

**University of Alberta**

**Differential impacts of native and introduced ungulates on Rough Fescue  
Grassland root production and turnover**

by

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A thesis submitted to the Faculty of Graduate Studies and Research  
in partial fulfillment of the requirements for the degree of

**Master of Science**

in

**Plant Ecology**

**Department of Biological Sciences**

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PREVIEW

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PREVIEW

## **Chapter 1. Overview of grassland root production and lifespans and comparisons of the impacts of native and introduced ungulates**

### **1.1 Root production**

Root production accounts for 30% of terrestrial biomass (Jackson *et al.*, 1996), and drives soil carbon (C) and nitrogen (N) cycling (Pineiro *et al.*; Post *et al.*, 1982; McNaughton *et al.*, 1997). Two categories based on diameter exist for roots: large roots ( $> 2$  mm) and fine roots ( $\leq 2$  mm). Large roots are primarily used for structure and photosynthate storage. Fine roots are a plant's water and nutrient foraging organs, the counterparts to leaves that accumulate CO<sub>2</sub> and sunlight. Research into static measures of standing root crop are extensive (Jackson *et al.*, 1996; Frank *et al.*, 1998; Steinaker & Wilson, 2008), but little is known about the mechanisms affecting fine root production and turnover (Eissenstat *et al.*, 2000).

Fine roots play at least two globally significant roles in ecosystem processes: nutrient acquisition and as the building blocks of soil organic carbon. Because of their short lifespans, which range from weeks to a few years (Sims & Singh, 1978; Gill *et al.*, 2002; Peek *et al.*, 2005; Stewart & Frank, 2008; Strand *et al.*, 2008), fine roots drive soil C and nutrient cycling (Jackson *et al.*, 1997; Strand *et al.*, 2008). Young roots of a diameter of  $< 1$  mm are the primary pathway for plant nutrient and water uptake (Bauerle *et al.*, 2008; Volder & Eissenstat, 2008). As conduits for photosynthate, fine roots in crops use as much as 50% of photosynthate for production and maintenance (Lambers 1987). The proportion of carbon used for maintenance differs between plant species, with grasses shunting three times as much C belowground as shrubs, most of which is lost to respiration (Carbone & Trumbore 2008). Much of the remaining C is transferred to the soil (Pineiro *et al.*).

Nowhere is the role of fine roots greater in proportion to large roots than grasslands. Large roots comprise up to 90% of belowground biomass in forest ecosystems, yet they account for only 3% in temperate grasslands (Jackson *et al.*, 1996; Jackson *et al.*, 1997; Pucheta *et al.*, 2004). Globally, grasslands generate  $13.6 \times 10^6$  Mg of fine roots per year, which is 17% of the global total (Jackson *et*



*al.*, 1997). Grass and rangelands cover greater than 50% of the Earth's terrestrial surface (Menke & Bradford, 1992), and are expanding as forests are removed to make areas managed for ungulate grazing (Woodward *et al.* 2004). Ungulates have large impacts on root production and turnover, but have not historically been present in all grasslands (Milchunas *et al.*, 1988; Milchunas & Lauenroth, 1993). As global ecosystems change from historical ecosystems to those with large herds of domestic ungulates, an understanding of how fine root production and turnover is affected by ungulate grazing is vital to making accurate models of global C and N cycles.

## **1.2 Knowledge gaps about native and introduced ungulate effects on belowground production**

Ungulate grazing is one of the prominent factors affecting above and belowground grassland primary production (McNaughton, 1979; McNaughton, 1984; Knapp *et al.*, 1999; Frank *et al.*, 2002). Under conditions of adequate moisture availability (Sims & Singh, 1978; Stohlgren *et al.*, 1999; Frank, 2007) and long histories of co-evolution between herbivores and plants (Milchunas *et al.*, 1988; Milchunas & Lauenroth, 1993; Pucheta *et al.*, 2004) ungulate grazing stimulates shoot and root production. However, grassland dynamics worldwide have shifted with the replacement of many large native ungulate herds by domestic cattle (Menke & Bradford, 1992; Riginos & Young, 2007). The impacts of changes from diverse assemblages to introduced monocultures, which differ in terms of composition and numbers of ungulates, are poorly understood. Furthermore, few studies have actually compared the impacts of native and introduced ungulates (Wisdom *et al.*, 2006), and none that I am aware of focus on belowground production.

Limited research to date has compared the effects of native and introduced ungulates on grasslands from North America and Africa (Wisdom *et al.*, 2006; Riginos & Young, 2007). In African systems, while most native ungulate communities remain intact they are dwindling as cattle management is applied to

increasing amounts of land (Riginos & Young, 2007). When cattle replace wild ungulates, tree and shrub encroachment may increase as grasses are forced to deal with greater stress aboveground (Roques *et al.*, 2001; Riginos & Young, 2007), or there may be a small reduction in forb biomass (Odadi *et al.*, 2007). There has been no investigation into cattle effects on African grassland root systems compared to native ungulates.

In North America, bison, elk and deer assemblages have been replaced almost completely by cattle (Allen, 1877; Soper, 1941; Murie, 1951; Hobbs, 1996). Native grazers (bison, *Bison bison*) and browsers (e.g., deer, *Odocoileus spp.*) have different impacts on plant aboveground production and ecosystem diversity than cattle (Plumb & Dodd, 1993; O'Neill *et al.*, 2003; Towne *et al.*, 2005). Cattle are more of a generalist herbivore than bison, consuming more forbs and browse, and less C<sub>4</sub> grasses (Plumb & Dodd, 1993). Compared to areas with bison, areas with cattle grazing have higher biomass of grasses and lower biomass of forbs (Towne *et al.*, 2005). The feeding and behavioural differences (e.g., wallowing) between bison and cattle result in higher diversity and abundance of native insects and rodents in bison areas, compared to those with cattle (Matlack *et al.*, 2001; Fay, 2003; Joern, 2005). Effects of North American native browsers mirror those of their African counterparts. Kay & Bartos (2000) found that cattle avoided feeding on aspen (*Populus tremuloides*) saplings, whereas native browsers reduced aspen stand regeneration, which increased native grass and forb abundance. However, like African systems, there have been no studies conducted that compare the effects of native and introduced ungulate effects on root production or turnover.

### **1.3 Predicting different impacts of native and introduced ungulates**

In North America, grasslands historically supported several large herds of migratory and resident species, including bison, elk and deer were the dominant ungulates. Bison are graminoid specialist grazers, while elk and deer forage in large part on tree and shrub foliage, as well as forbs and graminoids (Soper, 1941;

Murie, 1951; Soper, 1964; Merrill, 1994; Didkowsky, 2006). Since bison eradication in the late 1800's, cattle have become the dominant grazers, however there is little data about the relative impacts of these two grazing assemblages. However, the partitioning of resources by different ungulate species in a diverse native ungulate assemblage may result in different impacts on grassland production than cattle monocultures.

In African grasslands, theory has been developed suggesting that diverse assemblages partitioned resources to minimize inter-specific competition (McNaughton & Georgiadis, 1986; Voeten & Prins, 1999; Murray & Illius, 2000). For example, large ungulates (e.g., bison) with wide mouth / tongues crop closer to the ground than smaller ungulates (e.g., elk) (McNaughton & Georgiadis, 1986; Murray & Illius, 2000). However, smaller ungulates are able to select leafy parts of vegetation (e.g., browse from stems, or reproductive areas of grasses) (McNaughton & Georgiadis, 1986; Murray & Illius, 2000). During the growing season when food supplies are ample, this leads to reduced competition (Murray & Illius, 2000; Arsenault & Owen-Smith, 2002) and higher consumer productivity. By assuming that North American ungulate assemblages evolved in a similar fashion (to reduce competition by partitioning resources), I hypothesize that a diverse native ungulate assemblage will have a lower impact on belowground production and turnover than cattle monocultures.

#### **1.4 Thesis overview**

In 2003, the Precision Ranching Initiative was started to compare the relative impacts of native ungulates and cattle on Rough Fescue Prairie. The Rough Fescue Prairie is a savanna type habitat with aspen stands interspersed within rough fescue grassland. This thesis reports on the belowground component of a whole ecosystem study that investigated the impacts of native and introduced grazers on decomposition, ungulate behaviour, resource partitioning, and aboveground effects. My main thesis objective was to compare how native and introduced ungulates impact belowground primary production in Rough Fescue

Grassland. I hypothesized that a diverse native ungulates assemblage would have a lower impact on grassland aboveground production than cattle due to their varied foraging strategies, thereby leading to higher belowground production.

To test this hypothesis I examined belowground production in two ways. First, I investigated the interactive effects of ungulates and insects have on annual root production, and whether the nature of that interaction differed between native and introduced assemblages (Chapter 2). Second, I investigated how native ungulates and cattle affect fine root production, morphology, and turnover, including whether grazing has an interactive effect with other factors that affect root mortality (Chapter 3). The final Chapter contains a discussion about the ecological implications of my findings on the differential impacts of native and introduced grazers on belowground production (Chapter 4).

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PREVIEW

## Chapter 2. Non-additive effects of insects and ungulates on root growth in a native grassland

### 2.1 Introduction

Grassland communities are host to a diversity of herbivores. Insects and grasses have co-existed since the late Cretaceous (Labandeira & Sepkoski, 1993; Prasad *et al.*, 2005), and modern insects are now present in all the Earth's grasslands. Grazing mammals developed more recently in the Miocene as the climate dried and C<sub>4</sub> plants evolved (MacFadden, 1997; Vicentini *et al.*, 2008). Of the many vertebrates in grasslands ungulates are often the most obvious (MacFadden, 1997). Because of the potential for insect and ungulate herbivores to co-occur and feed within the same grassland, there is the potential for these two taxa to have interactive effects on plant growth and primary productivity.

Plant responses to insects are consistently negative. Regardless of the level of productivity, insects reduce grassland shoot production (Coupe & Cahill, 2003). Root biomass also decreases when insects feed above ground (Burlerson & Hewitt, 1982; Cain *et al.*, 1991; Alward & Joern, 1993). Rhizomes increase when insects are suppressed (Cain *et al.*, 1991), and shoot-feeding insects increase deep-root mortality (Coupe *et al.*, 2009). Compared to insects, ungulate effects are highly variable.

A survey of the literature suggests that ungulates are as likely to increase shoot and root production and biomass as they are to decrease it (Milchunas & Lauenroth, 1993; Knapp *et al.*, 1999). Ungulates can stimulate growth aboveground, causing compensation, such that despite off-take by the ungulates, the resulting total amount of shoot production is equal between ungrazed and grazed areas (Vinton & Hartnett, 1992; Turner *et al.*, 1993; Biondini & Manske, 1996; Hickman & Hartnett, 2002; Pucheta *et al.*, 2004). Overcompensation, where total shoot production is higher with grazing than without grazing, also occurs (McNaughton, 1984; Paige, 1992; Knapp *et al.*, 1999; Frank *et al.*, 2002; Towne *et al.*, 2005). In other examples, ungulates cause a reduction in shoot growth (Vandermaarel & Titlyanova, 1989; Bock & Bock, 1993; Towne *et al.*, 2005). Because grasslands typically have very high root:shoot ratios, changes in



root allocation and root growth have been identified as an important component of compensatory responses (Frank *et al.*, 2002). The results belowground have been as varied as those found aboveground, with belowground productivity increasing (Sims & Singh, 1978; Vandermaarel & Titlyanova, 1989; McNaughton *et al.*, 1998; Frank *et al.*, 2002; Pucheta *et al.*, 2004; Gao *et al.*, 2008), decreasing (Sims & Singh, 1978; Milchunas & Lauenroth, 1989; Knapp *et al.*, 1999; Gao *et al.*, 2008), or staying constant (Biondini *et al.*, 1998; McNaughton *et al.*, 1998; Frank, 2007) in response to ungulate grazing.

Both native and introduced ungulates can play a dominant role influencing plant production (McNaughton, 1984; Plumb & Dodd, 1993; Fritz *et al.*, 1996; Hobbs, 1996; Damhoureyeh & Hartnett, 1997), but few studies compare their relative effects (Wisdom *et al.*, 2006). On the northern Great Plains of North America, bison (*Bison bison*), elk (*Cervus canadensis*), and mule deer (*Odocoileus hemionus*) were historically the dominant ungulates (Allen, 1877; Murie, 1951; Soper, 1964). Today, cattle have largely replaced native ungulates, and native and introduced ungulates can have different effects on plant production (Damhoureyeh & Hartnett, 1997; Towne *et al.*, 2005). For example, The effects size of bison grazing on graminoid and forb biomass is 15% greater than that of cattle (Towne *et al.*, 2005), and both bison and cattle have subtle differences in their feeding preferences that leads to differences in plant community structure (Bock & Bock, 1993). These subtle differences may affect the type or direction of the interaction between ungulates and insects on grassland primary production.

Because the effects of ungulates on plant growth are substantially more varied than the effects of insects, the combined effects of these herbivore assemblages is difficult to predict. Nonetheless, understanding how insect and ungulate herbivory interactively affect plant production is essential our understanding of grassland community dynamics (Whiles & Charlton, 2006) and carbon cycling. To determine the independent and interactive effects of these herbivore guilds on plant productivity, we conducted a factorial experiment manipulating ungulate and insect densities in 50 hectares of rough-fescue

grassland. Secondly, we asked whether the composition of the ungulate assemblage (native or introduced) would influence any such interaction.

We show that the combined grazing of insects and ungulates, regardless of ungulate assemblage, has no effect on the aboveground plant productivity response to herbivory. In contrast, we demonstrate that insects eliminate the stimulatory effects of both native and introduced ungulates on root production.

## **2.2 Methods**

### **2.2.1 Study Site**

The experiment was conducted from May 2004 to September 2005 on 50 ha of the University of Alberta Research Ranch near Kinsella, Alberta, Canada (53.09° N, 111.55° W). The research ranch is located in the Aspen Parkland native subregion, a savannah type mosaic of aspen stands and rough-fescue prairie (Barbour & Billings, 2000). Lowlands are dominated by *Carex* spp. and clonal aspen (*Populus tremuloides*), and uplands are dominated by *Festuca hallii*, *Poa* spp., and *Hesperostipa* spp. Plant growth in the grassland habitat is both nitrogen and water limited (Lamb *et al.*, 2007). There is no history of cultivation at the field site, and the soil is a well-drained black chernozem. The dominant phytophagous insect orders are Hemipterans (aphids and leafhoppers) and Orthopterans (grasshoppers).

### **2.2.2 Experimental Design**

The site was divided into 6 paddocks averaging  $8.1 \pm 2.4$  (mean  $\pm$  s.d.) ha (Fig. 2.1). We used large paddocks, despite the limitations on sample size ( $n=3$ ), because it allowed the ungulates to choose their feeding patches within a paddock. This may be especially pertinent in regards to this study, as ungulates had a choice as to whether they would graze areas with insect damage. We also recognized there may be differences in this decision among native and non-native assemblages.

Each paddock was assigned one of two ungulate assemblage treatments: domestic cattle (*Bos taurus*), or simultaneous bison (*Bison bison*), elk (*Cervus canadensis*) and white-tailed deer (*Odocoileus virginianus*) grazing (hereafter the cattle and native treatments, resp.). Paddock assignments were clustered to reduce

the cost of bison fencing. The native grazing assemblage is similar to the assemblages that existed on the grassland prior to European settlement (Allen, 1877; Murie, 1951; Soper, 1964, Telfer and Scotter 1975). Bison-proof fences 3.65 m tall surrounded the native assemblage paddocks. Fencing around cattle paddocks was standard barbed wire fencing.

Grazing intensity was moderate for this region. A summer graze occurred from June 1 until July 15 and a fall graze occurred September 1 until October 15 in both of 2004 and 2005. Stocking densities of individuals per paddock were assigned based on an *a priori* 45-day stocking rate of 2.4 animal unit months (AUM) / ha (Society for Range Management, 1998). Estimates of AUM were calculated to obtain 50% vegetation removal based on allometric relationships between intake, body size and preliminary estimates of available forage (De Witt, 2009). Unpredicted effects of the age structure of the ungulate community resulted in actual stocking densities lower than expected (1.6 AUM / ha) in 2004 (De Witt, 2009). Stocking densities were increased to an average observed level of 2.5 AUM / ha in 2005. This achieved the desired vegetation removal (De Witt, 2009).

Within all six paddocks, a single 10 X 30 m large mammal exclosure (barbed wire in the cattle treatments, bison and deer proof fencing in the native treatments) was installed on the grassland. Inside and outside of each exclosure we placed a pair of 2.5 x 2.5 m plots, 2 m apart, in grassland habitats. We randomly sprayed one plot within each pair with Lorsban 4E (Dow Chemical; 48% active ingredient), a chlorpyrifos-based contact insecticide. Lorsban 4E is a cholinesterase inhibitor (Eto, 1974) and broad spectrum insecticide (Kenaga *et al.*, 1965). The insecticide was applied at 0.0875 ml Lorsban 4E m<sup>-2</sup> (approximately 4.2 mL Lorsban 4E in 1.44 L of water; (Coupe *et al.*, 2009). This concentration is recommended for control of adult grasshoppers in crops in this region (Johnson, 1998), and has been effectively used in prior studies at this field location (Coupe *et al.*, 2009). Spraying began the second week of May in both 2004 and 2005 and continued on a biweekly schedule until the end of August.

To assess the effectiveness of insecticide application in 2004, we sweep netted each treatment plot. Sweep netting occurred once in July, five days after insecticide application. After finding that insecticide reduced insect abundance in 2004 (Table 2.1), in July 2005 we sub-sampled the plots by randomly selecting one half of the paddocks and collected insects from each treatment plot with sticky traps (Tangle Trap on 20 X 30 cm yellow acetate cards).

### **2.2.3 Response measurements**

Plants were measured in the second year of the study (2005), prior to fall grazing, after 14 months of insecticide treatment and 3 applications of the ungulate grazing treatments (summer and fall 2004, and summer 2005). Relative root growth was estimated using an ingrowth coring method (Smit *et al.*, 2000), in which we dug a 30 cm deep, 20 X 20 cm hole in early May 2005, removed the roots, and backfilled the hole with root-free soil. At the end of the growing season (August 25, 2005), we re-cored the ingrowth hole to a depth of 20 cm using a 20 cm diameter root corer and separated the new root growth from the soil. All roots were separated from the soil by washing in a 1.00 mm mesh sieve, followed by drying at 60°C and weighing. Roots visually identified as dead were removed prior to weighing.

Concurrent with root sampling, we sampled aboveground vegetation by placing a 20 × 50 cm quadrat adjacent to the ingrowth cores. Living biomass was sampled by clipping at ground level. Samples were dried at 70 °C and weighed. Percent cover estimates were taken in late July, which corresponds to peak biomass during the growing season, within a 50 cm × 50 cm quadrat placed at the center of each plot.

### **2.2.4 Statistical Analyses**

To analyze the impact of ungulate and insect herbivores on root, shoot (grass and forb) and total production (the summation of root and shoot production) we used a nested general linear mixed model, using the MIXED procedure in SAS (v. 9.2, SAS, 2009). Fixed factors were ungulate grazing, insect suppression, grazing assemblage, and the interaction between insects and