the centre of the site so that, by March, the deer were mostly concentrated on the internal fields to the west where an extensive network of heavily travelled trails provided easy movement and escape routes. Outside these areas the white-tailed deer were easy prey for the coyotes, which moved with ease across the thinly crusted snow. By late March the remaining deer were lethargic, slow to flee humans, and being killed in increasing numbers. Fifteen deer carcasses showing signs of predation were located by April 2006. Two additional large males that died from undetermined causes.

In April 2006 very few signs of deer were found on site as the forest floor once again flooded. This is when migrating deer in agricultural settings typically disperse from winter yards (Brinkman et al. 2005, Nixon et al. 2007). As the site dried, spring forbs emerged. Shrub leaf-out began in May. At this time deer densities appeared to decrease on the small grassland patches within the forest and the forest itself. They all but abandoned the larger clearings in the forest that had supported them throughout the previous winter. Instead, deer were found to forage into the tallgrass prairie, notably passing through the northeast and southeast corners of the site. In late July numerous deer

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beds began to appear along the eastern edge of the tallgrass prairie, adjacent to a flowering canola field. Although the plants are considered to be toxic, the highly digestible flowers are not (Schwabb et al. 2001). A series of intensively used 45cm-wide movement trails suddenly emerged, emanating from the southeast corner of the aspen forest and leading to the same canola field. As soon as the canola stopped flowering, the bedding sites and trails were abandoned. The deer seemed to then migrate to the northern portion of the forest where they were found to be intensively grazing sunflower.

Preference Index

As expected, few of the site's uncommon and rare plants appeared in the quadrats. A total of 25 tallgrass prairie plant species of the 90 known to exist on the study site were found within the quadrats. Mean quadrat species counts for the vegetative cover survey was 7.35 (+/-2.27) with the contents of the quadrats being generally representative of the surrounding vegetation. This meant that a preference index value could not be assigned to all dietary components, typically the more rare forbs but also those plants not found on the dry prairies.

Preference Index scores for those plants found in the quadrats are detailed at Table 2.3 and Figure 2.7. These species represented only 24.12% (SE 2.09) of the entire diet for May until November. Of these, only eight plant species received a score > 1.0, meaning that they are selected more often than they occur. These were *Rumex* spp, *G. triflorium*, *Vicia* spp, *F. virginianus*, *Thalictrum*, *A. glauca*, *A. millifolium*, *M. fistulosa*, and *G.*

Table 2.3. Preference Index for forbs and shrubs found in the quadrats, using uncorrected values

Scientific Name	Common Name	May	Jun	Jul	Aug	Sep	Oct/Nov	Mean % Diet	% Prairie Biomass	<i>P</i> _{index}
<i>Bromus inermis</i>	Brome	1.6	1.7	2.1	0.6	2.7	2.7	1.9	6.371	-1.30
<i>Carex</i> spp	Sedge spp	38.1	2.7	5.3	1.3	0.4		7.97	0.506	-0.10
<i>Juncus balticus</i>	Baltic rush					0.5	0.5	0.17	2.150	-1.61
<i>Achillea millefolium</i>	Yarrow	0.7	4.7	1.7	0.8	1.0	1.0	1.78	0.248	1.97
<i>Agoseris glauca</i>	Large-flowered false dandelion	0.3	0.2		0.1			0.12	0.016	1.98
<i>Aster</i> spp.	Aster	1.1	0.4	0.4	0.6			0.50	1.727	-1.24
<i>Cirsium</i> spp.	Thistle		0.2	0.5	1.5	0.3	0.3	0.50	2.111	-1.44
<i>Fragaria virginiana</i>	Smooth strawberry	1.3	2.7	2.1		3.1	3.1	1.84	0.118	2.74
<i>Galium boreale</i>	Northern bedstraw	14.6	1.9	1.1	1.9	0.5	0.5	4.00	1.634	0.89
<i>Geum triflorum</i>	Three-leaved avens	7.1	3.5	4.0	0.4			3.00	0.081	3.60
<i>Helianthus</i> spp.	Sunflower spp	0.8		1.9	2.2			0.98	1.596	-0.49
<i>Monarda fistulosa</i>	Wild bergamot	0.5	0.6	4.8	6.7	0.5	0.5	2.62	0.557	1.55
<i>Petalostemon purpureum</i>	Purple prairie-clover							0	0.025	-3.26
<i>Rumex</i> spp	Dock	0.3	0.6	0.5	0.6	0.3	0.3	0.46	0.007	4.05
<i>Solidago</i> spp.	Goldenrod	0.5	3.0	0.5	1.9	2.5	2.5	1.68	2.639	-0.45
<i>Thalictrum</i> spp.	Meadow rue		1.3					0.26	0.033	2.04
<i>Vicia</i> spp.	Vetch spp	0.3	3.8	3.2	2.4	0.7	0.7	2.08	0.074	3.32
<i>Artemisia ludoviciana</i>	Prairie sage	2.6	1.3	0.1	0.4	0.1	0.1	0.90	2.238	-0.91
<i>Rosa</i> spp. leaf	Prairie rose			4.8	0.9			1.14	1.480	-0.26
<i>Symphoricarpos</i> leaf	Snowberry	1.1	0.4					0.30	incl above	
<i>Symphoricarpos</i> stem		1.3	1.1			18.8	18.8	4.24	5.543	-0.27
Total diet explained (%)		73.5	30.1	33	22.3	35.4	35	37.5	29.943	
						4.0	4.0	1.06	incl above	

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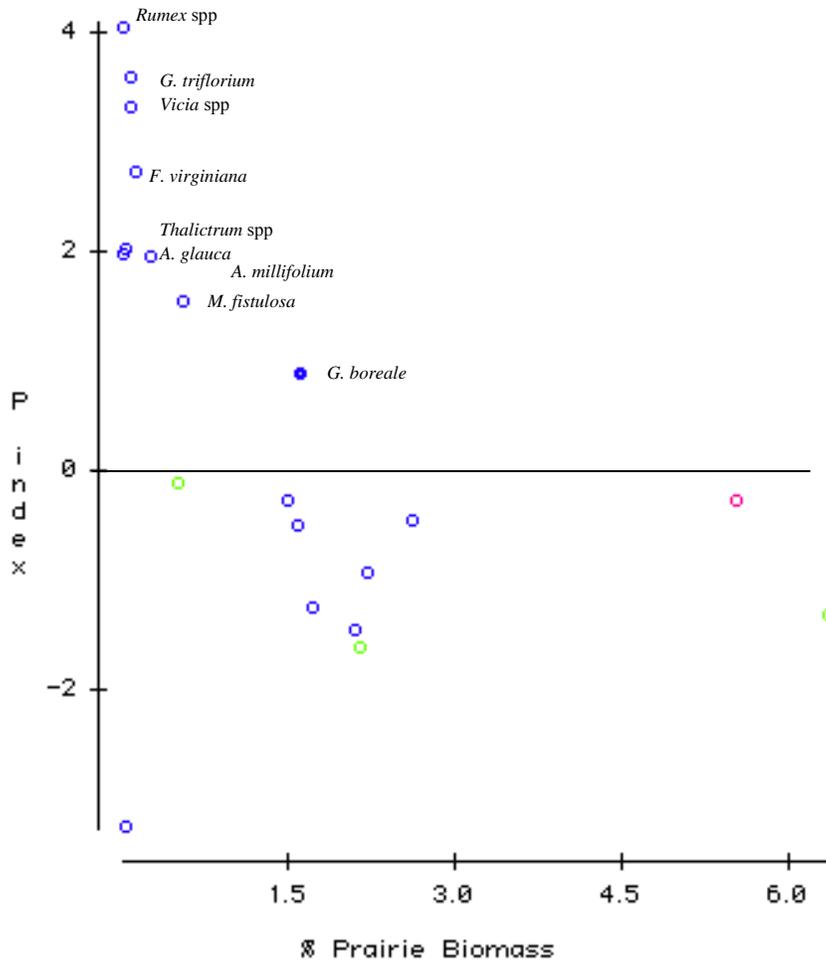


Figure 2.7. Species found within the quadrats under the greatest herbivore pressure. Those plants with scores >0 are under the most pressure from herbivory, as defined by the Preference Index (P_i). Other species are under greater pressure but were not found in the quadrats. Green: grasses, Blue: forbs, Red: shrubs.

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boreale. All other species were selected less often than they occurred on the prairie, as measured using the quadrats.

For those species not found in the quadrats but in the diets, three were deemed to be at very high risk from herbivory (Table 2.4). These were *Gallardia aristata*, *Oenothera biennis*, and *Penstemon gracilis*. All three of these are larger plants and thus readily located by deer, are rare or very rare on site, and constituted a relatively high proportion of the diet during the growing season. Only three *O. biennis* and two *G. aristata* stems were located on the study site in 2006. The *G. aristata* stems were found in the heavily traveled northeastern portion of the prairie and were completely consumed within days of flowering. The large intake of these plants despite their relative scarcity in the flowering stage suggests that the collective deer knowledge of the distribution of the site's flora is fairly complete. Similar to *G. aristata*, *P. gracilis* is a readily identifiable forb when in flower, could not be located during the vegetation surveys, but makes up a sizable portion of the deer diet. Its absence from the diet in August 2006 may suggest that crops in the diet displace this plant, reducing its associated risk.

At less risk but still under a good deal of pressure are *Andropogon* spp and *Stipa comata*. These native grasses still persist in small patches. When *Andropogon* began to seed out in August 2006 the stems were suddenly heavily grazed, completely reducing the plants. Both *Andropogon* and *S. comata* are consistent components in the annual deer diets, suggesting that this level of herbivory will persist with and without crops. *Erigeron* spp are considered to be at localized risk only where herbivory is the greatest. In the internal

Table 2.4. Prairie plants not found in the quadrats and consumed by white-tailed deer, using uncorrected values

Scientific name	Common Name	May	Jun	Jul	Aug	Sep	Oct	Mean % Diet	Occurrence Category	Risk of Extirpation
<i>Agropyron spp</i>	Wheatgrass, quackgrass	1.3	0.4	1.6	18.7	3.2	3.2	4.73	locally common	moderate - moderate -
<i>Andropogon spp</i>	Bluestem	1.9	0.4	0.5	0.4	2.0	2.0	0.82	uncommon	high
<i>Stipa comata</i>	Spear grass				1.7	0.5	0.5	0.83	rare	high
<i>Eleocharis spp</i>	Spike-rush					0.7	0.7	0.23	common	none
	Broad-leaved water plantain			0.7			0.7	0.14	marsh - common	none
<i>Alisma plantago</i>	plantain			2.0	0.4			2.68	rare	moderate
<i>Amorpha nana</i>	Dwarf wild indigo	9.3	1.7	2.0				0.74	rare	moderate
<i>Astragalus agretis</i>	Purple milk vetch	6.0	0.3	1.5	2.3	3.2	3.2	2.66	common	localized
<i>Erigeron spp.</i>	Dogbane spp		5.1	0.3	0.9			1.26	very rare	very high
<i>Gaillardia aristata</i>	Gaillardia								grazed-	
<i>Lactuca pulchella</i>	Blue lettuce	1.3		0.8		1.0	1.0	0.62	common	low
<i>Lathyrus spp.</i>	Wild peavane spp	3.8	1.8	2.6	1.7	0.4	0.4	2.06	uncommon	high
<i>Lithospermum canescens</i>	Hoary puccoon	1.4	0.8			3.5	3.5	1.14	uncommon	high
<i>Oenothera biennis</i>	Evening primrose		4.2	0.4	0.1			0.94	very rare	very high
	Lilac-flowered beardtongue			2.9		5.5	5.5	2.22	rare	very high
<i>Penstemon gracilis</i>	Arrow-leaved colts foot		2.7			1.1	1.1	0.22	marsh - common	none
<i>Petasites sagittatus</i>	Common plantain	0.7	1.3	0.8	0.4	0.1	0.1	0.66	edges - common	none
<i>Plantago major</i>	Potentilla spp		2.3		0.4	0.5	0.5	0.64	uncommon	low
<i>Potentilla sp. leaf</i>	Indian breadroot		1.3	0.5	0.2			0.40	rare	high
<i>Psoralea spp.</i>	Marsh hedge-nettle	2.3	0.5					0.56	marsh - rare	moderate

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prairie fields very few *Erigeron* stems were observed to flower in 2005, although as deer concentrated elsewhere in 2006 more flowers were observed. This species, along with a few others, appears to form the backbone of the native flora component in the white-tailed deer diet, being consumed whenever the deer can find it, but it also appears to tolerate heavy grazing. Another such plant appears to be *Lactuca pulchella*, most commonly found in the heavily grazed prairie in the northeast. It is not clear if it is preferentially grazed or if it is more of an accidental dietary component, consumed as the deer sample the plants they encounter. It persisted in the diet in small amounts throughout the year and is considered to be at Low risk.

DISCUSSION

Effects of Row Crops

Row-crops are not significantly buffering the native tallgrass prairie vegetation from the effects of high deer densities. As has been found elsewhere, white-tailed deer are grazing the native flora in order to maximize net energy gain, consuming plants in order of descending digestibility and when they are highest in nutritional value (Hakim 1998). When presented with row-crops, the deer selected them in large amounts but only when there was a nutritional advantage over the local native flora. Row-crops served principally as a nutritional bridge in April between snowmelt and leaf-out, and then in the fall as the relative nutritional advantage of native forages began to decline. Nixon et al. (1970) found a similar pattern in Ohio and Murphy et al. (1985) in Wisconsin, where grasslands and pastures were favoured in the spring and summer. The overall reduction in

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forb intake witnessed in August 2006 compared to that of the previous year was not even across all species, with *M. fistulosa* being the most notable example. Grazing intensity of certain favoured native species actually increased concurrent to the consumption of row-crops.

Within the forest's remnant tallgrass prairie fields the re-introduction of row-crops did reduce grazing pressure in the summer of 2006. Much of these internal fields, however, are already dominated by species associated with disturbance and possess little to no understory, including a dearth of otherwise ubiquitous grasses (Disturbance spp: 73.25%, SE 3.91, *Poa* spp: 16.5%, SE 2.7) (Chapter 3). This is not surprising given the intensity with which deer have been found to graze within forest gaps (Drolet 1978). Outside the forest's edge, the thermal shelter and southern exposures offered by the woodland's highly fragmented structure provided significant opportunity for the deer to satisfy both their thermal and foraging needs (Laurence 1990, Alverson et al. 1988), focussing deer herbivory in these areas (Vecellio et al. 1994).

Metric Preference Index

Many of the plants identified in the diet appear to be graze-tolerant; most plants assigned a high Preference Index were also common, such as *A. millifolium*, *F. virginiana*, and *Thalictrum*. This suggests that the native graze-intolerant species are too rare to appear in either the quadrats or the diet or that they have already become extirpated. Winter deer populations have generally exceeded 100 animals on Saint Charles Rifle Range since

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1983, except when extensive flooding has significantly reduced deer numbers throughout the region (Manitoba Conservation, unpublished data). When present in high densities, deer can collectively know where all favourable plant species are (Focardi et al. 1996), reducing the chance of them escaping selection.

Employing the Preference Index, only *A. glauca* is deemed to be at risk from white-tailed deer due to its high score and the enormous difficulty in locating flowering stems. Plants that persist in low densities are at greater risk of genetic depression and a subsequent reduction in germination rates. Thus if deer decrease stem abundance below a critical threshold, the plant may become extirpated without additional herbivory (Mendes 1991).

Of the other species with positive Preference scores, most continue to persist in abundance. Indeed, Anderson et al. (2005) found *M. fistulosa* and *Solidago (canadensis)* to thrive under intense white-tailed deer herbivory, likely due to their increased C:N ratios and lignin content (Rooney and Waller 2003, Chapter 4). *M. fistulosa* should be monitored, however, as it grows in isolated patches and is being consumed in very large quantities, possibly to offset the increased consumption of highly digestible row-crops (Chapter 4). Even graze-tolerant species may not be impervious to intensive grazing (Russell et al. 2001). *Rumex*'s high score is likely reflective of the plant's high density along Sturgeon Creek immediately north of the study site but its rarity among the quadrats. It is not believed to be at risk.

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Among the genus receiving a negative Preference Index rating was *Aster* spp., but there could be a danger in considering genus instead of individual species. *Asters* were grouped because this is how the fecal analysis was conducted, but not all *Asters* are equally resilient to herbivory. Anderson et al. (2005) found *Aster azereus* to be extremely intolerant and diminished in abundance under deer grazing. Drawe (1968) assigned *Aster aubulatus* var. *ligulatus* a low preference rating, although the effects on its abundance were not reported. The differences could be, in part, an artefact of their morphological variation by species (Olf and Ritchie 1998, Damhoureyeh and Harnett 2002, Spotswood et al. 2002).

The distribution in the diet of the site's two common *Asters* was similar ($F_{1,21} = 68.355, p < 0.0001$). *A. ericoides* is small, has many flowers, but has been found to respond poorly to deer herbivory in controlled experiments (Damhoureyeh and Harnett 2002).

Conversely, *A. laevis* is marginally larger, has numerous (but fewer) flower heads but with greater separation, reducing the possibility that all flower heads will be consumed at once. It is considered graze-tolerant. While both plants appear to be flourishing, it is possible that the resiliency of these two *Asters* differ.

Non-metric Preference Index

Two native grasses and seven other forbs found within the diet but not in the floristic survey do appear to be at risk. The grasses *Andropogon* spp and *S. comata* are of concern because of their limited remaining distribution and how completely the deer were found

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to consume them in late summer. Although deer do not consume large quantities of grass, their selective herbivory of favoured species has been found to suppress late seral grasses such as *Andropogon* spp. (Anderson and Briske 1995).

Of the forbs rated as being at a Very High risk of extirpation are *G. aristata*, *B. biennis*, and *P. gracilis*. Each of these was found flowering in very small numbers (two each for *G. aristata* and *O. biennis*) and appears to be over-represented in the diet. Although not important dietary components, their selection rate is out of proportion to their abundance. Rated as High are *Lathyrus* spp, and *L. canescens*, *Psoralea* spp. Deer can significantly reduce the percent cover of legumes and *Lathyrus venosus*, one of the two *Lathyrus* species found on the range, especially suffered in a 60-yr-old old field in Minnesota (Russell et al. 2001). On SCRR, *Lathyrus* spp. were very rarely found in flower and was a consistent component of the deer diet, present from May until December. Their dietary inclusion persisted even when row-crops were present. *Psoralea* spp., another legume, and *L. canescens* were rated as being at High risk because of their small physical size and their commonness in the diet. *L. canescens* was more commonly located on the prairie but its higher frequency did not appear to match the even higher rate of selection. It was, however, absent from the diet when crops were being grazed, suggesting that crops do provide a reprieve to at least some native forbs.

Rated as being at Moderate risk is *A. nana*. While this shrubby legume survives in two dense patches, a stochastic event could easily reduce their numbers (Simberloff and Gotelli 1984). It is actively grazed in the early summer and its inclusion in the diet

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persisted when row-crops were available. That said, another member of the genus, *A. canescens*, was found to be graze-tolerant (Anderson et al. 2005), suggesting that its continued selection may not pose a risk. *S. palustris* has been found to be intolerant of grazing and has therefore been rated as being at Moderate risk. It serves as one of the dietary spring bridge species even though it does not normally flower until the summer.

Of perhaps greatest concern are those forbs that do not appear in the diet or that are classified generically as Other Forbs. Of the spring-flowering forbs, 7.8% of the diet was unidentified. These small, fragile plants are least likely to survive digestion but are also perhaps under the greatest herbivorous pressure as the deer struggle to recover from the rigours of winter. *Viola* spp. for example, has been found to be consumed elsewhere but did not appear in the fecal analysis (Nixon et al. 1970). Similarly, it is unknown if the small number of rare flowering *Cypripedium calceolus* L var. *parviflorum* (small yellow lady slipper) located near the southeastern forest edge in the spring of 2005 were eventually grazed or only appeared due to the very wet soil conditions that year. They were not found again in 2006.

Short, small-seeded, and nitrogen-fixing plants as well as those on the wettest, most productive soils have been found to experience the heaviest losses due to habitat fragmentation (Leach and Givnish 1996). Small and nitrogen-rich plants were also among the most favoured by white-tailed deer and are at the greatest risk to be completely or nearly-completely consumed by deer. Nevertheless, unless the spring flowering plants are somehow identified in the diet, it is impossible to directly measure the effects of

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herbivory on them. An enclosure study would shed some light on this issue as plants still surviving but significantly repressed from herbivory could emerge.

The loss of the 2006-biomass samples prevented analysis of the enclosure study data from occurring, but within the second year of the enclosures two single stems of plants rare to the site were observed. These were *Artemisia frigida* (pasture sage), a graze-tolerant species, and *Aster praealtus* (willow aster). Not in an enclosure but located nearby was a single stem of *Lilium philadelphicum* (woody lily) which, like the *G. aristata*, promptly disappeared within days of flowering. Rare in a flowering state on the SCRR tallgrass prairie but appearing in another enclosure in 2006 was *Lathyrus venosus* (wild peavane). This suggests that the white-tailed deer are shaping the tallgrass flora in ways that may be limiting native diversity.

Actual Row-Crop Consumption

Fecal analysis failed to effectively identify the row-crop component of the diet. Judging from the swath grazed in the adjacent sunflower field, the intake of sunflower and canola flowers is likely significant. The *Helianthus* spp component of the December 2006 diet was reported to be 7.8%, *C. arvensis* was 21.2%, and the overall forb component 77.4% (Gooch, unpublished data). In light of the summer forb dietary values, this number is not credible; while *C. arvensis* was common where the deer were concentrated, *Helianthus* was not. This suggests that the sunflower component is being misreported as *Helianthus*

spp and that the percentage of this dietary element is being underreported, with a commensurate effect on the other plant classes.

The presence of sunflower and other crops is very likely increasing overall fitness amongst the local deer population and thereby increasing fecundity while decreasing mortality. Winter fat levels, so important in fending off mortality in harsh winters and increasing fecundity, are determined by summer forage intake (Hakim 1998). Fecundity rates are also influenced by the does' nutritional level in the early fall when in oestrus. A diet high in energy will enable the deer to reproduce more successfully at an early age and to maximize the number of twins delivered the following year (Verme and Ullry 1984). By ensuring a continual supply of high-energy foods after the native vegetation has declined in relative value, accessibility to row-crops crops reduces mortality (Dumont et al. 2000). In contrast to the 17 deaths on the study site in 2005, no carcasses were found in the winter of 2006. While certainly some deaths must have occurred, the mortality rate was much lower than the previous year when the deer were completely reliant upon the native vegetation. Elevated deer densities increase grazing pressure on the remaining phytomass.

MANAGEMENT IMPLICATIONS

Without the results from the exclosure study it was not possible to quantify the direct effects of white-tailed herbivory on the northern tallgrass prairie. Yet it is clear from these findings and the literature that the current white-tailed deer densities are having a

deleterious impact on the remnant northern tallgrass prairie, primarily forbs. The disturbance regime that the white-tailed deer are imposing does not reflect the nature of the disturbance under which the endangered ecosystem evolved (Fuhlendorf 2001), and by reducing deer densities to an ecologically acceptable level some of the negative effects of overgrazing can be reversed. The extirpation of functional plant groups will create opportunities for disturbance species to establish themselves and propagate on site (Anderson et al. 2001, Symstad 2005). Further, species present in only isolated patches are at greatest risk (Holt et al. 1995). Species that have become extirpated, however, may be lost forever unless sufficient seed banks exist within the soil. The emergence of some rare flowering stems within the exclosures does provide some hope that a measure of ecological rebound can indeed occur. Anderson et al. (2005) found that it took just 3 years for the tallgrass prairie outside of Chicago to begin to recover. To prevent further extirpations and ensure the proper ecological function of the tallgrass prairie, the population density should be reduced to 6-7 deer km⁻². This is the density that Anderson et al. (2005) found permitted the tallgrass prairie diversity to recover.

Any effort to reduce populations strictly through hunting is likely to be ineffective (Riley et al. 2003, Rutberg 1997, Giles and Findlay 2004), particularly now that rifle hunting has been excluded by provincial regulations. While hunting should be re-introduced, an organized cull will be required. A cull, however, is not a solution in of itself, as the underlying cause of the population irruption needs to be addressed (Jewel 1981). A local reduction in deer density will likely result in a net migration of deer due the social instability inherent in urban and agricultural deer communities (Brinkman et al. 2005,

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Nixon et al. 2007, Porter et al. 2004). More cost effective in the long term would be to leverage the white-tailed deer's optimal foraging habits to encourage them to choose not to reside on the site. Details are provided in Chapter 4, but this approach would see a deer fence erected around the perimeter of the endangered ecosystem, allowing populations to fluctuate and maintain healthy genetic diversity (Chesser 1991, Mathews et al. 1997) but separating the deer from row-crops, thereby eliminating the nutritional advantage they provide the resident deer. It is likely that some deer would relocate to the small southern woodlot when yarding was not necessary, but the grazing pressure placed on the tallgrass prairie to the north, opposite to the direction of travel for crops, would be significantly diminished.

Lastly, it is recommended that a forb stem-count study be conducted within the established exclosures in order to quantify the effects of white-tailed deer herbivory since 2005, and thereby secure a better understanding of the true effects of herbivory on the endangered tallgrass prairie.

LITERATURE CITED

- Alverson, W.S., Waller, M.W., and Solheim, S.L. 1988. Forests Too Edge: Edge Effects in Northern Wisconsin. *Conservation Biology*. 2:348-358.
- Anderson, R.C., Corbett, E.A., Anderson, M.C., Corbett, G.A., and Kelley, T.M. 2001. High white-tailed deer density has negative effect on tallgrass prairie forbs. *Journal of the Torrey Botanical Society*. 128:381-392.
- Anderson, V.J. and Briske, D.D. 1995. Herbivore-induced species replacement in grasslands: is it driven by herbivory tolerance or avoidance? *Ecological Applications*. 5:1014-1024.
- Anderson, R.C., Nelson, D., Anderson, M.A., and Rickey, M.A. 2005. White-tailed deer (*Odocoileus virginianus* Zimmermann) browsing effects in tallgrass prairie forbs: diversity and species abundance. *Natural Areas Journal* 25:19-25.
- Arnold, L.A. and Drawe, D.L. 1979. Seasonal food habits of white-tailed deer in the south Texas plains. *Journal of Wildlife Management*. 32:175-178.
- Atwood, E.L. 1941. White-tailed food habits of the United States. *Journal of Wildlife Management*. 5:314-332.
- Augustine, D.J. and Jordan, P.A. 1998. Predictors of white-tailed deer grazing intensity in fragmented deciduous forests. *Journal of Wildlife Management*. 62:1076-1085.
- Baker, R.H. 1984. Origin, Classification, and Distribution. Pages 1-18 *in* L.K. Halls, editor. *White-tailed Deer Ecology and Management*. Stackpole Books, Harrisburg, PA, USA.
- Bartolomé, J., Franch, J., Gutman, M., and Seligman, N.G. 1995. Technical Note: Physical factors that influence fecal analysis estimates of herbivore diets. *Journal of Range Management*. 48:267-270.
- Bergman, C.M., Fryxell, J.M., Gates, C.C., and Fortin, D. 2001. Ungulate foraging strategies: Energy maximization or time minimization. *Journal of Animal Ecology*. 70:289-380.
- Berteaux, D., Crete, M., Huot, J., Maltais, J., and Ouellet, J-P. 1998. Food choice by white-tailed deer in relation to protein and energy content of the diet: a field experiment. *Oecologia*. 115:84-92
- Bowers, M.A. 1997. Influence of deer and other factors on old-field plant community. Pages 310-326 *in* W.J. McShea and H.B. Underwood, editors. *The Science of Overabundance: deer ecology and population management*. Smithsonian Books, Washington D.C., USA

Chapter 2: Effects on the tallgrass prairie plants

- Brinkmann, T.J., Deperno, C.S., Jenks, J.A., Haroldson, B.S., and Osborn, R.G. 2005. Movement of female white-tailed deer: effects of climate and intensive row-crop agriculture. *Journal of Range Management*. 69:1099-1111.
- Brown, D.T. and Doucet, G.J. 1991. Temporal changes in winter diet selection by white-tailed deer in a northern deer yard. *Journal of Range Management*. 55:361-376.
- Bruinenberg, M.H., Valk, H., Korevaar, H., and Struik, P.C. 2001. Factors affecting digestibility of temperate forages from semi natural grasslands: a review. *Grass and Forage Science*. 57:292-301.
- Bullock, J. 2004. Plants. Pages 111-138 *in* *Ecological Census Techniques: A Handbook*. Editor W.J. Sutherland. Cambridge University Press, Cambridge, UK.
- Carpenter, L.H., Wallmo, O.C., and Gill, R.B. 1979. Forage Diversity and Dietary Selection by Wintering Mule Deer. *Journal of Range Management*. 32:226-229.
- Chamrad, A.D. and Box, T.W. 1968. Food Habits of White-Tailed Deer in South Texas. *Journal of Range Management* 21:158-164.
- Chase, J.M., Leibold, M.A., Downing, A.L., and Shurin, J.B. 2000. The effects of productivity, herbivory, and plant species turnover in grassland food webs. *Ecology*. 81:2485-2497.
- Chesser, R.K. 1991. Gene diversity and female philopatry. *Genetics*. 127:437-447.
- Coleman, J.E., Pederson, C., Hjermann, D.Ø., Holand, Ø., Moe, S.R. and Reimers, E. 2003. Do Wild Reindeer Exhibit Grazing Compensation During Insect Harassment? *Journal of Wildlife Management*. 67:11-19.
- Coulon, A., Guillot, G., Angibault, J.M.A., Aulagnier, S., Cargnelutti, B., Galan, M., and Hewison, J.M. 2006. Genetic structure is influenced by landscape features: empirical evidence from a roe deer population. *Molecular Ecology*. 15:1669-1679.
- Damhoureyeh, S.A. and Hartnett, D.C. 2002. Variation in grazing tolerance among three tallgrass plant species. *American Journal of Botany*. 89:1634-1643.
- Davitt, B.B. 1979. Elk summer diet composition and quality on the Colockum Multiple Use Research Unit, Central Washington. M.S. Thesis (unpublished). Washington State University, Pullman, WA, USA.

Chapter 2: Effects on the tallgrass prairie plants

- Ditchkoff, S.S. and Servello, F.A. 1998. Litterfall: An overlooked food source for wintering white-tailed deer. *Journal of Range Management*. 62:1 pp. 250-255.
- Drawe, D.L. 1968. Mid-Summer Diet of Deer on the Welder Wildlife Refuge. *Journal of Range Management*. 21:164-166.
- Drolet, C.A. 1978. Use of Forest Clear-cuts by White-tailed Deer in Southern New Brunswick and Central Nova Scotia. *Canadian Field-Naturalist*. 92:275-282.
- Dumont, A., Crête, M., Ouellet, J.P., Huot, J., and Lamoureux, J. 2000. Population dynamics of northern white-tailed deer during mild winters: evidence of regulation by food competition. *Canadian Journal of Zoology*. 78:764-776.
- Dumont, A., Ouellet, J.P., Crete, M., and Huot, J. 1998. Caractéristiques des peuplements frontiers recherches par le cerf de Virginie en hiver a la limite nord de son aire de repartition. *Canadian Journal of Zoology*. 76:1024-1036.
- Eberhardt, L.E., Hanson, E.E., and Caldwell, L.L. 1984. Movement and activity patterns of mule deer in the sagebrush-steppe region. *Journal of Mammalogy*. 65:404-409.
- Elliot, E.H. and Barrett, R.H. 1985. Dietary overlap among axis, fallow, and black-tailed deer and cattle. *Journal of Range Management*. 38:546-550.
- England, R.E. and DeVos, A. 1969. Influence of animals on pristine conditions on the Canadian grasslands. *Canadian Grasslands*. 22:87-94.
- Etter, D.R., Hollis, K.M., Van Deelan, T.R., Ludwig, D.R., Chelsvig, J.E., Anchor, C.L., and Warner, R.E. 2002. Survival and movements of white-tailed deer in suburban Chicago, Illinois. *Journal of Wildlife Management*. 66:500-510.
- Etzenhouser, M.J., Owens, M.K., Spangler, D.E., and Murden, S.B. 1998. Foraging behaviour of browsing ruminants in a heterogeneous landscape. *Landscape Ecology*. 13:55-65.
- Flinders, J.T. and Hansen, R.M. 1972. Diets and habits of jackrabbits in northeastern Colorado. Range Science Department Science Series No 12. Colorado State University, Fort Collins, CO, USA.
- Focardi, S., Marcellini, P., and Montrano, P. 1996. Do ungulates exhibit a food density threshold? A field study of optimal foraging and movement patterns. *The Journal of Animal Ecology*. 95:606-620.
- Free, J.C., Hansen, R.M, and Sims, P.L. 1970. Estimating Dry Weight of Food plants in Feces of Herbivores. *Journal of Range Management*. 23:300-302.

Chapter 2: Effects on the tallgrass prairie plants

- Fuhlendorf, S.D. and Engle, D.M. 2001. Restoring Heterogeneity on Rangelands: Ecosystem Management Based on Evolutionary Grazing Patterns. *BioScience*. 51:625-632.
- Garrod, R.C., Shoesmith, M.W., and Stewart, J.M. 1981. Rumen analysis of white-tailed deer, elk, and moose killed by hunters and vehicle collisions in Manitoba, 1975-1978. Manitoba Department of Natural Resources. MS Report No. 81-5.
- Giles, B.G. and Findlay, S.C. 2004. Effectiveness of a Selective Harvest System Regulating Deer Populations in Ontario. *Journal of Wildlife Management*. 68:266-277.
- Gray, P.B. and Servello, F.A. 1995. Energy intake relationships for white-tailed deer on winter browse diets. *Journal of Range Management*. 59:147-152.
- Hakim, S. 1998. Foraging strategies of white-tailed deer in northwestern Virginia, USA. Pages 222-225 in *Advances in Z. Zomborsky, editor. Deer Biology: Proceedings of the 4th International Deer Biology Congress*. Pannon University of Agriculture, Faculty of Animal Science, Kaposva, Hungary.
- Hansen, L.P., Nixon, C.M., and Beringer, J. 1997. Role of refuges in the dynamics of outlying deer populations: two examples from the agricultural Midwest. Pages 327-345 in *W.J. McShea and H.B. Underwood, editors. The Science of Overabundance: deer ecology and population management*. Smithsonian Books, Washington D.C., USA.
- Healy, W.M. 1997. Influence of deer on the structure and composition of oak forests in central Massachusetts. Pages 249-266 in *W.J. McShea and H.B. Underwood, editors. The Science of Overabundance: deer ecology and population management*. Smithsonian Books, Washington D.C., USA
- Helman, M.W. and Fulbright, T.E. 1997. Use of warm-season food plots by white-tailed deer. *Journal of Range Management*. 61:1108-1115.
- Hodgman, T.P., Davitt, B.B., and Nelson, J.R. 1996. Monitoring mule deer diet quality and intake with fecal indices. *Journal of Range Management*. 49:215-222.
- Holechek, J.L. and Gross, D.B. 1982. Evaluation of different diet calculation procedures for microhistological analysis. *Journal of Range Management*. 35:721-723.
- Holechek, J.L. and Valdez, R. 1985. Magnification and shrub stemmy material influences on fecal analysis accuracy. *Journal of Range Management*. 38:350-352.
- Holechek, J.L., Vavra, M., and Pieper, R.D. 1982. Botanical Composition Determination of Range Herbivore Diets: A Review. *Journal of Range Management* 35:309-315.

Chapter 2: Effects on the tallgrass prairie plants

- Holt, R.D., Robinson, G.R., and Gaines, M.S. 1995. Vegetation dynamics in an experimentally fragmented landscape. *Ecology*. 76:1610-1624.
- Howe, N, Shoesmith, M.W., and Stewart, J. 1974. Rumen contents of white-tailed deer in Manitoba. Manitoba Department of Mines, Resources, and Environmental Management. Research Branch. MS. Report. 74-17.
- Illius, A.W., and Gordon, I.J. 1993. Diet selection in mammalian herbivores: Constraints and tactics. Pages 157-181 in R.N. Hughes, editor. *Diet Selection: An Interdisciplinary Approach to Foraging Behaviour*. Oxford University Press, Don Mills, ON, Canada
- Jewel, P.A. and Holt, S. 1981. Introduction. Pages 1-7 in P.A. Jewel and S. Holt, editors. *Problems in Management of Locally Abundant Wild Mammals*. Academic Press, New York, New York, USA.
- Ji, L. and Peters, A.J. 2003. Assessing vegetation response to drought in the northern Great Plains using vegetation and drought indices. *Remote Sensing of Environment*. 87:85-98.
- Krausman, P.R., Kuenzi, A.J., Etchberger, R.C., Rautenstrauch, K.R., Ordway, L.L., and Hervert, J.J. 1997. Diets of desert mule deer. *Journal of Range Management*. 50:513-522.
- Ladd, D.M. 1995. *Tallgrass Prairie Wildflowers*. The Globe Pequot Press. Guilford, CT, USA.
- Land Resource Unit. 1999. *Soils and Terrain. An Introduction to the Land Resource*. Rural Municipality of Headingley. Information Bulletin 99-2, Brandon Research Centre, Research Branch, Agriculture and Agri-Food Canada. Brandon, Manitoba, Canada
- Laurance, W.F. 1990. Predicting the impacts of edge effect in fragmented habitats. *Biological Conservation*. 55:77-92.
- Leach, M.K. and Givinish, T.J. 1996. Ecological Determinants of Species Loss in Remnant Prairies. *Science*. 273: 1555-1558.
- Leitte, E.R. and Stuth, J.W. 1994. Influence of duration of exposure to field conditions on viability of fecal samples for NIRS analysis. *Journal of Range Management*. 47:321-314.
- Leslie, Jr., D.M., Vavra, M., Starkey, E.E., and Slater, R.C. 1983. Correcting for Differential Digestibility in Microhistological Analyses Involving Common Coastal Forages of the Pacific Northwest. *Journal of Range Management*. 36:730-732.

Chapter 2: Effects on the tallgrass prairie plants

- Loehle, C. and Rittenhouse, L.R. 1982. An Analysis of Forage Preference Indices. *Journal of Range Management*. 35:316-319.
- Martinez, A, Molina, V., Gonzalez, F., Marroquin, J., and Navar, J. 1997. Observations of white-tailed deer and cattle diets in Mexico. *Journal of Range Management*. 50:253-257.
- Mathews, N.E., Dewoody, J.A., Porter, W.F., Skow, L.C., and Honeycutt, R.L. 1997. Genetic Variation as a Predictor of Social Structure: Genetic Approaches for Studying Free-Ranging White-tailed Deer. Pages 99-119 *in* W.J. McShea, H.B. Underwood, and J.H. Rappole, editors. *The Science of Overabundance: Deer Ecology and Population Management*. Smithsonian Institute Press, Washington, USA.
- McCabe, T.R. and McCabe, R.E. 1984. Of Slings and Arrows: An Historical Retrospection. Pages 19-72 *in* L.K. Halls and C. House, editors. *White-tailed Deer Ecology and Management*. Stackpole Books, Harrisburg, PA, USA.
- McCabe, T.R. and McCabe, R.E. 1997. Recounting whitetails past.. Pages 11-26 *in* McShea, W.J and Underwood, H.B., editors *The Science of Overabundance*. Smithsonian Books, Washington D.C., USA.
- McCullough, D.R. 1997. Irruptive behavior in ungulates. Pages 69-91 *in* McShea, W.J and Underwood, H.B. editors. *The Science of Overabundance*. Smithsonian Books, Washington D.C., USA.
- Michael, E.D. Movements of white-tailed deer on the Welder Wildlife Refuge. *Journal of Wildlife Management*. 29:44-52
- Murphy, R.K., Payne, N.F., and Raymond, K.A. 1985. White-tailed deer use of an irrigated agricultural-grassland complex in central Wisconsin. *Journal of Wildlife Management*. 49:125-128.
- Nixon, C.M., Mankin, P.C., Etter, D.R., Hansen, L.P., Brewer, P.A., Chelsvig, J.E., Esker, T.L., and Sullivan, J.B. 2007. White-tailed deer dispersal behaviour in an agricultural environment. *American Midland Naturalist*. 157:212-220.
- Nixon, C.M., McClain, M.W., and Russell, K.R. 1970. Deer Food Habits and Range Characteristics in Ohio. *Journal of Wildlife Management*. 34 :870-886.
- Noy-Meir, I. 1981. Responses of Vegetation to the Abundance of Mammalian Herbivores. Pages 233-257 *in* P.A. Jewel and S. Holt, editors. *Problems in Management of Locally Abundant Wild Mammals*. Academic Press, New York, New York, USA

Chapter 2: Effects on the tallgrass prairie plants

- Olf, H. and Ritchie, M. 1998. Effects of herbivores on grassland plant diversity. *TREE*. 13:261-265.
- Parker, K.L., Robbins, C.T., and Haney, T.A. 1984. Energy expenditures for locomotion-by mule deer and elk. *Journal of Wildlife Management*. 48:474-488.
- Paterson, B.R. and Messier, F. 2000. Factors influencing killing rates of white-tailed deer by coyotes in eastern Canada. *Journal of Wildlife Management*. 64:721-732.
- Pauley, G.R., Peek, J.M., and Zager, P. 1993. Predicting white-tailed deer habitat use in northern Idaho. *Journal of Wildlife Management*. 57:904-913.
- Petraitis, P.S., Latham, R., and Niesenbaum, R. 1989. The maintenance of species diversity by disturbance. *The Quarterly Review of Biology*. 64:393-418.
- Pierce, R.M., Bowyer, R.T., and Bleich, V.C. 2004. Habitat selection by mule deer: forage benefits or risk of predation? *Journal of Wildlife Management*. 68:533-541.
- Porter, W.F., Underwood, H.B., Woodard, J.L. 2004. Movement behaviour, dispersal, and the potential for localized management of deer in a suburban environment. *Journal of Wildlife Management*. 68:247-256.
- Riley, S.J., Decker, D.J., Enck, J.W., Curtis, P.D., Lauber, T.B., and Brown, T.L. 2003. Deer populations up, hunter populations down: Implications of interdependence of deer and hunter population dynamics on management. *Ecoscience*. 10:455-461.
- Robbins, C.T. 1993. *Wildlife Feeding and Nutrition*, 2nd Edition. Academic Press, Toronto, Ontario, Canada.
- Rooney, T.P. 2001. Deer impacts on forest ecosystems: a North American perspective. *Forestry*. 74:201-208.
- Rooney, T.P. and Dress, W.J. 1997. Species loss over sixty-six years in the ground-layer vegetation of Heart's Content, an old-growth forest in Pennsylvania, USA. *Natural Areas Journal*. 17:297-305.
- Rooney, T.P. and Waller, D.M. 2003. Direct and indirect effects of white-tailed deer in forest ecosystems. *Forest Ecology and Management*. 181:165-176.
- Russell, F.L., Zippin, D.B., Fowler, N.L. 2001. Effects of White-tailed Deer (*Odocoileus virginianus*) on Plants, Plant Populations and Communities: A Review. *The American Midland Naturalist*. 146:1-26.
- Rutberg, A.T. 1997. The Science of Deer Management: An Animal Welfare Perspective. Pages 37-54 in W.J. McShea, H.B. Underwood, and J.H. Rapploe, editors. *The*

Chapter 2: Effects on the tallgrass prairie plants

Science of Overabundance: Deer Ecology and Population Management.
Smithsonian Books, Washington D.C., USA.

Saunders, K.D., Dehl, B.E., and Scott, G. 1980. Bite-count vs fecal analysis for range animal diets. *Journal of Range Management*. 33:146-149.

Schmitz, O.J. and Sinclair, A.R.E. 1997. Rethinking the role of deer in forest ecosystem dynamics. Pages 201-223 *in* W.J. McShea, H.B. Underwood, and J.H. Rapploe, editors. *The Science of Overabundance: Deer Ecology and Population Management*. Smithsonian Books, Washington D.C., USA.

Schwab, F.E., Pittoello, F.G., and Simon, N.P.P. 2001. Relative palatability of green manure crops and carrots to white-tailed deer. *Wildlife Society Bulletin*. 29:317-321.

Simberloff, D., and Gotelli, N. 1984. Effects of Insularisation on Plant Richness in the Prairie-Forest Ecotone. *Biological Conservation*. 29:27-46.

Sinclair, A.R.E. 1997. Carrying capacity and the overabundance of deer: a framework for management. Pages 380-394 *in* W.J. McShea, H.B. Underwood, and J.H. Rapploe, editors. *The Science of Overabundance: Deer Ecology and Population Management*. Smithsonian Books, Washington D.C., USA.

Sparks, D.R. and Malehek, J.C. 1968. Estimating percentage dry weights in diets using a microscope technique. *Journal of Range Management*. 21:264-265.

Spotswood, E., Bradley, K.L., and Knops, J.N.H. 2002. Effects of herbivory on the reproductive effort of 4 prairie perennials. *NMC Ecology*. 2:67-85.

Steuter, A.A. 1997. Bison. Pages 339-350 *in* Packard, S. and Mutel, C.F., editors. *The Tallgrass Prairie Restoration Handbook*. Island Press, Washington, DC, USA.

Stewart, K.M., Fulbright, T.E., and Drawe, L.E. 2000. White-tailed deer use of clearings relative to forage availability. *Journal of Wildlife Management*. 64:734-741.

Symstad, A.J. 2000. A Test of the Effects of Functional Group Richness and Composition on Grassland Invasibility. *Ecology*. 8: 99-109.

Takada, M., Asada, M., and Miyashita, T. 2004. Cross-habitat foraging by sika deer influences plant community structure in a forest-grassland. *Oecologia*. 133:389-394.

Tilghman, N.C. 1989. Impacts of white-tailed deer on forest regeneration in northwest Pennsylvania. *Journal of Range Management*. 53:524-535.

Underwood, Porter 1997. Reconsidering paradigms of overpopulation in Saratoga National Historical Park. Pages 185-197 *in* W.J. McShea, H.B. Underwood, and

Chapter 2: Effects on the tallgrass prairie plants

- J.H. Rapploe, editors. *The Science of Overabundance: Deer Ecology and Population Management*. Smithsonian Books, Washington D.C., USA.
- Vance, F.R., Jowey, J.S., McLean, J.S., and Switzer, F.A. 1999. *Wildflowers Across the Prairies*. Greystone Books, Toronto, ON, Canada.
- Vecellio, G.M., Yahner, R.H., and Storm, G.L. 1994. Crop damage by deer at Gettysburg Park. *Wildlife Society Bulletin*. 22:89-93.
- Verme, L.J. and Ullry, D.E. 1984. Physiology and nutrition. Pages 91-118 *in* L.K. Halls and C. House, editors. *White-tailed Deer: Ecology and Management*. Stackpole Books. Harrisburg, PA, USA.
- Walker, D.J. 2004. Development of a Preliminary GIS Database and Vegetation Framework for the St. Charles Rifle Range Tall Grass Prairie: Final Report. Prepared for World Wildlife Fund Canada.
- Weckerly, F.M. 1993. Intersexual resource partitioning in black-tailed deer: test of the body size hypothesis. *Journal of Range Management*. 57:475-494.
- Wiegand, T., Moloney, K.A., and Milton, S.J. 1998. Population dynamics, disturbance, pattern evolution: identifying the fundamental scales of organization in a model ecosystem. *The American Naturalist*. 152:321-337.
- Wilmshurst, J.F., Fryxell, J.M., and Hudson, R.J. 1995. Forage quality and patch choice by wapiti (*Cervus elaphus*). *Behavioural Ecology*. 6:209-217.

ABSTRACT

Intensive white-tailed deer (*Odocoileus virginianus*) herbivory can extirpate favoured tallgrass prairie flora, particularly forbs, but can also restructure woodlands and prevent forest regeneration. A study was conducted to determine if deer were either impeding or facilitating woody encroachment onto a remnant northern tallgrass prairie. Exclosures and paired plots were established along the aspen forest edge, and woody stems were counted and measured, by height class, over two years. Deer were found to reduce the mean height of *Rosa* spp stems while limiting the growth of *Amelanchier anifolia* and *Populus tremuloides*. Frost heave and small herbivores appeared to be more important in determining woody stem abundance. Indirectly, a correlation was found between where deer grazed and the abundance of woody stems and ruderals present on the grasslands ($r = 0.705$). Through fecal deposition, accelerated nutrient cycling, seed dispersal, trampling, and gap dynamics, white-tailed deer are degrading the remnant northern tallgrass prairie.

INTRODUCTION

When present in moderate to high population densities, large herbivores are capable of shaping woody vegetative cover through a number of pathways. Intensive browsing by African elephants (*Loxodonta africana*) and bison (*bison bison*) was an important source of ecological disturbance that sustained the African savannah and American prairies respectively, destroying woody stems through a combination of grazing and trampling

Chapter 3: Effect on woody growth

(Watkinson and Ormerod 2001, Guldemond and Van Aarde 2008, Hobbs and Heunneke 1992). While white-tailed deer (*Odocoileus virginianus*) are neither large enough nor present in sufficient numbers to transform woodlands into grasslands, they are capable of significantly modifying individual woody plant structures and preventing forest regeneration through intensive selective grazing and the consumption of tender reproductive and photosynthetic components (Alverson et al. 1988).

Because most woody species rely on vertical growth to gain competitive advantage, the reduction in stem height is an important limiting factor to their competitive success and, possibly, survival. In extreme cases, preferred plants can be eliminated altogether, although this outcome is most often limited to the more succulent understory forbs (Rooney and Dress 1997).

Conversely, large herbivores can degrade grasslands and promote forest expansion. Below ground, relative plant competitiveness can be modified by large herbivores through soil compaction and nutrient translocation (Knopps et al. 2002, Wilson and Tilman 1995, Hobbs 1996). Studies of wildebeest have shown how fecal deposits can alter soil nutrients, and especially nitrogen (N), as aboveground biomass is consumed and then deposited through feces at a new location (McNaughton 1979). The digestive process itself enhances N mineralization rates and, thus, its availability to plants. Increases in nutrients are one of the subtlest, but important, causes in the reduction of biodiversity (Hobbs and Heunneke 1992). Nitrogen loading of grasslands can change

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floristic composition, decrease plant diversity, and increase above ground productivity (Wedin and Tilman 1996).

Urine can also affect a similar shift (Knapp et al. 1999, Hobbs 1996, Rooney and Waller 2003). This point-adjustment of soil nutrients can cause the phyto-specific composition and competitiveness to change, especially where the redistributed nutrients have been limiting. With white-tailed deer concentrating inside or along the forest-grassland ecotone in order to reduce the distance travelled to preferred tallgrass prairie and row-crop foods (Chapter 4), the cumulative effects of micro-level nutrient infusion and gap dynamics imposed by deer could be sufficient to alter floristic composition towards higher C:N ratio and competitively inferior plants such as weedy and woody species and depress diversity of the tallgrass prairie (Maron and Connors 1996, Tilman 1988, Rooney and Waller 2003).

Fecal deposition can also facilitate the germination of seeds consumed by deer elsewhere. Acid scarification from seed digestion has been found to significantly enhance woody germination rates for *Amelanchier arborea* (Michx.f.) (Downey Serviceberry), likely an adaptation that has evolved as a response to herbivory (Robinson 1986). In laboratory trials, a mean of >30 forb and woody seeds germinated per white-tailed deer fecal group, with the most seeds being dispersed in October, January, and February (Myers et al. 2004). Due to their long gut retention times and landscape mobility, deer are considered an important vector for seed dispersal (Kellogg and Bridgham 2004) and could serve to facilitate woody encroachment onto grasslands.

Trampling of existing vegetation by large herbivores can also alter vegetative cover at the micro-site level by influencing inter-plant competition. By creating gaps in the canopy competitively inferior species can obtain greater sunlight and obtain advantage, allowing them to take hold where existing vegetation would normally preclude it (Hobbs and Heunneke 1992). Typically, tall ruderals such as wild bergamot (*Monarda fistulosa*) and Canada thistle (*Cirsium arvense*) are competitively inferior and will benefit from such a disturbance. This is especially true on fragile or moist soils where trampling can expose bare earth (Nuzzo 2005).

Numerous studies into the effects of intensive white-tailed browsing have been conducted within the mixed forests of the north eastern USA (Tilghman 1989, Côté et al. 2004, Healy 1997), the north-central USA (Alverson et al. 1988), and a few have looked at its effects on the tallgrass prairie (Anderson et al. 2005, Spotswood et al. 2002, Olf and Ritchie 1998), but with white-tailed populations irrupting (England and DeVos 1969, Baker 1984, McCabe and McCabe 1997), how these large ungulates are affecting the forest:tallgrass prairie ecotone that they inhabit is unclear. In Chapter 2 it was found that aspen forests provide a significant portion of the white-tailed deer diet during the winter months, and this browsing is often most intensive along the forest edge (Olson 1992, Alverson et al. 1998). It is therefore reasonable to suspect that if white-tailed deer are present in sufficient numbers, they can potentially alter forest composition and structure along the ecotone and encroachment onto the prairie.

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The objective of this study was to determine if, when present at high densities, white-tailed deer facilitate, retard, or have little overall impact on woody encroachment onto the study site's remnant northern tallgrass prairie. A second objective was to discover if white-tailed deer herbivory were altering the structure or composition of the woody vegetation along the forest: tallgrass prairie ecotone.

STUDY AREA

The primary study area is SCRR, a military rifle range and dismounted training area less than 2km west of Winnipeg, Manitoba, located in the Rural Municipalities of Headingley and Rosser (49° 55' North latitude, 97° 13' West longitude, elevation 238m). It comprises 280ha of remnant northern tallgrass prairie and 102ha of aspen forest. The site is flat and poorly to imperfectly drained with <2% slope. Soils are classified as Clayey Lacustrine (Gleysols and Black Chernozems) (Land Resource Unit 1999). As a result, it is not uncommon for low-lying areas such as the forest floors to be flooded in spring and during wet summers.

Today, the eastern half is generally characterized as a lower quality native prairie than the west, dominated by *Poa pratensis* and *Symphoricarpos occidentalis* instead of more *Agropyron* spp (wheatgrasses), *Koeleria cristata* (June grass), *Andropogon* spp (bluestem), and *Spiraea alba* as found on the western half. Since the 1880s, an aspen forest has become established and now covers over one third of the site. Although aspen encroachment continues locally, forest cover has remained relatively stable (2005). Less

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the grassy openings within the forest, the native prairie has been burned a number of times since 1996, the last being in spring 2005. Much of the southern half of the site is mowed as it supports the rifle ranges, obstacle course, and buildings.

Within a 25km radius of the site, land cover consists of 81.5% agriculture, 29.3% grasslands, including urban grasslands, 4.4% forage crops 2.1% forest, and 1.3% cultural. More immediately, the area within 6km of the study site is 52.3% agriculture, 10.4% cultural, 10.0% grasslands, 5.7% forage crops, and 2.8% forest (calculated using the MB Conservation 2004 Land Cover GIS layer). Approximately 4.5km to the south of the main study forest is the Assiniboine River, which flows east/west. Although such water barriers have not been found to be movement barriers, they do serve to restrict free movement of deer, especially where adequate resources exist on both sides of the water obstacle (Coulon et al 2006, Michael 1965, Eberhardt et al 1984). The land cover of the region to the south of this river was therefore not included in the above figures.

Additional details are found in Chapter 1.

METHODS

Direct Effects of Herbivory

Forests expand outward through a variety of mechanisms. Among these mechanisms are the establishment of stoloniferous shoots, abundant seed rain on adjacent lands, shading of competing extant plants and thereby depriving them of above ground resources,

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altering soil pH or chemistry, and increasing soil litter. The establishment of colonizing shrubs is often a precursor to the appearance of larger trees. In order to assess the direct effects of white-tailed deer herbivory on woody species along this important forest edge a series of three exclosure and paired plots, each measuring 10m x 10m, was established straddling the forest-prairie edge (Figure 3.1.a). Site selection was random. The exclosures were constructed of 48"-high steel pipe topped with three strands of 14-gauge steel wire, creating a 7'-high structure. This permitted all herbivores, less white-tailed deer, to freely enter the exclosures. Within each plot were three pairs of 0.5m x 1.0m quadrats located 1m and 3m each from the forest edge. Another three pairs of quadrats were located 1m and 3m inside the forest edge. Within the highly degraded internal prairie four 5m x 5m exclosures and paired plots were constructed in a fashion similar to those along the forest edge, but here only three 0.5m x 1.0m quadrats were established (Figure 3.1.b). Each of these four paired plots were located within 15m of the forest edge. An additional 5m x 5m paired plot (5B) was established 100m from the forest edge in a highly degraded prairie site that was dominated by woody species and ruderals. Due to the complex forest edge structure in this area the plot was only 40m laterally from the nearest copse of trees.

The paired plots were established in June 2005. In August 2005 and 2006 woody stems within all quadrats measuring between 0 - 2.0m were counted and measured, by height class. Classes were: <5cm, 5-24cm, 25-49cm, 50-74cm, 75-99cm, 100-124cm, 125-149cm, and >150cm. It was highly unlikely that stems taller than 175cm could be reduced by white-tailed herbivory. Pairwise *t*-tests were then conducted using a

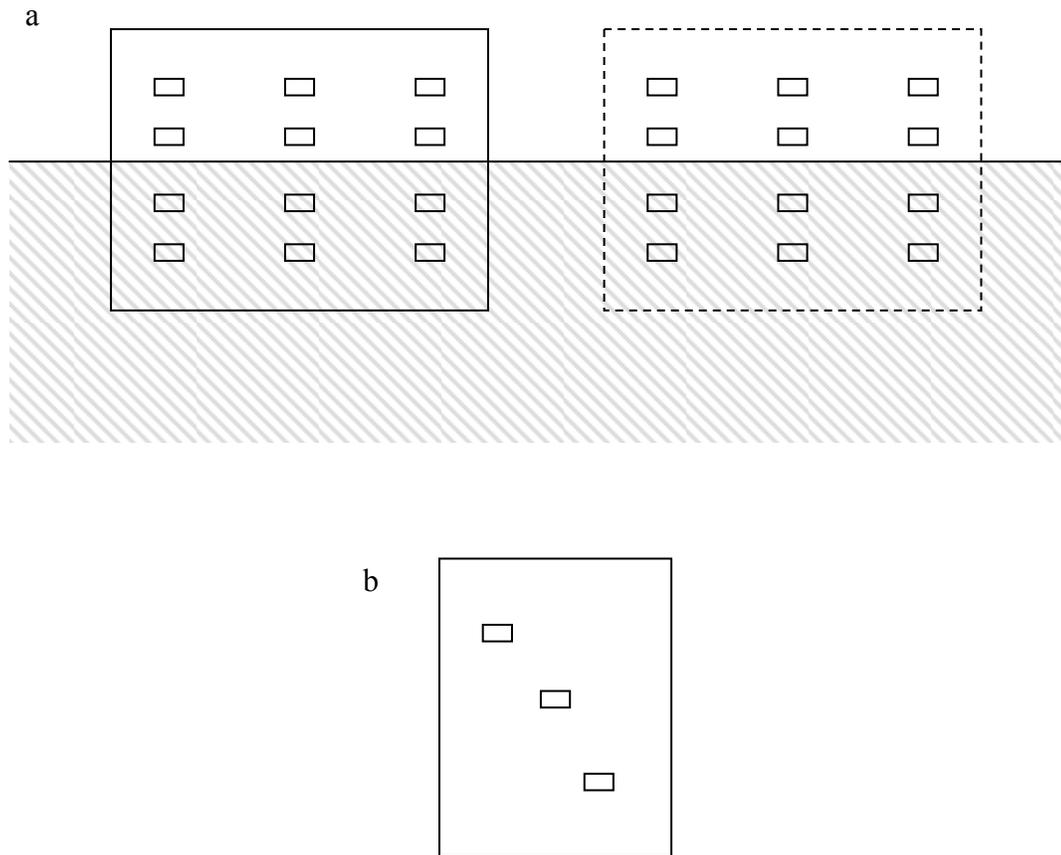


Figure 3.1. Enclosure Details. a. Forest edge plots were 10m x 10m. Quadrats measuring 1m x 0.5m were delineated with wire on the surface of the ground, and later enhanced with 9" nails at the corners. Paired plots are placed 3m to the south of the enclosures. b. Plots in the internal prairie measured 5m x 5m and the quadrats were similarly defined, although the placement of the quadrats within the plot differed. Paired plots were also placed to the south of the enclosures.

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Bonferonni Correction in order to ascertain if there were significant differences in abundance or height over time by species, treatment, and site region. Pairwise comparisons were also conducted to discover shifts in distribution, mean heights, and height classes. Next, Multiple Discriminate Analysis (MDA) was conducted between years and among treatments and regions to determine if woody cover within the exclosures was becoming more different than that within the paired plots and, thus, from exposure to deer herbivory.

Woody Plot Edaphics and Site Histories

One of the difficulties in determining the indirect effects of herbivory is that a baseline understanding of what has gone on before and the enduring site elements that exist must first be known to the extent possible. Although floristic composition is highly variable, it is a good proxy indicator of some historical disturbances and of relatively enduring characteristics such as drainage, soil texture, soil nutrients, and light levels. In short, like plant assemblages tend to grow in like sites with like histories. To this end, in mid-July 2006 a visual assessment survey was conducted of all eight woody exclosures. A 1m x 1m quadrat was placed into the centre of every exclosure and pair and plants present were recorded as a percentage of overall vegetation within the quadrat. This allowed data to be collected without altering plant dynamics or reducing woody stem heights. The observed vegetation was then classified into four categories: plants preferring moist conditions, dry conditions, those that typify disturbed sites, and ubiquitous plants (Table 3.1). Ubiquitous plants were those such as *poa* spp that can be found in most locations and are not

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Table 3.1. Plant Classification

<u>Dry</u>	<u>Moist</u>	<u>Disturbed</u>
<i>Aster ericoides</i>	<i>Agoseris glauca</i>	<u>Dry regions</u>
<i>Campanula rotundifolia</i>	<i>Amelanchier anifolia</i>	<i>Armetisia ludoviciana</i>
<i>Cirsium flodmanii</i>	<i>Anemone canadensis</i>	<i>Monardo fistulosa</i>
<i>Gallium boreal</i>	<i>Aster laevis</i>	<i>Solidago</i> spp
<i>Geum triflorum</i>	<i>Cypredium parviflorum</i> (rare)	(<i>missouriensis</i> and especially <i>rigida</i>)
<i>Helianthus maximillianni</i>	sandy	
<i>Lithospermum canescens</i>	<i>Elaeagnus commatata</i>	<u>Moist regions</u>
<i>Petalostemon purpureum</i>	<i>Erigeron</i> spp	<i>Asclepias speciosa</i>
(generalist habitat, but mostly dry)	<i>Fragaria virginiana</i>	<i>Amelanchier anifolia</i>
<i>Ratibida columnifera</i>	<i>Gentiana andrewsii</i>	<i>Cirsium arvense</i>
<i>Rosa</i> spp	<i>Heliopsis helianthoides</i>	<i>Symphoricarpos occidentalis</i>
<u>Sandy soils:</u>	<i>Lactuca pulchella</i> (heavy soil)	
<i>Glycorrhiza lepidota</i>	<i>Lilium philadelphicum</i>	
<i>Helianthus</i>	<i>Potentilla</i> spp	
<i>subrhomdoideus</i>	<i>Rubus</i>	
	<i>Rumex</i> spp	
	<i>Thalictrum dasycarpum</i>	
	<i>Vicia americana</i> (any moist environment, including shaded areas)	
	<i>Viola</i> spp (<i>pedatidia</i> and <i>nephrophilia</i>)	

necessarily indicative of any particular soil condition or past disturbance. Aggregate site similarity was then assessed by comparing vegetative cover types as a percentage of total cover by using a *t*-test with a Bonferonni correction value (0.025).

Disturbance Intensity Index (DI_i)

The next step was to devise a method to assess if white-tailed deer were encouraging woody recruitment on the tallgrass prairie through intensive selective grazing, trampling, nutrient translocation, woody seed dispersal, or a combination of all four. Instead of trying to develop a means of directly measuring these individual activities it was decided to create an indirect measure, or Disturbance Intensity Index (DI_i). By quantifying the intensity with which deer were moving through a series of points, and then assessing potential deer impacts by recording the type and nature of the vegetative cover associated with those points, it was speculated that the extent and effects of white-tailed deer activity on that site could be indirectly evaluated. Deer generally graze as they move, sampling and selecting an array of plants before moving on (Berteaux 1998). It was therefore assumed that where deer moved, they would inflict some degree of trampling, enrich soil nutrients by occasionally defecating, and graze preferred plants. Because woody species and ruderals are most commonly associated with disturbance (Hobbs and Huenneke 1992), and given that deer are effectively the only remaining source of disturbance other than fire on the study site, it was decided to use woody and ruderal growth as indicators of deer-induced disturbance.

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In September 2005, 20 additional points were established as detailed at Figure 1.3. Using a 1 x 1m quadrat, a clip, dry, and weigh methodology was employed to determine the exact floristic composition at each of these points. These points, extending into the prairie, were placed 100m apart along five transects emanating from the forest edge. As above, recorded quadrat cover was classified into four groupings: plants preferring moist conditions, dry conditions, those that typify disturbed sites, and ubiquitous plants. The problem with the forest edge plots was that Very Light and Light deer trails could not be discerned with confidence within the forest. To address this, five additional plots were established beside the forest edge paired plots 8 m from the forest along the same transect.

From each point four orthogonal transects were established. Where a deer trail intercepted one of these transects the distance from the centre point was recorded. These were called I-intercepts. Where a trail intercepted more than one transect line only the closest I-intercept measure was retained. Deer trails were rated as Medium, Light, and Very Light, which reflected their apparent intensity of use. Medium trails were those that were entrenched, had some bare earth, and were clearly visible. Trails classified as Light had very little exposed soil and were clearly distinguishable, suggesting use by several animals over several days. Trails termed as Very Light were perceptible but likely created fairly recently and may have been created by a single animal. Both of these light trail types tended to meander rather than move in a straight line. Trails that had greater than 20% bare earth and/or were deeply recessed into the field were not counted, as they were very likely simply movement trails and may not be in active use. Deer have been found to

move along sinewy routes while grazing, looking for preferred foods in a medium to high-density forage patch. Conversely, when moving between such patches white-tailed move with a greater sense of purpose, up to six times faster and thereby exerting far less influence on the site's vegetation and soil (Focardi et al. 1996). Deer bed locations were also recorded, although values were not assigned. While bedding will disturb the existing canopy, it was deemed that the density of deer trails in the vicinity of the beds would reflect this impact intensity. All measurements were taken and trails were mapped late July 2005 (Figure 3.2).

A Disturbance Intensity (DI_i) value was then assigned to each point,

$$DI_i = \sum di_i, \quad \text{where } di_i = \left[\frac{1}{(I_{nearest}^{0.7})} \right] w$$

where w is the weight given to each trail (Medium = 6, Light = 3, Very Light = 1) and $I_{nearest}$ is the nearest I-intercept. The exponent of 0.7 was selected in order to assign the greatest weight to those trails closest to the centre point, and primarily within 2m of the trail. Clearly, a point located near numerous well-used trails can be expected to suffer greater effects from trampling and grazing than those sites visited less frequently. The flat nature of the terrain and the absence of tall plants, both of which could influence deer grazing patterns, as well as the short distances measured from the sites reduce the risk of “smoothing” error commonly associated with Inverse Density Weighted (IDW) formulae (Achilleos 2008). This interpolation equation can be expected to be most accurate where

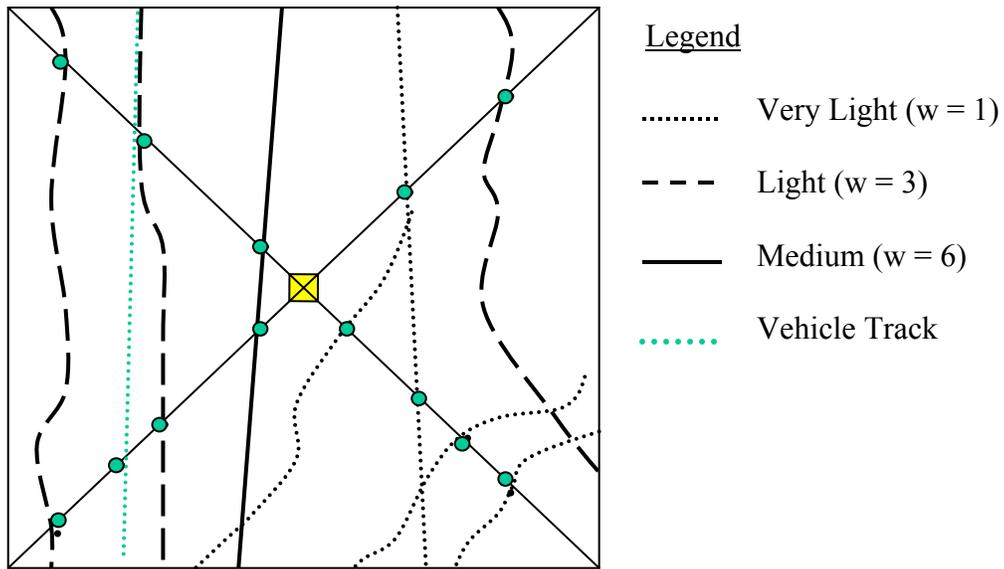


Figure 3.2. Disturbance Intensity Intercepts. The distance from the centre of the quadrat to the nearest point at which the deer trail intersected the four cardinal points was recorded. These distances were then weighted in accordance with the apparent usage frequency of the associated trail. Deer sometimes used vehicle tracks when moving through the tall grasses but no $I_{\text{intercept}}$ value was assigned to these.

the I-intercepts are most numerous and most evenly distributed about the point in question (Zimmerman et al 1999).

A limitation with this formula is that Light and Very Light trails may only reflect recent movement patterns whereas Medium trails may also represent between-feeding station movement corridors instead of grazing patterns. DI_i values were not calculated for the internal prairie plots (6A-D) because the trail network in the summer of 2005 was incredibly dense, making it all but impossible to differentiate individual trails. As the internal prairie is dominated by woody and ruderal species (all internal prairie plots have >59% of a combination of *Cirsium arvense*, *S. occidentalis*, and *Solidago spp*), the extensive grazing and trampling in this area lent support to the notion that the two measures could be correlated.

DI_i values were then correlated to disturbance species (ruderals + woody), distance from forest edge, and woody species (*S. occidentalis* + *Rosa*) scores to determine if there was a possible useful relationship between the pairs.

Because white-tailed deer are central-place feeders and an edge species, the intensity of deer-induced disturbance was expected to be greatest where they lived and loitered during the day (internal prairie – again, not measured), followed by the forest edge and then, to a decreasing degree, further from the forest edge species. The vegetative cover data was therefore grouped by these three locations (internal prairie, open prairie, and forest edge) and MDA was conducted to assess similarities between plots and among

site-types. The 5B plots are surrounded by woody growth and trees, although not on the forest edge itself. For this reason it was grouped with the forest edge plots.

RESULTS

Direct Effects of Grazing - Stem Counts

Four primary and one minor woody species were identified during the stem count process. *Symphoricarpos occidentalis* (western snowberry), a forest pioneering species, was ubiquitous and found in every quadrat. The next most common was *Rosa* (rose), which was present in 15 plots in 2005 and 17 in 2006. *Amelanchier anifolia* (saskatoon) was found in 8 and then 7 plots, primarily in the northeast (5 series) and in one of the internal prairie plots (6 series). Least common was *Populus tremuloides* (trembling aspen), located in four plots in 2005 and just two in 2006. Nine stems of *Rubus pubescens* (dewberry) were also found along the forest edge in one pair of plots but because of their small numbers and their disappearance the following year, they were not included in the analysis.

The total number of *S. occidentalis* and *P. tremuloides* stems decreased from 2005 to 2006 (Table 3.2). Whereas 1,047 *S. occidentalis* stems were counted in 2005, this dropped to 889 the following year (-15.1%). *P. tremuloides* stems declined from 62 to just 7, or by 88.7%. Meanwhile, *Rosa* experienced a slight increase in abundance from 81

Table 3.2. Total Stem Counts and Mean Heights, by Treatment

	<i>S. occidentalis</i>		<i>Rosa</i>		<i>A. anifolia</i>		<i>P. tremuloides</i>	
	Ht	Δ Ht	Ht	Δ Ht	Ht	Δ Ht	Ht	Δ Ht
<u>2005</u>								
Exclosure	43.75 (n = 443)	1.61	33.87 (n = 38)	4.66	44.5 (n = 50)	2.58	62.39 (n = 28)	24.42
Paired	45.36 (n = 604)		38.53 (n = 43)		47.08 (n = 52)		37.97 (n = 34)	
Total Stems (05)	(1047)		(81)		(102)		(62)	
<u>2006</u>								
Exclosure	49.0 (n = 426)	1.46	38.44 (n = 45)	3.73	63.25 (n = 53)	1.21	129 (n = 5)	20
Paired	50.46 (n = 463)		34.71 (n = 49)		62.04 (n = 46)		149 (n = 2)	
Total Stems (06)	(889)		(94)		(99)		(7)	

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stems in 2005 to 94 in 2006, or 16.0%. *A. anifolia* remained relatively stable, decreasing by just 3 stems from 102 to 99 (-2.9%).

The general decrease in *S. occidentalis* and *P. tremuloides* stems was not experienced equally across the site and between the treatments. *S. occidentalis* numbers remained relatively stable in the exclosures (443 in 2005, 426 in 2006) yet dropped within the paired plots from 604 to 463, or -30.9%. The greatest decreases were in the northeast while the greatest gains in stem counts occurred within the internal prairie. Conversely, *Rosa* stem numbers increased in the exclosures over time, from 38 to 45 (18.2%), as did the stems in the paired plots but to a marginally lesser degree, from 43 to 49 (14%). *P. tremuloides* numbers declined markedly in both treatments, from 28 stems within the exclosures in 2005 to just 5 in 2006 stems (-82.1%). Within the paired plots stems decreased even more, from 34 to just 2 (-94.1%). It should be noted that all *P. tremuloides* stems were counted in just three adjacent plots.

For two of the four species, mean stem height varied only marginally between years. *S. occidentalis*' mean stem height increased in both treatments by similar amounts (5.25cm exclosure, 5.10cm paired) whereas the *Rosa* in the exclosures increased slightly (4.58cm) while those in the paired plots decreased in height by 3.82cm, to 38.53cm. Both *A. anifolia* and *P. tremuloides*, however, experienced a large increase in stem height. Mean stem height for *A. anifolia* increased by 32.33cm to 76.83cm within the exclosures and a lesser amount - 14.97cm, or a height of 62.04cm – in the paired plots. The mean height for *P. tremuloides* in exclosures jumped from just 44.50cm to 113.11cm while those

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outside the exclosures rose from 47.08cm to 142.70cm, or almost a full metre. A difficulty with these numbers is that height increases varied widely within treatments (24.42cm within the exclosures and 20cm in the pairs) and the total numbers were small in 2006 ($n = 7$).

Pairwise comparison within treatments over time reveals greater changes (Figure 3.3). Conducting pairwise *t*-test analysis by treatment and year within species, significant differences were noted in all four woody plants, although to varying degrees. *S. occidentalis* experienced the greatest changes, varying significantly between treatment and years (2005X – 2006X: $p \leq 0.0001$, 2005P – 2006P: $p \leq 0.0001$). The variation between pairs and exclosures, however, actually decreased with time (2005: $p \leq 0.0001$, 2006: $p \leq 0.005$) suggesting that they were converging in stem height distribution. This convergence resulted from the reduction of stems found in the paired plot 5-24cm and the 25-49cm height categories (Figure 3.4). Conversely, *A. anifolia* distribution remained similar between treatments by year, although there was some limited movement towards differentiation over time (2005: $p = 0.1824$, 2006: $p = 0.0118$). In 2006 the *A. anifolia* stems in the pairs and the exclosures were significantly different from what they had been the previous year, indicating that both were undergoing a change of conditions (Paired: $p \leq 0.0001$, Exclosure: $p \leq 0.0001$).

Although total stem counts remained fairly constant over the two years, the differences between *Rosa* stems between the two treatments became significant over time (2005: $p = 0.3236$, 2006: $p = 0.0009$) as the mean stem height within the exclosures increased and

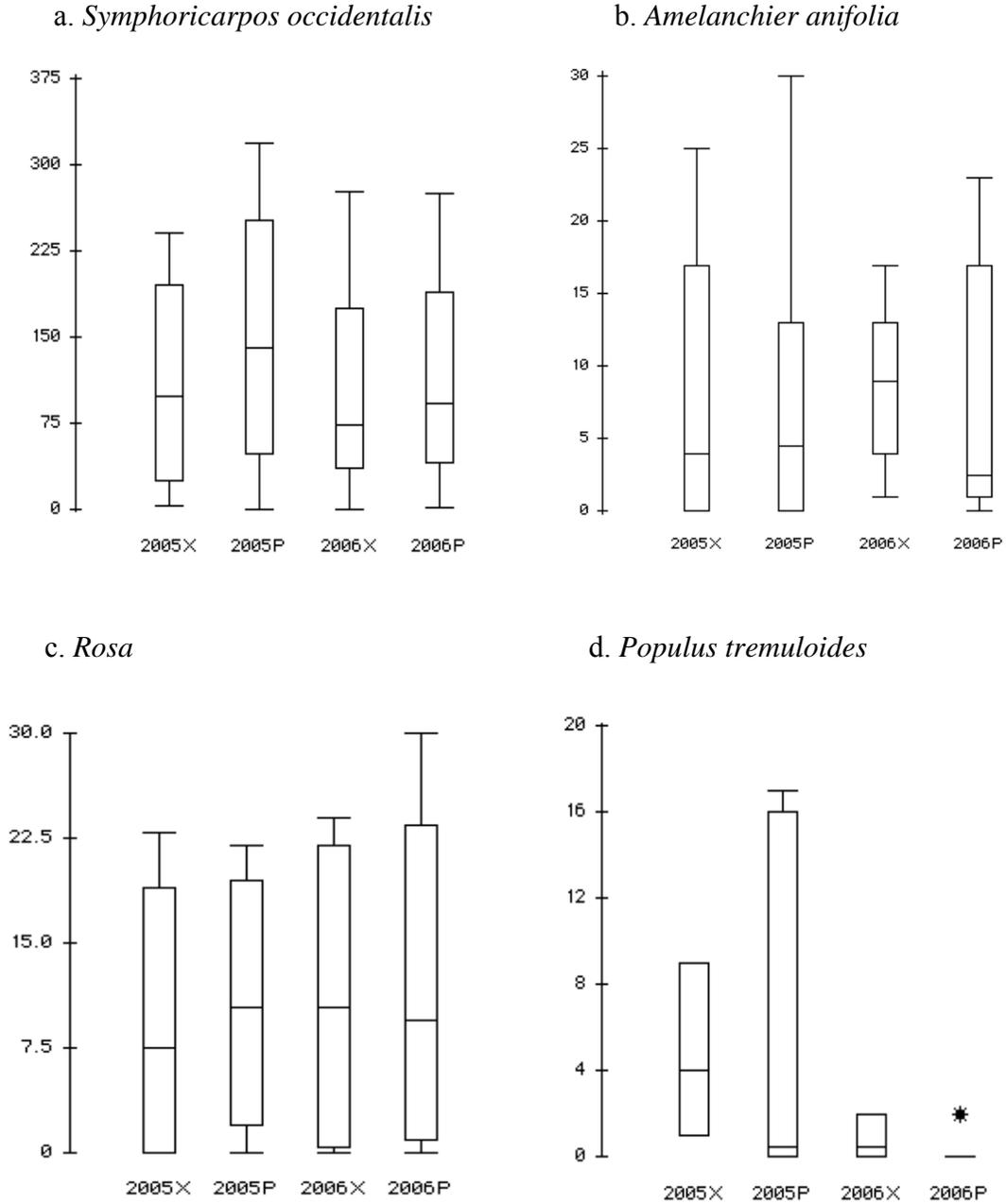
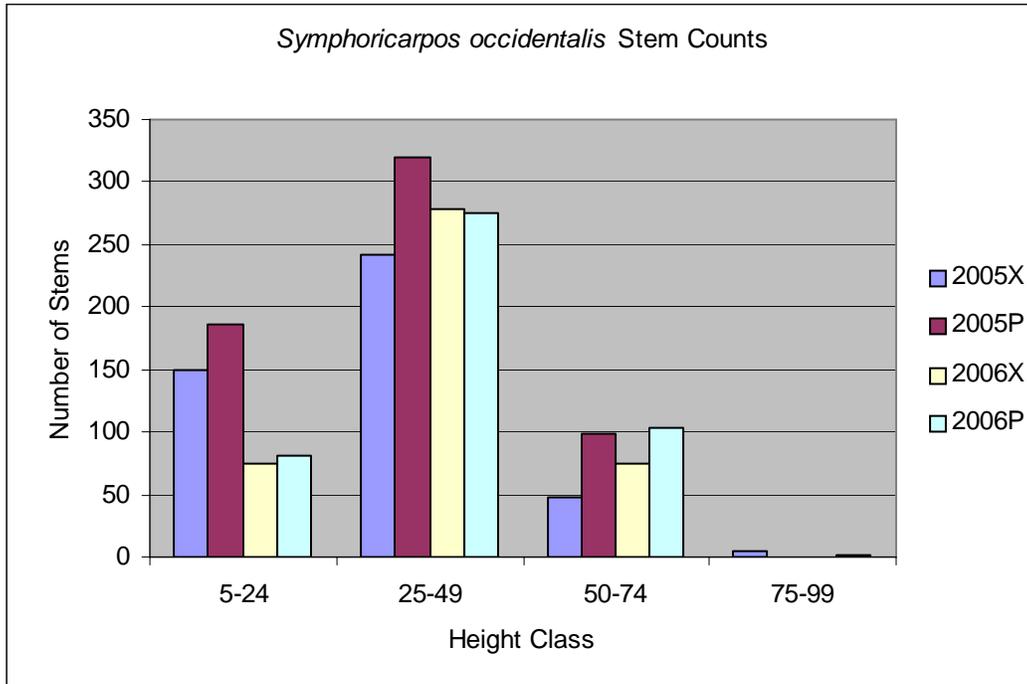
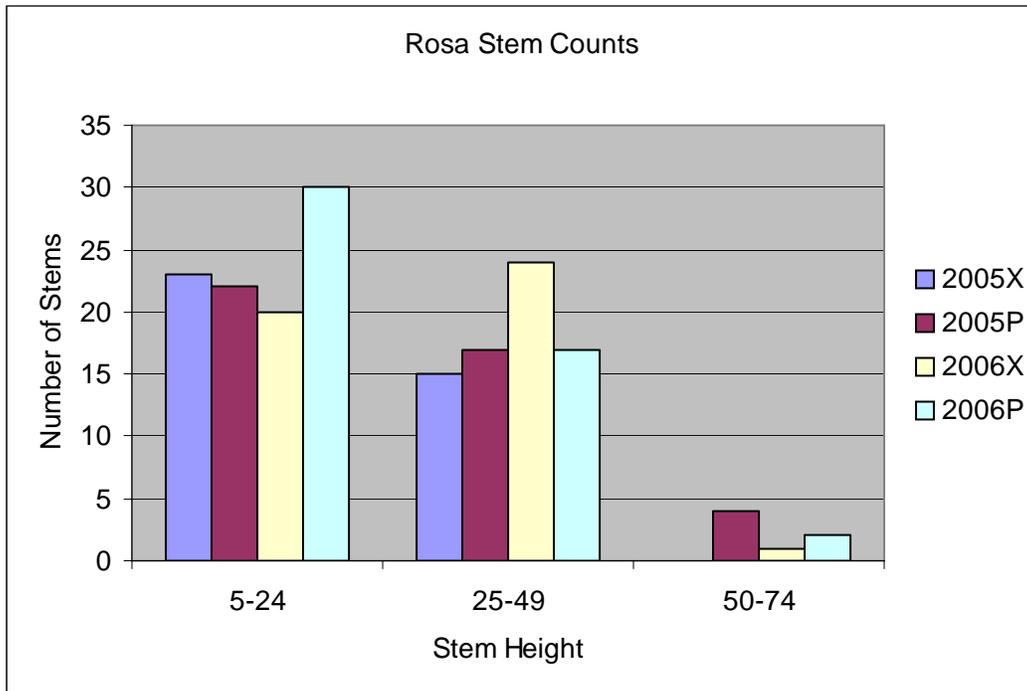


Figure 3.3. Pairwise Comparison of Woody Stems, by Treatment and Year.

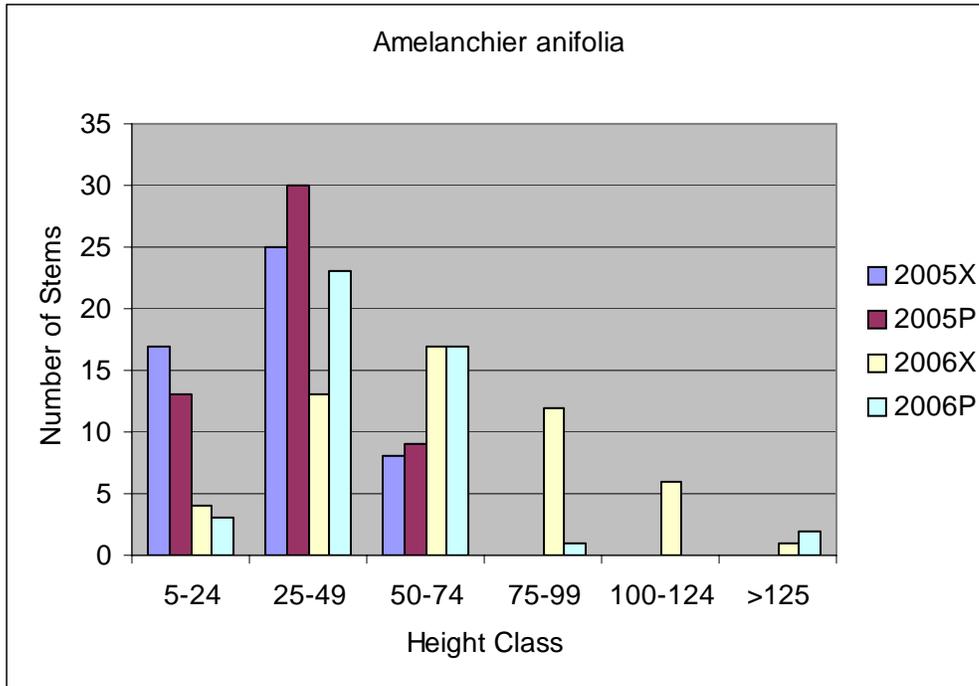
a)



b)



c)



d)

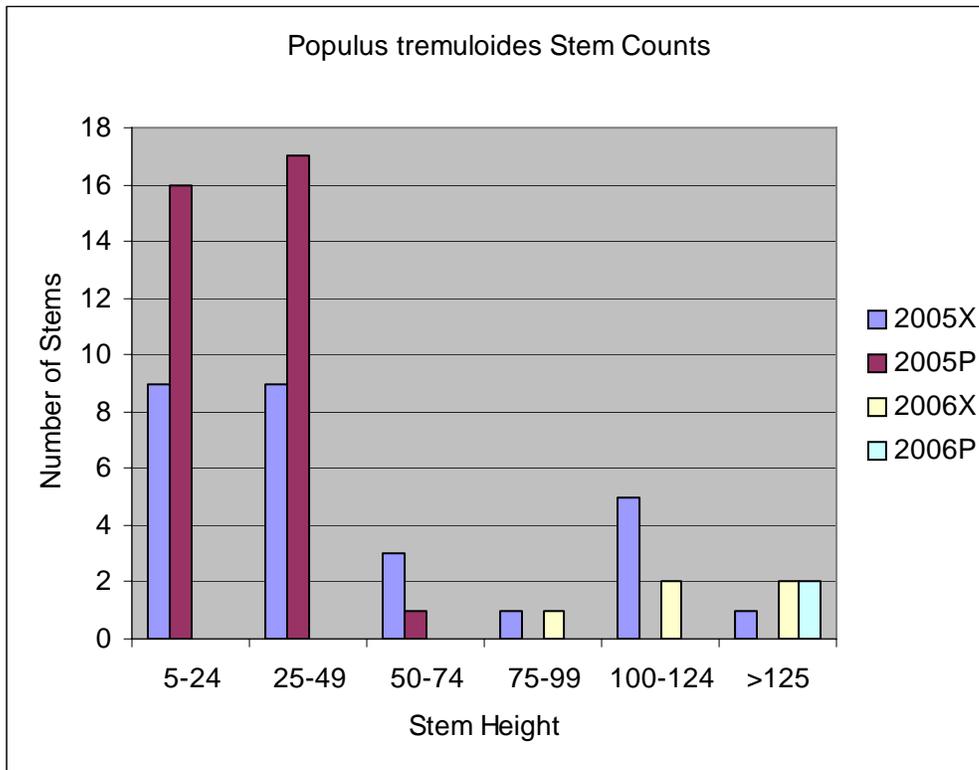


Figure 3.4. Stem Count Distribution, by Treatment and Year.

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within the paired plots decreased. The sharp decline in *P. tremuloides* stem numbers, and distribution makes effective pairwise comparisons with 2006 data difficult. The paired and exclosure plots were significantly different from the outset ($p \leq 0.0001$). What is evident is that virtually all of the stems of less than 125cm in height ($n = 54$) had either moved into the next height class or had disappeared altogether by September 2006. Twenty-two of these stems were within exclosures.

Changes in abundance and mean height class for two of the four species examined were uneven across the study site. *S. occidentalis* experienced the greatest growth within the 5 series exclosures and the least growth in 6 and 1 series. Within the pair plots the greatest losses were in the internal prairie while the best growth was the 3 and 5 series. *A. anifolia* saw the greatest amount of overall herbivory at all sites suffering losses of stems and, within paired plots, mean height. *Rosa* numbers were not conclusive by region and *P. tremuloides* occurred only in the 5 series.

MDA of the two years of woody data, grouped by treatment, did not reveal a statistically significant difference between the two sets of stem data over time ($\chi^2 = 9.91$, 12 df, Wilks $\lambda = 0.7756$, $p=0.623$) (Figure 3.5). *S. occidentalis* provided the greatest differentiation among groups (treatments) followed by *A. anifolia*. Whereas the former plant is ubiquitous, this latter plant was found on the smallest number of sites. Separation on Axis 2, however, is reinforced by *Rosa* and *P. tremuloides*, both of whose eigenvector supports that of *A. anifolia*. For *A. anifolia*, there was greater separation between treatments in

2006 than in 2005. Wildfire in April 2007 destroyed all small woody stems and prevented a subsequent data collection to see if this pattern was episodic or indicative of a trend.

Site History and Edaphic Variation

In a pairwise comparison of plant cover of the exclosures against that of all paired plots, no significant differences were found in the aggregated data (Figure 3.6). Most similar was the distribution of disturbance species ($p = 0.7999$) while the most different was the distribution of moisture-preferring plants ($p = 0.0597$). Although individual pairs showed signs of soil, moisture, and site history variation, they were collectively similar enough as to not be expected to have affected the data collected or the results obtained. Outlier data by treatment were typically similar between the plot and its pair, suggesting that paired plots shared similar abiotic conditions and site histories.

Further exploring plot relationships with cover type using percent plant cover as a proxy measure of site history and edaphics, MDA relating the cover in the internal prairie, forest edge, and open prairie revealed that the site groups are dissimilar, although the 95% confidence interval spheres for the forest edge and internal prairie plots are overlapping ($\chi^2 = 46.60$, $df = 6$, Wilks $\lambda = 0.3438$, $p < 0.00001$) (Figure 3.7). The ellipse for the open prairie is also much smaller than for the other two groupings, suggesting greater soil homogeneity among the grasslands. There is also greater separation over time of these plots from the internal prairie and forest edge plots along the Disturbance eigenvector. The internal prairie and forest edge plots are more dissimilar along the Dry

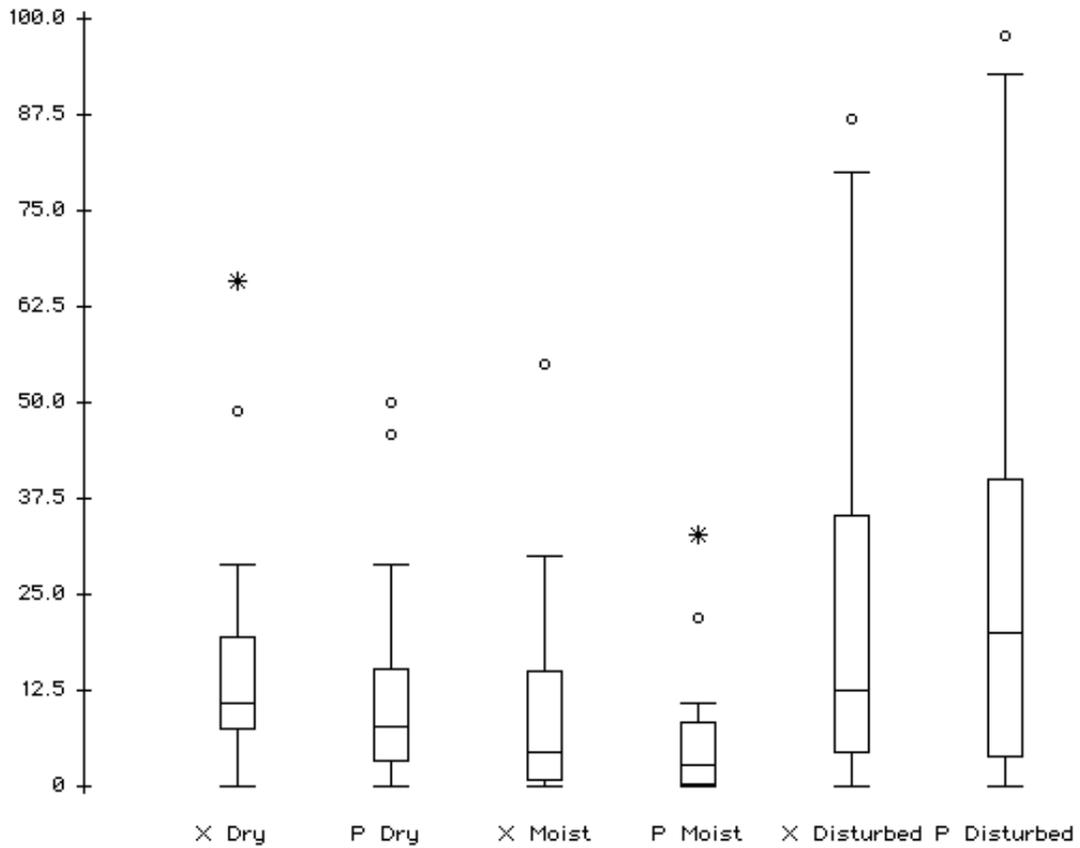


Figure 3.6. Comparison of Vegetative Cover Types by Treatment. The paired sets were not significantly different (Dry: $p = 0.3179$, Moist: $p = 0.0597$, and Disturbance: $p = 0.7999$).

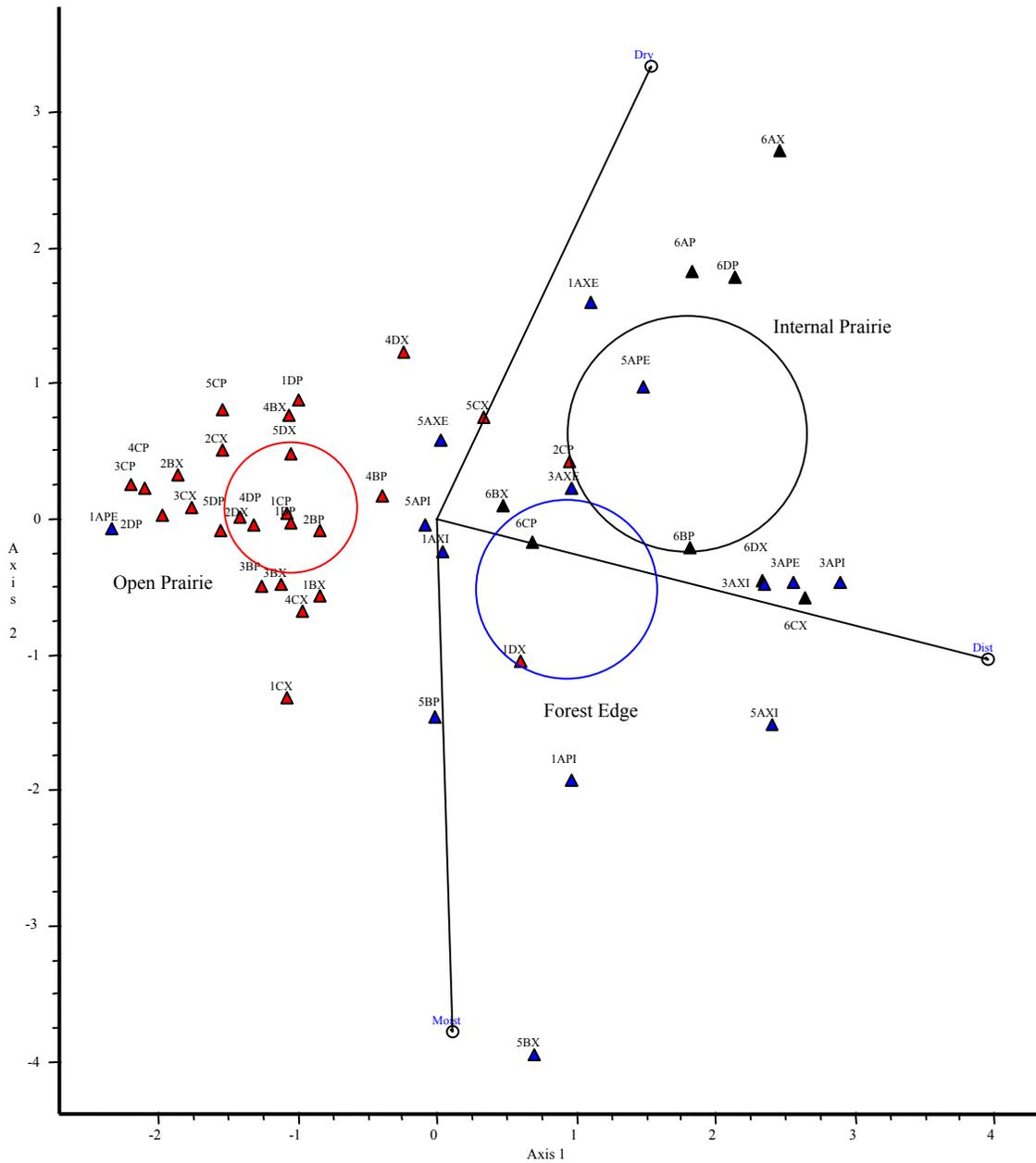


Figure 3.7. MDA of Vegetative Cover, by Location Type. The variance between groups of points was significantly different. The greatest between group variation was defined by Disturbance spp. $\chi^2 = 46.60$, Wilks $\lambda = 0.3438$, $df = 6$, $p < 0.00001$

and Moist eigenvectors than the Disturbance eigenvector. The variable representing Disturbance conditions was the canonical variate providing the greatest discrimination of the descriptors (0.84675) followed by Moist (0.784309) and then Dry (0.762478) conditions. All three variates, however, were important in discriminating among the groups of plots, suggesting that they are all useful indicators of site-specific growing conditions.

As expected, of the forest edge plots, those inside the forest were more heavily characterized by moisture-preferring plants than those just a metre or two away on the outside of the forest. A notable exception was a plot at 1A, which had very little disturbance vegetation and acted more like the open prairie plots. Its understory was principally grasses. Plot 6A, and particularly the exclosure, was characterized by dry vegetation. It had one of the lowest quantities of *S. occidentalis* despite being surrounded by it while, at the opposite end of the spectrum, the 5B exclosure acted more like an internal forest plot and was dominated by moisture-preferring plants (*A. anifolia* (25%) and *C. arvensis* (55%)).

Looking at MDA for the same data, but broken down by cover type and treatment, a similar pattern emerges (Figure 3.8). The confidence spheres between treatments are largely overlapping, indicating strong similarities by cover type on paired plots as well as among groups and therefore very similar site histories and abiotic factors. With the reduced data sets, however, the confidence spheres are larger and the separation of spheres by site-type is smaller. ($\chi^2 = 50.36$, $df = 15$, Wilks $\lambda = 0.3057$, $p < 0.0001$). The

change over time of both of these MDA analyses is statistically significant. Along the first axis, Disturbance vegetation accounted for the greatest amount of separation ($r = 0.802$). Along axis 2 Moist and Dry-preference species were most important ($r = -0.846$, $r = 0.623$) while along the third axis all three were important (Dry: $r = 0.710$; Disturbance: $r = 0.580$; and Moist: $r = -0.527$).

The results illustrated in Figures 3.6-3.8 suggest that the disturbance histories, edaphics, and other abiotic forces are, and have been, similar between paired plots and within the three main groupings – internal prairie, forest edge, and dry prairie.

Disturbance Intensity Index (DI_i)

The Disturbance Intensity (DI_i) values assigned to each of the plots are found at Table 3.3. The values tended to be greater along the forest edge than away from the forest along a given transect, although there were a few notable exceptions. The Pearson Product Moment correlation between DI_i and distance from the forest edge was -0.593 ($r^2 = 31.4$, $s = 91.61$, 17df), with DI_i values decreasing further into the prairie, although it appears that a few strong values from the forest edge plots are creating a much stronger relationship than would otherwise exist (Figure 3.9). This correlation is therefore likely overstated for all but those plots closest to the ecotone. The strength of the relationship between distance and the percent of disturbance vegetative cover is marginally weaker, where $r = 0.555$ ($r^2 = 26.7$, $s = 11.89$, 17df), but the regression line does bisect the majority of data points. The strongest relationship was between DI_i and the percent of

Table 3.3. Percent Disturbance Vegetation and Disturbance Intensity Index, by Plot

<u>Plot</u>	Distance from Forest <u>Edge</u> (m)	Percent Disturbance <u>Vegetation</u>	Percent Woody <u>Vegetation</u>	<u>DI_i</u>
<u>Open Prairie</u>				
1BP	100	25.83	3.06	1.95
1CP	200	13.19	6.14	3.65
1DP	300	1.37	1.14	2.45
2BP	100	12.91	4.78	1.34
2CP	200	3.56	1.88	2.00
2DP	300	10.43	3.32	2.45
3BP	100	5.19	3.53	1.21
3CP	200	1.56	0.0	1.71
4BP	100	4.55	1.48	0.21
4CP	200	9.83	3.46	1.52
4DP	300	4.37	5.09	1.30
5CP	200	2.32	2.54	2.04
5DP	300	8.29	1.56	2.08
<u>Forest Edge</u>				
1A	8	9.61	2.50	3.01
2A	8	8.91	3.82	7.96
3A	8	20.30	8.21	7.90
4A	8	36.10	0.53	4.65
5A	8	57.45	8.52	11.41
5B	60	14.27	4.05	6.68

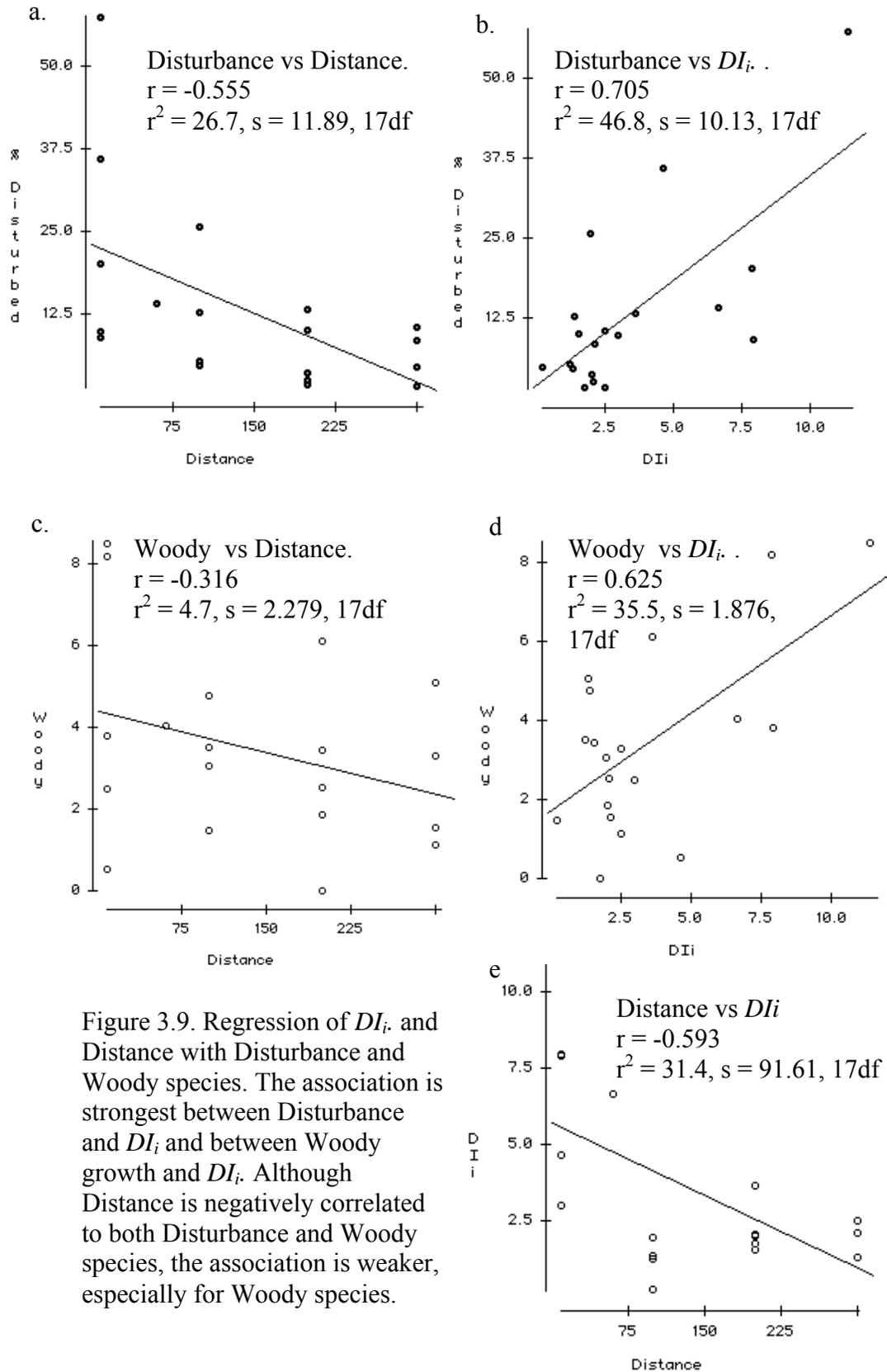


Figure 3.9. Regression of DI_i and Distance with Disturbance and Woody species. The association is strongest between Disturbance and DI_i and between Woody growth and DI_i . Although Distance is negatively correlated to both Disturbance and Woody species, the association is weaker, especially for Woody species.

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disturbance vegetation for each plot, with a r -value of 0.705 ($r^2 = 46.8$, $s = 10.13$, 17df). The strength of this relationship is reinforced by a single outlier in the form of plot 5A along the forest edge. A heavily disturbed site with a DI_i value of 11.41, 57.45% of its vegetative biomass can be classified as indicative of past disturbance. That said, the regression line falls within the centre of the majority of data points, suggesting that the results are reflective of the pattern. Woody species correlated almost as well with DI_i scores ($r = 0.625$, $r^2 = 35.5$, $s = 1.876$, 17df) as did Disturbance, but even more than Disturbance its correlation with DI_i is heavily influenced by a number of outlier points.

DISCUSSION

Direct Effects

Based on these results, white-tailed deer are not directly affecting woody stem abundance or recruitment on this remnant northern tallgrass prairie. Inside the forest they may be exerting a greater influence (Cadenasso and Pickett 2000) and may be preventing the two remaining *Quercus macrocarpa* (burr oak) specimens from reproducing through the complete consumption of the mast, a preferred food (Healy 1997, Murphy et al. 1985), but at such low population numbers *Q. macrocarpa* would not appear in the fecal analysis (plants representing < 0.1% of the overall diet were not reported). Within the internal prairie intensive white-tailed deer herbivory of *Salix spp* may be restricting their spread, as suggested by the distinct browse line on these shrubs, but neither *Q. macrocarpa* nor *Salix spp* appeared in any of the plots examined. These internal fields

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have been spatially stable over time (Walker 2004) but the associated woody and weedy cover does suggest heavy disturbance. It is possible that the very high forest edge:prairie area ratio may be preventing aspen forest encroachment through intensive herbivory and associated microclimate (Thilghman 1989, Laurance 1991) and that the deer are using these openings as they would small clear-cuts (Drolet 1978), but further research is required. Other herbivores, environmental and abiotic factors such as soil moisture, soil texture and nutrients, and both prescribed and wild burns are exerting a much greater influence. White-tailed deer are, however, altering the structure of the site's woody species.

The general decrease of total woody stem abundance across the study site was likely reflective of a number of factors. First are small herbivores in the form of lagomorphs, jackrabbits (*Lepus spp*), and especially meadow voles (*Microtus pensylvanicus*). Research has shown that the meadow vole can exact extensive damage to young stems within 30-40m of the forest edge, so long as they have good cover (Cadenasso and Pickett 2000, Higgans et al. 2000, Gill and Marks 2005). This would explain how so many stems under 75cm could simply disappear in relatively equally numbers both inside and outside of the exclosures. The quadrats were delineated by steel wire attached to the ground with steel pins, ensuring that precisely the same stems were measured in both years. Beyond 30m, the net influence of vole herbivory on woody invasions into old-fields is a complex interplay of shelter, plant competition, avian seed dispersal, and vole predation (Manson et al. 2001). Their influence on the open prairie therefore cannot be assumed.

Another factor may have been the excessive moisture levels of 2005 that flooded the forest floor for the duration of the summer. Although *P. tremuloides* favours micro topographic depressions and moist soils, as does *A. anifolia* and *S. occidentalis*, *Rosa* tends to be located in better-drained sites (Budd 1979, Lieffers et al. 2001). The unusually high moisture levels of 2005 may have parlayed into a die-off or even reduced recruitment in 2006. The high soil moisture may have also contributed to stem mortality caused by frost heave. Gill and Marks (2005) found that frost heave exposes the base of woody stems to desiccation the following growing season, especially in poorly drained sites, causing significant mortality. Given the dry summer conditions of 2006, it is very possible that stem counts were reduced as a result of such desiccation. *Rosa* was supported by better-drained soils, perhaps contributing to the marginal increase in stem counts between years.

The uneven stem recruitment and die-off rates across the plots and more particularly by region may have been indicative of site-specific variations in soil, drainage, and moisture. It also may have been reflective of seasonal and yearly shifts in deer movement patterns and density (Tilghman 1989), which, in turn, were largely a function of changing food distribution (Nixon et al. 1970). With the drying of the forest floor and the re-establishment of row crops in 2006 following their complete failure during the flood conditions of 2005, the site's resident deer spent far less time near the internal prairie plots, either scouring for food or loitering. Instead, they spent more time concentrated in the northeast, in the region of 5A and 5B, adjacent to a sunflower field and nearer to the

soybean field to the south. This shift could have resulted in increased browsing pressure being exerted in the 5 series plots and less in much of the rest of the site. The concurrent increase in *Rosa* stem height within the exclosures is difficult to interpret given the small number of stems counted.

Species-Specific Effects

The particularly dramatic decrease in *P. tremuloides* stems may also be attributable to two additional specific forces. First, aspen are intolerant of flooding, requiring strong sunlight and heat on the forest floor to trigger vigorous suckering (Archibold and Wilson 1978). The flood conditions of 2005 may have suppressed recruitment of the stems already present the following year, until the soil had sufficiently dried. The second cause may be related to the shift in deer movement and foraging patterns mentioned above. All stems less one were located in plots 5A and 5B and the increased presence of deer in that area led to a great deal of browsing pressure being placed on those plants as well as on the wire exclosures. During November and then again in December 2005 a single calf managed to break into the 5A exclosure and browsed the stems of all standing *P. tremuloides*. Without access to row-crop residue the deer were forced to rely completely on the site's native species. *P. tremuloides* leaves comprised from between 6.4 and 6.7% of the white-tailed deer diet from September to December 2005 and the consumption of stems rose to 11.1 during January – March 2006 (Chapter 2). In autumn most forage plants are low in protein, so aspen leaves may be an important source of browse, especially from saplings, which have the most nutritious leaves (Tew 1970, Einspahr and

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Harder 1978). As deer usually select the newest growth while browsing, this could have placed considerable stress on these plants in addition to that of the flood conditions the previous summer. Between extensive stem clipping by other herbivores, environmental stress, and intensive deer herbivory it appears that only the largest survived the two growing seasons.

The general trend of increased mean stem heights of all species across all treatments, less *Rosa* in paired plots, was possibly attributable to the improved growing conditions of 2006 as compared to 2005. After receiving approximately 150% of normal precipitation levels during the 2005 growing season, 2006 saw levels drop to less than half of the norm (SPI calculated using Environment Canada data as described by Ji and Peters 2003). Soil moisture levels, however, mitigated the drought conditions and provided good growing conditions. This likely permitted ample new growth and for new stems to survive, partially offsetting the losses of apical meristems and stems in general due to herbivory the previous year. Over the long term, however, the removal of apical meristems may have a significant impact on seed mass and reproduction of the most affected plants (Spotswood et al. 2002).

The convergence of *S. occidentalis* stem distribution between treatments in 2006 was probably a result of a three factors: small mammal herbivory reducing smaller stems and limiting recruitment in 2006, improved growing conditions that allowed surviving stems to increase in height, and white-tailed herbivory in the paired plots, mitigating height gains within those plots. This pattern would apply to all four woody stem species. It is not

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clear, however, why the mean height in the smallest height category of *Rosa* saw an increase from 2005 to 2006 while stems within the exclosures decreased slightly over the same period.

These same forces shaped the stem count and structure for *A. anifolia* but with slightly different results. While the two treatments over time remained significantly different, how they differed changed. All stems were located in the northeast region of the study site (plots 5A and 5B) and, although herbivorous pressure would increase in this area in the fall/winter 2006, it was perennially a favoured central place for the resident deer population. Due to the surrounding forest's structure, the site provided good thermal shelter and good bedding grounds until the snows became deeper and the risk of coyote predation became much greater (Stewart et al. 2000, Laurance 1991). This occurred in late December 2005. A locally rare native species highly favoured by white-tailed deer, all *A. anifolia* stems showed evidence of extensive browsing in both years. Thus, in many ways *A. anifolia* demonstrated the textbook effects of intensive deer herbivory. While small mammal herbivory likely reduced the number of smaller stems in both treatments, white-tailed deer herbivory in 2005/6 would have reduced the height of those remaining.

Snow depth on 21 January 2006 was measured to be 33cm, meaning that stems taller than this were still at risk of browsing from deer. With the good growing conditions of 2006 the surviving stems experienced considerable growth but deer herbivory persisted, continuing to reduce stems in the paired plots. As a result, a greater percentage of *A. anifolia* stems within the exclosures were free to grow into the 75-99cm, 100-124cm, and

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>150cm height classes. *Rosa* along the forest edge likely would have experienced the same winter browsing pressure, comprising of 6.1% of the total deer diet from Jan to March 2006, but the data is not as telling, possibly because whereas *A. anifolia* was located only in a highly browsed area, *Rosa* is more widespread and browsing intensity would have been more variable across the study site.

When comparing all data through MDA the growing, but still statistically insignificant, divergence between pairs and exclosures was expected given the large numbers of resident deer. That the greatest amount of divergence was accounted for by *S. occidentalis* is not surprising given the large numbers of stems counted. Yet this trend cannot be assumed to be permanent for all species as woody stem abundance and structure were the products of a number of factors, of which white-tailed herbivory was just one. Changes in deer distribution, movement and thus grazing patterns, small animal herbivory, fire, the presence/absence of adjacent row-crops, and weather would change how white-tailed directly effect woody growth.

Indirect Effects

Through browsing, trampling, nutrient translocation, and seed dispersal white tailed deer are providing a definite disturbance regime. Disturbance is important in maintaining a properly functioning ecosystem, and that of white-tailed deer can actually help displace aggressive invasive species when limited in scale (Kellogg and Bridgemen 2004). To be constructive, however, that disturbance must replicate the conditions under which the

subject ecosystem evolved. Otherwise, it can degrade that system and shift biotic composition and the floristic trajectory into a new direction. This appears to be the case with white-tailed deer on the remnant tallgrass prairie at the SCRR. Other than the re-introduction of controlled (and sometimes uncontrolled) fires in 1996, the white-tailed deer are the only major source of disturbance. While it has been seen that other small mammals can significantly alter woody stem counts along the forest edge and that they can cause soil disturbance, nutrient concentrations, and seed dispersal at the micro level by their sheer size, and home ranges, numerous deer can have a similar but much more dramatic impact (Vellend et al. 2003).

The separation of Open Prairie, Forest Edge, and Internal Prairie at Figure 3.6 reflects what is known about the site's history, suggesting that the above ground biomass is a good indicator of disturbance history and below ground resources such as organic matter, nitrogen, soil texture, moisture, drainage, and pH. The moderate correlation of the deer Disturbance Intensity Index to the nature of vegetation, to include the presence of the forest pioneering species *S. occidentalis* 300m away from the forest edge, supports the notion that white-tailed deer are having an indirect effect on woody encroachment and prairie degradation where they are present at high densities. The strength of this relationship will grow stronger as open high quality prairie is replaced with dense stands of shrubby growth and tall ruderals such as *C. arvensis* and *Solidago* spp. When the animal's view field is reduced due to high swards they tend to move in a much more tortuous manner, unable to see potentially more preferred foods, and trampling and grazing more intensively *in-situ* (Etzenhouser et al. 1998). The more intensive levels of

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grazing in these disturbed areas fuels a feed-back loop, whereby leaf and stem removal generate new growth that is higher in digestible energy, making the site more favoured by deer for future herbivory (Bruinenberg et al. 2001). Although the correlation of DI_i to woody species specifically was weaker than for Disturbance species ($r = 0.625$), it does suggest a cause-effect relationship. Given the complex relationship between vegetation, above ground and below ground resources, and site history, this correlation is still relatively strong.

S. occidentalis represented 70.9% of all the woody biomass used in this analysis and its presence in almost every plot examined and its correlation to deer movement patterns is important. *S. occidentalis* is a common stoloniferous plant but also propagates through large seed. Through these two means they often form dense stands, but these seeds are also consumed in large numbers by the white-tailed deer and are then deposited with their feces wherever they move. Large amounts of *S. occidentalis* seed were found in the deer feces collected throughout the site late October, including the extreme eastern edge of the tallgrass prairie. Seeds, of which most were *S. occidentalis* seeds, comprised of 1.2% of their diet in September-October and 3.9% of the diet in November-December 2005 (Chapter 2). While birds may disperse some seeds, deer are the most likely common vectors.

The ability of white-tailed deer to facilitate woody encroachment varies by location even where DI_i scores are similar. As illustrated in Figures 1.7 and 3.7, the aspen forest is largely confined to moist soils. These clayey soils are particularly susceptible to soil

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compaction and disturbance from trampling (Noy-Meir 1981). Thus plot 1A, with drier soils (44.15% sand and well drained), and moderate DI_i value – higher than those of the prairie but the lowest of the forest edge plots – had the least amount of disturbance vegetation. There are limits to this resilience, however. Plot 5A is also one of the few sandier locations near the forest edge (42.67%) but with a DI_i score of 11.41 and in a common deer bedding ground, it had the highest percentage of disturbance and woody cover.

Where N is limiting, ruderals and woody growth may also be restricted. Likely due to its previous cultivation history, soil N is lower on the open prairies than elsewhere (Chapter 1). Bearing evidence of this is also the large amount of *Solidago rigida* basal rosettes found amongst the tallgrass vegetation, typical of formerly cultivated fields because of the insufficient remaining soil N necessary to develop stems (Tilman 1988, Chapin et al. 1986). Plot 4A, for example, has a moderate DI_i rating (4.65) and an abundance of disturbance vegetation (36.10%), all in the form of *S. rigida* basal rosettes, yet only has very limited woody growth in the form of *Rosa* (0.53%). The addition of N through nutrient translocation could enable such disturbance species to become more dominant and enhance their growth plasticity (Garnier 1998).

Where deer sought thermal shelter during the day before foraging offsite into the neighbouring row-cropped fields, typically sown to plants with high crude protein and *in vitro* Dry Matter Digestibility (IVDMD) (Chapter 4), there were large accumulations of feces. Indeed, fecal concentrations were so dense that some deer trails became covered

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with a 45cm wide continuous layer (Figure 3.10). Although consuming these high N foods off-site, deer prefer to ruminate within thermal shelter such as a forest (Focardi et al. 1996) or among tall ruderals. Deer were often found bedding among *Solidago* spp and *C. arvensis* stems, and fecal concentrations are greatest in these areas. N-translocation may shift the competitive advantage from grasses to shrubs on the prairie, permitting shrubs to become more dominant (Kochoy and Wislon 2000, Collins et al. 1998). At sites where deer loitered, defecated, and grazed the effects of N deposition could be most acute; deer preferentially graze fertilized plants (Conover and Kania 1988), possibly exerting an ever-increasing degree of grazing pressure on the favoured flora at these locations and creating favourable conditions for graze-tolerant ruderals.

The internal prairie may be an extreme example of how these three indirect effects can come together in a self-sustaining cycle. Surrounded on all sides by forest, it provides perfect thermal cover and was once classified as high quality tallgrass prairie, an artefact of never having been tilled. Today, it is blanketed with *S. occidentalis* and several disturbance-preferring forbs (by cover, Disturbance spp: 73.25%, SE 3.91, *Poa* spp: 16.5%, SE 2.7), the soil is highly disturbed, and the ground is littered with a large amount of deer feces. A favourite winter deer refuge in 2005/6, they lived, browsed, and consumed countless *S. occidentalis* seeds in the internal prairie, excreting them in place. The feces would have accelerated nutrient mineralization, fertilizing the seeds and the plants immediately around the feces, ensuring a high recruitment rate of *S. occidentalis* and other disturbance species. Nitrate and total N levels in the internal prairie were the highest on the range (Chapter 1), encouraging many ruderals to establish a dominating

a)



b)



Figures 3.10. High concentrations of deer fecal deposition in high-use areas are very likely enhancing soil N and setting the conditions for future floristic shifts. These photos were taken just inside the forest about 5m from plot 5AX.

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canopy such that the more moist areas of the internal prairie have no understory. It has been suggested that diversity should be greatest where soil nutrients such as N are low to intermediate, introducing another form of competition within the ecosystem (Roberts and Gillam 1995).

There are limitations to the application of the Disturbance Intensity Index. First, it is unsophisticated as a modeling tool and can only serve to measure general relationships rather than to readily predict which points on a given site are at risk of deer-induced changes. Second, by recording trail density in the late fall the scores do not take into account areas grazed or frequented earlier in the year. Given that the deer were continuously shifting foraging patterns and habitat locations as different plants peaked in nutritional value, usage rates were fluid. Third, the method cannot explicitly differentiate between trails used simply for movement and those used for foraging. Nevertheless, it did correlate better with disturbance and woody growth than the Shannon and Simpson Diversity Indices, primarily because disturbance can actually increase floristic diversity by increasing the total number of species, even if only exotics.

White-tailed deer are directly affecting woody structure and, indirectly, woody growth and distribution, although the scale for each of these pathways has been inferred rather than directly measured and, thus, the weight accorded to each of these is not known.

MANAGEMENT IMPLICATIONS

Because white-tailed deer do not appear to be directly facilitating or affecting the recruitment or survival of the site's woody species, no management action is required in this regard in order to prevent the displacement of tallgrass prairie by aspen forest.

Certainly they are restructuring and possibly stressing preferred browse species such as *A. anifolia* but this is not currently a concern; wildfires and small mammal herbivory are exerting a far greater impact on the woody stems.

The indirect effects of white-tailed deer at high densities are of concern. Canopy destruction and soil disturbance through bedding and trampling, seed dispersal of *S. occidentalis* and other woody species, and nutrient translocation are likely facilitating tallgrass prairie degradation and helping to set the conditions for forest encroachment. While some deer-induced disturbance is desirable, their intensity at favoured locations such as the internal prairie and in the northeast is deleterious. To address this, active deer management needs to be introduced and controlled burns need to continue on the prairie, with consideration given to extending these burns to the internal prairie in an effort to mitigate some of the existing damage and to try to restore some of the native biodiversity that is disappearing.

LITERATURE CITED

- Achilleos, G. 2008. Errors within the Inverse Distance Weighted (IDW) interpolation procedure. *Geocarto International*. 23:429-449.
- Alverson, W.S., Waller, M.W., and Solheim, S.L. 1988. Forests Too Edge: Edge Effects in Northern Wisconsin. *Conservation Biology*. 2:348-358.
- Anderson, R.C., Nelson, D., Anderson, M.A., and Rickey, M.A. 2005. White-tailed deer (*Odocoileus virginianus* Zimmermann) browsing effects in tallgrass prairie forbs: diversity and species abundance. *Natural Areas Journal*. 25:19-25.
- Anthony, R.G. and Smith, N.S. 1977. Ecological Relationships Between Mule Deer and White-tailed Deer in Southern Arizona. *Ecological Monographs*. 47:255-277.
- Archibold, O.W. and Wilson, M.R. 1978. Spatial Pattern and Population Dynamics of *Populus tremuloides* in a Saskatchewan Aspen Grove. *Canadian Field-Naturalist*. 92:369-374.
- Baker, R.H. 1984. Origin, Classification, and Distribution. Pages 1-18 in L.K. Halls, editor. *White-tailed Deer Ecology and Management*. Stackpole Books, Harrisburg, PA, USA.
- Berteaux, D., Crete, M., Huot, J., Maltais, J., and Ouellet, J-P. 1998. Food choice by white-tailed deer in relation to protein and energy content of the diet: a field experiment. *Oecologia*. 115:84-92.
- Bruinenberg, M.H., Valk, H., Korevaar, H., and Struik, P.C. 2001. Factors affecting digestibility of temperate forages from seminatural grasslands: a review. *Grass and Forage Science*. 57:292-301.
- Budd, A.C. 1979. *Budd's Flora of the Canadian Prairie Provinces*. Research Branch Agricultural Canada Publication 1662, Minister of Supply and Services Canada, Ottawa, ON.
- Cadenasso, M.L. and Pickett, S.T.A. 2000. Linking forest edge structure to edge function: mediation of herbivore damage. *Journal of Ecology* 88:31-44.
- Chapin, F.S., Viousek, P.M., and Van Cleve, K. 1986. The nature of nutrient limitation in plant communities. *The American Naturalist*. 127:48-58.
- Collins, S.L., Knapp, A.L., Briggs, J.M., Blair, J.M., and Steinauer, E.M. 1998. Modulation of diversity by grazing and mowing in tallgrass prairie. *Science*. 280:745-747.

Chapter 3: Effect on woody growth

- Conover, M.R. and Kania, G.S. 1988. Browsing preference of white-tailed deer for different ornamental species. *Wildlife Society Bulletin*. 16:175-179.
- Côté, S.D., Rooney, T.P., Tremblay, J-P, Dussault, C, and Waller, D. 2004. Ecological Impacts of Deer Overabundance. *Annual Review of Ecology, Evolution, and Systematics*. 35:113-47.
- Coulon, A., Guillot, G., Angibault, J.M.A., Aulagnier, S., Cargnelutti, B., Galan, M., and Hewison, J.M. 2006. Genetic structure is influenced by landscape features: empirical evidence from a roe deer population. *Molecular Ecology*. 15:1669-1679.
- Drolet, C.A. 1978. Use of Forest Clear-cuts by White-tailed Deer in Southern New Brunswick and Central Nova Scotia. *Canadian Field-Naturalist*. 92:275-282.
- Eberhardt, L.E., Hanson, E.E., and Caldwell, L.L. 1984. Movement and activity patterns of mule deer in the sagebrush-steppe region. *Journal of Mammalogy*. 65:404-409.
- Einspahr, D.W. and Harder, M.L. 1978. Biomass and nutrient status of young quaking aspen stands. IPC Technical Paper Series Number 57. Institute of Paper Chemistry, Appleton, Wisconsin, USA.
- England, R.E. and DeVos, A. 1969. Influence of animals on pristine conditions on the Canadian grasslands. *Canadian Grasslands*. 22:87-94.
- Etzenhouser, M.J., Owens, M.K., Spangler, D.E., and Murden, S.B. 1998. Foraging behaviour of browsing ruminants in a heterogeneous landscape. *Landscape Ecology*. 13:55-65.
- Focardi, S., Marcellini, P., and Montrano, P. 1996. Do ungulates exhibit a food density threshold? A field study of optimal foraging and movement patterns. *The Journal of Animal Ecology*. 95:606-620.
- Garnier, E. 1998. Interspecific variation in plasticity of grasses in response to nitrogen supply. Pages 155-181 in G.P. Cheplick, editor. *Population Biology of Grasses*. Cambridge University Press. Cambridge, U.K.
- Gill, D.S. and Marks, P.L. 1991. Tree and shrub seedling colonization of old fields in central New York. *Ecological Monographs*. 61:183-205.
- Guldmond, R. and Van Aarde, R. 2008. The meta-analysis of the impact of African elephants on the African Savanna. *Journal of Wildlife Management*. 72:892-899.
- Healy, W.M. 1997. Influence of deer on the structure and composition of oak forests in central Massachusetts. Pages 249-266 in W.J. McShea and H.B. Underwood,

Chapter 3: Effect on woody growth

editors. *The Science of Overabundance: deer ecology and population management*. Smithsonian Books, Washington D.C., USA.

- Higgins, K.F., Stukel, E.D., Goulet, J.M., and Backlund, D.C. 2000. *Wild Mammals of South Dakota*. South Dakota Department of Game, Fish, and Parks. Pierre, South Dakota, USA.
- Hobbs, N.T. 1996. Modification of ecosystems by ungulates. *Journal of Wildlife Management*. 60:695-713.
- Hobbs, R.J. and Huenneke, L.F. 1992. Disturbance, Diversity, and Invasion: Implications for Conservation. *Conservation Biology*. 6:324-337.
- Ji, L. and Peters, A.J. 2003. Assessing vegetation response to drought in the northern Great Plains using vegetation and drought indices. *Remote Sensing of Environment*. 87. pp. 85-98.
- Kellogg, C.H. and Bridgham, S.D. 2004. Disturbance, herbivory, and propagule dispersal control dominance of an invasive grass. *Biological Invasions*. 6:319-329.
- Knapp, A.K., Blair, J.M., Briggs, J.M., Collins, S.L., Hartnett, D.C., Johnson, L.C., and Towne, E.G. 1999. The Keystone Role of Bison in North American Tallgrass Prairie. *Bioscience*. 49:39-50.
- Knopps, J.M.H., Bradley, K.L., and Wedin, D.A. 2002. Mechanisms of plant species impacts on ecosystem nitrogen cycling. *Ecology Letters*. 5:454-466.
- Kochy, M. and Wilson, S.D. 2000. Competitive effects of shrubs and grasses in prairie. *Oikos*. 91:385-395.
- Land Resource Unit. 1999. *Soils and Terrain. An Introduction to the Land Resource*. Rural Municipality of Headingley. Information Bulletin 99-2, Brandon Research Centre, Research Branch, Agriculture and Agri-Food Canada. Brandon, Manitoba, Canada.
- Laurance, W.F. 1991. Predicting the impacts of edge effect in fragmented habitats. *Biological Conservation*. 55:77-92.
- Lieffers, V.J., Landhausser, S.M., and Hogg, E.H. 2001. Is the wide distribution of aspen a result of its stress tolerance? Pages 311-323 *in* USDA Forest Service Proceedings RMRS-P-18.
- Manson, R.H., Ostfeld, R.S., and Canham, C.D. 2001. Long-term effects of rodent herbivores on tree invasion dynamics along forest-field edges. *Ecology*. 82:3320-3329.

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- Maron, J.L. and Connors, P.G. 1996. A native nitrogen-fixing shrub facilitates weed invasion. *Oecologia*. 105:302-312.
- McCabe, T.R. and McCabe, R.E. 1997. Recounting whitetails past. Pages 11-26 in W.J. McShea and H.B. Underwood, editors *The Science of Overabundance*. Smithsonian Books, Washington D.C., USA.
- McNaughton, S.J. 1979. Grazing as an Optimizing Process: Grass-Ungulate Relationships in the Serengeti. *The American Naturalist* 113:691-703.
- Michael, E.D. Movements of white-tailed deer on the Welder Wildlife Refuge. *Journal of Wildlife Management*. 29:44-52
- Noy-Meir, I. 1981. Responses of Vegetation to the Abundance of Mammalian Herbivores. Pages 233-257 in P.A. Jewel and S. Holt, editors. *Problems in Management of Locally Abundant Wild Mammals*. Academic Press, New York, New York, USA.
- Myers, J.A., Velland, M., Gardescu, S., and Marks, P.L. 2004. Seed dispersal by white-tailed deer: implications for long-distance dispersal, invasion, and migration of plants in eastern North America. *Oecologia*. 139:35-44.
- Murphy, R.K., Payne, N.F., and Raymond, K.A. 1985. White-tailed deer use of an irrigated agricultural-grassland complex in central Wisconsin. *Journal of Wildlife Management*. 49:125-128.
- Nixon, C.M., McClain, M.W., and Russell, K.R. 1970. Deer Food Habits and Range Characteristics in Ohio. *Journal of Wildlife Management*. 34 :870-886.
- Nuzzo, V. 2005. Element Stewardship Abstract for *Cirsium arvense*. The Nature Conservancy. Retrieved 13 October 2005.
<http://www.tncinvasives.ucdavis.edu/esadocs/documnts/cirsarv.pdf>
- Olf, H. and Ritchie, M. 1998. Effects of herbivores on grassland plant diversity. *TREE*. 13:261-265.
- Olson, R. 1992. White-Tailed Deer Habitat Requirements & Management in Wyoming. Department of Renewable Resources, University of Wyoming, B-964 February 1992.
- Roberts, M.R. and Gillam, F.S. 1995. Patterns and Mechanisms of Plant Diversity in Forested Ecosystems: Implications for Forest Management. *Ecological Applications*. 5:969-977.
- Robinson, W.A. 1986. Effect of fruit ingestion on Amelanchier seed germination. *Bulletin of the Torrey Botanical Club*. 113:131-134.

Chapter 3: Effect on woody growth

- Rooney, T.P. and Waller, D.M. 2003. Direct and indirect effects of white-tailed deer in forest ecosystems. *Forest Ecology and Management*. 181: 165-176.
- Scott, D. and Tilman, D. 1995. Competitive responses of eight old-field plant species in four environments. *Ecology*. 76:1169-1180.
- Spotswood, E., Bradley, K.L., and Knops, J.N.H. 2002. Effects of herbivory on the reproductive effort of 4 prairie perennials. *NMC Ecology*. 2:67-85.
- Stewart, K.M., Fulbright, T.E., and Drawe, L.E. 2000. White-tailed deer use of clearings relative to forage availability. *Journal of Wildlife Management*. 64:734-741.
- Tew, R.K. 1970. Seasonal Variation in the Nutrient Content of Aspen Foliage. *Journal of Wildlife Management*. 34:475-478.
- Tilghman, N.C. 1989. Impacts of white-tailed deer on forest regeneration in northwest Pennsylvania. *Journal of Wildlife Management*. 53:524-535.
- Tilman, D. *Plant Strategies and the Dynamics and Structures of Plant Communities*. 1988. Princeton University Press, Princeton, New Jersey, USA.
- Velland, M., Myers, J.A., Gardescu, S., and Marks, P.L. 2003. Dispersal of *Trillium* seeds by deer: implications for long-distance migration of forest herbs. *Ecology*. 84:1067-1072.
- Watkinson, A.R. and Ormerod, S.J. 2001. Grasslands, grazing, and biodiversity: editor's introduction. *British Ecological Society*. 38:233-237.
- Walker, D.J. 2004. Development of a Preliminary GIS Database and Vegetation Framework for the St. Charles Rifle Range Tall Grass Prairie: Final Report. Prepared for World Wildlife Fund Canada.
- Wedin, D.A. and Tilman, D. 1996. Influence of nitrogen loading and species composition on the carbon balance of grasslands. *Science*. 274:1720-1723.
- Wilson, S.D. and Tilman, D. 1995. Competitive Responses of Eight Old-Field Plant Species in Four Environments. 76: 1169-1180.
- Zimmerman, D., Pavlik, C., Ruggles, A. Armstrong, M.P. An experimental comparison of ordinary and universal kriging and inverse distance weighting. *Mathematical Geology*. 31:375-390.

ABSTRACT

Row-crops are a major factor contributing to white-tailed deer population irruptions across rural North America. What is not clear is if row-crops offset the net herbivorous pressure placed by these elevated ungulate densities on the adjacent native flora, or how row-crops shape that pressure. The nutritional values (NDF, ADF, ADL, AIA, IVDMVD, CP, GE, Total Ash) of two August diets (no crops 2005, crops 2006) with a single deer population on a northern tallgrass prairie were compared. Despite the large dietary compositional differences by treatment, the nature of the diet's fibre and digestibility remained very similar. Row-crops allowed net energy to be maximized through enhanced digestibility and reduced foraging effort; deer did not travel more than 1,250m to feed. CP was held constant despite higher levels found in crops (25% of the diet), suggesting that native foods low in CP were being selected to counterbalance the surplus in crops.

INTRODUCTION

In the 1970's numerous dietary composition studies were conducted for free ranging animals in an effort to better understand what particular species of herbivores were consuming and in what quantities (Carpenter et al. 1979, Garrod et al. 1981, Hunt 1979, Nixon et al. 1970). By the 1990s the focus had shifted from predominantly species-specific descriptive endeavours to developing dietary selection models and foraging theories, or from the descriptive to the analytical (Robbins 1993). What emerged as the underlying premise of most foraging and dietary theories was that an animal, provided a given set of food choices and environmental constraints, will seek to maximize its fitness

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by maximizing its net rate of nutritional intake (Provenza and Cincotta 1993, Sih 1993).

A product of this effort was Optimal Forage Theory, suggesting that the diet selected will reflect a combination of energy maximization and time minimization strategies (Provenza and Cincotta 1993, Westoby 1974, Wilshurst et al. 1995), with each species finding its own balance along the quantity-time continuum.

Optimal Forage Theory provides a sound framework in which to analyze diet selection, but the underlying mathematical model is not so sophisticated as to take into account the stochastic environment in which all creatures live (Houston 1993, Pyke 1984). Factors influencing the actual diet selected by a particular animal include, but are not limited to, current physiological state (Penry 1993), predator avoidance behaviours and strategies (Pierce et al. 2004), topography, vertical vegetative structures (Etzenhouser et al. 1998), forage accessibility, toxin minimization strategies (Robbins 1993), feed-back loop processes (Illius and Gordon 1993), individual preferences (Arnold and Drawe 1979, Provenza and Cincotta 1993), site knowledge, plant community distribution and structure (Berteaux et al. 1998), sex-based preferences resulting from habitat partitioning (Weckerly 1993), and animal grazing patterns (Berteaux et al. 1998). These numerous and often interdependent variables act to modify the final diet selected by an herbivore, reducing the predictive power of any nutritional maximization model. Thus, while large herbivores may strive to optimize their diets, absolute optimization is not possible (Westoby 1974, LaGory et al. 1985). Nevertheless, accepting that dietary optimization is the primary driver of large ungulate foraging behaviour, examining diet selection from a

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nutritional intake maximization perspective does allow the integration of digestibility with diet, or the consumer with its environment.

Common currencies used to measure nutritional intake are protein and energy (Berteaux et al. 1998), as studies show that many large herbivores are able to evaluate these two quantities within potential forages, either directly or indirectly through secondary compounds (Robbins 1993). The ability of white-tailed deer (*Odocoileus virginianus*) to innately know forage values has been questioned by Verme and Ullry (1984), but there is a growing body of work supporting the idea that they can discriminate overall forage quality, even if imperfectly (Berteaux et al. 1998). This research suggests that herbivores such as deer sample as they move between patches, a process referred to as partial selection. This partial selection behaviour provides both food intake and real-time nutritional information of all potential foods encountered (Illius and Gordon 1993). Using this information, deer can decide what to eat in order to best meet their nutritional needs. White-tailed deer have been found to select against protein in favour of energy once their physiological requirements have been met, suggesting that once sufficient levels have been achieved the animal will seek to maximize energy intake at a cost of protein (Berteaux et al. 1998).

The need to continually re-assess the nutritional value of available forage exists because these values are fluid. Vegetative matter is relatively low in digestible nutritional content, but these values vary diurnally, seasonally, and yearly depending on phenological stage (Stewart et al. 2000, Rao et al. 1973, Hanley and McKendrick 1985) and environmental

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factors such as available moisture and sunlight, soil nutrients, and recent disturbance (Lodge 1954, Bruinenberg et al. 2002, Sprinkle 2000). These factors also influence C:N ratios and the amount and location of digestible and indigestible compounds within the plant at a given time. As a general rule, plant components are highest in digestible energy when they are young, before large quantities of structural carbohydrates and silica develop and accumulate within the stems and leaves (Verme and Ullry 1984, Wilmshurst et al. 1995). This increase in poorly digestible and indigestible compounds decreases the overall digestibility of the flora. Young forbs and shrub leaves, fruits, seeds, and young roots have been found to have higher levels of digestible energy and protein, encouraging herbivores to preferentially select them for consumption (McConnell and Garrison 1966, Wilmshurst et al. 1995). Least digestible are mature shrub leaves and grasses. During drought conditions, plants can harden, further reducing their relative nutritional value (Short 1975, McConnell and Garrison 1966, Mountousis et al. 2008). Given all of these variables, optimizing dietary selection in order to maximize nutritional intake is an ongoing challenge.

How large forestomach ruminants extract nutrients from their selected diet also plays an important role in what they eat. Plant nutrients are locked up in two primary locations: the cell interior, which contains the fats, proteins, and non-structural carbohydrates (soluble sugars and starch), and the cell wall, which is composed of lignin, cutin, silica, and structural carbohydrates (pectin, hemicellulose, and cellulose). Non-structural carbohydrates and pectin are relatively simple to digest and the smaller particles and nonabsorbed metabolites pass quickly through the omasum into the abomasum, or true

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stomach, for enzymatic and acid hydrolysis (Robbins 1993). Among the plant classes, crops and forbs have the greatest percentage of digestible material, followed by shrub leaves and then grasses (Chapter 2). Yet the young leaves of shrubs and forb cell walls are more easily broken down by chewing and digestion than those of grasses and mature shrub leaves, meaning that the relative nutritional value of forbs and young shrub leaves may be greater than that indicated by its Dry Matter Digestibility (DMD) value (Short 1975, Mould and Robbins 1981).

To maximize the function of the rumen-reticulum, protein levels upon which the bacteria depend must be optimized. Too low a protein level will reduce the animal's ability to sustain the bacteria needed to extract nutrients even from a high-digestible energy diet. In extreme cases, it can result in death (Robbins 1993). More commonly, however, low CP intake limits growth, increases neonatal loss (Meyer et al. 1984), and reduces the rumen-reticulum's ability to digest NDF (Dorshorst and Grummer 2002). As a compensating strategy, animals on low protein diets ($\approx 7\%$) can become more efficient at extracting nutrients but body mass, and thus fitness, can decline (Asleson et al. 1997, Brown et al. 1995). Although results vary by study, likely due to amino acid composition of the proteins consumed (Robbins 1993) and the concentration of soluble digestion inhibitors (Hanley and McKendrick 1985), minimum white-tailed adult deer CP maintenance requirements range from 4-8% (Berteaux et al. 1998).

Increasing CP intake can enhance rumen function and nutrient extraction (Caton et al. 1988), yet excessive intake of CP does not enhance fitness as the rumen pH and

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biological value of the CP decreases (Robbins 1993). Further, excess nitrogen must be disposed of by renal excretion and, thus, requires increased water intake and the associated energetic costs of obtaining that water (Wildman et al. 2007). By optimizing CP intake, pH can be maintained within acceptable parameters (Köster et al. 1996). Because protein and energy tend to be closely correlated in most natural forages (Berteaux et al. 1998), selecting against protein while maximizing energy may lead to dietary decisions that are not readily apparent to the observer and defy simple linear regression explanations (Westoby 1974).

To access the nutrients contained within structural carbohydrates a symbiotic digestive process involving fibre-digesting bacteria and protozoa must occur within the rumen-reticulum. Although most of these compounds can be broken down into usable components within 48 hrs, the exact time required is curvilinear and the degree of efficiency varies by compound, gut retention times, and the constituency of the current gut rumen-reticulum content (Short 1975). Foods with high proportions of poorly digestible and indigestible structures increase gut retention times and reduce the animal's ability to consume additional biomass (Jung and Allen 1995, Allen 1996). Conversely, increased gut retention times permits the rumen-reticulum to further break down the structural carbohydrates, thereby extracting a larger portion of nutrients than would otherwise be the case (Penry 1993, Illus and Gordon 1993). This complex interplay of intake limitation and enhanced nutrient extraction renders dietary choices for large ruminants such as white-tailed deer extremely complex.

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The portion of the diet that cannot be digested – or at least very poorly digested - consists primarily the lignin, some cutin and suberin, and silica. This is excreted after the digestive process is complete (Verme and Ullry 1984). In the laboratory this component is known as Acid Insoluble Ash (AIA). Digestibility has been found to be negatively correlated with the natural marker AIA in other forestomach ruminants and monogastrics such as giraffes (Clauss et al. 2001), elephants (Pendlebury et al. 2005), and sheep (Van Keulen and Young 1977, Block et al. 1981). Similarly, Acid Detergent Lignin (ADL) has been found to be negatively correlated for elephants (Pendlebury et al. 2005) and cattle (Sunvold and Cochran 1991). The relationship for free-ranging white-tailed deer in an agricultural setting has not been established.

The proliferation of row-crop farming is thought to have caused white-tailed deer population densities to explode in many settings across North America (Côté et al. 2004, Nixon et al. 1970). There is a large body of work to suggest that as the availability of highly concentrated, highly digestible foods has increased, foraging energetic costs decreased while net rates of nutritional intake increased (Nixon 1991, Roseberry and Wolf 1998, Stewart et al. 2000). Approximately 25% more energy is spent by elk simply standing rather than laying, and similar figures have been found for other large ruminants (21-37%) (Parker et al. 1984). The act of foraging in the summer has been calculated to consume up to 22% of a white-tailed deer's daily energetic budget, but this cost can be exponentially minimized when favourable forage density increases, causing the animal to eat more and move less (Wickstrom et al. 1984).

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The first objective of this study was to determine what nutritional advantages are afforded white-tailed deer by row-crops. The second was to better understand why deer make the dietary choices they do. In the spring of 2005 flood conditions caused a catastrophic crop failure in the Winnipeg region, with no row-crops other than volunteer stems emerging from the soil. A drought followed in 2006 but persistent high soil moisture levels allowed the fields to be cultivated and a good crop to be harvested. These conditions afforded a very unique opportunity to compare diet selection and nutritional intake on the same site using essentially the same population of free ranging white-tailed deer when provided two different foraging environments.

STUDY AREA

The primary study area is SCRR, a military rifle range and dismounted training area less than 2km west of Winnipeg, Manitoba, located in the Rural Municipalities of Headingley and Rosser (49° 55' North latitude, 97° 13' West longitude, elevation 238m). It comprises 280ha of remnant northern tallgrass prairie and 102ha of aspen forest. The site is flat and poorly to imperfectly drained with <2% slope. Soils are classified as Clayey Lacustrine (Gleysols and Black Chernozems) (Land Resource Unit 1999). As a result, it is not uncommon for low-lying areas such as the forest floors to be flooded in spring and during wet summers.

Today, the eastern half is generally characterized as a lower quality native prairie than the west, dominated by *poa pratensis* and *Symphoricarpos occidentalis*, instead of more

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Agropyron spp (wheatgrasses), *Koleria cristata* (June grass), *Andropogon* spp (bluestem), and *Spiraea alba*. Since the 1880s, an aspen forest has become established on over one third of the site. Although aspen encroachment continues, forest cover has remained relatively stable (Walker 2004). Less the grassland openings within the forest, the native prairie has been burned a number of times since 1996, the last being in spring 2005. Much of the southern half of the site is mowed as it supports the rifle ranges, obstacle course, and buildings.

Within a 25km radius of the site, land cover consists of 81.5% agriculture, 29.3% grasslands, including urban grasslands, 4.4% forage crops 2.1% forest, and 1.3% cultural. More immediately, the area within 6km of the study site is 52.3% agriculture, 10.4% cultural, 10.0% grasslands, 5.7% forage crops, and 2.8% forest (calculated using the MB Conservation 2004 Land Cover GIS layer). Approximately 4.5km to the south of the main study forest is the Assiniboine River, which flows east/west. Although such water barriers have not been found to be movement barriers, they do serve to restrict free movement of deer, especially where adequate resources exist on both sides of the water obstacle (Coulon et al 2006, Michael 1965, Eberhardt et al 1984). The land cover of the region to the south of this river was not included in the above figures. Additional details are found in Chapter 1.

METHODS

Dietary Composition

Deer diets for August 2005 and August 2006 were determined through microhistological fecal analysis. Groups of fecal pellets were collected from across the study site in August 2005 ($n = 14$) and August 2006 ($n = 32$) and frozen within 4 hrs to minimize further decay (Kamler et al. 2003). Composite samples were then assembled using three pellets from each group. Only fresh pellets were collected to minimize plant epidermal decay and enhance dietary fidelity (Leitte and Stuth 1994). The higher number of pellet groups collected in the second year reflected the better understanding of white-tailed deer habitat preferences and movement patterns.

These composite samples were then sent to the Wildlife Habitat Nutritional Laboratory at Washington State University for microhistological analysis, using frequency-density conversion sampling procedures of Sparks and Malehek (1968), Flinders and Hansen (1972), Holchek and Vavra (1981), and Holechek and Gross (1982). The greatest single source of error during microhistological analysis is the technician's ability to properly identify the remaining epidermal fragments in the feces (Bartolome et al. 1995); by using the Washington State University laboratory this source of error was minimized. Relative cover (Davitt 1979) of plant cuticle and epidermal fragments were quantified for 25 randomly located microscope views on each of eight slides, for a total of 200 views. A 10 x 10 square grid mounted in the eyepiece of the microscope was used to measure the area

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covered by each positively identified fragment observed at 100x magnification. Larger magnification (200x to 450x) was used to aid in identification of discernable fragments (Holechuk and Valdez 1985). Measurements of the area covered were recorded by species. Percent diet composition was calculated by dividing cover of each plant by the total cover observed for all species, then multiplied by 100.

Fecal analysis is the only means of measuring dietary intake of free roaming wild herbivores, without sacrificing the animal (Saunders et al. 1980, Holechek and Gross 1982). The principle difficulty of this approach over rumen and oesophageal fistula analysis is that not all plant epidermal material survives the digestive process, resulting in under-reporting of easily digested plants. Forbs are the class most affected by this problem, and grasses, the least (Holechek and Gross 1982, Bartolome et al. 1995). To partially address this problem correction factors for the August 2005 and 2006 diets were calculated. This was done by recreating the measured diet using plant material harvested in August 2006 from the study site and then digesting that diet *in vitro* for 48hrs using steer inoculum. Microhistological analysis was then repeated on this digested sample and, using multiple regression, correction factors by species were derived (Leslie et al. 1983).

The more difficult problem arises for those plants that completely disappear or cannot be positively identified by species using fecal analysis due to their fragile epidermal cells. This occurs among some annual forbs (Free et al. 1970). For the purposes of this study the unidentified forb component, listed as “Other forbs” in both 2005 and 2006, was deemed to be with equal amounts of *Viola pedatidia* (Early prairie violet), *Ratibida*

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pinnata (Grey-headed coneflower), *Epilobium grandulosium* (Purple-leaved willow herb), and *Crepis tectorum* (Narrow-leaved Hawk's beard). None of these species were identified during fecal analysis and were locally rare (*Viola* spp and *C. tectorum*) or sparse (*E. grandulosium*). This latter species showed evidence of browsing while other studies have found that *Viola* spp are favoured by deer. Sunflowers were grown adjacent to the study site and deer were observed to intensively graze those plants. "Other shrubs" were assigned as *Spiraea alba*, common on the western half of the site and heavily browsed. "Other grasses" were assigned to be *Phleum pratensis* (Timothy) and *Agrostis scabra* (Rough hair grass). Plants not provided for the correction factor determination but found during fecal analysis were: *Astragalus agretis*, *Agoseris glauca*, *Gallardia aristata*, *Penstemon glacilis*, *Psorela* spp, *Lonicera dioica* and *Stipa comata*, totalling 7.4% and 2.9% of the 2005 and 2006 diets respectively. These plants were generally rare on the site and, although small numbers of certain plants were found earlier in the year, they could not be located in the fall for harvest. The analyses were therefore conducted without these species.

Forage Nutritional Content

The difficulty with assessing forage nutritional content is that most measures used are proximate. This is due to the difficulties associated with extraction, the uncertainty of how the subject animal uses some of the nutrients being measured, and knowing the biological value of the nutrients for the animal in question (Cullison 1982, Jung et al. 1997, Mould and Robbins 1981). To determine the nutritional content of the two diets, a

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second set of reconstituted diet using the aforementioned substitutes was dried and then subjected to a series of analyses. Crude Protein was calculated using the Kjeldah procedure with a CarbonNitrogen analyzer (LECO Truspee), a system based on the Dumas method of combustion. The resultant nitrogen value was multiplied by 6.25. AIKA C5000 bomb calorimeter was used to establish Gross Energy (GE) and total dietary lipids were extracted using petroleum ether, providing the Crude Fat values. Van Soest/Aknom detergent analysis using an Ankom 200 Fiber Analyzer was used to determine Neutral Detergent Fibre (NDF) and Acid Detergent Fibre (ADF). Acid Detergent Lignin was extracted using a 72% sulphuric acid method (Cullison 1982). Percent Acid Insoluble Ash (AIA), which represents lignin, silica, cutin, and suberin was determined by burning the ADL residue in a muffle furnace for 4 hrs at 500°C. *In vitro* DMD (IVDMD) was assessed by subjecting the dried composite samples to cattle rumen fluid for a 48hr period, as was the case when calculating the correction factors.

Nutritional values were determined for the major dietary components as well as for the composite dietary classes of Grasses and Shrubs for both treatment years. The principle dietary components were: *Agropyron* spp, *Cirsium arvense*, *Salix* spp, *Monarda fistulosa* leaves, *Triflorium/Melilotus* (50% each), wheat inflorescence, sunflower leaves, *Helianthus* leaves, and soybean leaves. Because all plant material gathered for nutritional analysis was collected in 2006, variations in plant nutrition between years due to year-specific environmental conditions were not captured. While some minor differences in nutritional value were likely (Montousis et al. 2008), the elevated soil moisture levels of

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2006 likely mitigated some of the effects that the hot dry summer of 2006 would have otherwise had.

Given of the complexity of the Forb class of the diet, with such a large number of species of which many could not be identified through microhistological analysis or located on site, its nutritional values were not directly measured. Instead, knowing the nutritional values by category for the forage classes of Grasses, Shrubs, and Total by year, it was possible to calculate the values for Forbs. In addition to Forbs, the remaining nutritional values of the diet that were not known were: Crops (0.0% in 2005, 25.7% in 2006), *Carex* (0.1%, 0.2%), and Mosses and Thorn (0.0%, 0.8%). Mosses and Thorns are of very low nutritional value and are generally believed to be consumed coincidentally to more favoured foods, at least when other choices are available. In 2006 0.7% of the 0.8% of this class was thorn, most probably consumed while eating *Cirsium* spp stalks and some *Rosa*. *Carex* was present in such small amounts that their exclusion was believed not to unduly skew the results. Lastly, Crops were absent from the 2005 diet but comprised a quarter of the August 2006 diet. Of this, only 0.3% was wheat with the remainder being soybean. The nutritional values for soybean were therefore used to represent the entire crop component.

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To calculate the annual nutritional values (y) for forbs, the following formula was used:

$$y_{i, \text{forbs}} = \frac{T_i - (\sum (\hat{y}_j \cdot w_j))}{W_{\text{forbs}}}$$

where T is the value of the nutrient i in the yearly Total Diet and i = Total Ash, GE, Crude Fat, NDF, ADF, ADL, AIA, IVDMD, and CP. The residual $\hat{y}_j = T_i - y_i$ for dietary component class j , where j = Grasses, Crops, and Shrubs, and w is the weighting for the residual. The weighting was the percent representation of dietary component class j in the Total Diet in August of that year.

There are three main sources of possible error with this approach. First, there was a small portion of the total diets that remained unknown (1.0%, 0.4%) while other portions were known by class but not by species. It was therefore not possible to perfectly reconstitute the diets. Second, not all known dietary components could be located on the research site and thus included when calculating the corrected diets or when calculating the nutritional values of the total diets and classes of forage. Third, because the digestive process is complex and dependant upon the precise composition of the diet, the sum of the parts is not necessarily equal to the whole, but the method provides a good approximation (Short 1975).

Energetics

To understand the relative advantages of particular dietary components in terms of energetics, the location and type of all vegetative cover in a 6km radius from the range was mapped. The distances from the centre of the study site's forest as well as the nearest edge of the forest were calculated. This was done by conducting a drive-by survey of all crops in the last week of July 2006. Given the narrow and irregular spacing of many of the old river lot fields, field edges were recorded using a Garmin Rhino 120 GPS (Garmin Ltd, Olathe Kansas, USA). All of these data were used to amend the base layer, which was compiled from Landsat Thematic Mapper (TM) imagery developed in 2001/2 using a pixel resolution of 30m (Manitoba Conservation). Crop field termini that could not be viewed from the road were ascertained with the aid of satellite imagery available from Google Earth. Cover was classified into sixteen categories. To be classified as Deciduous Forest it needed 75% - 100% of the forest canopy to be deciduous but could include small patches of grassland, marsh or fens less than two hectares in size. Grassland was defined as mixed native and/or tame prairie grasses and herbs, but could include scattered stands of willow (*Salix L.*), choke cherry (*Prunus virginiana*), pin cherry (*Prunus pensylvanica*) and saskatoon (*Amelanchier alnifolia*). There was normally less than 10% shrub or tree cover.

Because of the similarities between some barley and wheat varieties, bearded crops were grouped and classified as wheat/barley. Winter wheat was readily identifiable and was classified as such. Golf courses and recreational fields were identified as cultural lands.

On site, walking throughout the range every week and recording the locations of deer feces, bedding sites, and the deer themselves determined preferred habitat locations. It is possible that some favoured locations in less accessible areas of the forest were missed, but given the high deer numbers and small size of the study site, this error is not likely to be large.

Statistical Analysis

The dietary composition by year (no crop, crop) and by class was correlated by species and a single-tailed paired *t*-test was conducted to determine annual similarity. Nutritional values by year were then correlated using Pearson Product Moment and variance between years was measured by category and plant class. Each of the nutritional components was then compared across diets and dietary components using side-by-side bar charts in order to evaluate the importance of each component within the Total Diet. To assess any correlation between nutritional measures, all Total Diet categories were correlated for 2005 and 2006 using Pearson Product Moment and linear regression. Because of the non-linear relationship between some of the dietary components, especially at the species level, high correlations between some otherwise related measures such as CP and energy were not expected in all cases and some outliers were anticipated.

To better understand the relationship between dietary and nutritional components both Correspondence Analysis (CA) and Principle Component Analysis (PCA) were

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conducted with the SYN-TAX 2000 software package, using the nutritional components as the variables. CA is useful because it identifies relationships between the rows and columns of a set of data. (Legendre and Legendre 1998). In this case, it describes the relationship between dietary elements and their corresponding nutritional values. To correct for scale (differing units for GE), all values were normalized using x_i / x_{mean} and symmetrical weighting was applied to enhance the separation of the objects. This allowed the objects and variables to be projected while maximizing variation. PCA is valuable because it can summarize the greatest amount of variance among descriptors along a few independent variable axes (Legendre and Legendre 1998). In the case of the nutritional data, the length and direction of the eigenvectors calculated for each of the nutritional categories (variables) can explain the greatest amount of variance among the diets and dietary components (objects). Because it measures variance, there was no need to normalize the values.

RESULTS

Diet

The corrected diets for the absence/presence of crops are found at Table 4.1. Diets were not significantly different between treatments (Total Diet, $p = 0.9805$) or classes (Grasses, $p = 0.3858$; Forbs: $p = 0.3171$; Shrubs: $p = 0.4724$). Crops were absent in 2005 but comprised 25.4% of the corrected diet in 2006. Offsetting the consumption of crops, the intake of Grasses, *Carex* spp, Forbs, and Shrubs declined by 2.8%, 0.2%, 19.3%, 4

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Table 4.1. White-tailed Dewer Diets – Uncorrected and Corrected. Plants measuring less than 0.1% of the total diet were not included.

a. Grasses, Crops, and Carex

<u>Plant Species</u>	<u>Uncorrected Diets</u>			<u>Corrected Diets</u>		
	<u>Aug 05</u>	<u>Aug 06</u>		<u>Aug 05</u>	<u>Aug 06</u>	
<i>Agropyron</i> spp.	18.9	18.7		8.1	9.5	
<i>Andropogon</i> spp.	2.1	0.4		1.0	0.2	
<i>Bromus inermis</i>	4.7	0.6		1.8	0.3	
<i>Hordeum</i> spp.	1.0	0.9		0.3	0.4	
<i>Poa</i> spp.	2.8	0.4		0.7	0.2	
<i>Sporobolus heterolepsis</i>	2.1			1.8		
<u><i>Stipa comata</i></u>		1.7			0.7	
<u>Other Grasses</u>	2.4	1.1		<u>0.9</u>	<u>0.5</u>	
Total Grasses	34.1	23.8	%	14.6	11.8	%
Soybean		24.1			25.4	
Wheat		0.6			<u>0.3</u>	
Total Crops:	0.0	24.7	%	0.0	25.7	%
<i>Carex</i> spp.	1.2	0.4		0.4	0.2	
Total Sedge/Rush:	1.2	0.4	%	0.4	0.2	%

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b. Forbs

<u>Plant Species</u>	<u>Uncorrected Diets</u>		<u>Corrected Diets</u>	
	<u>Aug 05</u>	<u>Aug 06</u>	<u>Aug 05</u>	<u>Aug 06</u>
<i>Achillea millifolium</i>	1.3	0.8	2.3	1.1
<i>Agoseris glauca</i>		0.1		0.1
<i>Alisma plantago</i>	0.5		0.9	
<i>Amorpha nana</i>	1.0	0.4	1.7	0.5
<i>Aster spp.</i>		0.6		0.8
<i>Astragalus agretis</i>	1.2		2.2	
<i>Cirsium spp.</i>	2.8	1.5	4.2	3.9
<i>Erigeron spp.</i>	2.0	2.3	3.7	3.0
<i>Fragaria virginiana</i>	1.9		2.3	
<i>Gaillardia aristata</i>		0.9		1.2
<i>Galium boreale</i>	3.6	1.9	6.5	2.6
<i>Geum triflorum</i>	2.7	0.4	1.8	0.5
<i>Helianthus spp.</i>	0.1	2.2	0.2	1.8
<i>Lathyrus spp.</i>	2.8	1.7	5.2	2.3
<i>Lithospermum canescens</i>	2.1		3.0	
<i>Monarda fistulosa</i>	1.2	6.7	2.2	15.4
<i>Oenothera biennis</i>	0.5	0.1	0.9	0.1
<i>Penstemon gracilis</i>	4.5		8.3	
<i>Plantago major</i>	0.5	0.4	0.9	0.5
<i>Potentilla spp. leaf</i>	1.8	0.4	3.3	0.5
<i>Psoralea spp.</i>		0.2		0.3
<i>Rumex sp.</i>		0.6		0.4
<i>Solidago spp.</i>	1.8	1.9	3.3	2.6
<i>Stachys palustris</i>	2.0		6.5	
<i>Trifolium/Medicago/Melilotus</i>	0.5	1.6	0.9	3.5
<i>Vicia spp.</i>	0.5	2.4	0.9	2.2
Other Forbs	3.8	4.1	<u>7.0</u>	<u>5.6</u>
Total Forbs:	38.9	31.2	68.2	48.9
		%		%

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c. Shrubs and Others (Mosses and Thorns)

<u>Plant Species</u>	<u>Uncorrected Diets</u>			<u>Corrected Diets</u>		
	<u>Aug 05</u>	<u>Aug 06</u>		<u>Aug 05</u>	<u>Aug 06</u>	
<i>Amelanchier alnifolia</i> leaf	2.4			2.1		
<i>Amelanchier alnifolia</i> stem		0.9			0.6	
<i>Artemisia ludoviciana</i>	1.3	0.4		0.4	0.2	
<i>Lonicera dioica</i> leaf	1.7			0.9		
<i>Populus</i> spp. leaf	2.6	2.2		1.4	1.0	
<i>Populus</i> spp. stem	0.7			0.5		
<i>Rosa</i> spp. leaf		0.9			0.3	
<i>Rosa</i> spp stem	1.4			1.6		
<i>Rubus pubescens</i> leaf		2.8			1.3	
<i>Salix</i> spp. leaf	11.4	5.4		7.2	4.9	
<i>Salix</i> spp. stem	1.4	6.0		0.7	4.3	
<i>Symphoricarpos</i> leaf	2.1			1.4		
Other Shrub leaf	1.0			0.6		
Total Shrubs:	25.9	18.6	%	16.8	12.6	%
Mosses:	0.0	0.2	%		0.1	%
Thorn:	0.0	1.1	%		0.7	%
Total Other:	0.0	1.3		0.0	0.8	

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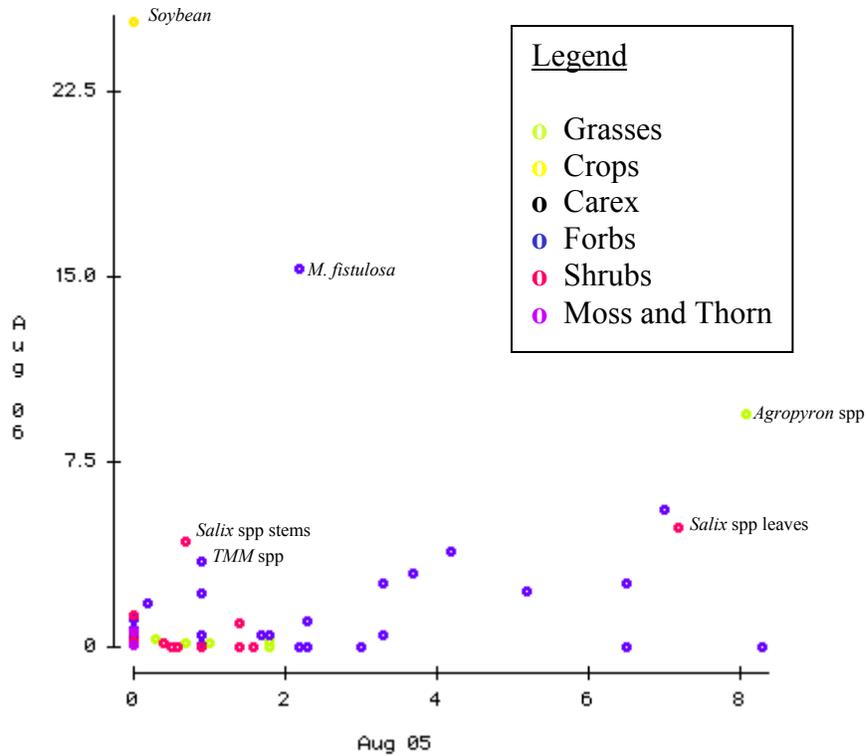


Figure 4.1. Corrected 2005 and 2006 Diets. Except for a sharp increase in consumption of *M. fistulosa*, the presence of crops reduced herbivorous pressure on most forbs, as measured as a percent of the diet. $r = 0.159$.

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.2%, while Mosses and Thorns increased by 1.5% of the total diet. As illustrated at Figure 4.1, the addition of crops to the 2006 diet also resulted in a reduction of grazing of all forbs, less *M. fistulosa*, which saw a sharp increase. Soybean was the principle crop consumed (25.4%) with a trace of wheat (0.3%). *Salix* spp stems also saw an increase (0.7 to 4.3%) whereas *Salix* spp leaves and most other woody species leaves and stems decreased.

Comparing the exact composition of the Total Diets, to include the quantities consumed by species, the diets were very poorly correlated ($r = 0.149$). This was due to a small number of species that were consumed in very different proportions between years. Of the 54 plant species and components identified over the two years, 28 appeared in both 2005 and 2006. Thirteen appeared only in 2005 while another 13 appeared only in 2006. On a presence/absence basis, the addition of crops created the greatest difference among Shrubs, Forbs, and then Grasses. Mosses and Thorns were not present in 2005, but they are likely only a coincidental dietary constituent as they have little or no nutritional value. Why Thorns did not appear in the 2005 diet despite *C. arvensis* being present in larger quantities than in 2006 is unclear. The addition of crops therefore reduced the total number of component species by just two in the overall diet although the volumes of many native species did decrease. With soybean and *M. fistulosa* removed from the data set, correlation between years increased to 0.580. Grasses were highly correlated, Shrubs less so ($r = 0.618$), and Forbs very poorly ($r = 0.137$). This was reflective of the general decrease in the consumption of forbs in the presence of crops. Sunflower was not found

during the fecal analysis despite its proximity to the site, being closer than soybean and between the forest edge and wheat, which was selected in small amounts.

Nutrition

The nutritional value of the diets, by Total Diet and by class between years, was very similar by all measures (Tables 4.2 and 4.3). Standard deviation of nutritional measures between years for the Total Diets was least for AIA (0.08%) and greatest for ADF (1.17%). Among the plant classes, Forbs experienced the greatest standard deviation across most nutritional indicators (Total Ash, ADF, AIA, and CP) but this never exceeded 4.95% (ADF). On the other end of the spectrum, both Grasses and Total Diets each had three categories in which the smallest standard deviations occurred. GE was excluded from the comparison because of its different unit of measure, although the GE values for Forbs varied far greater between years than any other class.

To better understand the interrelationships between individual nutritional components and markers, all nutritional values by category for all dietary classes (less Forbs, which was not directly measured) and their constituents were pooled across categories (Table 4.4). The greatest correlations were found between ADF and NDF ($r = 0.930$). Strongly negatively correlated were IVDMD with ADF (-0.874) and NDF (-0.821) while IVDMD was positively correlated with CP (0.802). The strong correlation between ADL and GE

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4.2. Dietary and Nutrient Composition, by Class and Year.

	Diet	%	Total Ash	GE	cals/gm	%	Crude Fat	%	NDF	%	ADF	%	ADL	%	AIA	%	IVDMD	%	CP
<u>total Diet</u>																			
	99.6	8.89	4648	4.09	44.77	30.15	8.63	0.5	57.8	12.92									
Aug 05	99	7.99	4635	3.74	45.8	31.81	9.16	0.38	58.13	12.48									
Aug 06	s	0.64	9.19	0.25	0.73	1.17	0.37	0.08	0.23	0.31									
<u>total Grasses</u>																			
	14.6	6.23	4666	1.98	74.88	42.1	5.93	1.07	43.18	7.43									
Aug 05	11.8	6.55	4668	2.08	74.46	45.03	8.64	0.73	41.48	6.81									
Aug 06	s	0.23	1.41	0.07	0.30	2.07	1.92	0.24	1.20	0.44									
<u>total Shrubs</u>																			
	16.8	5.26	5264	5.97	34.76	24.07	12.37	0.27	57.29	13.81									
Aug 05	12.6	4.87	5172	6.47	41.31	30.57	14.22	0.25	53.47	10.86									
Aug 06	s	0.28	65.05	0.35	4.63	4.60	1.31	0.01	2.70	2.09									
<u>total Forbs</u>																			
	68.2	10.41	4520	4.10	41.05	29.27	8.34	0.44	61.39	13.95									
Aug 05	48.9	8.41	4836	4.48	44.66	36.27	10.53	0.33	59.30	9.31									
Aug 06	s	1.4	223.49	0.27	2.55	4.95	1.76	0.08	1.48	3.28									
<u>total Crops</u>																			
	25.7	9.7	4155	1.90	38.80	19.10	4.10	0.40	68.10	22.40									
Aug 06																			

Table 4.3. Dietary and nutrient composition of principle dietary components.

<u>Species</u>	<u>% Diet (05,06)</u>	<u>Total Ash</u>	<u>GE</u>	<u>Crude Fat</u>	<u>NDF</u>	<u>ADF</u>	<u>ADL</u>	<u>AIA</u>	<u>IVDMD</u>	<u>CP</u>
	%	%	cals/gm	%	%	%	%	%	%	%
<u>Grasses</u>										
<i>Agropyron</i> spp. leaves	8.1, 9.5	5.52	4594	1.65	79.29	45.71	6.30	0.81	29.20	7.69
<u>Crops</u>										
Soybean*	0.0, 25.4	8.50	4537	2.90	42.60	37.00	7.40	0.20	71.10	21.70
Wheat (inflorescence only)	0.0, 0.3	5.46	4192	2.41	36.25	12.29	1.09	0.31	75.30	12.65
Sunflower leaves	0.0, 0.0	19.93	4028	2.37	17.35	11.66	1.16	0.42	79.60	27.26
<u>Forbs</u>										
<i>Cirsium arvense</i> (Oct)	4.2, 3.9	13.63	3778	2.98	39.06	26.44	4.13	0.16	75.90	19.16
<i>Helianthus max.</i> leaves	0.2, 1.8	13.34	4053	4.91	29.78	22.13	3.71	0.57	64.00	10.02
<i>Monarda fistulosa</i>	2.2, 15.4	7.58	4525	4.63	40.76	30.03	7.02	0.15	47.70	9.01
<i>Trifolium/Melilotus</i> (50% ea)	0.9, 3.5	9.60	4537	2.47	25.99	18.68	3.89	0.20	71.10	23.24
<u>Shrubs</u>										
<i>Salix</i> spp leaves	7.2, 4.9	9.78	4562	2.38	25.51	16.70	5.17	0.23	56.90	13.12

Although a minor component (wheat) or absent (sunflower) from the August diets, analysis was conducted as they form large components of white-tailed deer diet during other times of the year. C arvense, important in October and November, was analyzed in order to understand its nutritional value.

Table 4.4. Pearson Product-Moment Correlation of Nutrients.

	<u>Ash</u>	<u>GE</u>	<u>C. Fat</u>	<u>NDF</u>	<u>ADF</u>	<u>ADL</u>	<u>AIA</u>	<u>IVDMD</u>	<u>CP</u>
Ash	1.000								
GE	-0.699	1.000							
C. Fat	-0.137	0.503	1.000						
NDF	-0.628	0.280	-0.301	1.000					
ADF	-0.557	0.398	-0.057	0.930	1.000				
ADL	-0.559	0.865	0.678	0.294	0.503	1.000			
AIA	-0.288	0.072	-0.405	0.770	0.656	-0.026	1.000		
IVDMD	0.656	-0.568	0.004	-0.821	-0.874	-0.522	-0.584	1.000	
CP	0.708	-0.451	-0.210	-0.686	-0.712	-0.465	-0.467	0.802	1.000

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(0.865) was likely reflective of the manner in which GE is measured, as are the negative correlations of GE with CP and IVDMD (-0.451, -0.568). The bomb calorimeter only quantifies heat generated by dried matter when combusted, without differentiating among the various organic components (Robbins 1993). For plants with high IVDMD values, then, GE is likely a good measure for assessing available energy. For plants with low IVDMD, however, more caution may need to be exercised. Unlike what has been found elsewhere in the literature, AIA and IVDMD were poorly correlated (-0.584) (Sales and Janssens 2003, Block et al. 1981).

Evaluating the strength of the relationship between NDF, ADF, and AIA as indicators for digestibility in free ranging white-tailed deer, all three measures of fibre were plotted against IVDMD and regression analysis was conducted (Figure 4.2). ADF proved to be the best indicator of digestibility ($r^2 = 73.5$), closely followed by NDF ($r^2 = 64.9$). Surprisingly, AIA was a weak indicator ($r^2 = 29.4$).

By plant class, the greatest amount of digestible structural carbohydrates, hemicelluloses and some of the cellulose (NDF – ADF) were found in Grasses (32.78% in 2005, 29.43% in 2006). Next in descending order were Forbs (11.79%, 14.07%), Shrubs (10.69%, 10.74%), and Crops (-, 5.60). Total Diet digestible structural carbohydrates were 14.62% and 13.99%. This indicates that although Grasses have a low IVDMD value, the rumination process can release a fairly large amount of nutrients, partially explaining their importance in the diet.

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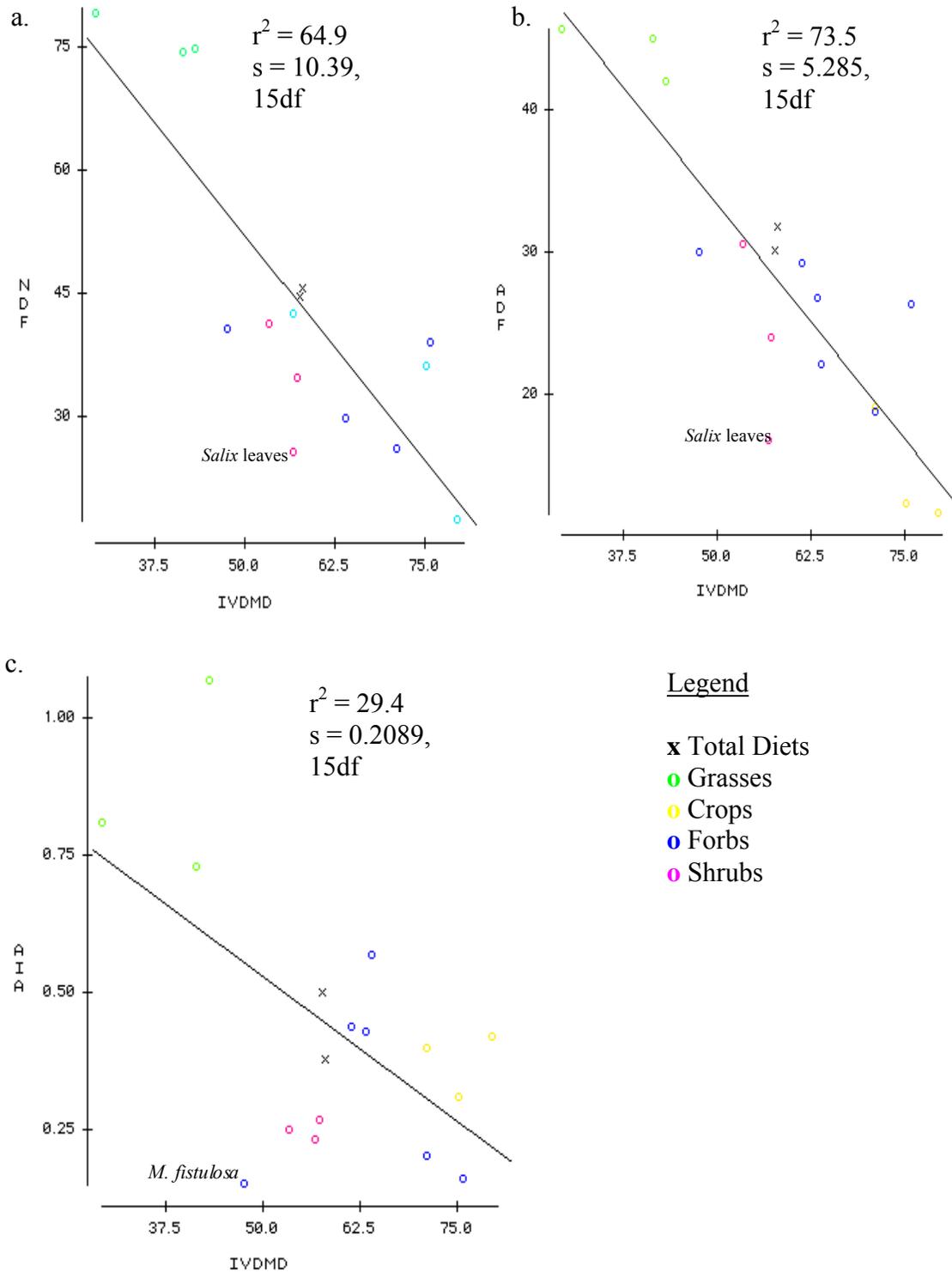


Figure 4.2. Relationship of fibre measures and digestibility. ADF was most highly associated with IVDMD, closely followed by NDF. AIA, a common marker for digestibility with tame forages in domestic livestock, was poorly correlated to digestibility for these free-ranging deer. All Diet Classes and Principle Dietary Components were used in the evaluation. The largest outliers are identified: *M. fistulosa* and *Salix leaves*.

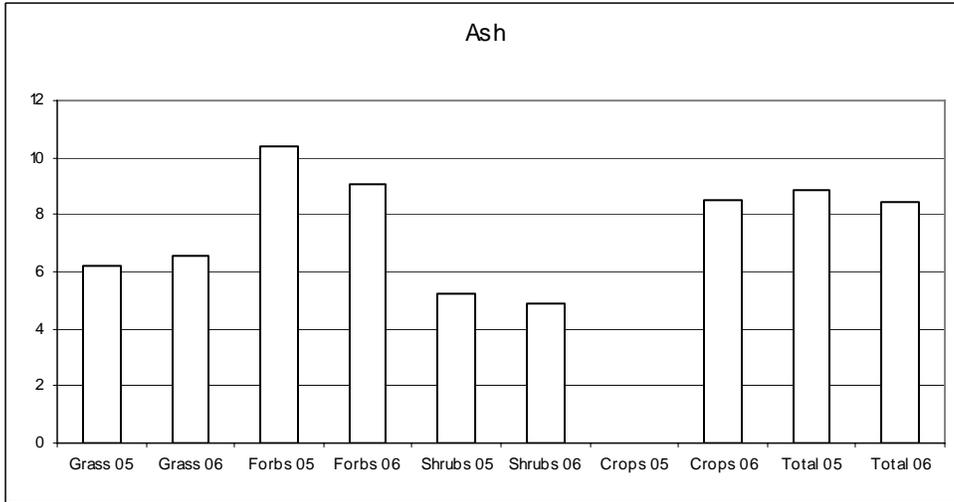
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As expected, correlation between the nutritional values of the plant classes and their major component species revealed that they were strongly associated. Grasses, made up of 55.5% *Agropyron* spp in 2005 and 78.6% in 2006, were almost perfectly correlated with that species ($r = 0.937, 0.967$), with increasing values as the proportion of *Agropyron* increased. *M. fistulosa* comprised 3.2% of all forbs consumed in August 2005 and 31.5% in August 2006, yet it was poorly correlated with overall Forb nutrient values (0.351%, 0.391%).

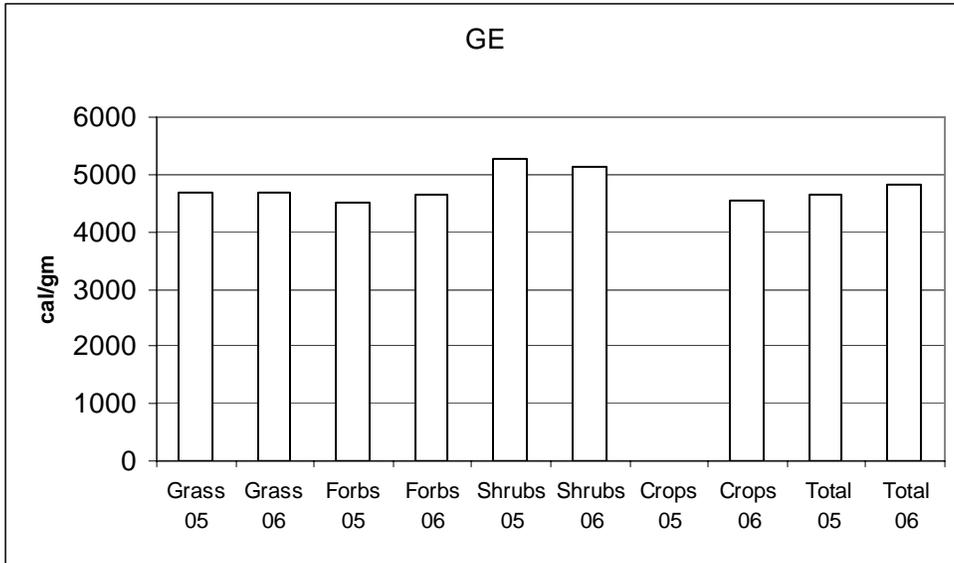
Comparing the nutritional values of the Total Diets and plant classes, several patterns emerge (Figure 4.3). Most importantly, although values for constituent classes changed when the class Crops was introduced, the Total Diet values remained relatively constant. Total Ash for Crops in 2006 was higher than that of the Grasses and Shrubs although marginally lower than that of Forbs they supplanted in 2006, resulting in a marginally lower overall Total Ash score for Total Diets in 2006 than 2005. GE remained very similar between years in all plant classes and for the Total Diet, with Crop values approximately equal to those of the Forbs they supplanted. Crude Fat increased very slightly in the grasses and a little more among the shrubs while the Crude Fat in Crops was much lower than that of Forbs. There was a net decrease in Crude Fat in the 2006 Total Diet. NDF levels for crops were very similar to those of Forbs in 2006, and Total levels remained static, although Shrub NDF did see a very slight increase. The higher values for ADF in Crops and the small increase in Grasses and Shrubs offset the decrease in Forbs, resulting in a net increase for Total Diet. ADL rose in 2006 in all classes,

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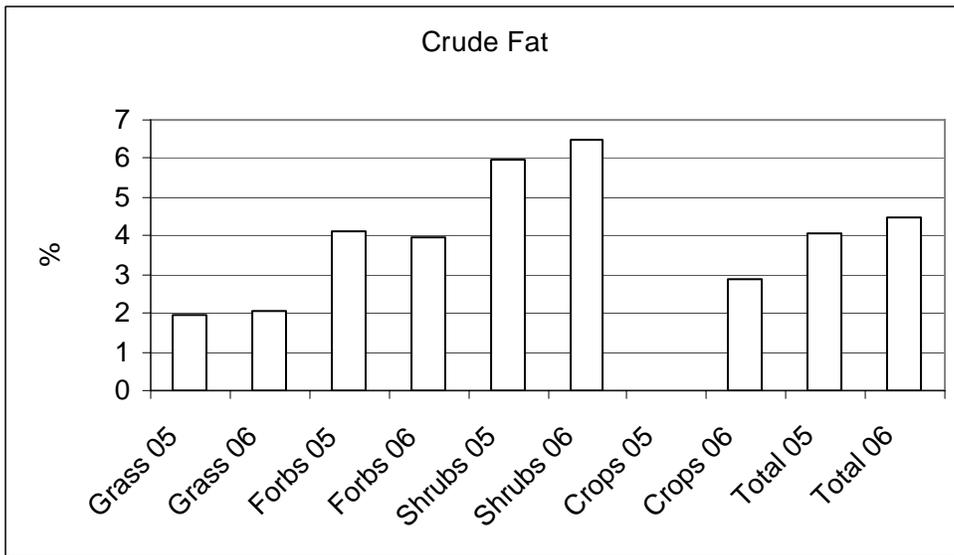
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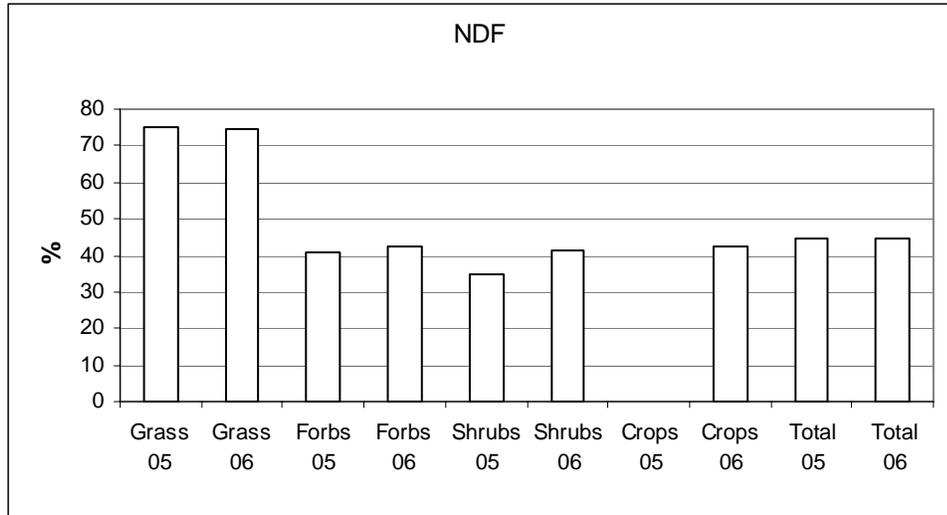
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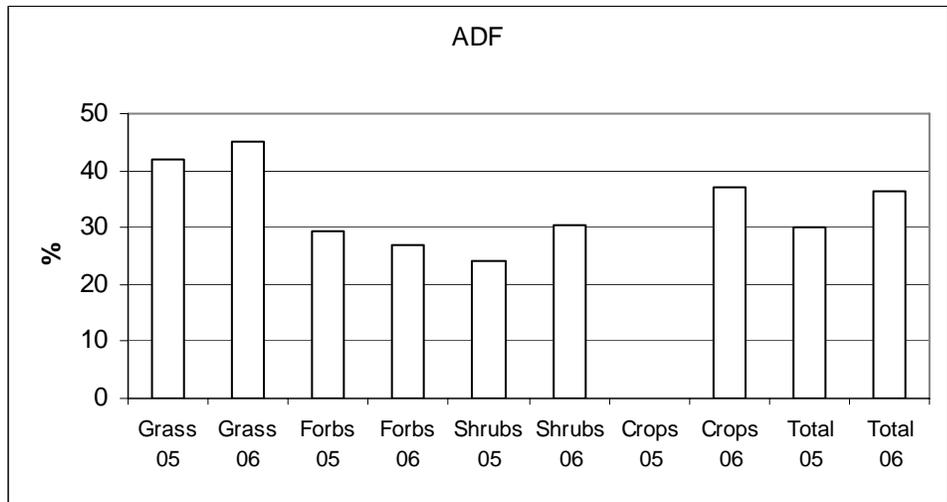
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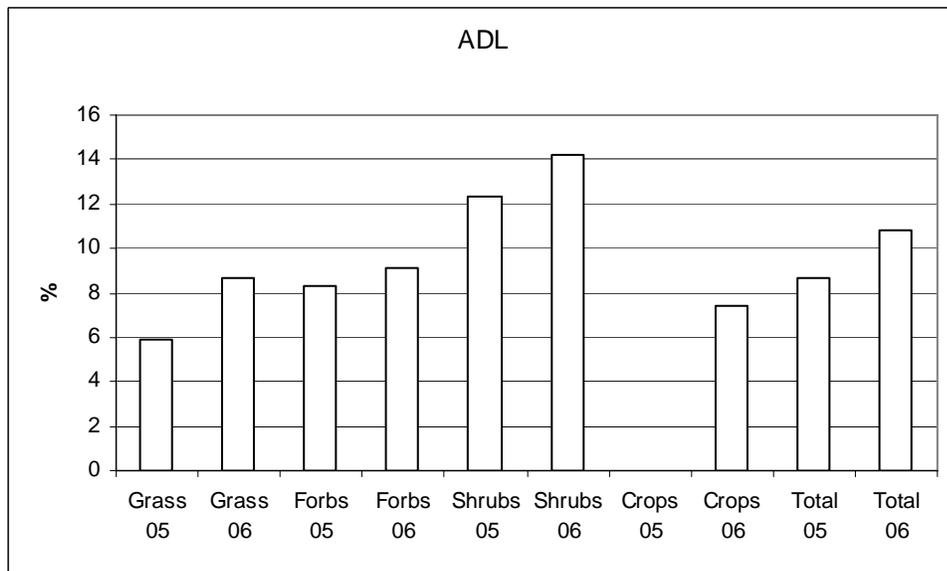
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f.



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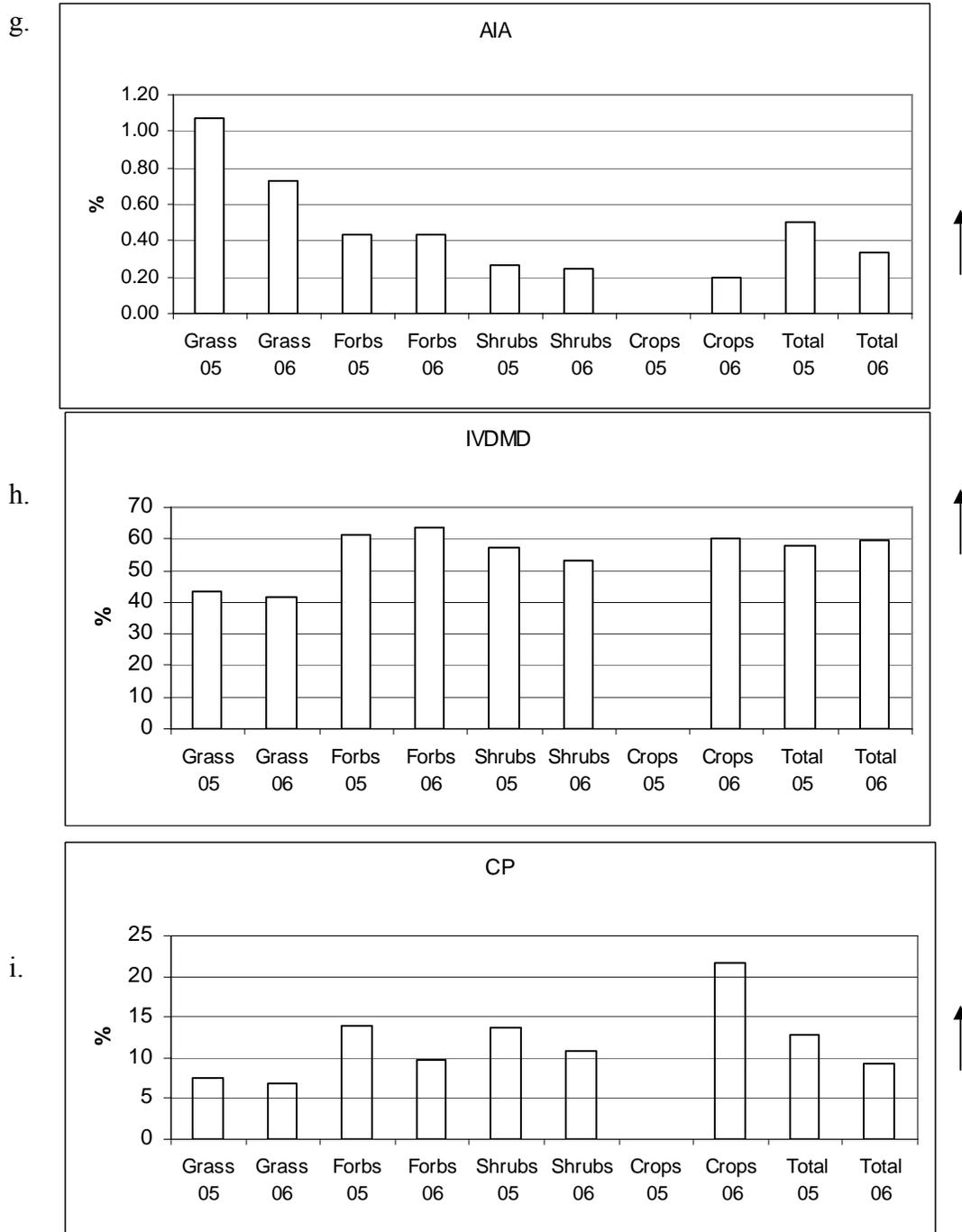


Figure 4.3. Bar graphs of dietary nutrients, by dietary class and year. Most Total Diet nutritional measures are very similar between years despite the different components in many of the classes, especially Forbs. The arrows indicate how the Total 06 diet would likely have been influenced if sunflower was indeed consumed in large quantities, as is suspected. In all cases, less NDF and IVDMD, the resultant values would have been even more similar to those of 2005.

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especially Grasses and Shrubs. ADL in Crops was less than that of Forbs. Grasses experienced a sizable decrease in AIA while that of Forbs and Shrubs remained relatively constant. The very low AIA values for Crops contributed to an overall decrease in AIA for Total Diets. IVDMD scores for Shrubs, Crops, and especially Forbs were very similar in both years and across classes, meaning that the Total Diet scores changed very little over time. Of the plant classes, only Grasses had IVDMD levels well below what is deemed to be necessary for animal maintenance (Gray and Servello 1995, Verme and Ullry 1984). Their persistence in the diet must be assumed to be because of other contributions they make to the animal's health.

Finally, the CP found in Crops was the highest of all plant classes, but the introduction of higher CP values in the 2006 diet was counterbalanced by the decrease among Forbs and Shrubs, again resulting in very similar CP values for Total Diets in both years. In almost all categories, deer appear to have adjusted the constituent components of their diet between treatments in order to maintain constant combined nutritional values while endeavouring to maximize net energy gains. Given the strong correlation between CP and IVDMD, maintaining CP levels constant while increasing IVDMD must have been a deliberate strategy (Figure 4.4).

Correspondence Analysis (CA)

Treating the nutritional values as variables and Total Diet, plant class, and principle species as objects, the data was analyzed using CA (Figure 4.5). The cumulative

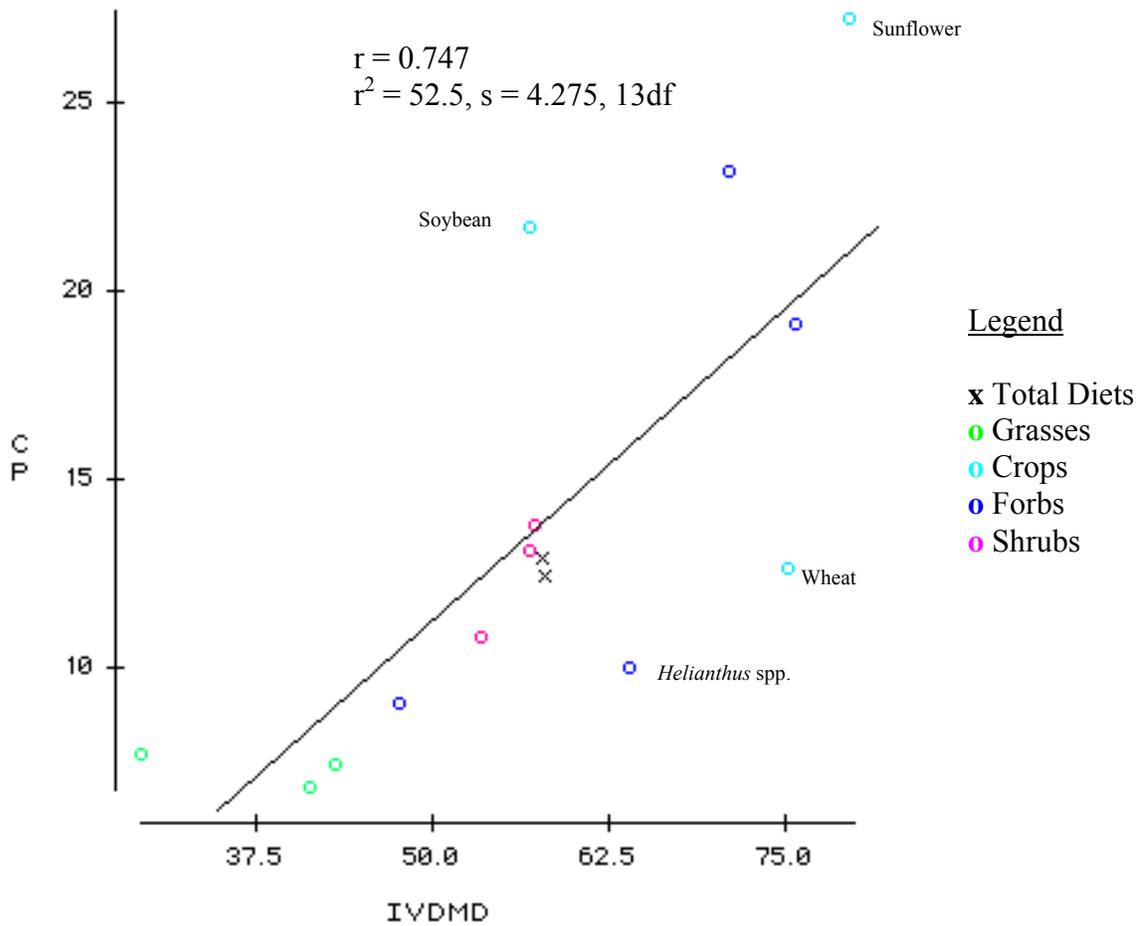


Figure 4.4. IVDMD plotted against CP. There is a strong linear relationship between these two nutritional measures. It is apparent that the high CP content of soybean in 2006 was offset by a corresponding reduction of CP elsewhere, largely from Forbs. The Total Diet CP and IVDMD values changed very little between the No Crop and Crop treatments, despite the high CP value of soybean.

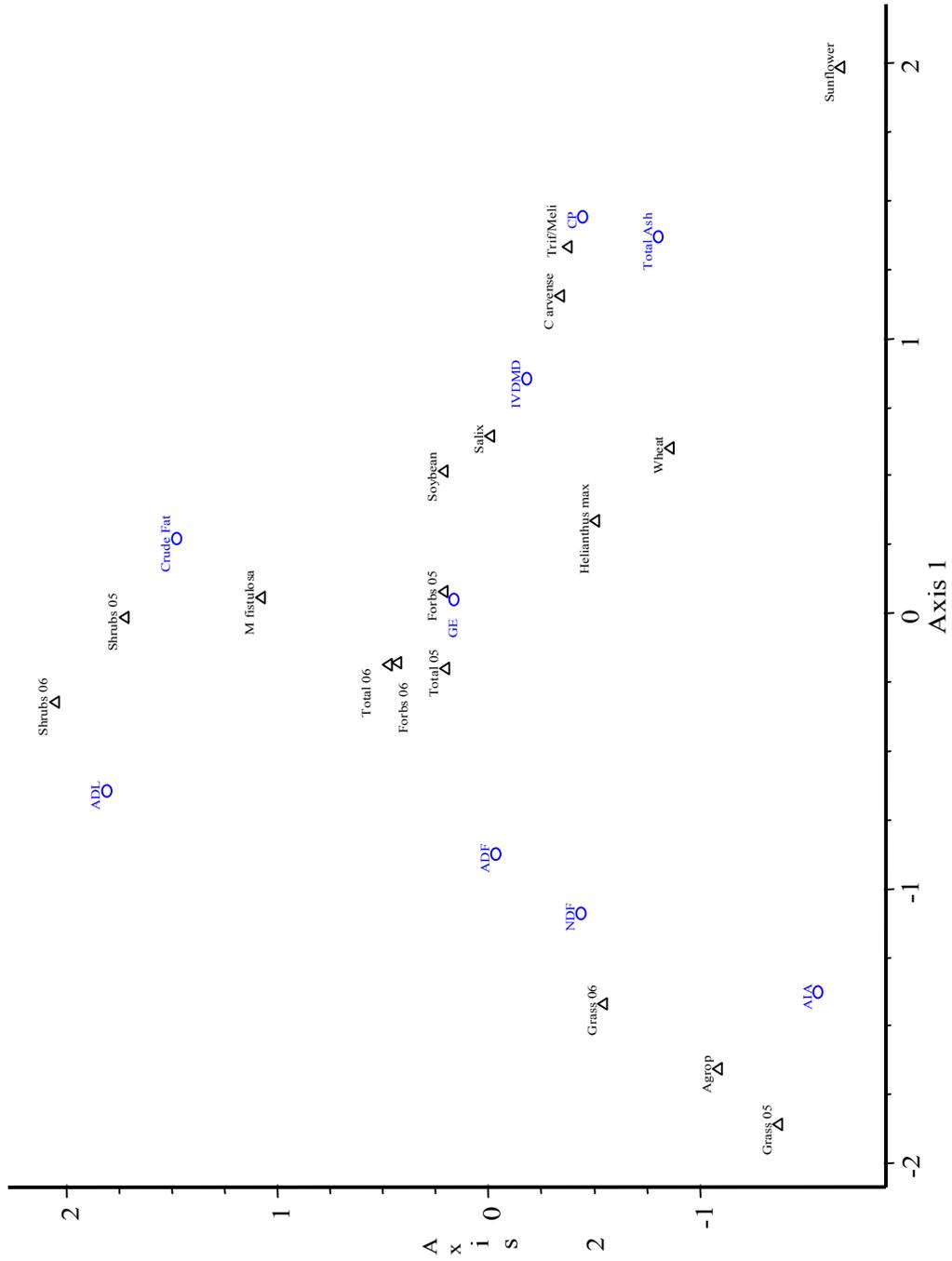


Figure 4.5. CA of Diet by Year and Component. Cumulative percentage of eigenvalues is: Axis 1 52.29%, Axis 2 82.55 %. All values were normalized by the mean to correct for scale and then symmetrical weighting was applied to enhance separation of the objects.

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percentage of eigenvalues was 52.29% on Axis 1 and 82.55% on Axis 2. The overall arch effect of the distribution of variables occurred because the data reflects an ecological gradient; diets and species high in digestible compounds tend to have lower non-digestible elements, allowing the majority of the data to be explained on a single axis (Legendre and Legendre 1998).

As expected from the data, each of the plant classes and the Total Diets were grouped closely together, with Total Diets being positioned centrally along with Forbs. Soybean, almost exclusively the only crop to appear in the 2006 diet, was located centrally to Forbs. By species, *Agropyron* spp was grouped with Grasses, *M. fistulosa* most closely to Shrubs, and wheat, *C. arvense*, *Trifolium/Melilotus (TM)*, and *Helianthus max* are loosely associated. The principle outlier was Sunflower. This crop, which did not appear in the corrected diet even though it was adjacent to the study site, had scores that were very dissimilar to those of all other dietary components and had comparatively high Total Ash and CP values and low NDF and ADL values. Its AIA was approximately at the mean value. The variables most closely associated with Grass are AIA and, to some degree, NDF. Aligned with Shrubs were ADL and Crude Fat whereas Total Ash, CP, and IVDMD were grouped more closely with the forb species and crops. GE was centrally located, suggesting that it played a minor role in explaining the dispersion of the objects.

Principle Component Analysis (PCA)

Analyzing the data with PCA, a large portion of the variance was explained along the first two axes (Axis 1: 51.81%, Axis 2: 26.11%, cumulative: 84.91%) (Figure 4.6).

Objects (plant classes and species) and variables (nutrient values) were dispersed in a manner similar to that of CA. The eigenvectors for GE and ADL, however, were very alike in both magnitude and direction, underscoring the previous observation that GE may be more of a reflection of total combustible energy vice digestible energy. Also notable were the opposing eigenvectors for IVDMD and ADF, portraying the strong negative correlation found previously. The eigenvectors for AIA and ADL were also negative in direction to that of IVDMD, but the angle of opposition was more acute. Last, the Euclidian distance separating Total Diets from their respective Forb components increased in 2006, likely because of the great increase in *M. fistulosa* consumption that year.

Energetics

Comparing diet to the vegetative cover survey, no off-site foraging occurred beyond 2,186m from the forest's centre or 1,250 from the forest edge (Table 4.5 and Figure 4.7).

This was to obtain soybean leaf; unprocessed soybeans contain biochemicals that interfere with the digestive process of at least some wildlife (Krapu et al. 2004). Alfalfa, which was part of the *Triflorium/Medicago/Melilotus* portion of the Forb diet, was located 1,623m from the forest centre but just 832m from the nearest forest edge.

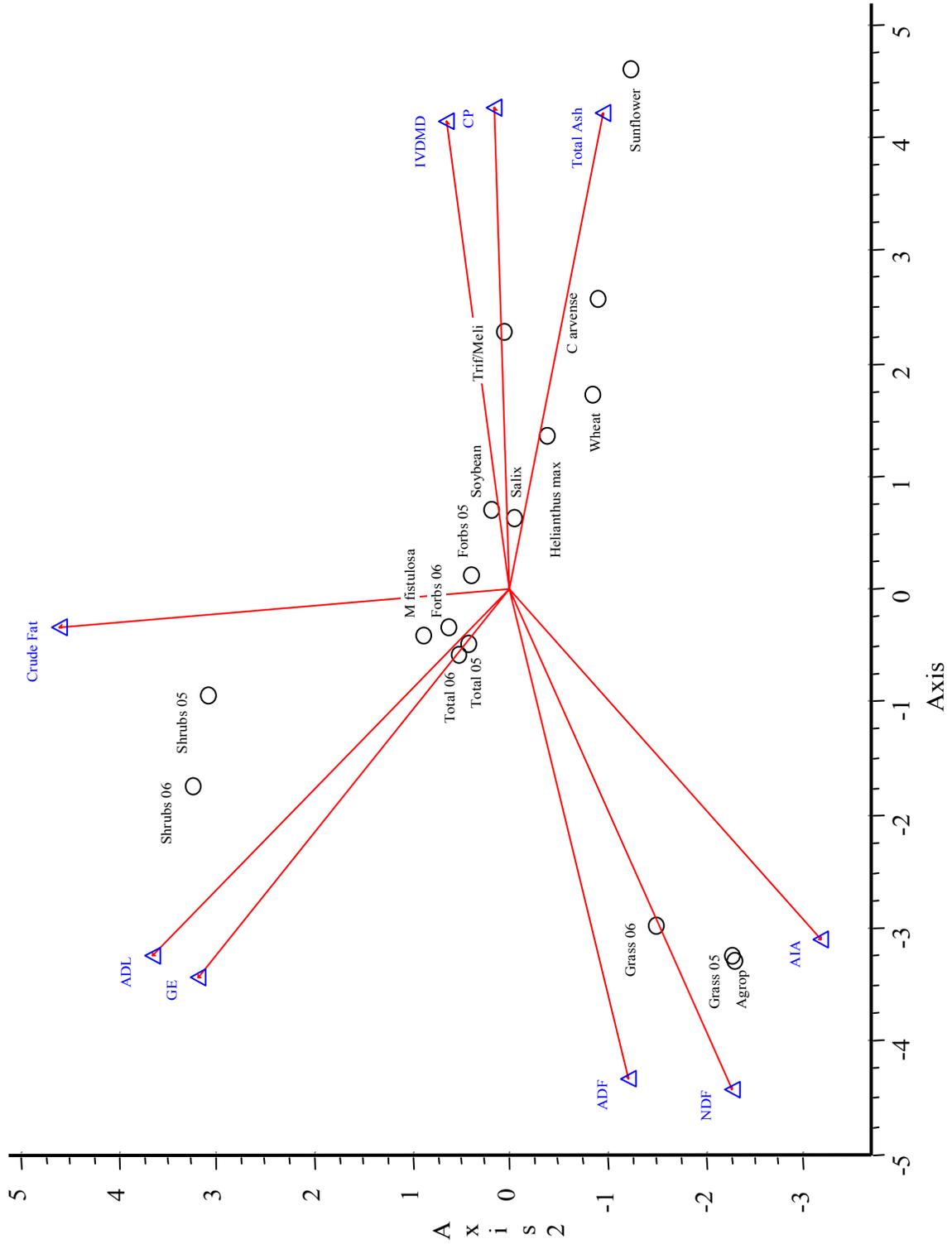


Figure 4.6. PCA of Dry Matter Nutritional Value. Percent eigenvalues for Axis 1 is 51.81%, Axis 2 is 26.11%, for a cumulative total of 84.91%.

Table 4.5. Shortest Distance to Forage. The distance from (a) the centre of the forest to the nearest source of each particular forage type and (b) from the nearest forest edge to each particular forage type. By relocating on site, deer were never required to travel more than 2000m from thermal shelter to forage

Crop	<u>Distance (m)</u>	
	Centre of Forest	Edge of Forest
Wheat/Barley	1355	576
Oats	498	30
Canola	625	156
Winter wheat	2421	1918
Sunflower	879	30
Soy bean	2186	1250
Flax	2778	2330
Hay	1623	878
Grass	0	0
Suburban	2780	2006

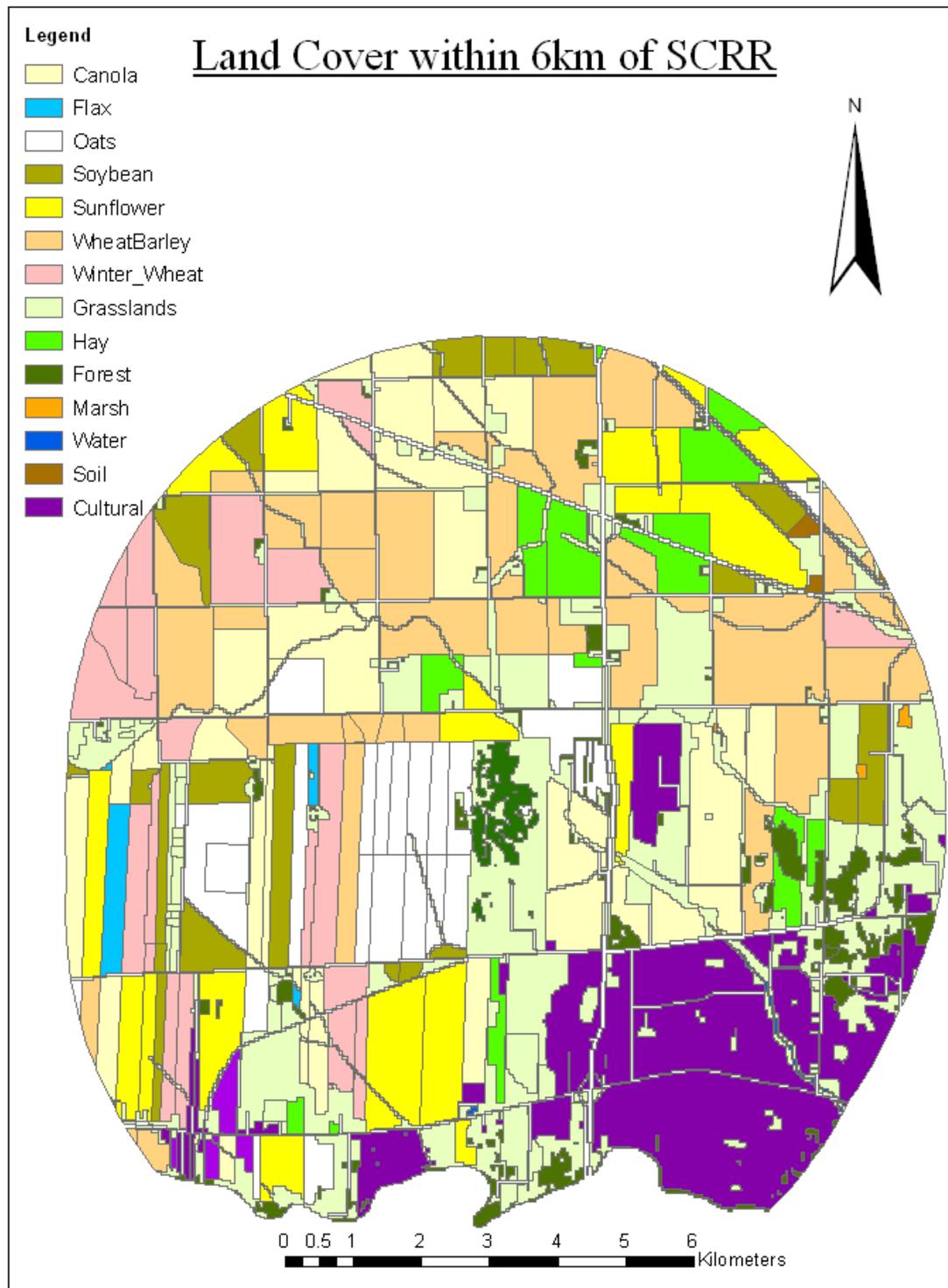


Figure 4.7. The cultural areas to the south and east (purple) are primarily sports fields, golf courses, and other recreational areas. Urban development begins in the southeast block east of the highway.

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Because of volunteer alfalfa in ditches and along field edges it is unclear if the consumption of *Medicago* occurred closer to home.

On-site, the deer shifted away from the clearings in the centre of the forest that they had inhabited and from which they obtained a large portion of their diet in 2005 and moved to the extremities of the forest, especially to the north and south. From the south they could more readily access soybean whereas in the north they could access wheat and tame hay (Figure 4.8). They also appeared to reduce foraging activity within the tallgrass prairie, perhaps seeking thermal shelter on site more than forage when crops were available. The continued concentration of deer in and along side of the northeastern portion of the aspen forest suggests both local intensive grazing and that the location served as a diurnal waiting area. Adjacent was a sunflower field, which separated the deer from the closest wheat field just 576m away although no sunflower appeared in the fecal analysis.

DISCUSSION

Nutrition

Despite a large overlap of constituent species in the white-tailed deer diets in both treatments, the diets themselves were significantly different in terms of the relative importance of each plant species in the overall diet. The presence of crops prompted a large reduction in the amount of native forages and browse consumed. This was especially true for Forbs and to a lesser extent Shrubs and Grasses. The variance in forb composition may have partly been the product of the very different moisture regimes that

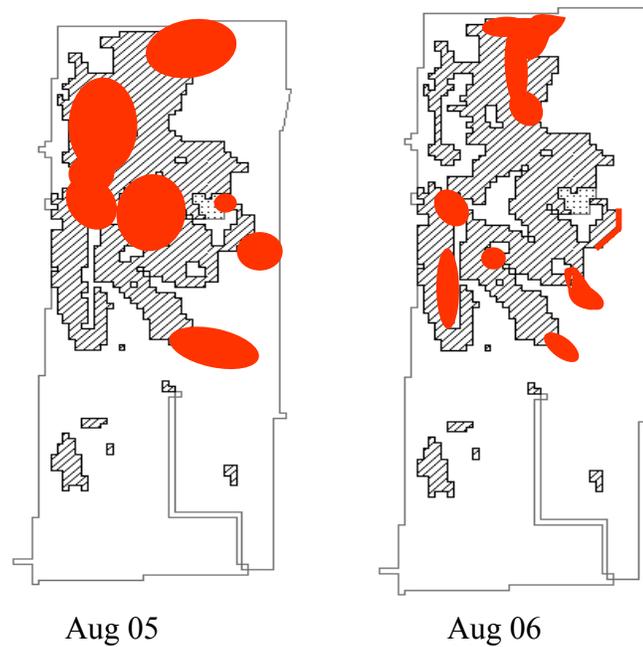


Figure 4.8. Deer habitat areas. The regions delineated in red indicate where the deer were found to spend the greatest amount of time during each of the years, as indicated by deer beds, feces, and animal presence.

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existed in each of the two years, shifting relative floristic composition and abundance as well as relative nutritional values. Nevertheless, the resultant total nutritional value of the two diets was remarkably similar as were many of the scores for many of the dietary measures, notably CP, IVDMD, NDF, and ADF.

These latter three measures underscore the congruities in digestibility of the two diets. This finding is especially interesting given that crops supplanted a quarter of the 2005 diet in 2006. These crops were almost completely soybean leaves, which have a very different nutritional profile than the plants they replaced. In particular, soybean had greater IVDMD and CP and lower ADL and ADF values than the Total Forbs they supplanted. The consistency of nutritional value of the two Total Diets despite the variations in constituent classes suggests that white-tailed deer are able to assess forage quality and to make dietary selection decisions based upon this assessment.

The introduction of high-energy row-crops in 2006 allowed the white-tailed deer to graze high energy, high protein, and easily digestible foods while reducing foraging effort. Rather than grazing across the tallgrass prairie in search of a host of small, often difficult-to-locate forbs and plants, the deer had only to walk to the soybean field to the southwest. Thereafter, little locomotive energy was necessary. Thus without an absolute nutritional gain the deer were able to realize a net energy gain through reduced search effort.

As expected, the deer managed to optimize protein intake by selecting a diet that offset the exceedingly high protein of soybean leaves, thus continuing to maximize energy

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intake. CP requirements for deer vary by age, sex, and time of year. Numerous studies have arrived at differing conclusions, but normal maintenance levels fall somewhere between 6-7% for adult deer with 16-17% meeting all climactic and physiological conditions (Meyer et al.1984, Aselson et al. 1997). The amount of accessible protein is usually assumed to be 70% of the plant's CP value, but the actual percentage varies greatly depending on the dietary protein concentration and the concentration of soluble digestion inhibitors (Hanley and McKendrick 1985). In beef cows on poor forage, digestion was maximized when protein levels of 11.1% were achieved (Köster et al. 1996), very similar to the 12.92% and 12.28% levels maintained by the white-tailed deer. The deer appear to have kept CP intake constant at least partly by actively selecting less digestible, high energy plants such as *M. fistulosa*, which is deficient in CP but high in fat and GE. They also continued to ingest Grasses, which are low in IVDMD but also in CP. Conversely, Forbs and to a lesser extent Shrubs, which are relatively high in CP, were selected less often.

Concurrent to optimizing, and thus selecting against over consumption of, CP in 2006, deer profited from the higher energy row-crops that were then available, maximizing intake. On their own, IVDMD values in Grasses are the lowest amongst all plant classes and is deficient for animal maintenance (Verme and Ullry 1084). It is possible, however, that Grasses remained important for their high hemicellulose content, as measured by the difference of NDF and ADF (32.78% in 2005, 29.43% in 2006). Accessed through rumen-reticulum digestion, it may have complimented the high digestibility and, thus, very high passage rates of soybean and succulent forbs. Not nearly as digestible as these

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other plants, Grasses and, to a lesser extent Shrubs, may have added the necessary fibre to maximize rumen-reticulum function and thereby maximize nutrient extraction. Rapid increases in dietary digestibility can disrupt the functioning of the rumen-reticulum, at least until the resident bacteria has had time to adapt (Berteaux et al. 1998, Verme and Ullry 1984). Given that the only crop found in the June and July 2006 diets was soybean, at uncorrected intake levels of 0.6 and 5.8% respectively (Chapter 2), the rapid increase of highly digestible soybean intake may have posed some difficulties if other less digestible forages had not been added to the diet.

Crude Fat values persisted over time in the Total Diet (4.09%, 3.74%), largely due to continued Shrub consumption intake (5.97%, 6.47%). Because Crude Fat is a measure of a heterogeneous mixture of high-energy compounds (Robbins 1993), especially in leaves, the precise nutritional value is difficult to ascertain, other than to observe that it would appear that the generally lower levels found in soybean were offset by a marginal increase in Shrubs.

Nutritional Markers

The failure of AIA and ADL to strongly correspond with IVDMD as has occurred elsewhere is puzzling, as AIA represents that portion of the diet that is almost completely indigestible. This discrepancy may be partially related to the relatively low digestibility of some native forages as compared to livestock feeds. Block et al. (1981) found that AIA was a less effective marker when digestibility levels were <50%. Reviewing their results,

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the correlation between AIA and IVDMD was not consistently strong until closer to 60%. IVDMD for Grasses were below 44% and only Crops were well above the threshold of 60%. Based on these findings the use of AIA as a digestibility marker for free ranging white-tailed deer is not recommended.

The much stronger linearity of ADF and IVDMD is, nevertheless, plausible. ADF largely represents what is left after the neutral detergent solubles, hemicellulose, and pectin are essentially removed during digestion, although some cellulose and lignin can be partially digested (Robbins 1993, Mould and Robbins 1981). Its advantage over NDF is that pectin, which is easily digested in the rumen and therefore does not degrade digestibility, is not removed by the NDF method. Dicots tend to have high levels of pectins (Bruinenberg et al. 2002) and, thus, elsewhere, their NDF values have been found to be weakly correlated with IVDMD (Solorio-Sanchez et al. 2000). NDF is more closely related to voluntary dry matter intake (VDMI) and inversely to gut retention (Allen 1996).

Thorn Intake

The nutritional value of *C. arvensis* was investigated in order to better understand why a ruderal, equipped with thorns as an anti-herbivory defence mechanism, was such a large part of the overall diet both with and without crops (4.2%, 3.9%). In feeding trials with tame white-tailed deer, the thorns of three thorny browse species in southern Texas and northern Mexico did not affect browse intensity, although the researchers speculated that

they have been more effective against lagomorphs and small herbivores (Cash and Fulbright 2005). Nutritionally, *C. arvensis* is similar to the cumulative nutritional values of the Total Forb diets, except that it has a higher IVDMD and CP, falling more in line with Crops but with lower AIA. This would make the cost of consumption worthwhile. The samples used were collected in October after senescence, when nutritional values may decrease as new growth stops and nutrients are translocated to the roots. The relatively constant rate at which this plant was selected in both years suggests that it is an important dietary element regardless of what other foods are available.

Undetected Dietary Components

The most difficult factor to take into account is the unknown. Because dietary composition was determined using fecal microhistological analysis, not all plants consumed could be identified, particularly those plants or plant structures that are highly digestible. Early spring/early summer forbs are particularly susceptible to complete digestion due to the fragile nature of their succulent structures (Free et al. 1970, Bartolomé et al. 1995), while flowers and some other fleshy tissues in general are also likely escaped detection. For example, certain plants known to be favoured by the white-tailed deer or whose stems bore evidence of recent herbivory failed to appear in the fecal analysis, notably domestic sunflowers and canola flowers.

Canola leaves are toxic to deer but many animals are attracted to the flowers (Schwabb et al. 2001). During the last week of July 2006 deer were observed moving in large numbers

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to the adjacent canola field to the east, cutting a 45cm-wide movement trail through the tallgrass prairie in the process and establishing numerous deer beds along the edge of the field. The following week, the trail and beds were abandoned. Next, sunflowers are highly digestible and, because of their thick stems and heavy leaves, there is a lower surface/volume ratio. The resident deer cleared a 20m swath in the area immediately next to the forest on the northern end of the study site during mid to late summer. It is possible that significant volumes of sunflower plants were consumed but that they did not appear in the feces. Further, the laboratory indicated that some of the *Helianthus* spp reported in the diet may have in fact been domestic sunflower.

If sunflower phytomass formed part of the actual 2006 white-tailed deer diet, the dietary and nutritional values found during this study would need to change. Re-examining the plant class and Total Diet comparisons in Figure 4.3, arrows have been placed to indicate the direction the 2006 Crop and Total Diet bars would need to be adjusted. The magnitude of these changes for the Total Diet cannot be accurately calculated given the complex interactions involved in digestion, yet it is possible that the net effect would be to increase correlations between Total Diets, with some exceptions. IVDMD would certainly increase. Referring to the placement of variables in PCA (Figure 4.6), the inclusion of sunflower would shift Total Diet 06 to the right as a result of the much higher IVDMD, CP, and Total Ash values. Based on the fibre values of sunflower it could be expected that gut retention times would decrease to some degree; the very low NDF value indicates that relatively few nutrients would be extracted in the rumen-reticulum, meaning that overall passage rates would increase and the degree of nutrient

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extraction from other feeds would be reduced (Robbins 1993). Net energy would also likely increase. This finding further supports the premise of Optimal Forage Theory that white-tailed deer seek to maximize energy intake.

Energetics

To maximize net energy gains the resident deer population continuously shifted their location within the study site's forest in order to be closer to its primary feeding stations. The avoidance of much of the forest during 2005 reflected the severe flooding conditions, pushing the animals onto the prairie edge during the day instead of inside, shaded from the sun's heat. But the deer also foraged across the site's open fields in 2005, reflected by the size of the areas in which they were moving, bedding, and defecating. In 2006 they continued to graze on site but also congregated more densely during the day, waiting to move off-site to forage and nearby crops. While does were likely more dispersed than males for about four weeks during fawning (Nixon et al. 1991), as a group the deer tended to congregate nearest to their preferred foods (Chapter 2). Vecellio et al. (1994) found that such concentrations of white-tailed deer could inflict intensive damage on crops. Near the deer congregating area located in the northeastern portion of the forest, every saskatoon (*Amelanchier anifolia*) stem, a favoured food for white-tailed deer, showed signs of recent browsing. Similar herbivorous pressure could be expected to be exerted on the native tallgrass prairie flora.

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There must be a clear net energy gain to induce herbivores to travel. Flax, a known deer food in Manitoba (Garrod et al. 1981), was located approximately 2.7km from the centre of the study site and 2.3km from the nearest edge yet was not consumed. The closest urban dwellings and their associated - and often browsed - ornamental plants (Schwab et al. 2001, Conover and Kania 1988) were 2km away but also did not appear in the diet. Soybean was 1,250m from the nearest forest edge and was consumed in large quantities while winter wheat, located 1,926m away, was completely avoided after spring leaf-out. These figures seem to support the finding that food plots within 1.5km of deer habitat are effective in attracting them to feed (Chapter 2). The reason for the presence of only trace amounts of summer wheat in August 2006 (winter wheat was harvested by end-July) despite its high nutritional value and close proximity (576m) is less obvious. This distance falls within the 670m radius from woodlands found to suffer greater crop predation (Vecellio et al. 1994). A possible explanation is that the deer were obtaining enough nutrients from the sunflower field adjacent to the north end of the study site that there was insufficient advantage to be had by travelling on to the wheat, an inferior food in almost every respect to sunflower. The presence of 0.3% wheat in the diet likely represents periodic sampling vice active selection. Further, soybean was located in the exact opposite direction to wheat, meaning that deer had to choose which crop they would consume. It is possible that some animals grazed both crops during different feeding sessions or that the site's deer divided themselves into sub-populations, one moving north and the other moving south. The absence of sunflower from the fecal analysis despite the strong evidence supporting its grazing makes a clear conclusion difficult.

MANAGEMENT IMPLICATIONS

Despite the high energy and IVDMD values of row-crops, it does not appear that they can provide a complete balanced diet for white-tailed deer. These large herbivores must therefore continue to rely heavily on other forages to meet their total nutritional requirements. What row-crops do provide, however, is a net increase in deer energy budgets by reducing foraging effort, ensuring that high population densities persist. Indeed, densities may continue to increase as high fecundity rates are maintained and mortality is minimized (Verme and Ullry 1984). All of this means that grazing pressure on the study site's remnant tallgrass prairie flora will persist, placing the survival of many favoured species at risk. Some species, such as *Gaillardia aristata*, *Astregalas agretis*, *Amorpha nana*, *Agoseris glauca*, *Oenothera biennis*, and *Lithospermum canadensis*, and *Lonicera dioctera* continue to appear in the diet but are only present in low to very low numbers. Other species, such as *Quercus macrocarpa*, may be prevented from reproducing as their mast, a favoured dietary element elsewhere, is completely consumed (Healy 1997, Murphy et al. 1985). At least some of the locally rare plants, such as *Lilium philadelphicum*, appear to be grazed shortly after they emerge, barely hanging on.

At high densities white-tailed deer can, collectively, know an entire site (Focardi et al. 1996). This may be the case at Saint Charles Rifle Range, encouraging deer to intensively graze all stems of their most favoured species. To reduce this risk posed to this endangered ecosystem there are two possible options. First is to reduce the resident deer population through active management. While useful, declining hunter numbers, land

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access restrictions, an unwillingness by hunters to kill antlerless deer, and the new restrictions on rifle hunting in the study area may reduce the effectiveness of this course of action (Riley et al. 2003, Brown et al. 2000). Further, given the instability of white-tailed deer populations in an agricultural landscape (Nixon et al. 2006), any local reductions would likely result in other animals moving onto the site.

A second option could be expensive in the short term but would leverage deer energy maximization strategies to advantage and possibly minimize ongoing population management costs. Because white-tailed deer will not forage from thermal cover at distances greater than 1,500m, placing a deer fence around the entire Rifle Range, leaving a standard 1.3m gate at the southern entrance, would force the deer to travel at least 1,620m to reach the nearest row-crop to the east and 2,085m to the west. While it is likely that some deer would remain on site, they would be at much greater risk of mortality through natural coyote predation and winter starvation, especially in years where the deer are forced to yard. During the winter without crops 17 dead deer were found (12.6% of the total population), in contrast to the 2 deer found in the winter of 2006 (1.4%). By eliminating the nutritional advantage afforded deer by row-crops, a more ecologically appropriate deer density and disturbance regime should evolve on the study site.

LITERATURE CITED

- Allen, M.S. 1996. Physical constraints on voluntary intake of forages by ruminants. *Journal of Animal Science*. 74:3063-3075.
- Arnold, L.A. and Drawe, D.L. 1979. Seasonal food habits of white-tailed deer in the south Texas plains. *Journal of Wildlife Management*. 32:175-178.
- Asleson, M.A., Hellgren, E.C., and Varner, L.W. 1997. Effects of seasonal protein restriction on antlerogenesis and body mass in adult male white-tailed deer. *Journal of Wildlife Management*. 61:1098-1107.
- Bartolomé, J., Franch, J., Gutman, M., and Seligman, N.G. 1995. Technical Note: Physical factors that influence fecal analysis estimates of herbivore diets. *Journal of Range Management*. 48:267-270.
- Berteaux, D., Crete, M., Huot, J., Maltais, J., and Ouellet, J-P. 1998. Food choice by white-tailed deer in relation to protein and energy content of the diet: a field experiment. *Oecologia*. 115:84-92.
- Block, E., Kilmer, L.H., and Muller, L.D. 1981. Acid insoluble ash as a marker of digestibility for sheep fed corn plants or hay and for lactating dairy cattle fed hay *ad libitum*. *Journal of Animal Science*. 52:1164-1169.
- Brown, T.L., Decker, D.J., Riley, S.J., Enck, J.W., Lauber, T.B., Curtis, P.D. and Mattfeld, G.M. 2000. The future of hunting as a mechanism to control white-tailed deer populations. *Wildlife Society Bulletin*. 28:797-807.
- Bruinenberg, M.H., Valk, H., Korevaar, H., and Struik, P.C. 2002. Factors affecting digestibility of temperate forages from semi-natural grasslands: a review. *Grass and Forage Science*. 57:292-301.
- Carpenter, L.H., Wallmo, O.C., and Gill, R.B. 1979. *Journal of Wildlife Management*. 32:226-229.
- Cash, V.W. and Fulbright, T.E. 2005. Nutrient enrichment, tannins, and thorns: effects on browsing of shrub and seedlings. *Journal of Range Management*. 69:782-793.
- Caton, J.S., Freeman, A.S., and Galyean, M.L. 1988. Influence of protein supplementation on forage intake, in situ forage disappearance, rumenal fermentation and digestion passage rate in steers grazing dormant blue gamma rangeland. *Journal of Animal Science*. 66:2262-2271.

Chapter 4: Nutritional advantage afforded by row crops

- Clauss, M., Lechner-Doll, M., Flach, E.J., Tack, C., and Hatt, J-M. 2001. Comparative use of four different marker systems for the estimation of digestibility and low food intake in a group of captive giraffes. *Zoo Biology*. 20:315-329.
- Conover, M.R. and Kania, G.S. 1988. Browsing preference of white-tailed deer for different ornamental species. *Wildlife Society Bulletin*. 16:175-179.
- Côté, S.D., Rooney, T.P., Tremblay, J-P, Dussault, C, and Waller, D. 2004. Ecological Impacts of Deer Overabundance. *Annual Review of Ecology, Evolution, and Systematics*. 35:113-147.
- Coulon, A., Guillot, G., Angibault, J.M.A., Aulagnier, S., Cargnelutti, B., Galan, M., and Hewison, J.M. 2006. Genetic structure is influenced by landscape features: empirical evidence from a roe deer population. *Molecular Ecology*. 15:1669-1679.
- Cullison, A.E. 1982. *Feeds and Feeding*, 3rd Edition. Reston Publishing Company. Reston, Virginia, USA.
- Davitt, B.B. 1979. Elk summer diet composition and quality on the Colockum Multiple Use Research Unit, Central Washington. M.S. Thesis (unpublished). Washington State University, Pullman, WA, USA.
- Dorshorst, M.E. and Grummer, R.R. 2001. Effects of day relative to parturition and dietary crude protein on rumen fermentation in prepartum transition cows. *Journal of Dietary Science*. 85:2290-2298.
- Eberhardt, L.E., Hanson, E.E., and Caldwell, L.L. 1984. Movement and activity patterns of mule deer in the sagebrush-steppe region. *Journal of Mammalogy*. 65:404-409.
- Etzenhouser, M.J., Owens, M.K., Spangler, D.E., and Murden, S.B. 1998. Foraging behaviour of browsing ruminants in a heterogeneous landscape. *Landscape Ecology*. 13:55-65.
- Flinders, J.T. and Hansen, R.M. 1972. Diets and habits of jackrabbits in northeastern Colorado. Range Science Department Science Series No 12. Colorado State University, Fort Collins, CO, USA.
- Focardi, S., Marcellini, P., and Montrano, P. 1996. Do ungulates exhibit a food density threshold? A field study of optimal foraging and movement patterns. *The Journal of Animal Ecology*. 95:606-620.
- Free, J.C., Hansen, R.M, and Sims, P.L. 1970. Estimating Dry Weight of Food plants in Feces of Herbivores. *Journal of Range Management*. 23:300-302.

Chapter 4: Nutritional advantage afforded by row crops

- Garrod, R.C., Shoesmith, M.W., and Stewart, J.M. 1981. Rumen analysis of white-tailed deer, elk, and moose killed by hunters and vehicle collisions in Manitoba. Department of Botany, University of Manitoba. Winnipeg, Manitoba, Canada.
- Gray, P.B. and Servello, F.A. 1995. Energy intake relationships for white-tailed deer on winter browse diets. *Journal of Range Management*. 59:147-152.
- Hanley, T.A. and McKendrick, J.D. 1985. Potential nutritional limitations for black-tailed deer in a spruce-hemlock forest, southeastern Alaska. *Journal of Wildlife Management*. 49:103-114.
- Healy, W.M. 1997. Influence of deer on the structure and composition of oak forests in central Massachusetts. Pages 249-266 *in* McShea, W.J and Underwood, H.B., editors. *The Science of Overabundance: deer ecology and population management*. Smithsonian Books, Washington D.C., USA
- Holchek, J.L. and Vavra, M. 1981. The effect of slide frequency observation numbers on the precision of microhistological analysis. *Journal of Range Management*. 34:337-338.
- Holechek, J.L. and Gross, D.B. 1982. Evaluation of different diet calculation procedures for microhistological analysis. *Journal of Range Management*. 35:721-723.
- Houston, A.I. 1993. The importance of state. Pages 10-13 *in* R.N. Hughes, editor. *Diet Selection: An Interdisciplinary Approach to Foraging Behaviour*. Oxford University Press, Don Mills, ON, Canada.
- Hunt, H.M. 1979. Summer, autumn, and winter diets of elk in Saskatchewan. *The Canadian Field Naturalist*. 93: 282-287.
- Illius, A.W., and Gordon, I.J. 1993. Diet selection in mammalian herbivores: Constraints and tactics. Pages 157-181 *in* R.N. Hughes, editor. *Diet Selection: An Interdisciplinary Approach to Foraging Behaviour*. Oxford University Press, Don Mills, ON, Canada
- Jung, H.G., and Allen, M.S. 1995. Characteristics of plant cell walls affecting intake and digestibility of forages by ruminants. *Journal of Animal Science*. 73:2774-2790.
- Jung, H.G., Mertens, D.R., and Payne, A.J. 1997. Correlation of acid detergent lignin and Klason lignin with digestibility of forage dry matter and neutral detergent fiber. *Journal of Dairy Science*. 80:1622-1628.
- Köster, H.H., Cochran R.C., Titgemeyer, E.C., Vanzant, E.S., Abdelgadir, I., and St-Jean, G. 1996. Effect of increasing degradable intake protein on intake and digestion of low-quality, tallgrass-prairie forage by beef cows. *Journal of animal Science*. 1996. 74:2473-2481.

Chapter 4: Nutritional advantage afforded by row crops

- LaGory, M.K., LaGory, K.E., and Taylor, D.H. 1985. Winter browse availability and use by white-tailed deer in southeastern Indiana. *Journal of Wildlife Management*. 49:120-124.
- Land Resource Unit. 1999. Soils and Terrain. An Introduction to the Land Resource. Rural Municipality of Headingley. Information Bulletin 99-2, Brandon Research Centre, Research Branch, Agriculture and Agri-Food Canada. Brandon, Manitoba, Canada.
- Legendre, P. and Legendre, L. 1998. *Numerical Ecology*, Second English Edition. Elsevier Science. Amsterdam, The Netherlands.
- Leitte, E.R. and Stuth, J.W. 1994. Influence of duration of exposure to field conditions on viability of fecal samples for NIRS analysis. *Journal of Range Management*. 47:321-314.
- Leslie, Jr., D.M., Vavra, M., Starkey, E.E., and Slater, R.C. 1983. Correcting for Differential Digestibility in Microhistological Analyses Involving Common Coastal Forages of the Pacific Northwest. *Journal of Range Management*. 36:730-732.
- Lodge, R.W. 1954. Effects of grazing on the soils and forage of mixed prairie in southwestern Saskatchewan. *Journal of Range Management*. 7:166-170.
- Kamler, J, Homolka, M., and Kráčmar, S. 2003. Nitrogen characteristics of ungulates faeces: effect of time exposure and storage. *Folia Zoology*. 52:31-35.
- Krapu, G.L., Brandt, D.A., and Cox, R.R. 2004. Less waste corn, more land in soybeans, and the switch to genetically modified crops: trends with important implications for wildlife management. *Wildlife Society Bulletin*. 32:127-136.
- McConnell, B.R. and Garrison, G.A. 1966. Seasonal Variations of available carbohydrates in bitterbrush. *Journal of Wildlife Management*. 30:168-172.
- Meyer, M.W., Brown, R.D., and Graham, M.W. 1984. Protein and Energy Content of White-tailed Deer Diets in the Texas Coastal Bend. *Journal of Wildlife Management*. 48:527-534.
- Michael, E.D. Movements of white-tailed deer on the Welder Wildlife Refuge. *Journal of Wildlife Management*. 29:44-52.
- Mould, E.D. and Robbins, C.T. 1981. Evaluation of detergent analysis in estimating nutritional value of browse. *Journal of Wildlife Management*. 45:937-947.

Chapter 4: Nutritional advantage afforded by row crops

- Mountousis, I, Papanikolaou, K., Stanogias, G., Chatzitheodoridis, F, and Roukos, C. 2008. Seasonal variation of chemical composition and dry matter digestibility of rangelands in NW Greece. *Journal of Central European Agriculture*. 9:547-556.
- Murphy, R.K., Payne, N.F., and Raymond, K.A. 1985. White-tailed deer use of an irrigated agricultural-grassland complex in central Wisconsin. *Journal of Wildlife Management*. 49:125-128.
- Nixon, C.M., Hansen, L.P., Brewer, P.A., and Chelsvig, J.E. 1991. Ecology of white-tailed deer in an intensively farmed region of Illinois. *Wildlife Monographs*. 118
- Nixon, C.M., Mankin, P.C., Etter, D.R., Hansen, L.P., Brewer, P.A., Chelsvig, J.E., Esker, T.L., and Sullivan, J.B. 2006. White-tailed deer dispersal behaviour in an agricultural environment. *American Midland Naturalist*. 157:212-220.
- Nixon, C.M., McLean, M.W., and Russell, K.R. 1970. Deer food habits and range characteristics in Ohio. *Journal of Wildlife Management*. 34: 870-886.
- Parker, K.L., Robbins, C.T., and Hanley, T.A. 1984. Energy expenditures for locomotion by mule deer and elk. *Journal of Wildlife Management*. 48:474-488.
- Paterson, B.R. and Messier, F. 2000. Factors influencing killing rates of white-tailed deer by coyotes in eastern Canada. *Journal of Wildlife Management*. 64:721-732.
- Pendlebury, C., Odongo, N.E., Renjifo, A., Naelitz, J., Valdes, E.V., and McBride, B.W. 2005. Acid-insoluble ash as a measure of dry matter digestibility in captive African elephants (*Loxodonta africana*). *Zoo Biology*. 24:261-265.
- Penry, D.L. 1993. Digestive constraints on diet selection. Pages 32-55 in R.N. Hughes, editor. *Diet Selection: An Interdisciplinary Approach to Foraging Behaviour*. Oxford University Press, Don Mills, ON, Canada.
- Pierce, R.M., Bowyer, R.T., and Bleich, V.C. 2004. Habitat selection by mule deer: forage benefits or risk of predation? *Journal of Wildlife Management*. 68:533-541.
- Provenza F.D. and Cincotta, R.P. 1993. Pages 78-101 in R.N. Hughes, editor. *Diet Selection: An Interdisciplinary Approach to Foraging Behaviour*. Oxford University Press, Don Mills, ON, Canada.
- Pyke, G.H. 1984. Optimal Foraging Theory: A Critical Review. *Annual Review of Ecological Systematics* 15:523-575.
- Rao, M.R., Harbers, L.H., and Smith, E.F. 1973. Seasonal change in nutritive value of bluestem pastures. *Journal of Range Management*. 26:419-422.

Chapter 4: Nutritional advantage afforded by row crops

- Riley, S.J., Decker, D.J., Enck, J.W., Curtis, P.D., Lauber, T.B., and Brown, T.L. 2003. Deer populations up, hunter populations down: Implications of interdependence of deer and hunter population dynamics on management. *Ecoscience*. 10:455-461.
- Robbins, C.T. 1993. *Wildlife Feeding and Nutrition*, 2nd Edition. Academic Press, Toronto, Ontario, Canada.
- Roseberry, J.L. and Woolf, A. 1998. Habitat-population density relationships for white-tailed deer in Illinois. *Wildlife Society Bulletin*. 26:252-258.
- Sales, J. and Janssens, G.P.J. 2003. Acid-insoluble ash as a marker in digestibility studies: a review. *Journal of Animal and Feed Sciences*. 12:383-400.
- Saunders, K.D., Dehl, B.E., and Scott, G. 1980. Bite-count vs fecal analysis for range animal diets. *Journal of Range Management*. 33:146-149.
- Schwab, F.E., Pittoello, F.G., and Simon, N.P.P. 2001. Relative palatability of green manure crops and carrots to white-tailed deer. *Wildlife Society Bulletin*. 29:317-321.
- Short, H.L. 1975. Nutrition of southern deer in different seasons. *Journal of Wildlife Management*. 39:321-329.
- Sih, A. 1993. Effects of ecological interactions on forager diets: competition, predation, risk, parasitism, and prey behaviour. Pages 182-211 *in* R.N. Hughes, editor. *Diet Selection: An Interdisciplinary Approach to Foraging Behaviour*. Oxford University Press, Don Mills, ON, Canada.
- Solorio-Sanchez, F.J., Armendariz-Yanez, I., and Ku-Vera, J. Chemical composition and *in vitro* dry matter digestibility of some fodder trees from South-east Mexico. *Livestock Research for Rural Development*. 12:4. Retrieved 05 January 2009, from <http://www.lrrd.org/lrrd12/4/solo124a.htm>.
- Sparks, D.R. and Malehek, J.C. 1968. Estimating percentage dry weights in diets using a microscope technique. *Journal of range Management*. 21:264-265.
- Stewart, K.M., Fulbright, T.E., and Drawe, L.E. 2000. White-tailed deer use of clearings relative to forage availability. *Journal of Wildlife Management*. 64:734-741.
- Sprinkle, J. 2000. *Supplementation during drought*. CL1170. Cow-Calf Management Library, University of Arizona, Arizona, USA.
- Sunvold, G.D., and Cochran, R.C. 1991. Technical note: evaluation of acid detergent lignin, alkaline peroxide lignin, acid soluble ash, and indigestible acid detergent fiber as internal markers for prediction of alfalfa, bromegrass, and prairie hay digestibility by beef steers. *Journal of Animal Science*. 69:4951-4955.

Chapter 4: Nutritional advantage afforded by row crops

- Van Keulen, J., and Young, B.A. 1977. Evaluation of acid-insoluble ash as a natural marker in ruminant digestibility studies in *Journal of Animal Science*. 4:282-287.
- Vecellio, G.M., Yahner, R.H., and Storm, G.L. 1994. Crop damage by deer at Gettysburg Park. *Wildlife Society Bulletin*. 22:89-93.
- Verme, L.J. and Ullry, D.E. 1984. Physiology and nutrition. Pages 91-118 in L.K. Halls and C. House, editors. *White-tailed Deer: Ecology and Management*. Stackpole Books. Harrisburg, PA, USA.
- Walker, D.J. 2004. Development of a Preliminary GIS Database and Vegetation Framework for the St. Charles Rifle Range Tall Grass Prairie: Final Report. Prepared for World Wildlife Fund Canada
- Weckerly, F.M. 1993. Intersexual resource partitioning in black-tailed deer: test of the body size hypothesis. *Journal of Range Management*. 57:475-494.
- Westoby, M. 1974. An analysis of diet selection by large generalist herbivores. *American Naturalist*. 108:290-304.
- Wickstrom, M.L., Robbins, C.T., Hanley, T.A., Spangler, D.E., and Parish, S.M. 1984. Food intake and foraging energetics of elk and mule deer. *Journal of Wildlife Management*. 48:1285-1301.
- Wildman, C.D., West, J.W., and Bernard, J.K. 2007. Effect of dietary cation-anion difference and dietary crude protein on performance of lactating dairy cows during hot weather. *Journal of Dairy Science*. 90:1842-1850.
- Wilmshurst, J.F., Fryxell, J.M., and Hudson, R.J. 1995. Forage quality and patch choice by wapiti (*Cervus elaphus*). *Behavioural Ecology*. 6:209-217.

THE RESEARCH

Although the effects of intensive white-tailed deer herbivory on a tallgrass prairie have recently been examined elsewhere (Anderson et al. 2001, Anderson et al. 2005), possibly nowhere else have the effects been examined within such a complex setting as a prairie within an agro-urban-fragmented forest landscape. Therefore, while this study provides site-specific insight into white-tailed deer-tallgrass prairie dynamics, it also has applications beyond those of SCRR. This is especially true given that flooding prevented the planting of row-crops in 2005, making it possible to evaluate diet selection and nutritional intake of essentially a single group of free-ranging white-tailed deer with and without access crops. This has not been done before. While some of the observations made during this study agreed with those found elsewhere, others did not.

Similar to the findings of Anderson et al. (2001, 2005), the tallgrass prairie of SCRR is now being degraded by the direct effects of white-tailed deer herbivory. The importance of tallgrass prairie plants in general, and forbs in particular, within the deer diet even when row-crops are available means that elevated deer densities are consuming most of the available phytomass of preferred species. While row-crops propel and sustain high deer populations, it is the native plants that continue to form the bulk of dietary intake. As such, certain locally rare plants such as *Lilium philadelphicum* and *Gallardia aristata* may fleetingly emerge from the soil, but they and many other favoured species are quickly grazed before they can flower, repressing numbers of graze-intolerant species and placing their continued survival in doubt.

Deer do not appear to be directly influencing aspen encroachment onto the prairie, although they are restructuring woody growth. White-tailed deer are also, however, indirectly degrading the quality of the prairie through a combination of over-grazing, nutrient translocation, seed dispersal, trampling, and gap dynamics. In extreme cases, an over-story of invasives and ruderals has supplanted the original floristic cover, virtually eliminating all understory plants. On the eastern half of the site, previous cultivation practices have reduced organic matter and nitrogen, retarding aspen encroachment and the dominance of ruderals, but deer may be shifting inter-species plant competitive dynamics by enhancing soil nutrients. This mechanism merits further study.

The white-tailed deer's effort to maximize energy while optimizing CP and, thus, rumen-reticulum function both with and without access to crops was not entirely unexpected. What was surprising was the high degree with which this was achieved given the large number of variables involved. Also surprising was the importance of a small number of native tallgrass plants in the optimization process, placing those plants at even greater risk of extirpation.

Contrary to findings in numerous studies involving an array of monogastrics and ungulates, ADF, and not AIA, was found to be the best nutritional marker; it was highly correlated to IVDMD. This was likely due to the relatively low IVDMD values of a number of the native dietary components.

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Based on these findings, it is clear that the white-tailed deer of SCRR are exerting a deleterious effect on the northern tallgrass prairie's flora. An active ecological management plan needs to be developed and implemented if the ecosystem is to be preserved for the future.

MANAGEMENT STRATEGIES

Introduction

A century after the primary ecological disturbance engines of North America's tallgrass prairie were eliminated, it is remarkable that the small remnant tract located on the SCRR even persists as a functioning -albeit heavily altered – ecosystem. Donated by a benefactor to the Department of the Militia at the dawn of the twentieth century (Prairie Habitats 1994), it was spared from complete subjugation to agricultural practices, although it has nevertheless suffered severely from anthropological intervention. In the southern portion where the rifle firing butts are located the grasses have been mowed for decades, only a very few native species such as *Erigeron* persist as weeds, along with the dandelions. In the Danger Area immediately behind the butts the drier eastern half was put to the till for several decades while the wetter west was hayed. While these lands now lay dormant the *Salix* swales noted in the 1880s have expanded to become a large aspen parkland forest. Where the forest has not taken hold, the prairie flora that was as recently as the mid 1990s rated as “High Quality” (J. Morgan, pers comm) can now be considered to be highly degraded.

Today, some steps are being taken to preserve this ecological treasure. SCRR currently falls under the ecological stewardship of 17 Wing, Winnipeg. Part of the DND, it must comply with ecological stewardship regulations as set forth in the Species at Risk Act (SARA) (Bidlake 2004) and DND Sustainable Development Strategy (SDS), which includes Goals of preserving biodiversity and heritage sites (DND 2006). To this end controlled burns have been re-introduced to the eastern portion of the site located within the Danger Area.

Disturbance Regimes

Because intensive bison grazing of the northern tallgrass prairie was historically infrequent, greater fuel loads would have accumulated on these grasslands, leading to more frequent and hotter wildfires than perhaps occurred elsewhere in the Great Plains. Fire, therefore, may have been the most important ecological driver of this ecosystem. Fire does appear to be having some positive effect in retarding aspen encroachment. It is also likely suppressing the accumulation of soil N that, in turn, would allow conditions conducive to weedy invasive found within the internal prairies to repeat themselves there.

White-tailed deer do provide a grazing disturbance regime but it is ecologically inappropriate, as these ruminants graze plants and in a manner that does not replicate the conditions under which the ecosystem evolved. Elevated deer densities that have persisted since the 1980s and the establishment of intensive row cropping in the region

have significantly increased grazing pressure on the site's most favoured and rare plants. A number of these have very likely become extirpated while others are now clearly at risk. Even some forbs and grasses that are generally considered to be graze-tolerant could be in danger as deer consume them in such large quantities in an effort to optimize their dietary intake and, thus, fitness. The re-introduction of a more appropriate grazing regime by either highland cattle or, more preferably, bison is feasible and would further restore the function, structure, and composition of this tallgrass prairie (Gooch 2005).

Population Control

Although the mounting number of deer-automobile collisions in the Winnipeg region has drawn public attention, it has not had a noticeable impact on local deer densities. It is not serving as an effective population control measure and the highway does not seem to be acting as an effective deer migration barrier, as assessed from regional seasonal deer migration and population distribution dynamics (Gooch, unpublished data). Deer hunting is an increasingly ineffective means of deer population control as the sport declines in popularity but would be of some value on SCRR in reducing numbers (Riley et al. 2003, Rutberg 1997, Giles and Findlay 2004). Deer hunting has been prohibited on the site by 17 Wing for close to a decade and, since 2006, rifle hunting has been provincially prohibited as the City of Winnipeg expands. An organized cull is necessary if deer numbers are to be reduced to the recommended to 6-7 deer km⁻² as described in Chapter 2.

Before implementing a cull of deer, however, an aggressive public information campaign would need to be conducted (Decker and Purdy 1988). An endearing animal, the question of deer population control typically polarizes the community along predictable lines (Rutberg 1997). Unless they have personally experienced economic loss or damage, the public generally does not support population controls (Henderson et al. 2000, Stout et al. 1993, Decker and Gavin 1987). The irony is that while the general populous can be expected to rally in support of this non-native species, they will do so ignorant of their exacting toll on the native tallgrass prairie ecosystem that is quintessentially “Western”.

Causes of Overabundance

Largely due to the spatial instability of white-tailed deer populations in an agricultural setting (Nixon et al. 2006), any effects of a deer cull would be short lived (Jewel 1981). A permanent solution requires the addressing of the underlying causes of deer overabundance. There are two of these. The first is the presence of row-crops within 1.5km of the site’s forest. These crops provide a variety of highly digestible, high-energy foods during the critical periods. The result is reduced white-tailed deer winter mortality through enhanced net energetic gains, increased fecundity, and thus even greater population densities, with a corresponding increase of herbivorous pressure on the native flora. It is not possible to influence what the region’s farmers grow, so it must be assumed that this practice will continue. Indeed, with the rise in demand for bio-diesel corn was planted for the first time in years just north of SCRR in the summer of 2007. Corn is highly favoured by deer (Murphy et al. 1985, Nixon et al. 1970). In Chapter 4 the

establishment of a deer fence around the perimeter of the site was proposed as a means of naturally discouraging elevated deer densities without deleteriously affecting the genetic health of the deer herd or requiring repeated culls. If built strong enough to contain bison this fence could be used in conjunction with the re-introduction of bison grazing. The grazing intensity would be heavy but would only need to occur infrequently. The cost for such a fence and handling facility would be approximately \$125,000 (Gooch 2005).

The second cause of overabundance is the presence of the aspen forest and the thermal shelter and browse it affords. As this forest increases in size, it can sustain even higher deer densities, even during harsh winters. Although the deer do influence woody stem abundance and structure on the tallgrass prairie, their ability to alter woody encroachment rates except in perhaps isolated points where deer densities are the highest is negligible, as discovered in Chapter 3. An example would be on the internal prairie fields and northeastern edge of the forest, where deer densities during flood conditions were particularly high. At these points exclosures were damaged as deer aggressively consumed all tender woody growth and the effects of trampling, nutrient translocation, and seed dispersal were particularly acute. As urbanization and human activity continues to degrade and eliminate other forest refuges for Winnipeg's white-tailed deer (Gooch, unpublished data), the SCRR forest has become an increasingly important deer habitat, particularly during deep snow accumulations and crop failures. This can only serve to amplify the risk posed by white-tailed deer on this remnant grassland.

Restoration

The reduction and eventual elimination of the aspen forest on SCRR would be challenging to achieve but ecologically appropriate. It would also negate the need for a deer fence. By eliminating the aspen forest the deer would not congregate on the site and subject favoured plants to over-grazing. The retention of willow swales and some small copses of forest on the wettest lands would provide some deer habitat and allow some limited disturbance to persist, but at more ecologically appropriate levels. The elimination of the forest would also allow for controlled burns to be applied in the heavily degraded internal prairie fields. This would denitrify the soils and potentially suppress the growth of some of the weedy species that are now dominant and allow smaller native plants to re-establish themselves.

Such tenacious ruderal species as *C. arvensis* may persist, but late spring burning should reduce its abundance and hinder its spread by reducing its stem height and encouraging the growth of competitive grasses (Edwards et al. 2000). This effort may need to be combined with targeted herbicide application (Nuzzo 2005) and preceded by over-seeding with native competitively aggressive grasses such as *Andropogon* spp (Molt 1990). Over-seeding would prevent existing or other invasive species from becoming establishing in the gaps and on the bare earth once the current weedy cover was burned (Solecki 1997, Packard 1997, Packard and Ross 1997). Grassland seeds do not generally remain viable in the soil for more than 35-40yrs, especially on wet soils (Oosting and

Humphreys 1940, Dekker 2000), so the elimination of weedy and species may not result in the automatic emergence of favourable native flora.

The reduction of aspen forest cover would be a difficult task to accomplish and would require numerous years to complete. In response to stress, aspen send up dense stands of shoots; the cutting or girdling of the trees would likely result in aggressive regeneration (Solecki 1997). Yet combined with prescribed burn regime, the removal of aspen trees could be achieved. The method employed would have to be designed so as to not disturb the soil or surrounding vegetation, otherwise opportunities would be created for invasive weedy species to take hold. How many and which trees should be removed per year would need to be decided, but it likely would be best to first eliminate those stands that still have a tallgrass prairie understory, thereby presenting the least opportunity for invasives to become established. These sites would also require the least amount of active restoration after the woody stems were removed. To minimize the thermal cover afforded the deer while they forage onto the tallgrass prairie, deforestation should also initially target the small fragments, copses, and woody “peninsulas” (Yahner 1988). The significant reduction in forest size would not only present less shelter for local deer, it would increase the size of the remnant tallgrass prairie.

The SCRR northern tallgrass prairie remnant is an ecological island, subject to the speciation, invasion, and extinction processes that form the body of island biogeography (Wu and Vankat 1995). Imbedded within an agricultural landscape on the edge of a major urban centre, it is cut off from potential native flora immigration. Indeed, it is under

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continual pressure from the non-native species that surrounds it. As canopy gaps are created or native species and functional groups are removed, the opportunity for non-native immigration increases (Symstad 2005). Genetic drift occurs and genetic bottlenecks form, reducing the long-term prospects for the ecosystem to persist islands (Simberloff and Gotelli 1984, Menges 1991, Jennersten 1988). Removing most of the aspen forest will, concurrently, increase the abundance and habitat niches for the remaining native flora and fauna and, thus, robustness.

Other than deforestation, the size of the remnant tallgrass prairie can be increased in two additional ways. First, the practice of regularly mowing the grasslands south of the actual rifle range and buildings should be stopped, thereby allowing the prairie flora to slowly re-emerge. Just as occurred on the formerly cultivated and hayed lands to the north, at least some tallgrass prairie species should migrate into these areas through seed dispersal or vegetative reproduction (Johnson and Anderson 1986), especially if they are subjected to controlled burns as well. Second, the practice of leasing the parcel of land to the north for agriculture should also be reconsidered. Because of the length of time that field has been tilled active restoration such as seeding would likely be necessary, although relatively simple to do (Morgan 1997). The considerable ecological advantage is that it would increase the size of the remnant and the distance from the existing forest edge to row-crops.

Increasing the size and health of the tallgrass prairie remnant is important to its long-term survivability, but its management and stewardship must be viewed at the landscape level.

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As urban expansion continues the City of Winnipeg will, in the relatively near future, engulf SCRR. From a military operational perspective this has implications on 17 Wing's ability to continue to use the range. From an ecological perspective, the risk of invasion by non-native flora species will increase (Moffat et al. 2004) and active and appropriate tallgrass management will be hindered as the use of prescribed burns is inevitably challenged. Bison grazing the grasslands would also become a liability, as the DND would be expected to ensure no one placed himself or herself in harm's way (Dr. King, Winnipeg Zoo, pers comm). As such, the DND, Province of Manitoba, and the Rural Municipalities of Headingley and Rosser should strike a joint Working Group to begin to consider future courses of action. While legal stewardship and control of the site resides entirely with the DND, given that SCRR is the second largest tallgrass prairie site in Manitoba, all stakeholders including the province need to assume both moral and fiscal responsibility for its survival, working towards a common understanding and objective (Samson et al. 2004, Rondeau 2001, Holl and Howarth 2000). The municipalities are necessary in that they would need to implement any zoning changes, ideally creating an agricultural buffer between the remnant and urban development.

CONCLUSION

The northern tallgrass prairie of SCRR is unique in that it represents a critically endangered ecosystem (Samson et al. 2003), even though it's constituent plants are not individually endangered. Some species are, however, uncommon. The emergence of the aspen forest and establishment of intensive row-cropping has set the conditions for

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ecologically threatening white-tailed deer densities to explode, placing the ecosystem's continued survival in question. Due to its small size, isolation from other tallgrass prairie genetic sources, and pending urban encroachment, the long-term future of this ecosystem is in serious jeopardy unless a comprehensive management plan is developed and implemented. A new integrated approach to conservation needs to be adopted before greater damage occurs (Samson et al. 2003). Once the functioning system has been lost, it could take several centuries of work and investment to restore (Samson and Knopf 1994).

LITERATURE CITED

- Anderson, R.C., Corbett, E.A., Anderson, M.C., Corbett, G.A., and Kelley, T.M. 2001. High white-tailed deer density has negative effect on tallgrass prairie forbs. *Journal of the Torrey Botanical Society*. 128:381-392.
- Anderson, R.C., Nelson, D., Anderson, M.A., and Rickey, M.A. 2005. White-tailed deer (*Odocoileus virginianus* Zimmermann) browsing effects in tallgrass prairie forbs: diversity and species abundance. *Natural Areas Journal* 25:19-25.
- Bidlake, L.J. 2004. An Evaluation of CFB Shilo's Responsibilities under the Federal and Provincial Species at Risk Legislation. Brandon, Manitoba, Canada.
- Decker, D.J. and Gavin, T.A. 1987. Public Attitudes Toward a Suburban Deer Herd. *Wildlife Society Bulletin*. 15:173-180.
- Decker, D.J. and Purdy, K.G. 1988. Toward a Concept of Wildlife Acceptance Capacity in Wildlife Management. *Wildlife Society Bulletin*. 16:53-57.
- Dekker, R.M., Verweij, J.P., and Fresco, L.F. 2000. Soil seed bank dynamics in hayfield succession. *Journal of Ecology*. 88:594-607.
- Department of National Defence. 2006. Sustainable Development Strategy: Environmentally Sustainable Defence Activities, 4th Iteration. Retrieved 07 January 2006, <http://www.admie-smaie.forces.gc.ca/dge/sds-sdd/docs/sds-sdd-06-eng.pdf>
- Edwards, G.R., Bourdot, G.W., and Crawley, M.J. 2000. Influence of herbivory, competition, and soil fecundity on the abundance of *Cirsium arvense* in acid grasslands. *Journal of Applied Ecology*. 37:321-334.
- Giles, B.G. and Findlay, S.C. 2004. Effectiveness of a Selective Harvest System Regulating Deer Populations in Ontario. *Journal of Wildlife Management*. 68:266-277.
- Gooch, S.J. 2005. Feasibility Study: Re-introducing large ungulate grazing onto the Saint Charles Rifle Range (SCRR). Prepared for the 17 Wing Environmental Officer March 2005, Winnipeg, Manitoba, Canada.
- Henderson, D.W., Warren, R.J., Newman, D.H., Bowker, J.M., Cromwell, J.S., and Jackson, J.J. 2000. Human Perceptions Before and After a 50% Reduction in an Urban Deer Herd's Density. *Wildlife Society Bulletin*. 28:4.
- Holl, K.D. and Howarth, R.B. 2000. Paying for restoration. *Restoration Ecology*. 8:260-267.

- Jennersten, O. 1988. Pollination in *Dianthus deltoides* (Caryophyllaceae): Effects of Habitat Fragmentation on Visitation and Seed Set. *Conservation Biology* 2:359-366.
- Jewel, P.A. and Holt, S. 1981. Introduction. Pages 1-7 in P.A. Jewel and S. Holt, editors. *Problems in Management of Locally Abundant Wild Mammals*. Academic Press, New York, New York, USA.
- Johnson, R.G. and Anderson, R.C. 1986. The seed bank of a tallgrass prairie in Illinois. *American Midland Naturalist*. 115:123-130.
- Menges, E.S. 1991. Seed Germination Percentage Increases with Population Size in a Fragmented Prairie Species. *Conservation Biology* 5:158-164.
- Moffat, S.F., McLachlan, S.M., and Kenkel, N.C. 2004. Impacts of land use on riparian forest along an urban-rural gradient in southern Manitoba. *Plant Ecology*. 174:119-135.
- Molt, C. 1990. Restoring the prairie. *Bioscience*. 40:804-809.
- Morgan, J.P. 1997. Plowing and Seeding. Pages 193-215 in S. Packard and C.F. Mutel, editors. *The Tallgrass Restoration Handbook: for prairies, savannas, and woodlands*. Island Press, Washington, D.C., USA.
- Murphy, R.K., Payne, N.F., and Raymond, K.A. 1985. White-tailed deer use of an irrigated agricultural-grassland complex in central Wisconsin. *Journal of Wildlife Management*. 49:125-128.
- Nixon, C.M., Mankin, P.C., Etter, D.R., Hansen, L.P., Brewer, P.A., Chelsvig, J.E., Esker, T.L., and Sullivan, J.B. 2006. White-tailed deer dispersal behaviour in an agricultural environment. *American Midland Naturalist*. 157:212-220.
- Nixon, C.M., McClain, M.W., and Russell, K.R. 1970. Deer Food Habits and Range Characteristics in Ohio. *Journal of Wildlife Management*. 34 :870-886.
- Nuzzo, V. 2005. Element Stewardship Abstract for *Cirsium arvense*. The Nature Conservancy, retrieved 13 October 2005.
- Oosting, H.J. and Humphreys, M.E. 1940. Buried viable seeds in a successional series of old field and forest soils. *Bulletin of the Torrey Botanical Club*. 67:253-273.
- Packard, S. Interseeding. Pages 163-191 in S. Packard and C.F. Mutel, editors. *The Tallgrass Restoration Handbook: for prairies, savannas, and woodlands*. Island Press, Washington, D.C., USA.

Chapter 5 – Ecological Sustainment

- Packard, S. and Ross, L.M. 1997. Restoring remnants. Pages 63-95 *in* S. Packard and C.F. Mutel, editors. *The Tallgrass Restoration Handbook: for prairies, savannas, and woodlands*. Island Press, Washington, D.C., USA.
- Prairie Habitats. 1994. Prototype Vegetation Management Plan: Department of National Defence, Canadian Forces Base Winnipeg, Winnipeg, Manitoba, Canada.
- Riley, S.J., Decker, D.J., Enck, J.W., Curtis, P.D., Lauber, T.B., and Brown, T.L. 2003. Deer populations up, hunter populations down: Implications of interdependence of deer and hunter population dynamics on management. *Ecoscience*. 10:455-461.
- Rondeau, D. 2001. Along the way back from the brink. *Journal of Environmental Economics and Management*. 48:156-182.
- Rutberg, A.T. 1997. The Science of Deer Management: An Animal Welfare Perspective. Pages 37-54 *in* W.J. McShea, H.B. Underwood, and J.H. Rapploe, editors. *The Science of Overabundance: Deer Ecology and Population Management*. Smithsonian Books, Washington D.C., USA.
- Samson, F. and Knopf, F. 1994. Prairie Conservation in North America. *Bioscience* 44: 418-421.
- Samson, F.B., Knopf, F.L., and Ostlie, W.R. 2004. Great Plains ecosystems: past, present, and future. *Wildlife Society Bulletin*. 32:6-15.
- Samson, F.B., Knopf, F.L., McCarthy, C.W., Noon, B.R., Ostlie, W.R., Rinehart, S.M., Larson, S.G., Plumb, G.E., Schenbeck, G.L., Svingen, D.M., and Byer, T.W. 2003. Planning for population viability on Northern Great Plains national grasslands. *Wildlife Society Bulletin*. 31:986-999.
- Solecki, M.K. 1997. Controlling invasive plants. Pages 251-301 *in* S. Packard and C.F. Mutel, editors. *The Tallgrass Restoration Handbook: for prairies, savannas, and woodlands*. Island Press, Washington, D.C., USA.
- Stout, R.J., Stedman, R.C., Decker, D.J., and Knuth, B.A. 1993. Perceptions of Risk from Deer-Related Vehicle Accidents: Implications for Public Preferences for Deer Herd Size. *Wildlife Society Bulletin*. 21:237-249.
- Simberloff, D., and Gotelli, N. 1984. Effects of Insularisation on Plant Richness in the Prairie-Forest Ecotone. *Biological Conservation*. 29:27-46.
- Symstad, A.J. 2000. A Test of the Effects of Functional Group Richness and Composition on Grassland Invasibility. *Ecology* 8: 99-109.

Chapter 5 – Ecological Sustainment

Wu, J. and Vankat, J.L. 1995. Island biogeography: theory and applications. Pages 371-379 in W.A. Nierenberg, editor. *Encyclopaedia of Environmental Biology*, Vol. 2. Academic Press, San Diego, California, USA.

Yahner, R.H. 1988. Changes in wildlife communities near edges. *Conservation Biology*. 2:333-339.