University of Alberta

Plant Litter Influences on Soil Moisture and Production in Aspen Parkland Grasslands

By

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ABSTRACT

Soil moisture limits production in arid and semi-arid grasslands. Even in more mesic systems, including the Aspen Parkland, moisture management is increasingly important in mitigating recent increases in drought and future climate change. To better understand the effectiveness of litter as a tool for reducing water stress and augmenting production, the role of litter in regulating temporal and spatial soil moisture dynamics was examined in 2007 using two field experiments. Abundant litter up to 14,000 kg/ha increased soil moisture in native and tame grassland despite negative impacts to early season growth via reductions in soil temperature and light. Litter also enhanced grass recovery following mid-season defoliation, in part due to positive influences on soil moisture. At the landscape level, litter strongly controlled soil moisture over and above range site conditions, and enhanced mid-season shoot biomass, leading to a better predictor of production.

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1. INTRODUCTION

1.1. Background

The importance of adequate soil moisture for plant growth is widely recognized as a key variable constraining the production and distribution of plant species and communities across local, landscape and biome scales (Chapin et al. 2002, Holechek et al. 2004). The connection between moisture and plant growth becomes particularly important in prairie systems where precipitation and soil moisture are the primary limiting factors regulating production (Rogler and Hass 1947, Coupland 1958, Smoliak 1956, Rauzi 1964, Smoliak 1986, Laurenroth and Sala 1992). Soil water is a function of a number of abiotic influences. These include precipitation, temperature, wind and topographic position (Weaver and Rowland 1952, Facelli and Pickett 1991, Bork et al. 2001, Salve and Allen-Diaz 2001), as well as soil characteristics such as the extent of development (i.e. organic matter), texture, structure, depth and resulting water-holding capacity (Wilcox et al. 1988, Dormaar and Carefoot 1996, Laio et al. 2001, Porporato et al. 2001, Salve and Allen-Diaz 2001).

Despite strong abiotic controls, plant and plant residues can influence the distribution and availability of soil moisture, particularly at small scales across the landscape (Dyksterhuis and Schmutz 1947, Weaver and Rowland 1952, Knapp and Seastedt 1986, Facelli and Pickett 1991, Naeth et al. 1991a). Understanding the influence of organic matter, plant litter and live plant biomass on soil moisture provides a means of managing for the optimization of grassland productivity within the context of seasonal or yearly variation in precipitation and temperature. Plant residues and live plants can affect soil moisture storage and recharge by improving the water-holding capacity of soils, increasing the rate of precipitation infiltration, and altering evapotranspiration rates (Holland and Coleman 1987, Wilcox et al. 1988, Naeth et al. 1991a, Naeth et al. 1991b, Dormaar and Carefoot 1996).

Understanding how litter can impact soil moisture is important in the development of planned management strategies to increase water conservation and promote more efficient water use by plants in semi-arid environments (Willms et al. 1986, Willms et al. 1993). Water management may be particularly important during drought years in more mesic grasslands such as the fescue grasslands of central Alberta where current relatively stable and sufficient moisture inputs may be replaced with lower and more variable rainfall under climate change scenarios (IPCC 2001, Schindler and Donahue 2006). In this context, the manipulation of vegetation, litter and soil organic matter provides a key means of managing for the long-term sustainability of plant production by developing more stable microclimates at the soil surface.

To better understand the influence of plant litter on temporal and spatial soil moisture dynamics in mesic grasslands and associated plant production, two field studies were conducted in the Aspen Parkland ecoregion of central Alberta. These studies examined the relationships among litter, microclimate and production at the community and landscape level, respectively.

1.2. Linking Litter, Soil Moisture and Plant Production

In Chapter 2, past studies on the importance of soil moisture in regulating plant production are examined and summarized. Regulation of water balance by litter and defoliation is also reviewed to understand how the derivative effects of common land-use practices can influence and be used to manage both soil moisture and plant production. Of particular interest is the importance of the relationship of litter on soil moisture, and then in turn, to plant production in more mesic grassland systems that do not regularly experience moisture limitations. The influence of plant litter on other microclimatic variables is also examined in the context of the positive and negative pathways through which litter can influence soil surface conditions and ultimately, plant establishment and growth.

In Chapter 3, replicate field studies were used to analyze temporal soil moisture dynamics throughout the growing season under potential threshold litter loads ranging from 260 – 13,900 kg/ha on an ungrazed native prairie and 150 – 20,500 kg/ha on an ungrazed tame plant community. Plant production and re-growth following defoliation were also examined in relation to both litter and soil moisture. An important goal of this study was to determine whether and how excessive litter loads influence soil moisture drawdown after rainfall, as well as how these temporal processes were influenced by clipping, a surrogate for grazing, which is the dominant land use on grasslands in the area.

In Chapter 4, soil moisture sampling was conducted across a landscape under naturally variable litter loads and under variable topographic and soil conditions. This study was implemented to determine whether the soil moisture and production patterns observed under the higher litter loads of Chapter 3 would still be apparent in a more typical landscape. More importantly, this study examined the importance of litter in maintaining soil moisture levels relative to other range site characteristics.

Chapter 5 summarizes and synthesizes the findings of these field studies and suggests potential uses of litter in the context of managing soil moisture and plant production in mesic rangelands. Finally, conclusions are drawn regarding the importance of measuring litter in assessing the health of rangelands as well as the importance of litter in maintaining ecosystem resilience.

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2. UNDERSTANDING SOIL MOISTURE, LITTER AND DEFOLIATION: A LITERATURE REVIEW

2.1. The Aspen Parkland

Alberta has 7.6 million hectares of rangelands, with 750,000 ha in the Aspen Parkland ecoregion (Vance et al. 1983), which is a tension zone between the Dry Mixedgrass Prairie to the south and the Boreal forest to the north (Moss 1932). The Parkland is located in the cool temperate climatic zone where plants are limited by low temperatures during the winter and spring and by water stress in the summer towards the end of the growing season (Environment Canada 2005a). Landscapes of the area are known as 'knob and kettle' topography, consisting of undulating and hilly terrain derived from past glaciations (Coupland 1961) and soil parent material consisting of glacial till (Coupland and Brayshaw 1953). Upland soils are typically Black or Dark Brown Chernozems, developed under productive grasslands with more rainfall, lower average temperatures and higher humidity than the Mixedgrass Prairies to the south (Moss and Campbell 1947, Coupland 1961).

Parkland landscapes are dominated to a large extent by trembling aspen (*Populus tremuloides* Michx.) groves which appear as patches within a mosaic of prairie grassland. Aspen preferentially occurs on moister north-facing slopes and depressional areas, while open grasslands occupy the drier south-facing slopes and hilltops. Shrublands, including *Symphoricarpos occidentalis* Hook., *Rosa arkansana* Porter and *Elaeagnus commutata* Bernh. *ex* Rydb, often occupy the ecotone between aspen forest and grasslands (Wheeler 1976). Aspen abundance in the landscape increases in the northern part of the Parkland, while grassland becomes increasingly prevalent in the south of this region (Moss 1932).

The typical native grassland of the Parkland is the rough fescue prairie dominated by *Festuca hallii* (Vasey) Piper. The *Stipa-Agropyron* community that is typical of the southern Mixedgrass Prairie also occurs on drier sites, particularly hilltops (Coupland and Brayshaw 1953). Most grasses in the fescue prairie are cool season that use available early spring and fall soil moisture more rapidly than warm season grasses (Conard and

Youngman 1965). Plants are more productive in the fescue prairie than grasslands of southeastern Alberta due to greater moisture availability during the growing season (Coupland 1961). Nonetheless, moisture deficit can significantly limit production at this northern latitude, particularly on south-facing slopes (Coupland 1961, Bork et al. 2001) and during periodic drought (Wilson 2007).

The fescue grassland historically evolved with grazing by wild ungulates such as bison, elk and deer, and continues to be used by these wild ungulates along with domesticated livestock, primarily cattle. Summer grazing is commonly practiced by ranchers across the region (McCartney 1993). Tame pastures, areas cultivated and seeded with introduced forage species, are also common in the area and are an important source of supplemental forage for area ranchers. Other major regional land-use activities over the past century include cultivation and annual crop production, together with oil and gas exploration, which have contributed to habitat fragmentation and non-native plant invasion (Environment Canada 2005a, Alberta Energy 2008). Fire suppression is largely responsible for the spread of aspen into historic grassland areas (Bailey and Wroe 1974, Anderson and Bailey 1980). Collectively, these activities have significantly reduced the area of fescue grassland to less than 10% of its original size and have raised conservational concerns for the region (Alberta Agriculture and Rural Development 2003, McGinley 2007).

2.2. Regional Drought and Climate Change Concerns

North American grasslands are characterized by periodic droughts, although these events tend to occur less frequently in northern prairies (Dix 1964). Nonetheless, the period since European settlement has been the wettest century in the past two millennia, with an unusually stable climate (Schindler and Donahue 2006). Droughts in previous centuries appear to have been frequent and long, and the regional climate generally drier, suggesting recent climate changes may simply represent a return to more 'normal' conditions. Notably, severe drought in the 1990s and beyond, peaking with the driest year on record in central Alberta during 2002 (Bonsal and Wheaton 2005, Wheaton et al.

2005), has raised concerns over future land use and demonstrated the importance of identifying management strategies to mitigate drought.

Climatic warming is caused by greenhouse gas emissions (i.e. CO_2, CH_4, and NO_2) that increase the quantity of water vapor in the atmosphere. Together, these compounds increase the efficiency with which the atmosphere traps and re-radiates longwave radiation to the earth's surface (Chapin et al. 2002). Climate change is not only expected to increase global mean temperatures, but also augment the global hydrologic cycle, by which both evaporation and precipitation will increase on a global scale (Chapin et al. 2002). Due to their position in the interior of the continent, the Canadian prairies are warming faster than the global average, with temperature increases of 1-4°C recorded in the last 80-118 years, and a reduction of 14-24% of precipitation over the same time span (Schindler and Donahue 2006). Climate models also predict additional warming over the next century, causing up to a 55% increase in evaporation in some areas of the prairies. Although rainfall may also be higher, it is unlikely to be sufficient to counteract expected increases in evapotranspiration, indicating that the future will be much drier in the western Prairie Provinces (Canadian Institute for Climate Studies 2005). Climate warming combined with increasingly severe drought conditions and increasing human habitation in the Canadian prairies may well result in marked limitations in the quantity and quality of water in the region (Schindler and Donahue 2006). Consequently, water management strategies will become increasingly important for supporting ongoing land-use activities, including proactive methods for conserving soil moisture on rangelands in order to maintain adequate plant production and ecosystem health.

2.3. Plant Growth and Resource Controls on Net Primary Production

2.3.1. General Patterns

Net primary productivity is the net carbon gain by vegetation. Climatic controls over NPP are exerted primarily through the availability of belowground resources (Chapin et al. 2002). Plants allocate biomass to minimize limitations by any single resource, and biomass allocation to roots maximizes the acquisition of these belowground resources. Nonetheless, biomass must also be allocated to leaves to maximize carbon gain from photosynthesis, and to seeds for sexual reproduction (Enquist and Niklas 2002). Plants can increase the acquisition of a resource by producing more root or leaf area, by increasing the activity of the appropriate tissue, or by retaining biomass for a longer time (Chapin et al. 2002). In general, plants allocate production to roots when water or nutrients limit growth, and allocate new biomass preferentially to shoots when light is limiting (Reynolds and Thornley 1982). With increasing precipitation, the over-riding importance of water as a limiting factor decreases (Sims and Singh 1978), and soil nitrogen, light availability, herbivory and fire become increasingly important in determining production and plant community dynamics (Burke et al. 1998). Temperature can also have a large influence on the timing and growth-rate of plants, and on their water-use efficiency (Willms and Jefferson 1993).

2.3.2. Soil Moisture Influences on Plant Production

Even in mesic grasslands, water is one of the factors that strongly controls net primary production (Coupland 1958, De Jong and MacDonald 1975, Smoliak 1986, Lauenroth and Sala 1992, Bork et al. 2001), with several mechanisms by which water can influence plant production. The various effects of climate, soil and vegetation on the local hydrologic cycle are united through the key linkage to soil moisture, which in turn, modifies the effect of the climatic water balance on plants (Rodriguez-Iturbe et al. 2001). Although soil moisture is often the most limiting resource directly controlling vegetation production (Lauenroth and Sala 1992, Rodriguez-Iturbe et al. 2001), moisture can additionally effect production by altering nitrogen mineralization rates and associated soil nutrient supply (Chapin et al. 2002).

Soil moisture also exerts strong effects on production potential of an ecosystem by influencing species composition, community structure and organization. Different species and types of plants vary significantly in their demands on soil moisture under the same environmental conditions (Chapin et al. 2002). Water use of individual plants is somewhat dependent on the size and distribution of the root system. Although root systems in drier environments tend to be shallow and widespread, relative to above-ground plant size, rooting depths, lateral root spreads and total root biomass tend to increase with greater adaptation to arid conditions (Schenk and Jackson 2002). The root:shoot ratio also increases in plants that are adapted to drier climates (Schenk and Jackson 2002), thereby ensuring a sufficient root mass to supply the water needed by the existing shoot. Finally, root size and orientation can influence moisture depletion among various soil horizons (Sala et al. 1992), altering the spatial distribution of soil water.

In limiting NPP, the frequency and duration of water stress in plants is generally determined by the interaction of temperature and precipitation. Increasing temperatures and decreasing precipitation decrease the water supply for plant growth (Dix 1964). The negative response of plants to water stress begins when stomatal closure is induced by moisture deficits, and enters its final stage once the permanent wilting point is reached (Brutsaert and Chen 1995, Brutsaert and Chen 1996, Porporato et al. 2001). The permanent wilting point is the level of soil moisture at which plants stop transpiring and plant parts become permanently damaged from insufficient moisture (Laio et al. 2001a). Even so, plants are able to extract up to 75% of plant-available soil water before beginning to show signs of moisture stress (Waring and Running 1998). Seedling establishment is the most critical life stage for moisture to be available, and the degree and duration of moisture stress during this period can be critical for regulating growing season production (Willms and Jefferson 1993). In northern grasslands, including those of the Aspen Parkland, snowmelt is a critical component of spring soil moisture recharge and can also have large impacts on shoot establishment and resultant total summer growth (Naeth et al. 1991b, Viessman and Lewis 2003).

2.4. Soil Moisture

2.4.1. The Hydrologic Cycle

On a local scale, the hydrologic cycle consists of inputs from precipitation, surface water inflows, and groundwater movement to the surface. The outputs of the hydrologic cycle include plant interception losses leading to evaporation, soil water evaporation, transpiration from plants, surface runoff, and percolation into groundwater (Viessman and Lewis 2003). Plant available soil water consists of water that infiltrates from the soil surface and percolates into the rooting zone, as well as groundwater inputs up into the rooting zone (Laio et al. 2001). Precipitation in the form of rain or snow is the major input that renews soil moisture, and actual deposition of this moisture into the soil depends on the amount of rainfall, antecedent soil moisture conditions, topography, vegetation cover and soil type, among other variables (Chapin et al. 2002).

Water intercepted by vegetation and trees may be equivalent to the total precipitation input for relatively small storms (Walsh and Voight 1977, Naeth et al. 1991a). Most interception loss occurs during the initial storm period with the rate of interception decreasing rapidly thereafter (Viessman and Lewis 2003). Water stored on plant and litter surfaces eventually becomes depleted through evaporation, with different plants demonstrating different capacities to intercept water depending on leaf biomass and associated leaf area. Different types of litter may variably influence water interception based on the density and water-holding capacity of the litter (Flory 1936, Weaver and Rowland 1952, Walsh and Voight 1977, Thurow et al. 1987, Naeth et al. 1991a).

Water that escapes interception, or exceeds the interception capacity of plant and litter surfaces, can take several paths as it reaches the ground. Some water will fill depressions and eventually evaporate, whereas some water will infiltrate into the soil and flow beneath the soil surface to replenish both the upper soil layers and the groundwater reservoir (Viessman and Lewis 2003). Infiltration is influenced by the type and extent of vegetation cover, rooting patterns, the condition of the soil crust and associated soil channels, soil physical properties, and rainfall intensity (Rauzi 1960, Johnson 1962, Branson and Owens 1970, Tromble et al. 1974, Thurow et al. 1986, Wilcox et al. 1988, Dormaar and Carefoot 1996, Spaeth et al. 1996). Once water infiltrates into the soil, downward water movement is determined by topography and characteristics of the underlying soil profile such as texture and porosity (Schenk and Jackson 2002). Infiltration can therefore vary spatially due to variability of soil and above- and belowground vegetation characteristics (Rauzi 1960, Meeuwig 1970, Wilcox et al. 1988, Pierson et al. 2002). Infiltration can also vary temporally based on antecedent moisture conditions. Soils have a greater potential infiltration gradient and moisture movement when the wetting front is at the soil surface, as in dry soils. Thus, infiltration capacity is initially greater than the rainfall rate, yet as the wetting zone expands with increasing soil water content, the potential infiltration gradient will decline (Viessman and Lewis 2003).

Once infiltration capacity equals rainfall rate, the soil surface becomes saturated and a film of water develops on the soil surface until overland flow commences (Horton 1933, Laio et al. 2001a, Viessman and Lewis 2003). Impaction of raindrops on an unprotected soil can reduce the hydraulic conductivity by sealing open pores at the soil surface and thereby increasing overland flow (Weaver and Flory 1934, Thurow et al. 1986, Chapin et al. 2002). Subsurface flow may be another important source of water runoff when the upper horizon is shallow and highly permeable to surface flow (Freeze and Cherry 1979).

Once in the soil, water is subject to evapotranspiration. Evaporation is the process by which water is transferred from the land and water masses to the atmosphere during heating (Viessman and Lewis 2003). Transpiration is the loss of water specifically from plants when soil moisture is taken up by vegetation and eventually evaporated as it exits the stomata during photosynthesis. The rate of transpiration is directly related to the rate of plant growth (Chapin et al. 2002). Evapotranspiration often constitutes the largest component of moisture loss in the hydrologic cycle (Viessman and Lewis 2003), and depends on soil moisture content, solar radiation, vapor pressure of the overlying air, temperature, wind, atmospheric pressure, and the nature of the evaporating surface including vegetation (Weaver and Rowland 1952, Facelli and Pickett 1991a, Dormaar and Carefoot 1996, Laio et al. 2001a). After abundant rainfall, the rate of evaporation and transpiration is dependent on the available solar and wind energy supply, but as soil moisture declines, rates of water loss also becomes dependent on the extent of stomatal closure within plant leaves (Brutsaert and Chen 1995, Brutsaert and Chen 1996), with increasing water shortages forcing plants to reduce growth to conserve water. Below the permanent wilting point, soil moisture depletion occurs mostly through evaporation from the soil surface (Laio et al. 2001a).

2.4.2. Soil Water-Holding Capacity

Water storage in the soil occurs primarily in pores between soil particles. Water-holding capacity of the soil depends on its total pore volume and associated pore surface area, which in turn, depends on soil depth and the proportion of soil volume not occupied by mineral and organic matter (Viessman and Lewis 2003). Porosity is also dependant on soil texture, plant root density, and the action of small animals (Weaver and Rowland 1952, Laio et al. 2001a, Laio et al. 2001b). Shallow soils hold less water than deep valley-bottom soils, while rocky or sandy soils hold less water than fine soils (Salve and Allen-Diaz 2001, Chapin et al. 2002). Compaction of the soil layer also impacts water holding capacity by reducing open pore volume (Wilcox et al. 1988, Chapin et al. 2002).

Once water enters the soil, it moves downward under the force of gravity until soil matric forces responsible for the adsorption of water to soil particles exceed the gravitational potential (Porporato et al. 2001, Viessman and Lewis 2003). The field capacity of a soil is the quantity of water retained by a saturated soil once gravitational water has drained to groundwater (Viessman and Lewis 2003). Nonetheless, leakage losses continue to occur with gravity after field capacity has been reached, with the rate of loss at the lowest boundary of the soil layer rapidly decreasing as the soil dries and the hydraulic conductivity falls (Laio et al. 2001a). Fine textured soils with high clay content can hold more water against gravity than sandy soils because of the large surface area of pores relative to each unit of soil volume (Laio et al. 2001b, Salve and Allen-Diaz 2001). However, finer soils have a greater permanent wilting point, therefore reducing the amount of water extractible by plants during transpiration (Laio et al. 2001a).

Organic matter further enhances the field capacity of a soil because of its hydraulic characteristics, its wide range of pore sizes, and its effect on soil structure (Wilcox et al. 1988, Dormaar and Carefoot 1996, Chapin et al. 2002). Soils with high organic matter content tend to aggregate into spheroidal structures that increase the rate of water infiltration through the macro-pore spaces between aggregates (Holechek et al. 2004). Because of its structural characteristics, organic matter can hold up to twice as much water per unit volume as mineral soil (Naeth et al. 1991a).

Overall, stored soil water supports evaporation and transpiration during time periods when these processes exceed ongoing precipitation inputs. Declines in soil moisture during periods without precipitation are the result of systematic drawdown of stored water (Chapin et al. 2002), which culminates in drought for vegetation when soil moisture is no longer adequate to meet the demands of evapotranspiration.

2.5. Land Management Influences on Soil Moisture and Forage Production

2.5.1. Litter Influences on Soil Moisture

Plant litter, defined as any dead or partially decomposed plant material either standing above or lying on the soil surface, can be used to manage and conserve soil moisture as it augments infiltration and reduces both evaporation and run-off. Yet litter can reduce available water by intercepting, absorbing and holding moisture before it reaches the ground, particularly during small rainfall events (Weaver and Rowland 1952, Naeth et al. 1991a, Pierson et al. 2002). Interception depends on the density and water-holding capacity of litter (Flory 1936, Weaver and Rowland 1952, Naeth et al. 1991a), with roots, standing litter and coarse organic matter retaining more water than medium, fine or very fine organic matter (Naeth et al. 1991a). The hydrophobic properties of litter also impact interception, with drier litter showing greater water repellency (Walsh and Voight 1977). The ability of litter to intercept and retain soil water may be the driving factor influencing the net positive or negative effect of litter on the water balance of a site (Facelli and Pickett 1991a).

Litter increases rainwater infiltration into the soil via the important inputs of organic matter and by reducing the rate of splash erosion at the soil surface, (Dormaar and Carefoot 1996). In the absence of litter, raindrops striking bare soil can destabilize soil aggregates and cause small soil particles to be washed into the soil pore space resulting in a continuous cemented layer that reduces or prevents water entry into the ground (Kincaid and Williams 1966). Heavily grazed areas with reduced plant and litter cover have decreased water infiltration rates, as have annual pastures that generally have higher proportions of bare ground than perennial grasslands (Naeth et al. 1991b, Gill et al. 1998). In general, litter has important positive influences on the rate of water entering the soil in a large number and variety of grassland systems (Weaver and Rowland 1952, Rauzi 1960, Johnson 1962, Wilcox et al. 1998, Pierson et al. 2002).

Soil surface crusting with splash erosion in the absence of litter can also increase the incidence of overland flow and associated soil erosion (Troeh et al. 1980). By creating a rougher surface and interfering in the flow-path of water (i.e. forcing water to move in a more sinuous pattern), litter reduces water runoff and sediment erosion by reducing the flow-rate of water across the soil surface. This effect of litter on runoff has been shown in a number of range, vegetation and soil types, including semi-arid and mesic grasslands, as well as tame pastures (Weaver and Flory 1934, Dyksterhuis and Schmutz 1947, Rauzi 1960, Johnson 1962, Meeuwig 1970, Gill et al. 1998).

Both living plants and litter, by acting as an insulating layer on the soil surface, can further maintain soil moisture levels by reducing incident solar radiation and associated thermal heating, and thereby reduce the evaporation of soil water (Flory 1936, Dyksterhuis and Schmutz 1947, Hopkins 1954, Sauer 1978, Holland and Coleman 1987, Willms et al. 1993, Dormaar and Carefoot 1996). Plant cover can also reduce evaporation by increasing relative humidity at the soil surface, either by decreasing surface temperatures or by trapping moist air under foliage. Increased humidity maintains a hydrologic equilibrium between the atmosphere, vegetation and soil components at their interface (Facelli and Pickett 1991a). The ability of litter to reduce wind impacts at the soil surface can also be very important for reducing evaporation (Weaver and Rowland 1952). Litter decreases evaporation by up to 75% after irrigation compared to exposed soil (Weaver and Rowland 1952).

Heavy plant litter loads can trap snow in the spring and reduce the influence of spring winds on evaporating snow and recent snowmelt (Rice and Parenti 1978, Knapp and Seastedt 1986). Areas with abundant litter retain snow longer and increase the effectiveness of spring soil moisture recharge to field capacity (Sauer 1978, Naeth and Chanasyk 1995). Increased grazing that reduces litter loads significantly affects the ability of Alberta grasslands to capture snow (Willms and Chanasyk 2006).

2.5.2. Litter Influences on Plant Production

By increasing infiltration and reducing evaporation at the soil surface, litter conserves soil moisture and increase plant production in many environments, predominantly those where soil water is particularly limiting (Willms et al. 1986, Willms et al. 1993). Even in more mesic temperate regions where cooler temperatures and the short growing season are thought to be more limiting to plant production, high litter loads on tame pastures increase plant productivity during periods of drought and moisture stress (Page and Bork unpublished data). In the moist conditions of the Tallgrass Prairie, most forbs and woody species can increase in biomass and reproductive effort under high litter loads, potentially through changes in soil moisture status (Abrams et al. 1987). Nonetheless, excessive water retention by litter may reduce the water available to plants in these ecosystems and induce moisture stress under some conditions (Weaver and Rowland 1952, Walsh and Voight 1977, Knapp and Seastedt 1986).

Conversely, in the more arid Mixedgrass Prairie, several studies have found that litter reduces water stress and increases long-term plant productivity (Smoliak 1965, Willms et al. 1986, Willms et al. 1993). Shallower rooting depths and a limited depth of infiltration of precipitation results in more rapid loss of plant available soil water in these semi-arid grasslands, and therefore increases the importance of litter cover in reducing evaporation (Willms et al. 1986). However, Willms et al. (1993) found that the relationship between plant litter and productivity in the Mixedgrass Prairie is less pronounced when water is unavailable for conservation, or when moisture levels are high and less limiting to plant growth.

Litter can influence production by reducing incoming photosynthetically active radiation (PAR) via reflection or absorbtion of light energy (Knapp and Seastedt 1986). Shading by litter follows the Beer-Lambert extinction law, with an exponential decrease in PAR transmittance as litter increases, and with different types of litter showing different extinction coefficients (Facelli and Pickett 1991b). In the Tallgrass Prairie, PAR levels below a dense litter mat can be 1-5% of levels above the litter surface (Weaver and Rowland 1952, Knapp and Seastedt 1986). Reduced PAR can prevent or delay the germination, emergence and seedling establishment of plant species that respond positively to light and may therefore have important influences on the resulting plant community (Grime 1979, Sydes and Grime 1981, Hamrick and Lee 1987, Facelli and Pickett 1991a, Facelli and Pickett 1991b). Light reduction by litter can also reduce plant densities, tillering, and associated production in grasslands due to physiological changes that reduce the plant's ability to fix carbon early in the year (Weaver and Rowland 1952, Haslam 1971, Knapp and Seastedt 1986, Willms 1988). Specific structural and physiological induced plant responses to high litter include reduced leaf thickness, specific leaf mass, stomatal density and conductance, and modifications in leaf photosynthetic pigment content (Knapp 1985, Knapp and Gilliam 1985).

Litter influences plant production by altering the temperature at the soil surface. By intercepting solar radiation, litter insulates the soil from sharp temperature increases and creates time lags in the soil profile to diurnal and seasonal temperature fluctuations (McKinney 1929, Weaver and Flory 1934, Evans and Young 1970, Facelli and Pickett 1991a). Litter can also lengthen the growing season by delaying soil freezing, but conversely may have detrimental effects on early season plant growth and total growing season production by delaying soil warming and thereby shortening the effective growing season (Dyksterhuis and Schmutz 1947, Penfound 1964, Knapp and Seastedt 1986, Facelli and Pickett 1991a). Natural litter loads in the Tallgrass Prairie decrease soil temperatures by up to 8°C (Weaver and Rowland 1952, Hulbert 1969), resulting in plants that develop more slowly and flower more sparsely (Weaver and Rowland 1952, Rice and Parenti 1978). Tillering can also be reduced with lower temperatures due to lower surplus energy for allocation to vegetative reproduction (Langer 1963). The reduction of soil thermal amplitude under litter mats may also impede the germination of seeds whose dormancy is broken by fluctuating temperatures (Thompson et al. 1977, Grime 1979), which in turn, may reduce plant diversity (Weaver and Rowland 1952). In contrast, lower temperatures under litter may positively influence plant re-growth following mid-summer defoliation based on the presence of temperatures closer to optimum for plant growth (Frank et al. 2002).

The physical barrier of the litter mat itself may reduce production, as plant mortality can occur as seedlings essentially grow themselves to death. Plants beginning growth under heavy litter must utilize stored energy producing shoots able to penetrate through the litter mat before becoming photosynthetically self sufficient (Sydes and Grime 1981, Hamrick and Lee 1987). Litter may also prevent seeds from reaching the soil and thereby inhibit the emergence of seedlings or sprouts (Facelli and Pickett 1991a). Generally, the position and size of the cotyledons during emergence (Grime 1979, Knapp and Seastedt 1986) and the shape, size and compactness of the litter mat (Facelli and Pickett 1991a) will determine the success of different plant species in establishing under the litter layer.

Litter can facilitate plant production by augmenting the soil nutrient status through the accumulation of organic matter on the ground surface. This organic matter is eventually incorporated into the soil, with the rate of nutrient release related to the physiochemical properties of the litter (Facelli and Pickett 1991a). Litter can also directly affect the chemical composition of rainfall reaching the soil surface through leaching (Knapp and Seastedt 1986), thereby increasing soil nutrient status. In contrast, litter may hamper nutrient cycling through reductions in temperatures and microbial activity, thereby slowing decomposition and mineralization rates (Knapp and Seastedt 1986).

2.5.3. Defoliation Influences on Soil Moisture

Grazing is a common land use in the Aspen Parkland and across most grasslands of the Great Plains (Environment Canada 2005b). Grazing can reduce litter loads, but also significantly affect soil moisture by means of affecting evapotranspiration. Grazing can increase soil water by removal of leaf area, reducing photosynthetic surfaces and ultimately lowering transpiration rates (Buckhouse and Coltharp 1976, Leriche et al. 2002). Grazing may also reduce root biomass (Holland et al. 1992), and therefore decrease the spatial extent of water-extraction in the rooting zone (Naeth et al. 1991b). Grazing is particularly effective at increasing soil moisture when applied earlier in the season coincident with high plant growth rates and maximum water use, and in doing so, may increase soil water availability later in the growing season compared to ungrazed areas (Buckhouse and Coltharp 1976, Naeth et al. 1991b).

Grazing can also reduce soil moisture content. Plant biomass can have a similar impact as plant litter in increasing infiltration and reducing soil evaporation (Naeth et al. 1991b, Leriche et al. 2002, Donker et al. 2006). Several studies in Alberta prairies have found grazing to reduce water at all measured soil profile depths (Donker et al. 2006), with the greatest reductions in deeper soil horizons (Naeth et al. 1991b).

2.5.4. Defoliation Influences on Plant Production

Defoliation, commonly through grazing by cattle in the Aspen Parkland, can significantly affect plant production by reducing leaf area and removing NPP (Weaver 1958). Defoliation results in a complex set of positive and negative, direct and indirect impacts on NPP through influences on PAR interception, soil water availability, plant nutrient content and productivity, and root:shoot allocation patterns (Holland et al. 1992, Leriche et al. 2001). For instance, defoliation can positively influence productivity by increasing light availability to lower leaves via a reduction in self-shading (Jameson 1963), leading to an increase in the photosynthetic rate of remaining tissues (Doescher et al. 1997). More often, defoliation reduces total growing season biomass as many plants are susceptible to growing-season biomass removal (Willms 1991).

Altered allocation of assimilates between above and belowground plant parts is another important effect of defoliation. A number of greenhouse studies have shown that defoliation will, at least temporarily, reduce root growth (Jameson 1963, Holland et al. 1992, King et al. 1995, Leriche et al. 2001). Field studies on biomass allocation have shown more contradictory results, but tend to show that defoliation has little effect on grassland belowground production (McNaughton et al. 1998). Where it does occur, altered photosynthate allocation in favor of shoot re-growth can reduce water and nutrient uptake ability and eventually affect the drought resistance of the plant community (Frank et al. 2002). Nonetheless, temporary diversion of resources to re-growing shoots may be important for promptly restoring photosynthetic tissues (McNaughton et al. 1998).

Moderate grazing levels can also have important influences on plant community composition. Climate and past grazing history may dictate whether species diversity and species density increase or decrease under defoliation pressures (Collins and Barber

1986, Milchunas and Lauenroth 1993, Hild et al. 2001), and whether absolute species counts or relative abundances are more strongly effected (Willms et al. 2002, Grace and Jutila 1999). Selective grazing may also alter the community composition through animal preferences for certain species (Holechek et al. 2004), effects not present in controlled defoliation studies using clipping as a proxy for grazing.

2.6. Summary

While much is known about soil moisture dynamics and the importance of moisture for plant production, few studies have examined the impact of litter threshold levels on the microenvironment (including soil moisture) and associated production levels in mesic grasslands like those in the Aspen Parkland. Little is also known about the interaction between litter and defoliation and their combined influences on plant production, particularly as mediated by soil moisture. A better understanding of short-term temporal regulation of soil moisture by litter and other ecosite variables will provide important information for developing prescriptive management strategies for reducing long-term variability in moisture and corresponding plant production in these areas.

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3. SOIL MOISTURE AND PRODUCTION RESPONSES TO VARIABLE LITTER AND DEFOLIATION

3.1. Introduction

The importance of studying soil moisture dynamics in water-limited systems arises from concerns over maintaining ecosystem resilience and plant production under a variable climate. Even in cool temperate grasslands like those of the Aspen Parkland of western Canada, where moisture is just adequate for the low evapotranspiration of the region (Coupland 1961), predictions under current climate change models make it necessary to proactively manage soil moisture. Although it is unclear whether future precipitation will increase or decrease in the Aspen Parkland, evaporation rates are likely to get higher with rising temperatures, and drought is likely to become more frequent and severe as the climate becomes more variable (Schindler and Donahue 2006). Understanding and manipulating plant litter effects on soil moisture can be an important tool for managing hydrologic function in these grasslands, as litter can variably effect rainfall interception, surface evaporation, infiltration and runoff (Facelli and Picket 1991).

Consequently, litter can be important for both increasing and preserving near-surface soil moisture levels. Litter can increase soil moisture through its impact on water infiltration and by slowing surface runoff (Weaver and Rowland 1952, Thurow et al. 1986, Naeth et al. 1991b, Dormaar and Carefoot 1996). Moisture levels are sustained by litter through shading effects and the consequent reduction in evaporation under lower soil surface temperatures (Dyksterhuis and Schmutz 1947, Knapp and Seastedt 1986). Evaporation is also reduced through the creation of a vapor barrier below the litter surface, which maintains higher levels of relative humidity and reduces water loss from the soil (Facelli and Pickett 1991). In some instances, litter can lead to lower soil moisture levels, particularly as it intercepts rainfall and reduces the amount of water reaching the soil surface (Knapp and Seastedt 1986, Naeth et al. 1991a). A better understanding of the role of litter is therefore important for optimizing the positive effects of litter on soil water. Specific information about the role of litter in rangelands may be uniquely important when examining production in agricultural systems that are not always water limited, particularly as litter can detrimentally affect plant growth by reducing surface temperature (Weaver and Rowland 1952, Rice and Parenti 1978) and the penetration of photosynthetically active radiation (Sydes and Grime 1981, Knapp 1985, Knapp and Seastedt 1986), or by increasing the physical barrier through which seedlings must grow during establishment (Sydes and Grime 1981, Hamrick and Lee 1987).

To better understand litter as a tool for moisture retention in managed grasslands, it is important to understand how litter may interact with common land-use practices like grazing. Litter and defoliation may exhibit particularly strong interactions during the period of plant re-growth subsequent to biomass removal as moisture has been found to be critical to plant phenological development (Willms and Jefferson 1993). The interaction of litter and defoliation may also alter our interpretation of appropriate litter levels for management (as in Adams et al. 2003), particularly if total growing season forage production can be linked to augmented soil moisture levels under optimum litter loads. Although this question is of practical concern, it has not been previously examined in a field setting.

In this study, two field sites located in the Aspen Parkland of central Alberta were used to examine soil moisture and plant production responses to varying litter loads and examine the interaction between litter and defoliation. The study sites provided a unique opportunity for examining moisture dynamics under highly variable litter levels in both native and tame grasslands. Specific research questions examined in this study include: (1) whether litter and defoliation alter the micro-environment at the soil surface, including soil moisture depletion, within native and tame grasslands of the Aspen Parkland, (2) whether litter, in combination with defoliation, alters forage production and plant community characteristics in the Aspen Parkland, and (3) whether vegetation changes can be linked to observed microenvironmental changes created by litter modification.

3.2. Materials and Methods

3.2.1. Study Area

This research was conducted at the University of Alberta Kinsella Research Station, approximately 150 km southeast of Edmonton, Alberta (53° 05' N; 11° 33' W) within the Aspen Parkland natural subregion. Two study sites were assessed representing a naturalized native and tame grassland, respectively. Both sites were in late seral condition, and ungrazed by livestock for more than 10 years, resulting in large accumulations of plant litter at both the Native (~5500 $kg^{\cdot}ha^{-1}$) and Tame (~7000 $kg^{\cdot}ha^{-1}$) sites. The area has a dry sub-humid climate, with annual precipitation generally between 400-500 mm, and mean annual temperature of 1.5° C, a summer mean of 15° C, and a January mean of -12.5° C. Elevation averages 690 m asl (Environment Canada 2005).

Both study sites were located within the lower elevations of a relict glacial spillway, although there is no seasonal flooding in most years. While the Tame Site was on a slightly elevated lower slope of the valley with a 2.5° grade, the Native Site was situated approximately 500 m north of the Tame site on a flat alluvial outwash about 1 m above the bottom of the spillway.

Soils at the Native Site were Dark Brown Chernozems, with an Ah horizon approximately 16 cm deep. An extensive gravel layer (70% of soil matrix) was present starting 11 cm below the surface, with abundant carbonates and mottles indicating a perched water table. Most roots were located in the top 20 cm of the soil, but extended to 33 cm below the surface. Soils at the Tame Site were also Dark Brown Chernozems, with an Ah horizon 30 cm deep. Gleying and mottling was evident 56 cm below the surface. Most roots were located in the top 15 cm of the soil, and extended 55 cm down.

At the Native Site, dominant grassland vegetation consisted of *Festuca hallii* (Vasey) Piper, *Poa pratensis* L. and *Agropyron smithii* Rydb. Although forbs were uncommon, small amounts of *Galium boreale* L., *Achillea millefolium* L. and *Taraxacum officianale* Weber were present. The shrub *Symphoricarpos occidentalis* Hook was also present. The Tame Site consisted primarily of *Bromus inermis* Leyss, *Agropyron repens*

(L.) Beauv and *Poa pratensis*, but had a moderate infestation of *Cirsium arvense* L. Scop., with few other forbs.

3.2.2. Experimental Design and Treatments

At both the Native and Tame sites, 45 plots were laid out in a randomized complete block (RCB) design, with 5 replicate blocks containing each of 9 treatments. All plots were 1.5 m by 1.5 m in size, and included a 0.25 m unsampled buffer along the perimeter. Blocks were set up as a square with three rows of three connected plots, and 1 m pathways to provide access for sampling. At the Native Site, blocks were dispersed across the lowland at similar elevations above the water table. At the Tame Site, blocks were adjacent to each other and parallel to the slope and were separated by 1 m walkways.

Treatments included 3 litter modifications crossed with 3 defoliation treatments in a factorial design. Litter treatments included 1) removal of all litter by clipping standing dead vegetation and hand scraping the litter layer, 2) an untreated *in situ* litter treatment with original litter levels (~5500 kg/ha in Native and ~7000 kg/ha in Tame), and 3) a double litter treatment. The latter was derived by randomly assigning the litter taken from each of the litter removal plots and spreading it evenly over the top of one of the existing litter plots, thereby providing double litter plots of ~11,000 kg/ha and ~14,000 kg/ha on the Native and Tame sites, respectively. Litter treatments were imposed in late September and early October of 2006 after a severe frost had killed aboveground vegetation. In this investigation, litter refers to all standing dead, detached and partially decomposed plant material of any size that is recognizable as plant material, not incorporated into the mineral soil and located on the surface of the soil mineral horizons. By the spring of 2007, even attached litter in *in situ* and double litter plots had been compressed by winter snow and was lying within 5 cm of the soil surface.

Three defoliation treatments were additionally imposed on the litter plots in mid-June 2007. Defoliation included either 1) heavy defoliation with clipping of all living plant material to 2.5 cm stubble height, 2) light defoliation with clipping of all living plant material to a 6.5 cm stubble height, or 3) an undefoliated check with no removal of plant material. As litter had been compressed to the soil surface by snow, no litter was removed during implementation of the defoliation treatment.

3.2.3. Field Sampling

At each site, sampling was conducted in early May, June, July and August of 2007 and included measures of environmental conditions and vegetation. Soil moisture and temperature, light interception, litter depth, foliar cover of vascular plants, and plant growth stage were sampled monthly. In addition, above and below-ground plant biomass, litter biomass, vascular plant species composition (by cover), height of focal grass species (*Poa pratensis* at Native Site, and *Bromus inermis* at Tame Site) and seedhead densities were measured in early August 2007. Volumetric soil moisture was also assessed in early August, as was Canada thistle density at the Tame Site.

3.2.3.1 Environmental Measures

Soil moisture was quantified in the top 10 cm of mineral soil using a TDR-MLX2 moisture probe. Moisture was measured for five consecutive days following significant rain events to obtain differential drying (i.e. soil moisture depletion) curves under the different litter treatments. Four moisture readings were taken per plot per day to account for spatial variability within plots. In plots with heterogeneous slope or topography, or containing anthills (Tame Site), all moisture readings were consistently taken in the same plot location over the five days. During June, rain occurred between the fourth and fifth day, so only four consecutive days of moisture readings were available.

Volumetric soil moisture was quantified in August 2007 in the fifth plot of each block to calibrate the TDR soil moisture readings. Soil cores 20 cm^3 in size (1.9 cm diameter by 7 cm deep) were taken in the corner of each plot after removing the litter layer. Cores were weighed fresh, oven-dried at $105^{\circ}C$ for three days, and re-weighed dry. Soil bulk density was calculated for each core with the following equation:

$$[\text{weight of dry soil} / \text{bulk volume of the soil}] \quad (1)$$

Gravimetric soil moisture was calculated as follows:

$$[(\text{weight of wet soil} - \text{weight of dry soil}) / \text{weight of dry soil}] * 100\% \quad (2)$$

Volumetric soil moisture was calculated with the following equation:

$$[\text{gravimetric soil moisture} * \text{dry bulk density}] \quad (3)$$

Soil temperature was measured monthly using a garden temperature probe in the first 5 cm of mineral soil. Temperature was measured at about mid-day (12-2 PM) on clear, sunny days to minimize variation unrelated to plot characteristics. August soil temperatures at the Tame Site were taken earlier in the morning (9 AM).

Light interception was measured with a LICOR sun-fleck ceptometer and reported as photosynthetically active radiation (PAR). In May, prior to plant growth, PAR was measured above and below the litter layer to assess light penetration to the soil surface. Measurements were taken across the entire plot with a segmented light probe. During June, July and August, PAR was measured above and below the current year's vegetation to assess light interception by current year plant biomass. Above-canopy PAR was measured as a single reading of the entire wand, while below-canopy PAR was measured as the average of ten readings on a segmented wand. Percent light interception was calculated using the following equation:

$$[(\text{above canopy PAR} - \text{below canopy PAR}) / \text{above canopy PAR}] * 100\% \quad (4)$$

3.2.3.2 Vegetation Assessment

Total foliar cover of live vascular plants was measured each month using a Daubenmire quadrat (0.10 m^2) (Daubenmire 1959) positioned in each plot. Overlapping foliage allowed estimates of foliar cover to exceed 100%. Quadrats were randomly relocated in the plot each month, but care was taken to ensure unusual features were avoided (e.g. occasional anthills, etc.).

Litter depth was measured all months in a representative area of the plot with a ruler from the top of the mineral soil to the average height of the litter lying on the ground surface.

Above ground biomass was sampled in a 0.25 m^2 quadrat within each plot in August 2007. All vegetation was harvested to a 1 cm stubble height and sorted by growth form (grasses and forbs). Where present, Canada thistle was sampled separately from the forbs in the Tame plots. Samples were dried at 65 °C for five days to constant mass and weighed to determine biomass. All weights were converted to kg/ha for statistical analysis. Litter biomass was also measured in August 2007, and was sampled within the same 0.25 m^2 quadrat used for quantifying above ground plant biomass. As the standing litter was flattened to the ground in all plots, this litter was clipped around the edges of the quadrat and to ground level to remove all attached litter. Detached litter was subsequently removed by hand raking the quadrat area. All litter was dried at 65 °C for five days to constant mass and weighed. Root biomass was sampled with a single 295 cm^3 (5 cm diameter by 15 cm deep) soil core per plot. Soil samples were sieved through a 0.5 mm screen, and following washing, extracted roots were dried at 65°C for three days to constant mass and weighed.

Vegetation composition was assessed through estimation of the percent cover of each species within the biomass quadrat prior to harvest in August. Composition data were used to derive species richness values per plot (number of species / 0.25 m^2). Species diversity was quantified for the cover data using Shannon's Diversity Index:

$$H' = \Sigma Pi * \ln Pi, \qquad (5)$$

where pi is the proportion of all species abundance consisting of species i.
Finally, species evenness was obtained by applying Pielou's J index (Pielou 1977):

$$J = H'/\log \text{species richness}) \qquad (6)$$

The development of focal grass species was monitored throughout the growing season. Plant growth stage and number of leaves per plant were quantified for each plot in each month based on an ocular assessment of plant morphology. Phenological development was evaluated on dominant *Poa pratensis* at the Native Site, and *Bromus inermis* at the Tame Site. Growth stage was numerically coded to specify whether the plant was 1) in its basal growth stage, 2) had initiated stem elongation, 3) reached advanced stem elongation, or 4) had emergent seedheads.

Plant height was measured in August on eight *Poa pratensis* plants (Native Site) and eight *Bromus inermis* plants (Tame Site) randomly chosen in each plot. Height was measured from the soil surface to the top of the longest leaf. The eight values in each plot were averaged to obtain a plot mean prior to analysis.

Seedhead densities were estimated in August by counting the number of seedheads on grass plants within the entire plot (no./2.25 m^2). Seedheads were not distinguished by species. Thistle shoot densities were taken by counting all thistle stems within the entire plot at the Tame Site (no./2.25 m^2). Both measures were converted to no./ m^2 for subsequent analysis.

3.2.4. Data Analysis

Data were analyzed separately for the Native and Tame sites due to differences in past management, dominant plant species, and soil types. Local climatological data for May, June and August 2007 were obtained from the Kinsella Research Station headquarters located less than 2 km south of both sites. These data were not available for July due to data logger failures and consequently, these climate data were obtained from the next closest Environment Canada weather station at Viking, Alberta, approximately 20 km west of Kinsella. Environmental data for the rainfall events prior to sampling as well as for air temperatures during the soil moisture depletion sampling periods in May, June, July and August 2007 are shown in Appendix 1.

Statistical analyses were completed using Proc Mixed in SAS 9.1.3 for a random complete block (RCB) design. Vegetation cover, light interception, leaf number and growth stage of the dominant grass were run as a repeated measures ANOVA using month as the repeated time effect. The main effect of litter was analyzed over all four months, and the litter*defoliation treatment analyzed separately only for the post-defoliation measurements in July and August. All other variables were analyzed with regular mixed model ANOVA.

Prior to analysis, all data were checked for normality and homogeneity of variances, and data not meeting these assumptions were log or square root transformed. For the Native Site, forb biomass and the root:shoot ratio were log transformed; percent rough fescue cover and seedhead density were square root transformed; and light interception by litter was doubly transformed (McCune and Grace 2002). For the Tame Site, Canada thistle biomass, thistle cover, total regrowth biomass, seedhead density and light interception by litter were log transformed. Soil temperature in May was square root transformed, and total growing season biomass was transformed using both applications. While the final F-statistic and significance tests are presented based on the transformed data where applicable, the presentation of final results uses LSmeans and standard errors from the original data to maintain data clarity. Statistical significance for all tests was set at $P \leq 0.05$.

Leaf number and growth stage data for both the Native and Tame sites did not conform to either normality or homogeneity of variances, and were initially run using repeated measures analysis with the non-parametric Proc GENMOD in SAS. GENMOD is not able to account for the random block variable in the experimental design, and the leaf number and growth stage were therefore re-run using the parametric Proc MIXED, which gave similar, but slightly more conservative standard error estimates and mean comparisons than GENMOD. Because the data from the MIXED procedure was more conservative, these results are presented.

Simple regressions were also run on the leaf height of the dominant grass species at the Native and Tame Sites using Proc REG in SAS to examine the influence of moisture on leaf re-growth following defoliation. A multiple regression was also run on May vegetative cover at the Native Site to examine the influence of the microenvironment on early rates of plant growth.

3.3. Results

3.3.1. Native Site

3.3.1.1. Environmental Responses

TDR soil moisture was affected by litter but not defoliation in all months of sampling at the Native Site (Table 3.1). Soil moisture also declined markedly over the five days of sampling following individual rainfall events in each month (see Figs. 3.1A-D). During May, plots with litter removed were lower in moisture than those with litter ($P=0.02$), but only on the day after the rainfall event (Fig. 3.1A). In June, the double litter plots had greater soil moisture than the other treatments ($P<0.0001$) on each of the first three days following rainfall (Fig. 3.1B), and by day four, all litter treatments differed from one another in moisture content ($P<0.0001$). Over the 4 days of monitoring in June, total decreases in moisture within the double (-2.8±0.7%) and *in situ* (-4.0±0.7%) litter treatments were similar ($P>0.05$), but remained below ($P<0.005$) that of plots where litter was removed (-6.8±0.7%). Differential soil moisture responses following rainfall during July were not apparent under the various litter treatments (Fig. 3.1C). The lone soil moisture response in July was in the total moisture loss over the five day interval ($P=0.02$), with litter removal plots (-13.2±1.1%) showing a greater loss of moisture ($P<0.006$) than treatments where litter remained (-10.1±1.1% and -11.8±1.1%). In August, soil moisture differences were strongly affected by litter treatments ($P<0.0002$) on all days of sampling, with the litter removal plots consistently lower in moisture than the others (Fig. 3.1D). The *in situ* treatment had less soil moisture than the double litter treatment by day five. Total loss of soil moisture was again greatest ($P<0.0001$) in August for the plots lacking litter (-8.3±0.4%), followed by the *in situ* (-6.6±0.4%) and double litter (-5.1±0.4%) treatments. Finally, volumetric soil moisture measurements were relatively poorly correlated with the TDR soil moisture readings, with the relationship between the two variables demonstrating a slope of -0.49 and an R-square of 0.36 (Appendix 2).

Similar to soil moisture, the litter treatments but not defoliation had an ($P<0.0001$) effect on soil temperature in each month (Table 3.1). In May, June and July, plots with all litter removed had soils warmer than the others by ~3°C, while the double litter plots had soils that were 2-3°C cooler than the others, including the *in situ* treatment (Fig. 3.2). In August, the *in situ* and double litter treatments were similar in temperature, but remained cooler than plots with litter removed.

Litter treatments also had a strong effect on the amount of light intercepted before reaching the soil surface ($F_{2,42}=63.51$, $P<0.0001$). Plots with litter removed intercepted only 10.7±1.2% of light, which remained well below ($P<0.0001$) the amount of light intercepted by litter in both the *in situ* (94.3±1.2%) and double litter (99.7±1.2%) plots.

3.3.1.2. Production Responses

Significance tests for biomass of plant re-growth following defoliation (August biomass only) and total growing season biomass (June defoliated biomass plus August re-growth biomass) are shown in Table 3.2. Levels of total shoot re-growth were affected by both litter ($P=0.002$) and defoliation ($P<0.0001$), largely due to strong effects of litter ($P=0.002$) and defoliation ($P<0.0001$) on the grass rather than the forb component. Patterns of grass and total re-growth biomass among litter treatments were similar (Table 3.3), with greater biomass in the *in situ* litter treatment compared to both the litter removal and double litter treatment. Not surprisingly, defoliation effects on re-growth biomass were even more pronounced ($P<0.0001$), with the undefoliated plots (2695±161 kg/ha) containing the most biomass, followed by the lightly defoliated plots (1810±118 kg/ha) and the heavily defoliated plots (1239±118 kg/ha). Forb biomass was unaffected by litter and defoliation.

Conversely, only litter treatments showed significant effects on total accumulated growing season (June defoliated plus August re-growth) biomass (Table 3.2). Litter had a strong effect ($P<0.0001$) on both grass and total shoot biomass, with *in situ* litter plots containing the most biomass and the double litter plots the least (Table 3.3). Litter also significantly affected forb biomass ($P=0.03$), with litter removal plots containing the most forb biomass ($P<0.05$) and *in situ* plots the least. Neither litter nor defoliation affected root biomass or the root:shoot ratio of vegetation at the Native Site (Table 3.2), although litter effects on the root:shoot ratio were significant at $P=0.10$, with the double litter treatment showing a greater ratio than plots containing *in situ* litter (Table 3.3).

3.3.1.3. Plant Development Responses

The average height of *Poa pratensis* was influenced by both the litter ($F_{2,36}=68.44$, $P<0.0001$) and defoliation ($F_{2,36}=79.57$, $P<0.001$) treatments, but not by their interaction ($F_{4,36}=0.54$, $P=0.70$). *Poa* plants were shorter ($P<0.05$) in litter removal plots (22.6±0.07 cm) than under the *in situ* (33.6±0.7 cm) and double (32.8±0.7 cm) litter treatments. Heavy defoliation produced the shortest plants in August (24.8±0.7 cm), followed by light defoliation (27.0±0.7 cm) and undefoliated plots (37.2±0.7 cm).

August soil moisture on day five of measurement accounted for much of the variation in *Poa* height in defoliated plots (*Poa* height = -8.84 + 1.91 soil moisture on day 5, R^2 = 0.69).

The number of leaves per *Poa pratensis* plant was significantly affected by litter ($F_{2,7.37}$=130.22, P<0.0001), month ($F_{3,10}$=5.70, P=0.02), and the litter by month interaction ($F_{6,12}$=11.39, P=0.0002) over the four sampling months. Changes in the number of *Poa* leaves through time under the different litter treatments are shown in Figure 3.3. Treatment differences were most pronounced in May, with increasing similarity over the subsequent months. Conversely, defoliation had no effect on *P. pratensis* leaf number ($F_{2,36}$=0.54, P=0.59).

The phenological development (i.e. most advancedgrowth stage) of *Poa pratensis* was also significantly affected by litter ($F_{2,44}$=23.81, P<0.0001), sampling month ($F_{3,44}$=103.50, P<0.0001), and their interaction ($F_{6,44}$=12.56, P<0.0001). While *Poa* development in May and August were identical across litter treatments, there was more rapid plant development in the litter removal plots during June and July (Fig. 3.4). Defoliation ($F_{2,36}$=44.99, P<0.0001) and the defoliation by month interaction ($F_{2,36}$=12.24, P<0.0001) also had a strong impact on *Poa* growth stage in July and August. Defoliated plots (heavy = 1.1±0.2, light =1.6±0.2 growth stage) showed a strong reduction (P<0.0001) in growth stage in July compared to undefoliated plots (3.4±0.2 growth stage). Although the growth stage of *Poa* in defoliated plots (3.1±0.1, 3.3±1 stage) had increased by August, it remained lower (P<0.0001) than the undefoliated plots (4.0±0.1 stage).

Seedhead density in August responded to both the litter ($F_{2,32}$=94.58, P<0.0001) and defoliation ($F_{2,32}$=234.36, P<0.0001) treatments, and to the litter by defoliation interaction ($F_{4,32}$=51.59, P<0.0001). Differences between treatment combinations are summarized in Table 3.4. Defoliation of either intensity reduced seedhead production (P<0.05) in comparison to the true check (16.2±6.1 seedheads/m^2) to levels below 4 seedheads/m^2. While the double litter plots contained similar seedhead densities to the *in situ* check (P>0.10), litter removal resulted in a large increase (P<0.0001) in seedheads to 166±6.1 seedheads/m^2, but only in the absence of defoliation.

3.3.1.4. Plant Community Responses

Total vegetation cover was effected by both litter ($F_{2,16.4}$=78.62, P<0.0001) and month of sampling ($F_{3,13.6}$=205.18, P<0.0001), but there was no interaction between litter and month ($F_{6,16.4}$=1.45, P=0.26). In all months, litter removal plots contained the most vegetation cover and double litter plots the least (Fig. 3.5). Most of the variation in plant cover at the start of the growing season was related to variation in soil temperature and light interception by litter (May cover = 10.1 + 3.4*soil temperature – 0.16*light interception; R^2 = 0.89). Defoliation also affected total vegetation cover in July and August ($F_{2,68}$=60.21, P<0.0001), with the most cover in undefoliated plots (61.7±3.0% and 63.8±3.0%), followed by lightly defoliated plots (52.9±3.0% and 54.5±3.0%), and heavily defoliated plots (38.3±3.0% and 40.5±3.0%).

Patterns in August vegetation cover were primarily driven by the grass component, which responded significantly to both litter ($F_{2,32}$=28.66, P<0.0001) and defoliation ($F_{2,32}$=20.32, P<0.0001), but not the litter by defoliation interaction ($F_{4,32}$=0.57, P=0.68). Grass cover was greatest in the litter removal plots (62.2 ± 3.2%), then the *in situ* plots (46.9 ± 3.2%), and lowest in the double litter plots (37.2 ± 3.2%), and was also greatest in the undefoliated plots (58.2 ± 3.2%), then the lightly defoliated plots (50.8 ± 3.2%), and showed the least cover in the heavily defoliated plots (37.3 ± 3.2%). Patterns in grass cover under the litter treatments were driven primarily by the dominant grasses *Poa pratensis* ($F_{2,32}$=9.08, P=0.0008) and *Festuca hallii* ($F_{2,32}$=15.81, P<0.0001). *P. pratensis* cover was greater in the litter removal treatment (45.9± 4.4%) compared to the *in situ* (31.0 ± 4.4%) and double litter (29.6± 4.4%) treatments. In a close parallel, *F. hallii* cover was similar under the litter removal (11.3± 1.6%) and *in situ* (11.2± 1.6%) litter treatments, and lowest under the double litter treatment (3.7± 1.6%). Only *P. pratensis* responded significantly to defoliation ($F_{2,32}$=9.30, P=0.0007), with the undefoliated (42.2± 4.4%) and light defoliation (39.3± 4.4%) treatments containing greater cover than the heavy defoliation treatment (25.1± 4.4%). Forb cover was unaffected by either litter ($F_{2,36}$=0.99, P=0.38) or defoliation ($F_{2,36}$=1.24, P=0.34).

Species richness was influenced by litter ($F_{2,36}$=7.51, P=0.002), with more species present (P<0.05) in the litter removal plots (5.5± 0.4 species) compared to the *in situ*

(3.9± 0.4 species) or double (3.5± 0.4 species) litter plots. Many of the species that responded to litter treatment (i.e. removal) were forbs ($F_{2,36}$=4.22, P=0.02). Species evenness responded to defoliation ($F_{2,32}$=3.49, P=0.04) but not litter ($F_{2,32}$=2.12, P=0.14), with heavily defoliated plots (1.7±0.1) showing greater evenness (P<0.05) than either the lightly defoliated (1.3±0.1) or undefoliated (1.4±0.1) plots. Shannon's diversity index was unaffected by either litter ($F_{2,32}$=1.98, P=0.15) or defoliation ($F_{2,32}$=0.70, P=0.50).

3.3.2. Tame Site

3.3.2.1. Environmental Responses

Soil moisture values at the Tame Site were affected by litter in June, July and August (Table 3.5). Soil moisture also declined over the five days of sampling following rainfall at this site (see Figs 3.6A-D). In May, litter treatments showed no difference in soil moisture (P>0.05) on any day after rainfall despite a trend for the litter removal treatment to have more moisture (Fig. 3.6A). During June, while individual moisture measurements did not differ (P>0.05) (Fig. 3.6B), total decreases in moisture differed (P< 0.0001) between the double (-2.4±0.7%), *in situ* (-4.3±0.7%) and litter removal plots (-6.8±0.7%). Differential soil moisture responses to the litter treatments were also apparent on the first and fourth day (P<0.05) following rainfall in July, with the litter removal treatment containing more moisture than the double litter plots at those times (Fig. 3.6C). Total moisture loss over the five day interval in July also differed (P=0.04) between litter treatments, with litter removal plots (-11.2±1.3%) showing a greater loss of moisture (P=0.02) than the *in situ* litter plots (-8.6±1.3%). In August, soil moisture differences were strongly affected by litter treatments (P<0.003) on days 3, 4 and 5 following rainfall, with the litter removal plots consistently lower in moisture than the others (Fig. 3.6D). Total loss of soil moisture in August was again greatest (P<0.0001) for the plots lacking litter (-6.4±0.4%), followed by the *in situ* (-3.2±0.4%) and double litter (-2.0±0.4%) treatments.

Soil moisture was also affected by the defoliation treatment on the second day after rainfall in July (P=0.02), with the heavily defoliated plots (24.0±2.7%) containing more moisture (P=0.006) than the undefoliated plots (20.4±2.7%). Defoliation also affected soil moisture on the second day following rainfall in August (P=0.02), with heavily defoliated plots (23.1±1.2%) again containing more moisture (P=0.007) than undefoliated plots (21.4±1.2%). Finally, volumetric soil moisture measurements at the Tame Site were strongly correlated with the TDR soil moisture readings, with the relationship between the two variables demonstrating a slope of 0.61 and an R-square of 0.91 (Appendix 2).

The litter treatments but not defoliation had a significant (P<0.0001) effect on soil temperature in each month (Table 3.5). In May, June and July, plots with litter removed had soils warmer than the other treatments by ~4°C, while the double litter plots had soils that were 1-3°C cooler than the *in situ* treatment (Fig. 3.7). Conversely, in August, the *in situ* and double litter treatments were similar in temperature, and both were warmer than plots with litter removed. The litter by defoliation interaction also influenced soil temperature (P=0.03) in July (Table 3.5), with greater temperature differences between defoliated treatments in litter removal plots (Δ=2.4°C) than in *in situ* (Δ=0.9°C) or double (Δ=0.4°C) litter treatments.

Litter treatments had a strong effect on the amount of light intercepted before reaching the soil surface ($F_{2,38}$=140.99, P<0.0001). Plots with litter removed intercepted only 26.5±3.1% of light, which remained well below (P<0.0001) the amount of light intercepted by litter within the *in situ* (99.5±3.1%) and double litter (100.0 ± 3.1%) plots.

3.3.2.2. Production Responses

Significance tests for Tame Site biomass of both plant re-growth following defoliation (August biomass only) and total growing season biomass (June defoliated biomass plus August re-growth biomass) are shown in Table 3.6. Total shoot re-growth was influenced by both litter (P=0.006) and defoliation (P<0.0001), and corresponded to the effects of litter (P=0.02) and defoliation (P<0.0001) on the grass rather than the forb component. Grass re-growth biomass was greater in the litter removal plots than in the double litter plots, and total shoot re-growth biomass was greater in the litter removal plots than in either treatment containing litter (Table 3.7). Similar to the Native Site, defoliation also had a large effect on re-growth biomass (P<0.0001), with the undefoliated plots (4363±354 kg/ha) containing more biomass than either the lightly defoliated plots (2366±354 kg/ha) or heavily defoliated plots (2228±354 kg/ha). Thistle and other forb biomass did not respond to either the litter or defoliation treatment (Table 3.6).

The litter treatment also had a strong effect on grass ($P<0.0001$) and shoot ($P<0.0001$) total growing season (June defoliated plus August re-growth) biomass (Table 3.6). Litter removal plots contained the most grass and shoot biomass, while double litter plots contained the least overall shoot biomass (Table 3.7). Defoliation also influenced total shoot biomass ($P=0.05$), with undefoliated plots (4393±461 kg/ha) containing more total biomass than lightly defoliated plots (3524±461 kg/ha): heavily defoliated plots (4107±461 kg/ha) had similar ($P>0.05$) biomass to the other two treatments. Neither litter nor defoliation affected total forb biomass.

Root biomass responded weakly to the defoliation treatment ($P=0.06$), with more root mass in undefoliated plots (13785±959 kg/ha) than lightly defoliated plots (10424±959 kg/ha). Heavily defoliated plots (12053±959 kg/ha) were similar ($P>0.05$) in biomass to the other defoliation levels. Conversely, the root:shoot ratio of vegetation responded to litter ($P=0.05$), with the double litter treatment showing a greater ratio than the litter removal treatment (Table 3.7).

3.3.2.3. Plant Development Responses

The average height of the dominant grass, *Bromus inermis*, was influenced by defoliation ($F_{2,32}=83.57$, $P<0.0001$) and the litter by defoliation interaction ($F_{4,32}=3.42$, $P=0.02$), but not by the main litter effect ($F_{2,32}=1.23$, $P=0.31$). As expected, plants were significantly ($P<0.0001$) shorter in lightly (37.2±1.9 cm) and heavily (33.2±1.9 cm) defoliated plots than in undefoliated plots (53.9±1.9 cm). Within lightly and heavily defoliated plots, *Bromus* plants increased in height with increasing litter, while in undefoliated plots, plant height decreased with increasing litter (Fig. 3.8). August soil moisture on day four of measurement accounted for some of the variation in *B. inermis* height in defoliated plots (plant height = 13.6 + 1.05 soil moisture on day 4; $R^2 = 0.24$).

The number of leaves per *Bromus inermis* was significantly affected by litter ($F_{2,11.6}$=11.69, P=0.002) and month of sampling ($F_{3,10}$=125.47, P=0<0.0001), but not by the litter by month interaction ($F_{6,12}$=1.27, P=0.34). *Bromus* leaf counts under different litter treatments over the four sampling months are shown in (Fig. 3.9). Plants in the litter removal plots consistently had more leaves (P<0.01) than in the other treatment plots, with the exception of August. Defoliation ($F_{2,36}$=101.3, P<0.0001) and the defoliation by litter interaction ($F_{4,36}$=4.66, P=0.004) also affected *B. inermis* leaf counts. The number of leaves on *Bromus* decreased (P<0.0001) from undefoliated plots (9.4±0.2 leaves) to the lightly (5.6±0.2 leaves) and heavily (5.0±0.2 leaves) defoliated treatments. While leaf counts increased (P<0.05) with increasing litter in defoliated plots, they decreased with more abundant litter in undefoliated plots (Fig. 3.10).

The phenological development (or growth stage) of *Bromus inermis* was significantly affected by litter ($F_{2,12.2}$=10.01, P=0.003), month ($F_{3,34.9}$=255.56, P<0.0001), and the litter by month interaction ($F_{6,35.5}$=4.14, P=0.003) during 2007. Growth stage was generally most advanced in litter removal plots (Fig. 3.11). Defoliation ($F_{2,33.1}$=79.63, P<0.0001) and the defoliation by litter interaction ($F_{2,33.1}$=5.84, P=0.001) also had a strong impact on growth stage in July and August. As expected, plants in undefoliated plots had the most advanced growth stage (3.7±0.1 stage) (P<0.01), followed by the light defoliation (2.7±0.1 stage) and then the heavy defoliation treatment (2.4±0.1 stage). Development of *Bromus* was most advanced (P<0.05) with increasing litter in the presence of defoliation, but decreased with increasing litter in the absence of defoliation (Fig. 3.12).

Seedhead density across the Tame Site responded to both the litter ($F_{2,32}$=2.80, P=0.08) and defoliation ($F_{2,32}$=25.85, P<0.0001) treatments, but not to the litter by defoliation interaction ($F_{4,32}$=0.73, P=0.58). Seedhead density was greater (P<0.10) in litter removal plots (6.5±0.5 seedheads/m^2) compared to *in situ* litter (1.7±0.5 seedheads/m^2) and double litter (0.7±0.5 seedheads/m^2) plots. Light defoliation (0.21±0.5 seedheads/m^2) and heavy defoliation (0.30±0.5 seedheads/m^2) also reduced seedhead production (P<0.0001) in comparison to the undefoliated plots (8.3±0.5 seedheads/m^2).

3.3.2.4. Plant Community Responses

Total vegetation cover at the Tame Site was impacted by litter ($F_{2,44}$=127.96, P<0.0001), month of sampling ($F_{3,44}$=203.72, P<0.0001) and their interaction ($F_{6,44}$=6.63, P<0.0001). Litter removal consistently led to the greatest cover, with double litter plots the least (Fig. 3.13). Differences in cover between treatments were greatest in June. Defoliation ($F_{2,32.2}$=25.55, P<0.0001), month ($F_{1,36}$=18.5, P<0.0001), and the defoliation by month interaction ($F_{2,36}$=3.53, P=0.04) also affected cover in July and August, respectively, with the most cover in undefoliated plots (70.7±5.5% and 72.3±5.2%), then lightly defoliated plots (51.1±5.5% and 59.5±5.2%), and the least in heavily defoliated plots for July but not August (45.7±5.5% and 59.2±5.2%).

Similar to the Native Site, patterns in August vegetation cover at the Tame Site were driven primarily by the grass component, which responded significantly to both litter ($F_{2,32}$=22.63, P<0.0001) and defoliation treatments ($F_{2,32}$=6.54, P<0.004), but not the litter by defoliation interaction ($F_{4,32}$=1.19, P=0.33). Grass cover was greater (P<0.05) in the litter removal plots (63.1 ± 5.0%) than the *in situ* litter plots (45.6 ± 5.0%) and the double litter plots (40.0± 5.0%), and was also greater (P<0.05) in the undefoliated plots (57.1 ± 5.0%) compared to the light (45.7 ± 5.0%) and heavily defoliated (46.0 ± 5.0%) plots. Cover of *Bromus inermis* was influenced only by litter ($F_{2,32}$=3.45, P=0.04), showing more cover (P=0.01) in litter removal plots (31.7±3.3%) than double litter plots (22.7±3.3%), with *in situ* litter plots (26.1±3.3%) similar to the other two treatments (P>0.05). *Poa pratensis* cover was also influenced by litter ($F_{2,32}$=21.23, P<0.0001), with litter removal (23.9±2.0%) containing greater cover (P<0.05) than either the *in situ* plots (13.1±2.0%) or the double litter plots (9.7±2.0%). *Agropyron* spp. responded to defoliation at P<0.10 ($F_{2,32}$=3.05, P=0.06), with the undefoliated plots (9.3± 3.4%) showing greater cover (P<0.01) than either the lightly defoliated (5.9± 3.4%) or heavily defoliated (6.5± 3.4%) plots. Finally, forb cover was unaffected by either litter ($F_{2,32}$=0.91, P=0.41) or defoliation ($F_{2,32}$=0.96, P=0.39), as was thistle cover (litter: $F_{2,32}$=0.21, P=0.81; and defoliation: $F_{2,32}$=0.34, P=0.71).

The litter treatment had no effect on species richness ($F_{2,32}$=0.39, P=0.68), species evenness ($F_{2,32}$=0.07, P=0.93) or Shannon's diversity index ($F_{2,32}$=0.11, P=0.90) at the

Tame Site. Defoliation also had no effect on richness ($F_{2,32}$=0.39, P=0.68), evenness ($F_{2,32}$=1.02, P=0.37) or diversity ($F_{2,32}$=0.24, P=0.79).

Canada thistle stem density responded significantly to litter at $P<0.10$ ($F_{2,32}$=3.06, P=0.06), but not to the defoliation treatment ($F_{2,32}$=0.14, P=0.87). Litter removal plots (14.3±1.4 thistle /m^2) contained more ($P<0.05$) thistle per m^2 than both the *in situ* (10.5±1.4 thistle /m^2) and double (10.7±1.4 thistle /m^2) litter plots.

3.4. Discussion

3.4.1. Environmental Responses

3.4.1.1. Litter and Defoliation Influences on Soil Moisture

At the Native Site, litter affected soil moisture content while defoliation did not. The capacity of litter at this site to reduce evaporative losses appeared more important in maintaining greater soil moisture than through the reduction in transpiration resulting from the removal of phytomass with defoliation. The greatest soil moisture content the day following rainfall was always recorded in either the double or *in situ* litter plots. This result is somewhat surprising as heavy litter treatments were expected to have a greater effect on rainfall interception and associated water loss immediately following precipitation than was found (Weaver and Rowland 1952, Knapp and Seastedt 1986, Naeth et al. 1991a), particularly as the litter treatments used here consisted of large amounts of standing and coarse organic matter known to be very effective at intercepting rainfall in Aspen Parkland grasslands (Naeth et al. 1991a). Therefore, the benefits of the moderate to high litter levels at the Native Site more than compensated for any moisture losses in this experiment.

July *in situ* litter plots had lower moisture content than litter removal plots, providing some evidence of greater interception potential after small rainfall events (Walsh and Voight 1977). Due to the high amount of litter present in these litter plots, particularly those with double litter, it is probable that interception losses occurred in the other months as well. Consequently, during and immediately following precipitation, the litter removal plots may well have had greater near-surface soil moisture levels than the other treatments. However, significant surface evaporation would have occurred in these litter removal plots within the 24 hours prior to the initial TDR readings resulting instead in the lower observed moisture values on the first day of measurement. Comparative evaporation rates during this time period would probably have been lower in the *in situ* and double litter plots due to decreased temperature and increased relative humidity under the litter layer (Dix 1964, Facelli and Pickett 1991), leading to the more favorable moisture readings after 24 hours.

At the Tame Site, both litter and defoliation had an effect on soil moisture, with litter apparently less important compared to the Native Site for most months. Litter removal plots contained the greatest soil moisture levels on the first measurement day in May, June and July, highlighting the effectiveness of litter in potentially intercepting precipitation and reducing soil moisture recharge at the Tame Site. This effect may have been due to the greater litter biomass at the Tame Site, and may have been exacerbated by the large component of wide-leaved grasses like *Bromus inermis* and *Agropyron repens* within the litter mat, which together may have had a larger capacity to intercept precipitation than the more narrow-leaved *Poa pratensis* and *Festuca halli* that dominated the litter layer at the Native Site (Thurow et al. 1987, Naeth et al. 1991a).

Greater initial moisture readings within *in situ* and double litter plots at the Native Site may have also resulted from litter influences on water infiltration. However, the presence of residual litter on the litter removal plots, along with high plant cover and the absence of physical soil crusts, diminish the likelihood that infiltration was significantly hampered in any of the treatments (Johnson 1962, Dormaar and Carefoot 1996). Nonetheless, increasing litter has been found to have a positive association with infiltration, although there is evidence of an upper asymptote for this relationship (Meeuwig 1970).

By the fifth day of measurement in June, July and August at the Native Site, double litter plots had the greatest moisture levels. At the Tame Site, moisture was either similar between treatments or highest in double litter plots. Greater ending moisture levels in the double litter and *in situ* litter plots was likely due to the effect of litter on reducing evaporation over the five days of measurement (Knapp and Seastedt 1986, Dormaar and Carefoot 1996). However, greater current-year growth of plant leaf area in litter removal plots may also have resulted in increased transpiration during the growing season (Naeth et al. 1991b), and may therefore also account for the greater total moisture loss over the five days of measurement. Overall, these moisture dynamics highlight the complex role of litter in changing infiltration, reducing evaporation and maintaining near-surface soil moisture following rainfall.

Litter had a particularly strong relationship with observed soil moisture in June at the Native Site and in August at both sites, corresponding to the months with greatest rainfall input prior to sampling. Near-surface soil moisture is most affected by rainfall (Salve and Allen-Diaz 1991), and greater recent water inputs may have amplified the effects of litter and live plants on soil water dynamics, particularly moisture conservation, during these times. Litter also appears to have had important effects on reducing evaporation of soil moisture in May and July. At the Native Site, litter was closely associated with soil moisture only on the first day of May, possibly due to greater surface evaporation of rainfall in litter removal plots. May had the highest levels of soil moisture, corresponding to recent inputs from snowmelt (Naeth et al. 1991b), and water may have been more available for rapid evaporation on the soil surface over the first two measurement days if rainfall input initially exceeded soil storage capabilities (Laio et al. 2001a). Finally, despite a lack of treatment differences on each day of measurement, July soil moisture depletion at the Native Site was also greatest in litter removal plots, again likely due to evaporation of recent rainfall from more exposed soils, particularly as July had the highest ambient temperatures (See Appendix 1) (Weaver and Rowland 1952).

Although excessive litter levels were expected to have both positive (reducing evaporation and increasing infiltration) and negative (rainfall interception) effects on soil moisture, this study found that, with a few exceptions, the net influence of litter quantity on near-surface soil moisture was generally positive. Other studies with high litter levels have shown varied results. In the Tallgrass Prairie in particular, litter effects on rainfall interception often result in a net reduction in soil moisture (Weaver and Rowland 1952, Knapp and Seastedt 1986). Nonetheless, increased infiltration and reduced evaporation under litter can offset interception losses and be important for moisture retention in more arid Mixedgrass grasslands (Willms et al. 1986, Naeth et al. 1991a).

The presence of a defoliation effect at the Tame and not the Native Site may be due to greater plant production at the Tame Site. Defoliation at the Tame Site resulted in greater observed moisture in heavily defoliated plots than undefoliated plots, likely indicative of reduced transpiration associated with a smaller plant canopy (Naeth and Chanasyk 1995, Leriche et al. 2002). Other studies have shown contradictory results regarding the effect of defoliation on soil moisture (Buckhouse and Coltharp 1976, Naeth et al. 1991b, Salve and Allen-Diaz 2001), particularly as some of these studies examined defoliation through grazing with cattle, thereby complicating the relationship with trampling and consequent changes in soil physical properties and associated infiltration (Donkor et al. 2006). In general, defoliation results in a tradeoff between reduced evapotranspiration with the removal of leaf area, thereby prolonging soil water availability, and reduced infiltration and higher evaporation rates with biomass removal (Buckhouse and Coltharp 1976, Salve and Allen-Diaz 2001, Leriche et al. 2001).

The inverse relationship at the Native Site between volumetric and TDR moisture values is also noteworthy, although the small sample size (n=5) is likely susceptible to sampling error, with two data points driving the negative relationship. Furthermore, unlike the TDR sampling where multiple readings were taken across each plot, volumetric sampling reflected only a single soil core from the corner of each of the 5 plots, which would make the latter data highly susceptible to microsite induced variation in soil moisture. With variable moisture within a plot, it is possible that the two data points driving the negative relationship were taken in plots with greater spatial moisture variability on the day of measurement. Nevertheless, if the trend in the data is correct, the presence of salts may also explain why modeled soil moisture declined as actual soil moisture increased. Low moisture levels may increase the salt concentration at this lowland site, with magnesium and sodium sulfate common in soils of the area (Last and Ginn 2005), resulting in increased conductivity and altered modeled moisture values (Inoue et al. 2008). Conversely, high soil moisture could dilute the salt and reduce conductivity, yielding lower modeled soil moisture values with the TDR probe.

3.4.1.2. Litter and Defoliation Influences on Soil Temperature

Litter also influenced soil temperature, with the warmest temperatures found within the litter removal plots in all months at the Native Site and in most months at the Tame Site. Differences in soil temperature are likely the result of the shading effect of litter, with both the *in situ* litter and double litter plots blocking over 90% of incoming solar radiation at both sites. Litter has consistently been found to have a strong influence on reducing soil temperature in other studies (Weaver and Flory 1934, Weaver and Rowland 1952, Evens and Young 1970, Knapp and Seastedt 1986). The thicker litter layer of the double litter plots also appeared to provide a better insulating layer, leading to a cooler soil compared to the *in situ* litter plots in May, June and July. The similar temperatures under the two litter treatments in August was likely the result of the added shading effect of the greater quantity of plant biomass in the *in situ* litter plots during peak biomass of the growing season at both sites. Live plant biomass had an effect on temperature at the Tame Site in July, particularly in the plots where litter was removed. Generally, the influence of litter on reducing temperature has important implications for moisture by reducing evaporation rates (Facelli and Pickett 1991).

Soil temperature patterns at the Tame Site in August differed from the other months, with warmer temperatures in the double litter plots and cooler temperatures in the litter removal plots. This anomaly may be due to August sampling occurring early in the morning, while measurements in the other months were taken mid-day after the sun had heated the soil. Collectively, these results demonstrate the buffering effect of litter, by which it shades the soil from solar heating during the day, and insulates the soil from infrared heat loss at night by reducing convective cooling (Knapp and Seastedt 1986).

3.4.2. Production Responses

3.4.2.1. Litter Influences on Total Growing Season Aboveground Biomass

Biomass patterns were markedly different at the Native and Tame Sites. At the Native Site, the *in situ* litter plots yielded the greatest biomass both for measures of total growing season and re-growth biomass. Reduced biomass in the litter removal plots may be due in part to the large increase in seedhead production in these plots, with the removal treatment acting as a stimulant for sexual reproduction within *Poa pratensis* tillers. Other studies have also found that litter can reduce seedhead production in some grass species (Weaver and Rowland 1952, Knapp and Seastedt 1986, Willms et al. 1886), presumably by reducing the light needed to promote floral induction in grasses. It appears that vegetation in litter removal plots invested energy early in the growing season into seedhead production, which in turn, would have re-allocated energy away from growth and production of leaf biomass (Chapin et al. 2002), thereby reducing overall biomass levels.

Increased energy investment into seedhead production may also explain inconsistencies between patterns in vegetative cover and biomass responses to the different litter treatments at the Native Site. Consistently high plant cover in the litter removal plots likely corresponds to a high tiller density rather than leaf area, and the lack of correspondence with the biomass data can best be explained by differences in individual tiller weight under litter treatments. Willms et al. (1986) found that rough fescue tillers were more abundant (i.e. denser) but weighed less and were shorter in litter removal plots compared to plots with litter (see also Willms et al. 1993). Although unmeasured, increased tillering in the litter removal plots would likely have been stimulated by increased temperature and light (Langer 1963), as shading by litter has been found to reduce plant basal cover (Weaver and Rowland 1952).

Shorter observed heights of *Poa pratensis* in the litter removal plots are a further indication of decreased per-plant biomass with reduced litter cover, as well as a fundamental trade-off between reproduction, whether sexual or asexual, and growth in these plants. Taller plants and increased per-tiller biomass under litter is also linked to the augmented soil moisture content under moderate and high litter loads in this and other studies (Willms 1988, Donker et al. 2002), with reduced evaporation leading to moisture levels more optimal for sustaining vegetative growth and biomass production over the growing season (Willms et al. 1993).

Conversely, the Native Site double litter treatment resulted in reduced plant biomass compared to the *in situ* litter plots, likely due to the overriding negative influence of heavy litter loads on early season plant development. Plant cover patterns under the different litter levels also did not vary over the growing season, indicating that the initial ecological processes acting in May to suppress cover in the double litter plots and release cover in the litter removal plots, continued to influence plots over the growing season. Heavy litter can reduce early season seed germination and plant establishment through reducing temperature, blocking light from reaching the soil surface, and acting as a mechanical barrier to plants (Weaver and Rowland 1952, Sydes and Grime 1981, Hamrick and Lee 1987). It is likely that all three of these mechanisms acted to reduce May plant densities and cover in the double litter plots, with the effect carrying over through to August. Further, leaf production and plant growth stage were also significantly delayed in litter plots, probably in response to the same soil surface environmental variables that affected vegetation cover (Ganskopp et al. 2007). Thus, the positive influences of high soil moisture that were associated with greater plant biomass within the *in situ* litter plots do not appear sufficient to similarly benefit plants in the double litter plots at the Native Site.

In contrast, total production in the Tame Site was stimulated by the reduction of litter, with the litter removal plots demonstrating greater grass and total shoot biomass over the growing season. Warmer temperatures and greater light at the soil surface during the initial spring growth period in the litter removal plots likely acted as a release on the production of grasses (Dibbern 1947, Tan et al. 1978). This effect of litter removal on Tame Site plant production was also evident in greater vegetation cover and greater *Bromus inermis* leaf counts during the early growing season, as well as in the advanced phenological development of *B. inermis* throughout the growing season. Similar to the Native Site, high litter loads appeared to delay shoot establishment by reducing solar radiation at the soil surface and by acting as a physical barrier to initial plant growth (Knapp and Seastedt 1986, Page and Bork unpublished data).

3.4.2.2. Litter Influences on Aboveground Re-Growth Biomass

Post-defoliation re-growth biomass was similar between the litter removal and double litter plots at the Native Site despite less accumulated total growing season biomass under heavy litter. As initial delays in spring growth from low light and cool temperatures resulted in an overall decrease in total growing season production within the double litter plots, this result suggests there may indeed be an upper maximum amount of litter for optimizing forage availability in this community. Nevertheless, heavy litter loads did appear to improve re-growth after defoliation relative to plots with litter removed, presumably through the benefit of decreased evaporation (Willms et al. 1993) and enhanced moisture availability (Willms and Jefferson 1993), particularly during the dry months of June and July. Augmentation of post-defoliation plant re-growth by litter was further evidenced in the measurements of *Poa pratensis* height in August, with double litter plots producing taller plants than litter removal plots. Thus, even very high and seemingly excessive litter loads may have important effects on improving plant growth potential after mid-season defoliation. Although increased moisture appears to account for most of the variation in re-growth at the Native Site, prior allocation of energy to seedhead production in grasses within the litter removal plot, leading to decreased energy reserves to respond to defoliation, may also be important (Chapin et al. 2002). Further, plants that were more developmentally advanced at defoliation may have had more advanced senescence, with growth shutting down after defoliation compared to plants that had not produced seed by the defoliation treatment.

Litter presence also had some positive influences on plant re-growth following defoliation at the Tame Site. Despite large differences in total growing season production, *in situ* litter plots had similar grass biomass as litter removal plots for August-only biomass measures. Furthermore, while plant growth parameters, including the height, leaf number per tiller and growth stage of *Bromus inermis,* decreased with lower litter biomass in undefoliated plots, they responded positively to high litter loads in defoliated plots. Again, this positive influence of litter on post-defoliation plant re-growth is likely due, at least in part, to the ability of litter to conserve greater levels of soil moisture over time.

3.4.2.3. Defoliation Influences on Accumulated Aboveground Production

Native Site defoliation treatments did not impact total growing season shoot production, but did have a predictable impact on the re-growth biomass post-clipping, with the amount of biomass removed during the defoliation treatment clearly correlated to the amount of plant material present at final harvest. Defoliation also severely impacted seedhead production, indicating that clipped plots, even in the absence of litter, did not recover their reproductive effort after defoliation by the end of August.

Defoliation at the Tame Site also had no significant effect on total growing season grass biomass, but shoot biomass was altered, likely due to the combined trends of grasses and forbs. The light defoliation treatment resulted in significantly less shoot biomass than the undefoliated treatment, but the heavily defoliated plots remained similar to the other treatments. It should also be noted that the consistent re-growth biomass values in the lightly and heavily defoliated plots may be due to the elongated growth form of the tame grasses at the time of June defoliation, as clipping occurred below most leaf attachment points on elongated tillers, resulting in similar removal of leaf mass and intercalary meristems in both the 2.5 and 6.5 cm defoliation treatments (Voltaire 1994, Holechek 2004). This contrasts with the defoliation treatment at the Native Site, where bunchgrasses with low leaf attachments had noticeably different amounts of biomass remaining after the clipping treatment.

Defoliation also predictably affected Tame Site July vegetation cover, which decreased with increasing defoliation severity and corresponding stress on the plants (Bai et al. 2001). In August, the foliar cover difference between undefoliated and defoliated plots was reduced from that seen in July, potentially indicative of a minor interaction with litter and the effect of litter on soil moisture and associated re-growth.

3.4.2.4. Patterns in Belowground Biomass

Root biomass in the first 15 cm of the soil was not affected by litter at either site. At the Tame Site, the defoliation treatment exhibited a trend towards lower root mass in clipped plots. Defoliation causes stress on the plant's photosynthetic capacity, which can result in the re-allocation of assimilates from roots to shoots to improve resource acquisition through photosynthetic pathways (Ryle and Powell 1975). It is also possible that root responses to defoliation were delayed for a growing season, or that any root death following defoliation was not detected due to the proximity of the August harvest to the initial clipping treatment. Although greenhouse studies have shown that defoliation can have a strong effect on reducing short-term root growth (Jameson 1963, King et al. 1995), field studies have shown that grazing can have little effect on belowground biomass in grasslands (McNaughton et al. 1998).

Differences in the root:shoot ratio under the litter treatments at the Native Site appear to be due to changes in shoot biomass among litter plots, particularly the *in situ* and double litter, rather than changes in root biomass. At the Tame Site, lower shoot biomass values in the double litter plots is the likely cause for the increased root:shoot ratio.

3.4.3. Plant Community Responses

Forb richness and biomass responded positively to litter removal at the Native Site, likely due to increased temperatures and light at the soil surface under this treatment. Diurnal temperature fluctuations and sufficient light are critical for seed germination of a number of species (Thompson et al. 1977, Grime 1979, Sydes and Grime 1981). The increase in forb richness also appeared responsible for increasing the total species richness in the litter removal plots. However, because the forb component of the community was quite minor compared to the grasses, changes in forb production and richness did not alter the overall community structure sufficiently to impact species evenness and diversity at the Native Site. In other studies, litter influenced species diversity, specifically by hindering the establishment and growth of some species while favoring others (Willms et al. 2002, Facelli and Pickett 1991). In the case of perennial grasslands, these changes often lead to a simplified community dominated by only a few competitive grasses.

Cover of the dominant grass species was also impacted by the litter treatment at the Native Site, but again not enough to alter diversity or evenness. *Poa pratensis*, considered a common naturalized species in this area, responded positively to the outright removal of litter. In contrast, *Festuca halli,* the dominant native grass of the region, responded more to the level of litter, with less cover in the double litter plots compared to the other treatments. Together, the responses of these two grasses to the litter treatments appeared to determine overall responses of vegetation cover at this site, and indicate that while the absence of litter may favor *Poa* over time, moderate litter (i.e. 5,500 kg/ha) may favor *Festuca*.

Defoliation at the Native Site impacted species evenness, which was greatest in the heavily defoliated treatment. Other studies in the region have found a similar effect of grazing on relative species abundances (Willms et al. 2002, Bai et al. 2001). This increased evenness is likely due to the negative effect of severe defoliation on the species pool at the site rather than on competition between species, particularly as plant cover was low in plots with litter and clipping was non-selective (Grace and Jutila 1999). Surprisingly, defoliation did not impact *F. hallii*, a preferred forage species and a known decreaser under grazing (Willms et al. 1985), possibly due to the lack of selectivity in the defoliation treatment. *P. pratensis*, the dominant grass at this site, unexpectedly responded negatively to the heavily clipped treatment, indicating that this species may be tolerant of lighter levels of defoliation, at least initially on the range sites examined here.

Neither litter nor defoliation significantly affected species richness, evenness or diversity at the Tame Site. This may be due to low species counts at this site, which in turn, likely reflects prior land management. In addition to having been ploughed and seeded to rapidly growing tame grasses, the prolonged absence of grazing at this site would have allowed dominance by only a few competitive species. The lack of change in community parameters could also be related to the absence of a significant response by *Cirsium arvense* to either treatment, although *C. arvense* did show a trend towards increasing density, cover and biomass with decreasing litter. Litter removal likely acted as a release for *Cirsium* growth through soil warming, as this species is known to prefer these conditions, presumably created here by litter removal. *Cirsium* did not appear particularly competitive under this treatment, however, as it responded proportionally to the other plant species. Further, although defoliation treatments were also non-significant on *C. arvense*, increasing defoliation intensity resulted in a trend towards reduced *C. arvense* cover and post-defoliation biomass, but also an increase in *C. arvense* density. Increases in *C. arvense* density are known to result during regrowth from prior non-selective defoliation of *Cirsium* stems (Grekul and Bork 2007), and exhibit variable competitive abilities depending on the severity of defoliation (Amor and Harris 1977, De Bruijn and Bork 2006).

3.5. Conclusions

This study demonstrates that litter abundance between 11,000 and 14,000 kg/ha appears to provide positive impacts on soil moisture in lowland sites of the Aspen Parkland ecoregion by maintaining moisture in the soil for longer periods after moderate to heavy precipitation events. However, high litter loads may also negatively impact plant growth early in the growing season, likely due to reduced temperature and light, and the formation of a mechanical barrier to plant growth, and in the case of small rainfall events, by the short-term loss of water via interception. Although retarded early growth may reduce overall accumulated forage yields in tame pastures, litter levels greater or equal to 5500 kg/ha demonstrated consistent positive relationships with grass production within undefoliated native pasture systems. Litter also positively affected grass recovery and re-growth following mid-season defoliation in both tame and native pastures, in part due to apparent important influences on soil moisture.

Table 3.1: ANOVA F-value results for type 3 tests of fixed effects of litter (L) and defoliation (D) on soil moisture, total moisture lost over the 5 days of measurement, and temperature throughout the growing season in 2007 at the Native Site.

Variable	Moisture Day 1	Moisture Day 2	Moisture Day 3	Moisture Day 4	Moisture Day 5	Total Moisture Lost	Soil Temp
May							
L	$F_{2,38}=4.33^{*}$	0.36	1.34	0.22	1.11	2.40	559.25^{***}
June							
L	$F_{2,38}=19.83^{***}$	16.79^{***}	20.39^{***}	25.89^{***}	-	9.33^{**}	250.83^{***}
July							
L	$F_{2,32}=1.49$	1.27	1.38	1.52	1.60	4.39^{*}	112.69^{***}
D	$F_{2,32}=2.21$	0.70	0.57	1.30	0.88	2.95	2.69
L*D	$F_{4,32}=1.28$	1.28	1.54	0.80	1.27	1.12	1.12
August							
L	$F_{2,32}=12.24^{***}$	11.28^{**}	27.73^{***}	34.37^{***}	102.91^{***}	22.30^{***}	38.15^{***}
D	$F_{2,32}=0.15$	0.97	0.61	0.03	0.28	0.00	2.73
L*D	$F_{4,32}=0.83$	2.51	1.37	1.08	2.17	0.63	0.45

*,**,*** Indicate significance at $P\leq0.05$, $P\leq0.01$, and $P\leq0.0001$, respectively.

Table 3.2: ANOVA F-value results for type 3 tests of fixed effects of litter and defoliation on re-growth and total biomass at the Native Site in August 2007.

Variable	Litter	Defoliation	Litter*Defoliation
Re-growth Biomass (August)			
Grass	$F_{2,32}$=7.78**	$F_{2,32}$=58.27***	$F_{4,32}$=2.42
Forbs^{+}	$F_{2,32}$=2.03	$F_{2,32}$=1.28	$F_{4,32}$=0.23
Shoot Total	$F_{2,32}$=7.87**	$F_{2,32}$=72.55***	$F_{4,32}$=2.25
Total Biomass (June + August)			
Grass	$F_{2,32}$=12.71***	$F_{2,32}$=0.02	$F_{4,32}$=0.11
Forb+	$F_{2,32}$=3.86*	$F_{2,32}$=0.60	$F_{4,32}$=0.56
Shoot Total	$F_{2,32}$=13.06***	$F_{2,32}$=0.00	$F_{4,32}$=0.19
Root Biomass	$F_{2,32}$=0.38	$F_{2,32}$=1.13	$F_{4,32}$=1.52
Root:Shoot Ratio^{+}	$F_{2,32}$=2.79	$F_{2,32}$=0.34	$F_{4,32}$=0.89

*,**,*** Indicate significance at $P\leq0.05$, $P\leq0.01$, and $P\leq0.0001$, respectively

+ Log transformed

Table 3.3: Summary LSmeans and standard errors of re-growth and total biomass (kg/ha) among the litter treatments at the Native Site. Within a row, means with different letters differ, P<0.05.

Variable	Litter Removed	*In Situ* Litter	Double Litter	SE
Re-growth Biomass (August)				
Grass	1780 b	2180 a	1680 b	120
Forbs	33 a	15 a	56 a	21
Shoot Total	1810 b	2190 b	1740 b	120
Total Biomass (June + August)				
Grass	2600 b	3140 a	2180 c	160
Forbs	69 a	19 b	61 ab	24
Shoot Total	2660 b	3160 a	2240 c	160
Root Biomass	16600 a	15110 a	15350 a	1360
Root:Shoot Ratio	6.4 ab	5.0 b	7.2 a	0.8

Table 3.4: Summary LSmeans (±SE) of seedhead density among litter and defoliation treatments at the Native Site in August 2007. Means with different letters differ, P<0.05.

Defoliation	Litter Treatment	Mean Seedhead Density (seedheads/m^2)
Heavy Defoliation	Litter Removal	1.4 ± 6.1 d
	In Situ Litter	0.0 ± 6.1 d
	Double Litter	0.4 ± 6.1 d
Light Defoliation	Litter Removal	3.8 ± 6.1 c
	In Situ Litter	0.6 ± 6.1 d
	Double Litter	0.3 ± 6.1 d
Undefoliated	Litter Removal	166.0 ± 6.1 a
	In Situ Litter	16.2 ± 6.1 b
	Double Litter	10.4 ± 6.1 b

Table 3.5: ANOVA F-value results for type 3 tests of fixed effects of litter and defoliation on soil moisture, total moisture lost over the 5 days of measurement, and temperature throughout the growing season in 2007 at the Tame Site.

Variable	Moisture Day 1	Moisture Day 2	Moisture Day 3	Moisture Day 4	Moisture Day 5	Total Moisture Lost	Soil Temp
May							
L	$F_{2,38}$=0.78	1.78	1.12	1.27	0.09	1.00	867.13***
June							
L	$F_{2,38}$=2.27	0.13	0.37	1.80	-	14.44***	84.52***
July							
L	$F_{2,32}$=4.27*	1.78	3.04	3.47*	0.32	3.60*	85.38***
D	$F_{2,32}$=1.30	4.29*	0.59	2.52	0.47	0.23	1.21
L*D	$F_{4,32}$=0.19	1.30	0.76	1.23	1.49	1.13	3.00*
August							
L	$F_{2,32}$=2.17	1.98	7.01**	9.62**	35.11***	39.73***	14.39***
D	$F_{2,32}$=2.31	4.23*	2.59	0.55	1.25	2.93	0.94
L*D	$F_{4,32}$=1.34	0.64	0.59	0.60	1.07	2.07	0.62

*,**,*** Indicate significance at $P \leq 0.05$, $P \leq 0.01$, and $P \leq 0.0001$, respectively.

Table 3.6: ANOVA F-value results for type 3 tests of fixed effects of litter and defoliation on re-growth and total biomass at the Tame Site in 2007.

Variable	Litter	Defoliation	Litter*Defoliation
Re-growth Biomass (August)			
Grass	$F_{2,32}$=4.59*	$F_{2,32}$=24.85***	$F_{4,32}$=1.78
Forbs	$F_{2,32}$=1.75	$F_{2,32}$=1.02	$F_{4,32}$=0.15
Thistle^{+}	$F_{2,32}$=0.66	$F_{2,32}$=1.44	$F_{4,32}$=0.64
Shoot Total^{+}	$F_{2,32}$=5.97**	$F_{2,32}$=40.72***	$F_{4,32}$=2.20
Total Biomass (June + August)			
Grass	$F_{2,32}$=13.23***	$F_{2,32}$=2.17	$F_{4,32}$=0.35
Total Forb	$F_{2,32}$=1.24	$F_{2,32}$=1.06	$F_{4,32}$=0.71
Shoot Total$^{+\#}$	$F_{2,32}$=15.68***	$F_{2,32}$=3.31*	$F_{4,32}$=0.34
Root biomass	$F_{2,36}$=0.39	$F_{2,36}$=3.07	$F_{4,36}$=1.03
Root:Shoot Ratio	$F_{2,32}$=3.36*	$F_{2,32}$=0.08	$F_{4,32}$=0.73

*,**,*** Indicate significance at $P \leq 0.05$, $P \leq 0.01$, and $P \leq 0.0001$, respectively.
+Log transformed
Square root transformed
+# Double transformed

Table 3.7: Summary LSmeans and standard errors of re-growth and total biomass (kg/ha) among the litter treatments at the Tame Site. Within a row, means with different letters differ, $P<0.05$.

Variable	Litter Removal	*In Situ* Litter	Double Litter	SE
Re-growth Biomass (August)				
Grass	3100 a	2600 ab	2210 b	350
Forbs	3 a	1 a	9 a	4
Thistle	470 a	310 a	250 a	130
Shoot Total	3580 a	2910 b	2470 b	350
Total Biomass (June + August)				
Grass	4590 a	3520 b	2760 b	460
Forbs	530 a	340 a	260 a	130
Shoot Total	5120 a	3850 b	3020 c	460
Root Biomass	12190 a	12830 a	11440 a	960
Root:Shoot Ratio	2.8 b	3.4 ab	3.9 a	0.5

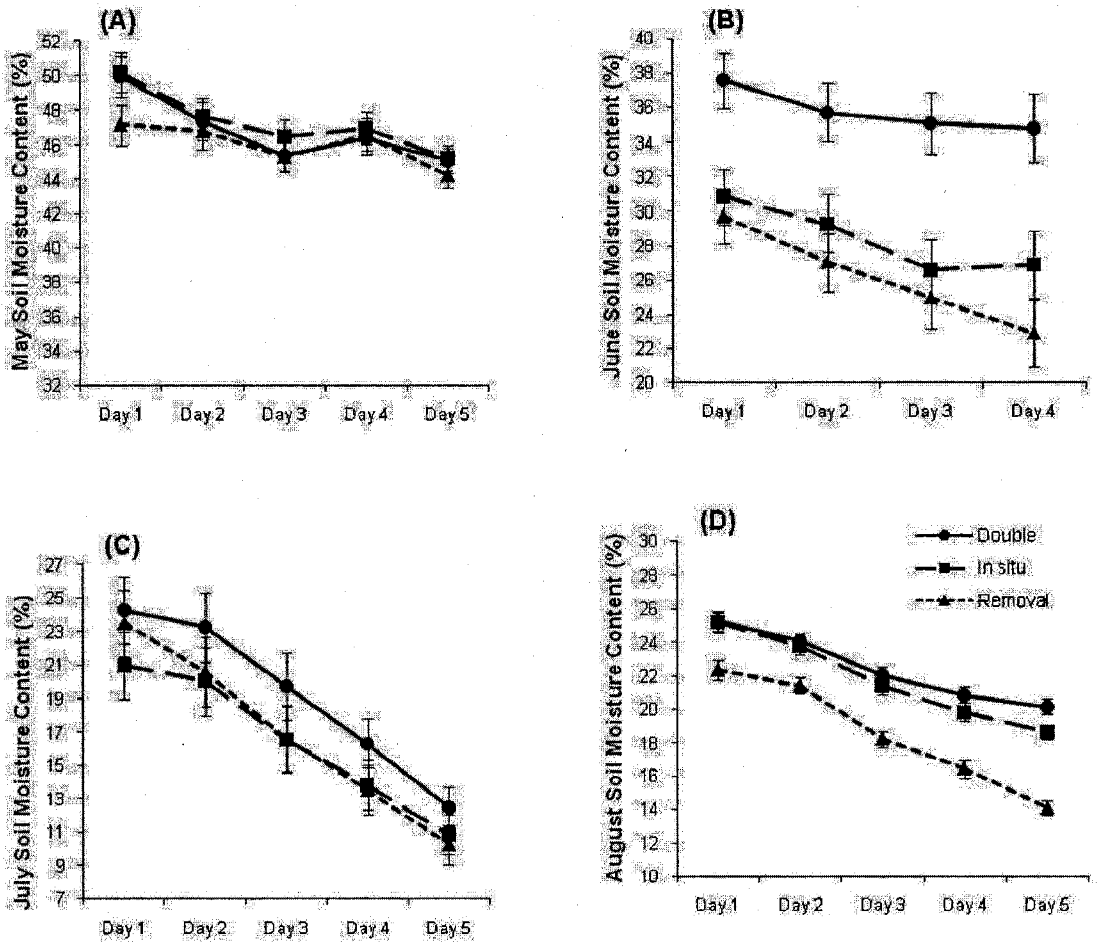

Figure 3.1: Patterns of mean (±SE) soil moisture (%) depletion up to 5 days after rainfall under varying litter treatments at the Native Site in each of May (A), June (B), July (C) and August (D) of 2007.

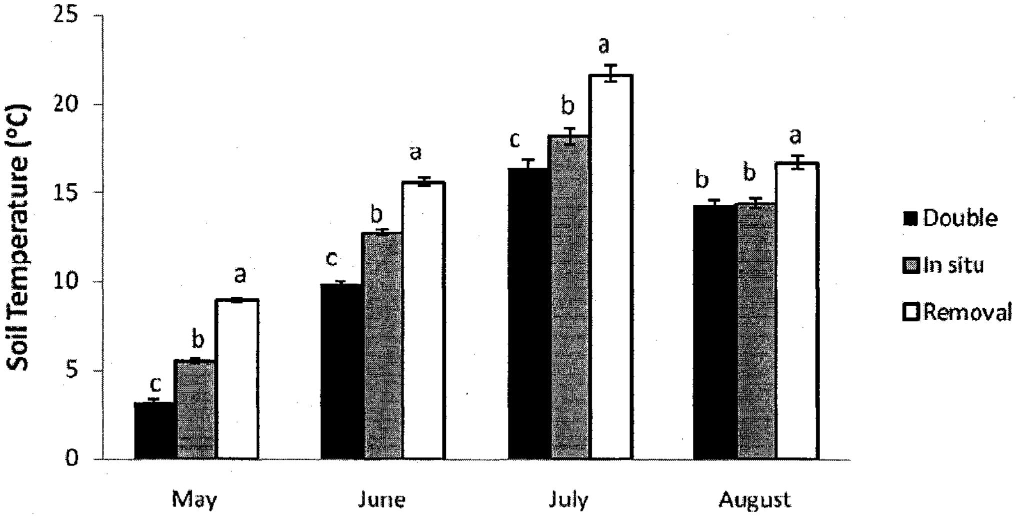

Figure 3.2: Mean (±SE) soil temperature (°C) under the three litter treatments during each of May, June, July and August 2007 at the Native Site. Within a month, means with different letters differ, $P<0.05$.

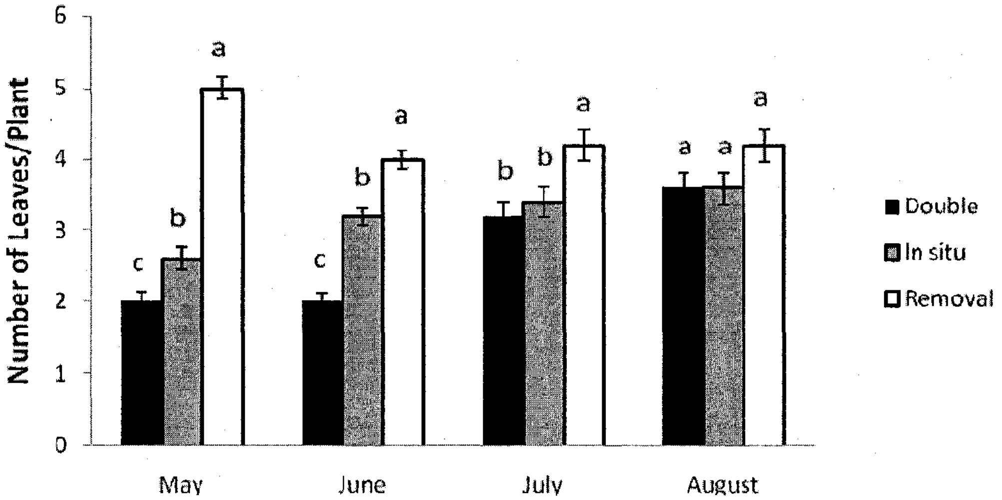

Figure 3.3: Mean (±SE) leaf counts of *Poa pratensis* plants under the three litter treatments during each of May, June, July and August 2007 at the Native Site. Within a month, means with different letters differ, $P<0.05$.

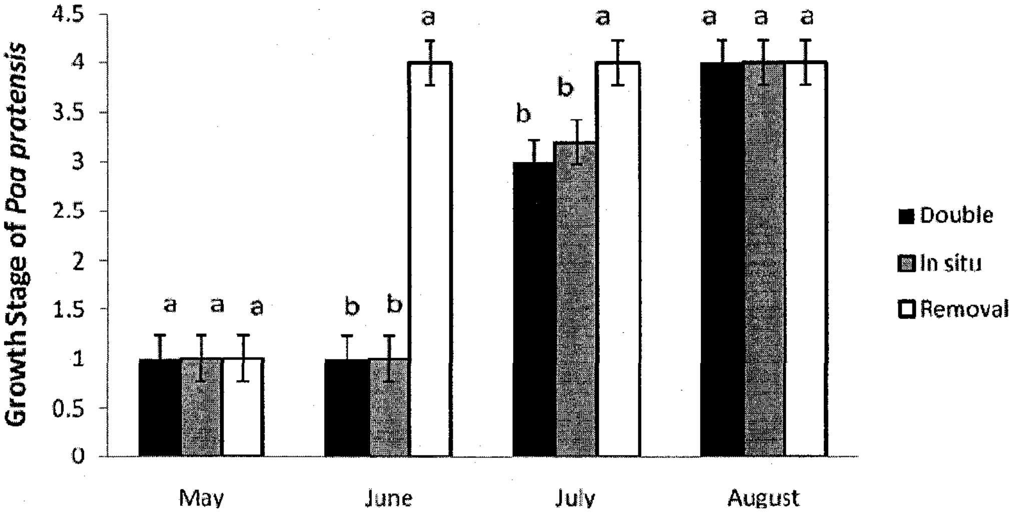

Figure 3.4: Mean (±SE) growth stage of *Poa pratensis* within the three litter treatments during each of May, June, July and August 2007 at the Native Site. Within a month, means with different letters differ, P<0.05.

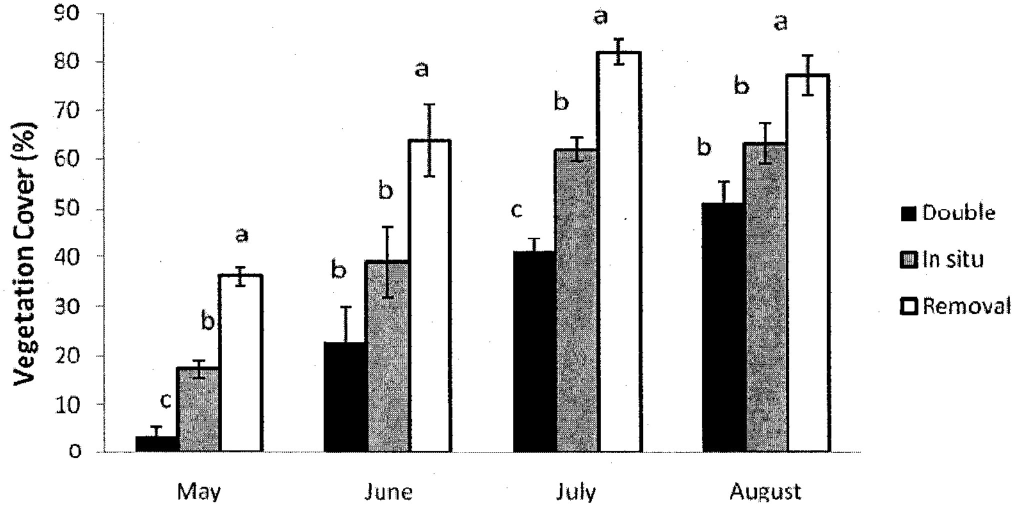

Figure 3.5: Mean (±SE) total vegetation cover (%) under the three litter treatments during each of May, June, July and August 2007 at the Native Site. Within a month, means with different letters differ, P<0.05.

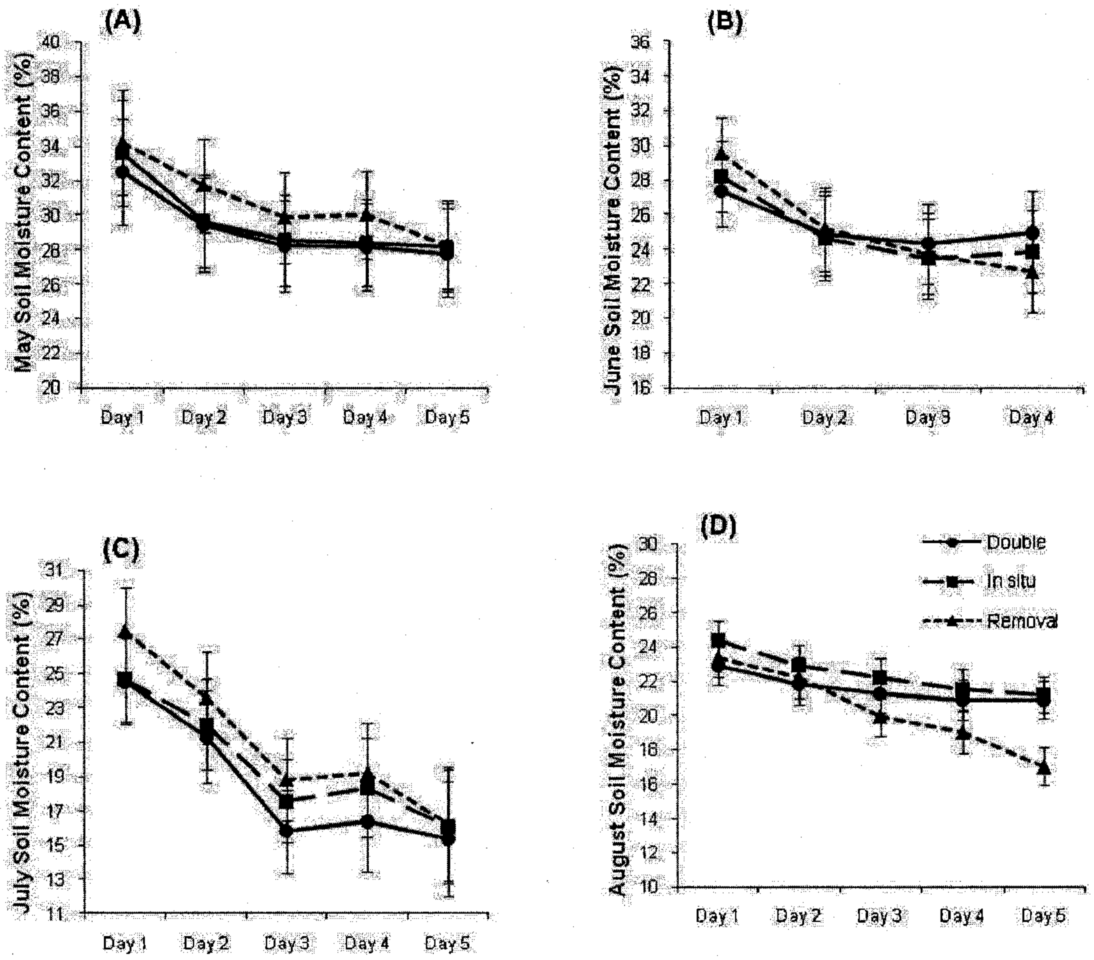

Figure 3.6: Patterns of mean (±SE) soil moisture (%) depletion up to 5 days after rainfall under varying litter treatments at the Tame Site in each of May (A), June (B), July (C) and August (D) of 2007.

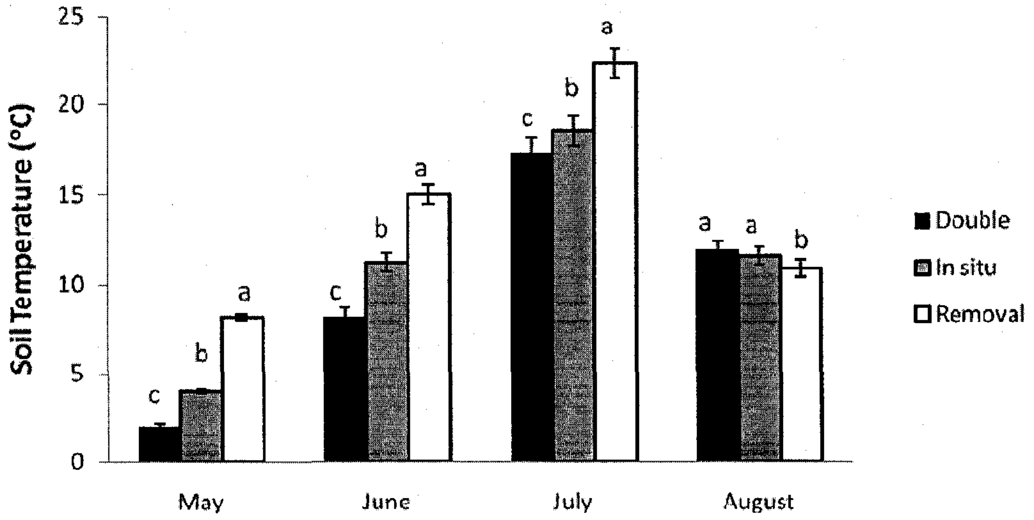

Figure 3.7: Mean (±SE) soil temperature (°C) under the three litter treatments during each of May, June, July and August 2007 at the Tame Site. Within a month, means with different letters differ, P<0.05.

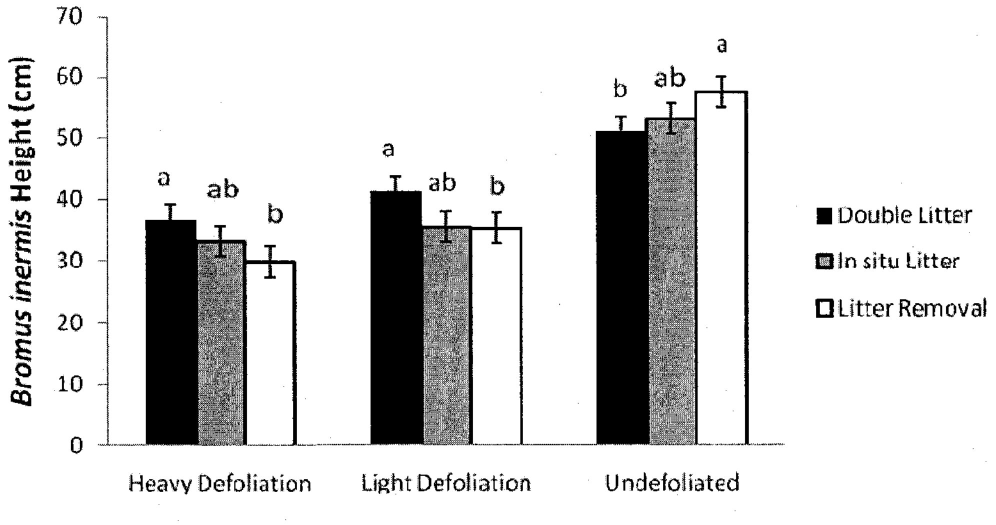

Figure 3.8: Mean (±SE) height of *Bromus inermis* under the litter and defoliation treatments in August 2007 at the Tame Site. Within a defoliation treatment, means with different letters differ, P<0.05.

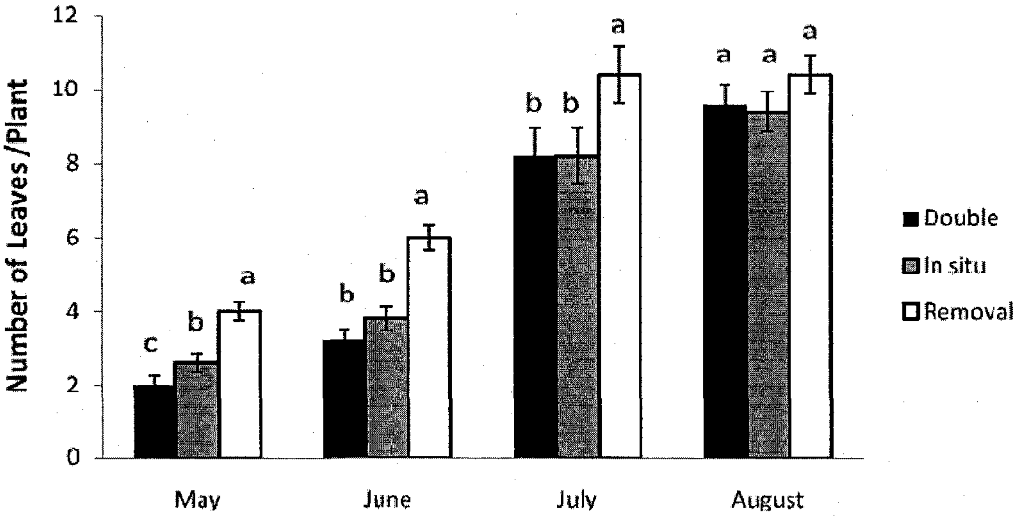

Figure 3.9: Mean (±SE) leaf count on *Bromus inermis* under the three litter treatments during each of May, June, July and August 2007 at the Tame Site. Within a month, means with different letters differ, P<0.05.

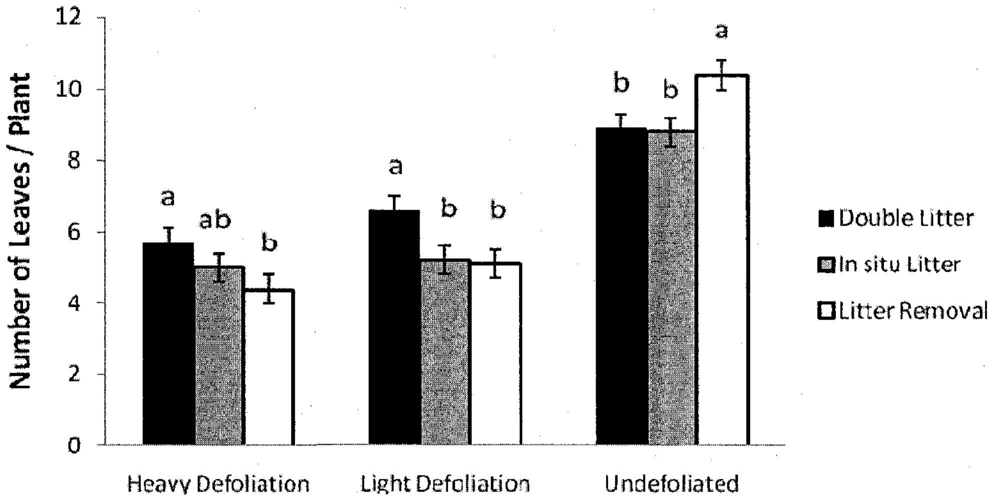

Figure 3.10: Mean (±SE) leaf count of *Bromus inermis* plants under the litter and defoliation treatments in August 2007 at the Tame Site. Within a defoliation treatment, means with different letters differ, P<0.05.

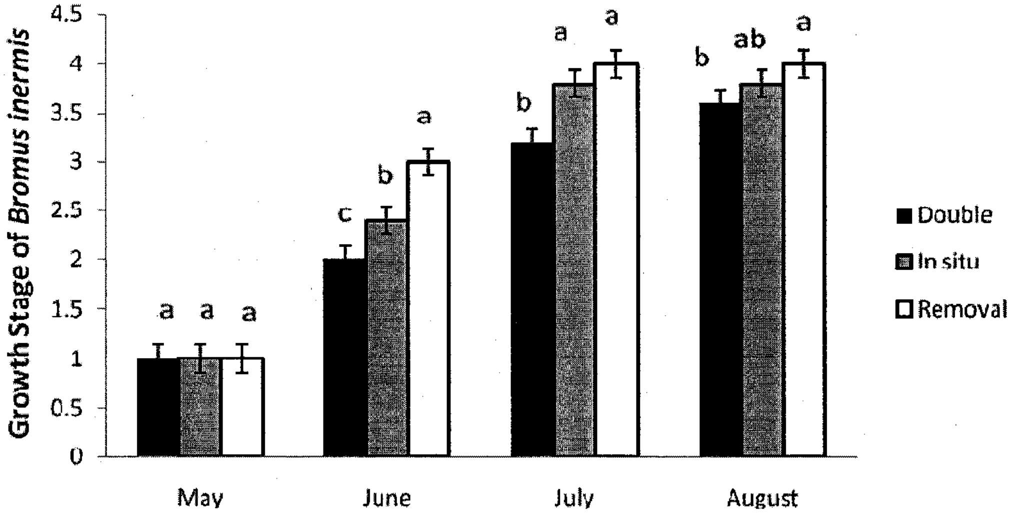

Figure 3.11: Mean (±SE) growth stage of *Bromus inermis* under the three litter treatments during each of May, June, July and August 2007 at the Tame Site. Within a month, means with different letters differ, P<0.05.

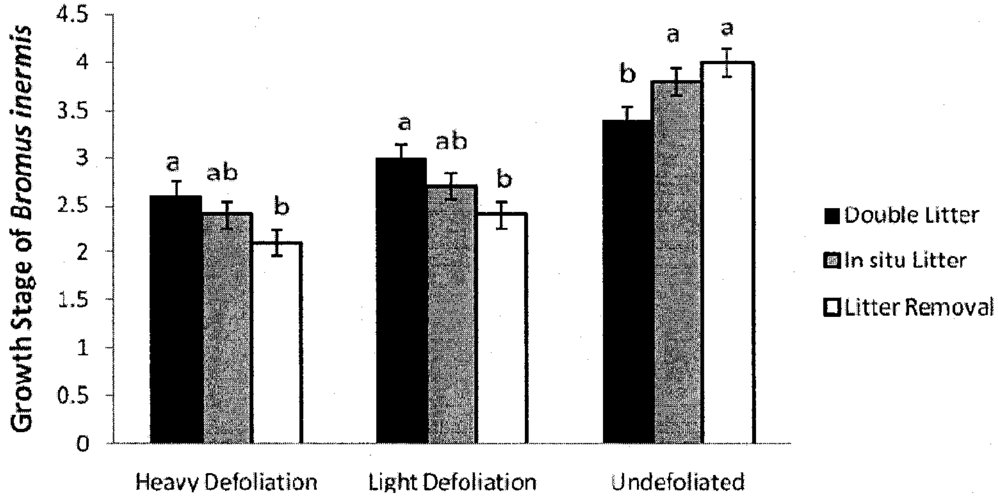

Figure 3.12: Mean (±SE) growth stage of *Bromus inermis* under the litter and defoliation treatments in August 2007 at the Tame Site. Within a defoliation treatment, means with different letters differ, P<0.05.

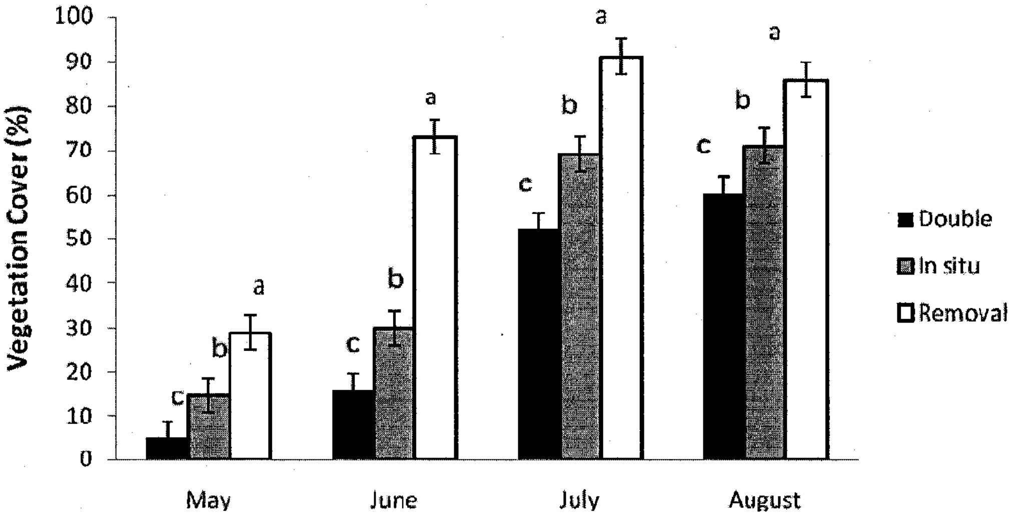

Figure 3.13: Mean (±SE) total vegetation cover (%) under the three litter treatments during each of May, June, July and August 2007 at the Tame Site. Within a month, means with different letters differ, P<0.05.

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4. THE RELATIVE IMPORTANCE OF LITTER IN REGULATING TEMPORAL AND SPATIAL SOIL MOISTURE DYNAMICS AND PLANT PRODUCTION.

4.1. Introduction

Plant productivity in rangelands is closely dependent on soil moisture availability (Coupland 1958, Lauenroth and Sala 1992). Near-surface soil moisture is most affected by precipitation (Salve and Allen Diaz 2001), and understanding moisture dynamics in the upper soil layers is important as most plant roots occur in this zone within water-limited grasslands (Schenk and Jackson 2002). Soil moisture levels vary both temporally throughout the growing season and spatially across the landscape, in turn affecting the potential for plant growth. An understanding of this variation is important for managing soil moisture within rangelands, particularly where soil moisture is a primary limitation for plant growth.

Aside from the primary influence of climate, near-surface moisture is influenced by soil, topography and vegetation characteristics. Observed levels of soil water are strongly correlated with intrinsic soil properties such as texture, organic matter and depth, which effect moisture recharge during rainfall and subsequent infiltration and soil water-holding capacity (Wilcox et al. 1988, Naeth et al. 1991a, Laio et al. 2001a, Salve and Allen-Diaz 2001). Soil moisture is also strongly influenced across the landscape by topography, which may change spatial patterns of water runoff and deposition (Horton 1933, Meeuwig 1970, Bork et al. 2001, Salve and Allen-Diaz 2001), as well as evaporation through surface exposure to solar radiation (Chapin et al. 2002). Moreover, soil characteristics such as texture and organic matter content, and associated water holding capacity and infiltration, may vary from uplands to lowlands, thereby changing hydrologic properties of the local range site (Landi et al. 2004). Nonetheless, few if any of these factors can be manipulated to increase soil moisture through management practices.

Conversely, the manipulation of plants, and in particular plant litter, has been found to be very effective at maintaining greater soil water in most grassland ecosystems (Weaver and Rowland 1952, Johnson 1962, Knapp and Seastedt 1986, Thurow et al. 1986, Holland and Coleman 1987, Dormaar and Carefoot 1996). Soil moisture depletion is heavily dependent on vegetation influences such as root and shoot biomass, plant cover and leaf area, which exert a strong influence through transpiration (Buckhouse and Coltharp 1976, Brutsaert and Chen 1995, Laio et al. 2001a, Chapin et al. 2002). Plant litter can reduce runoff (Dyksterhuis and Schmutz 1947, Rauzi 1960, Meeuwig 1970), increase water infiltration into the soil (Weaver and Rowland 1952, Dormaar and Carefoot 1996) and reduce evaporative losses through shading and lowering soil temperatures (Dyksterhuis and Schmutz 1947, Hopkins 1954, Holland and Coleman 1987), thereby increasing productivity (Willms et al. 1986). Despite these benefits, litter may also reduce soil moisture by intercepting a significant portion of rainfall (Walsh and Voight 1977, Knapp and Seastedt 1986, Naeth et al. 1991a), particularly during small precipitation events. Excessive litter may also negatively influence production by reducing light penetration to the soil surface (Weaver and Rowland 1952, Knapp 1985, Hamrick and Lee 1987) and physically impeding early season shoot growth (Sydes and Grime 1981, Hamrick and Lee 1987). Consequently, litter becomes more important as a management tool in ecosystems where its positive influence on moisture conservation outweighs its negative effects on early plant development (Weaver and Rowland 1952, Willms et al. 1986).

While the importance of litter in moisture conservation has long been accepted on arid and semi-arid rangelands (Johnson 1962, Meeuwig 1970, Thurow et al. 1986, Willms et al. 1986), an understanding of soil moisture dynamics and its role in maintaining plant production is becoming increasingly important within more mesic cool-temperate grasslands, particularly in the face of future climate change predictions (IPCC 2001). The Aspen Parkland is a broad tension zone in western Canada situated between the semi-arid Mixedgrass Prairie to the south and mesic Boreal forest to the north (Moss 1932), and as such has been strongly influenced by temporal variation in climate during the past (Coupland 1961). Although the Aspen Parkland does not typically experience acute moisture stress, recent occurrences of drought along with future projections of climate change towards a warmer, drier climate (Schindler and Donahue 2006) have raised concerns over managing for moisture shortages. Despite the obvious importance of litter in moisture conservation, little is known of the importance of litter relative to other range site characteristics in regulating soil moisture dynamics and associated community production in the Aspen Parkland.

This study examined the effectiveness of naturally-occurring litter levels at maintaining grassland soil moisture on a south-facing hillslope in the Aspen Parkland. Specific research questions that were addressed included: (1) does litter consistently have a positive influence on maintaining moisture in the soil following precipitation events in the Alberta Aspen Parkland, (2) what is the contribution of litter in influencing near-surface soil moisture content relative to other topographic, soil and biotic factors, and (3) does the influence of litter on moisture and temperature translate into measureable changes in plant production?

4.2. Materials and Methods

4.2.1. Study Area

The study was conducted within the Aspen Parkland natural subregion, approximately 150 km southeast of Edmonton, Alberta at the University of Alberta Kinsella Research Station (53° 05' N; 111° 33' W). The landscape at the station is dominated by rolling knob and kettle topography, with all study plots located on grasslands of a south-facing slope at elevations ranging from 680 m to 700 m asl. The area has a dry subhumid climate, with a mean annual precipitation of 400-500 mm and mean annual temperature of 1.5 °C. Mean summer temperatures are 15 °C (Environment Canada 2005).

Soils at the study site were relatively well drained and fertile. Upper and mid slopes were Dark Brown Chernozems with a mean Ah horizon depth of 17 and 13 cm, respectively. Lower slopes were Orthic Black Chernozems with an average Ah depth of 20 cm, and contained a gravel layer approximately 35 cm below the soil surface with some evidence of impeded drainage (i.e. mottling). Roots were most prevalent in the first 13, 11 and 14 cm of soil for upper-, mid-, and lower- slopes, respectively.

Dominant grasses at the site included *Stipa curtiseta* (A.S. Hitchc) Barkworth, *Festuca hallii* (Vasey) Piper, *Festuca saximontana* Rydb., *Agrostis stolonifera* L., and *Poa pratensis* L.. Dominant forbs included *Achillea millefolium* L., *Commandra umbellata* (L.) Nutt., *Galium boreale* L., and *Solidago missouriensis* Nutt.. *Rosa arkensana* Porter was also prevalent. Total litter loads, representing both standing dead material and that of coarse and fine (i.e. mulch) material in the litter layer on the soil surface, ranged from 500 to 7000 kg/ha among plots. While the study area had been historically grazed by cattle in the fall of each year, the area had been rested from grazing for 4 years prior to this study.

4.2.2. Experimental Design

Thirty 1.5 by 1.5 m plots were randomly laid out across a south-facing slope of the study site in mid-April 2007. All plots contained *Festuca hallii*, the dominant grass of late seral grasslands in the area. Seven plots were situated on the more xeric upper portion of the slope, 12 plots on the mid-slope, and 11 plots on the mesic lower-slope. To ensure variable litter conditions among plots within each landscape position, litter was removed by hand raking from 6 of the mid-slope plots and 4 of the lower slope plots in mid-April. Plots used in this study therefore represented a wide range of litter loads, and included natural variation in topography, range sites, and associated plant communities (Table 4.1). In this study, litter refers to all standing dead, detached and partially decomposed material recognizable as vegetation and not incorporated into the mineral soil.

4.2.3. Field Sampling

At each plot, sampling was conducted after rainfall in early May, June, July and August of 2007 and included measures of environmental, soil and vegetation characteristics. Soil moisture and temperature, ground cover including the total cover of vascular plants, together with litter depth, litter biomass and above ground plant biomass, were sampled monthly. Along with these monthly measures, plot slope, aspect, position, Ah horizon depth and below ground biomass were assessed in early July. During early August, vascular plant density and cover by individual species, soil bulk density and volumetric soil moisture content were measured.

4.2.3.1. Environmental Measurements

Soil moisture (%) was measured in the top 10 cm of the mineral soil using a TDR-MLX2 moisture probe. Moisture was measured for five consecutive days following a precipitation event early in each sampling month to obtain differential soil moisture depletion curves. Four moisture readings were taken per plot per day in random plot locations to account for moisture heterogeneity. Soil temperature was measured using a garden temperature probe in the first 5 cm of the mineral soil. Temperature was measured close to the middle of the day (between 12 and 2 PM) on clear, sunny days to minimize variation unrelated to plot characteristics.

Volumetric soil moisture content was quantified within all plots in August 2007 to calibrate the TDR soil moisture probe. A 20 cm^3 soil core (1.9 cm diameter, 7 cm deep) was extracted from each plot and immediately weighed. Cores were then oven-dried at 105 ^{o}C for three days and re-weighed dry. Soil bulk density was then calculated with the following equation:

$$[\text{weight of dry soil} / \text{bulk volume of the soil}] \tag{1}$$

Gravimetric soil moisture was calculated as follows:

$$[(\text{weight of wet soil} - \text{weight of dry soil}) / \text{weight of dry soil}] * 100\% \tag{2}$$

Finally, volumetric soil moisture was calculated using the following equation:

$$[\text{gravimetric soil moisture} * \text{dry bulk density}] \tag{3}$$

4.2.3.2. Vegetation Measurements

Ground cover and total vascular plant cover were estimated using a 20 x 50 cm Daubenmire quadrat (0.10m^2) (Daubenmire 1959) positioned randomly in each plot. Quadrats were randomly relocated each month by a grid, and were restricted to areas not previously harvested. Ground cover measures assessed the percent cover of rock, litter, bare soil and cryptogams. Vascular plant foliar cover was an ocular measurement of the proportion of the quadrat occupied by live plant biomass.

Above ground biomass was sampled in each plot using a 0.1m^2 Daubenmire quadrat. All vegetation was harvested to a 1 cm stubble height and sorted to growth form (grasses, forbs or shrubs). Samples were then oven-dried at 65 °C for five days and weighed. Weights were converted to kg/ha for analysis. Litter biomass was also measured monthly from the biomass quadrats. Standing litter was sorted from live plant biomass at harvest, and detached litter and mulch removed from the soil surface by hand raking. All litter was then dried in a 65 °C oven for five days and weighed, with values converted to kg/ha for analysis. Litter depth was measured in a representative area of the plot from the top of the mineral soil to the average height of the loose partially decomposed or undecomposed litter layer on the soil surface.

Below ground root biomass was measured from a single 295 cm^3 (5 cm diameter by 15 cm deep) soil core per plot in July. Soil was removed through a 0.5 mm sieve, and roots were rinsed to remove all remaining soil. Extracted roots were then dried in a 65 °C oven for three days and weighed.

In early August, detailed vegetation composition was determined through the estimation of percent cover of each species within the biomass quadrat prior to harvest. These compositional data were used to determine species richness values as the number of species per 0.1m^2. Species diversity was calculated using Shannon's Diversity Index:

$$H' = \Sigma(Pi*\ln Pi), \quad (4)$$

where Pi is the proportion of all cover made up of species i. Species evenness was obtained using Pielou's J index (Pielou 1977):

$$J = H'/\log(\text{species richness}) \quad (5)$$

4.2.3.3. Range Site Measurements

Slope gradient in each plot was measured using a Suunto clinometer, with two individuals stationed 5 meters apart on the uphill and downhill sides of the plot: slope measurements therefore accounted for the steepest slope angle of each plot. Aspect was measured using a compass, with direction identified from the steepest part of the plot. A direct south-facing slope was designated 180°, with southwest or southeast aspects quantified through deviations from south in degrees. Due to drying winds from the west, southwest slopes were assumed to be the driest. The topographic position of each plot was designated an ordinal category from 1 at the top of the slope to 8 at the base of the slope.

Depth of the Ah soil horizon was measured in a small soil pit within each plot. Horizon boundaries were identified as the average region of color change between the Ah horizon and the underlying Bm horizon.

4.2.4. Soil Analysis

Soil removed during extraction of the July root biomass was used to measure soil organic matter content, texture, and soil moisture content at field capacity and permanent wilting point in the laboratory. Soil organic matter content was measured using ash content and the percent loss-on-ignition (LOI) method. Organic matter was oxidized by heating samples to 375 °C and the LOI calculated using the following equation:

$$[(\text{dry sample wt} - \text{sample wt after ignition})/\text{dry sample wt}] * 100\% \quad (6)$$

Soil texture was measured with a particle size analysis conducted using Bouyoucos hydrometer method of mechanical analysis (Bouyoucos 1962).

Soil moisture content at permanent wilting point (PWP) was determined by applying 15 bars of pressure to saturated soil samples in a pressure chamber, while soil moisture content at field capacity (FC) was determined by applying 1/3 bars of pressure to saturated samples. All PWP and FC moisture content measures were duplicated, with samples remaining in the pressure chamber for two days during the first replication, and four days during for the second replication. Samples were subsequently weighed wet, placed in a 105° C dryer for two days and reweighed dry. Soil moisture content (SMC) at PWP and FC were calculated using the following equation:

$$\text{SMC} = [\text{wt of the water in the soil} / \text{wt of dry soil}] * 100\% \quad (7)$$

Plant available soil moisture (PASM) was calculated using the following equation:

$$\text{PASM} = \text{MC at FC} - \text{MC at PWP} \quad (8)$$

4.2.5. Data Analysis

Local climatological data for May, June and August 2007 were obtained from the Kinsella Research Station headquarters located less than 2 km south of the study site. Data were not available for July due to data logger failures and consequently these climate data were obtained from the Environment Canada weather station at Viking, Alberta, approximately 20 km west of Kinsella (see Appendix 1).

Prior to analysis, all data were checked for normality by examining skewness using column summaries in PC ORD Version 5. All variables with a skewness coefficient greater than 1 (Ah horizon depth, soil organic matter content, mean litter depth, and August litter weight) were log transformed.

In order to determine the influence of litter and range site on soil moisture and production, the following steps were followed:

- **Step 1:** Reduce correlated variables to limit multicollinearity in subsequent analyses. Reduced variable include litter, soil and topographic range site characteristics, and the plant community.
- **Step 2:** Determine the influence of litter and range site characteristics on soil moisture, soil water-holding capacities and soil temperature using bivariate correlations and stepwise multiple regression models.
- **Step 3:** Determine the influence of soil moisture, moisture content at field capacity and permanent wilting point, and soil temperature on plant production using bivariate correlations and regression models.
- **Step 4:** Determine the influence of litter and range site characteristics on plant production using bivariate correlations and stepwise multiple regression models.
- **Step 5:** Determine the relationship between plant community characteristics and plant production patterns.

Generally, these steps were performed to examine the pathways by which litter and range site influence production as illustrated below:

1. **Litter vs. Soil vs. Topography → Microenvironment → Production**

Vs.

2. **Litter vs. Soil vs. Topography → Production**

Data analysis steps are described in more detail below.

4.2.5.1. Reduction of Litter Variables

To determine whether litter parameters differed across sampling months, the litter variables were tested using a repeated measures mixed model ANOVA in SAS 9.1.3 with month of sampling as the classification variable. Mean litter cover, litter depth, May to July litter biomass, and August litter biomass (for August analyses), were determined as the best characterizations of litter for subsequent analysis. A bivariate correlation test was then run on these leading measures using Proc CORR in SAS 9.1.3 to determine the interrelationship between the different estimations of litter. The best litter measurements were also tested for correlation with soil and topographic variables to examine whether litter varied predictably across the landscape with any other range site variable.

4.2.5.2. Reduction of Range Site Variables

A bivariate correlation analysis was run on the soil and topographic variables to examine inter-correlation between predictor variables for subsequent regression analysis with soil moisture. Due to the presence of several significant correlations, a Principal Component Analysis (PCA) (Pearson 1901, Hotelling 1933) was run on all of the independent range site characteristics (sand, silt, clay, OMC, bulk density, Ah depth, position, aspect and slope) in PC-ORD in order to create a smaller subset of principal components based on the inter-correlated variables. This analysis addressed the problem of multicollinearity by deriving new components (i.e. variables) that were orthogonal compared to the original data (McCune and Grace 2002, Gotelli and Ellison 2004). Reducing the number of independent variables also addressed the problem of small sample size and reduced the likelihood that subsequent multiple regression models were fit to random noise in the data (McCune and Grace 2002). The PCA analysis was run with a correlations cross-products matrix and the solution was not rotated. Principal components were interpreted based on their eigenvectors, grid overlays and correlations of variables with axes.

4.2.5.3. Reduction of Plant Composition Data

To characterize the vegetation community, a Non-metric Multidimensional Scaling (NMS) ordination was run on the vascular plant cover data from August using a Sorensen distance measure in PC-ORD (Kruskal 1964, Mather 1976). A random starting configuration was used, and dimensionality was assessed using a Monte Carlo test. The real data was run 250 times, as was the randomized data for the Monte Carlo test. A total of 500 iterations were used to obtain the final stable solution with a final instability of 0.00001. Ordination axis scores were interpreted based on Pearson and Kendall correlations with all species found across the site.

4.2.5.4. Linking Litter and Range Site to Observed Soil Moisture

To evaluate the relationship between litter and soil moisture content, bivariate correlations were run for litter depth and weight with observed soil moisture measurements taken on each day following rainfall in May, June, July and August 2007. As litter can also affect soil moisture evaporation rates by moderating soil temperature, correlations between litter and soil temperature were examined in each sampling month. Original soil and topographic variables were then tested for bivariate correlation with observed moisture measurements, identified field capacity and permanent wilting point values, as well as with temperature measurements using Proc CORR in SAS.

4.2.5.5. Comparing Litter and Range Site Influences on Soil Moisture

To determine the importance of litter in regulating soil moisture content relative to the other range site variables, a multiple regression analysis was run on each observed soil moisture measurement with the reduced range site principal components, litter weight and above-ground plant biomass (to test for moisture depletion through transpiration) as independent variables. Because the research question behind this analysis was exploratory in nature, Proc STEPWISE was used in SAS, and the MAXR option used for model evaluation (McCune and Grace 2002). The best one variable and the best multiple variable model for each soil moisture measurement was determined using the Mallows' statistic (Mallows 1973), and was based on the lowest C(p) value for the different model options.

Similar multiple regression analyses were run on moisture content for permanent wilting point, field capacity, and plant available soil water to examine hypothesized dependencies of these variables on the first two principle components derived from soil texture, bulk density and soil organic matter content. A stepwise multiple regression analysis was also run on the monthly soil temperature measurements to determine the relative influences of litter weight, plant biomass, slope, aspect and plot position. Soil properties were not regressed on temperature as they were thought to effect temperature mostly through indirect pathways via their impacts on soil moisture (Wigneron et al. 2008).

4.2.5.6. Linking Soil Moisture and Temperature to Plant Production

Simple bivariate correlation analyses were run on the moisture and vegetation production measurements to assess the relationship of all plant production measurements (biomass of grass, forbs, shrubs, total shoots and roots, along with the root:shoot ratio and vegetation cover) with field measured near-surface soil moisture, moisture content at field capacity and permanent wilting point, plant available soil water, and soil temperature. Yet, as plant production both effects and is affected by soil moisture and temperature, the directional influence of all microclimatic measurements were also tested on both total shoot and root biomass. First, simple regressions were run using Proc REG in SAS to examine how strongly each moisture and temperature measure influenced plant production. Next, to determine the relative importance of these different variables on shoot and root biomass, a stepwise regression analysis was run in SAS using the MAXR option and Mallows' statistic for model selection of the best one-variable model. Multiple-variable models were not determined due to intercorrelation between the different measurements of soil moisture and temperature.

4.2.5.7. Linking Litter and Range Site to Plant Production

The link between above- and belowground plant production with litter and original range site variables (soil texture, organic matter content, bulk density, slope, aspect and landscape position) was initially examined through bivariate correlation analyses. To examine the relative influence of litter biomass and reduced range site variables (topographic and soil principal components) on shoot and root biomass, stepwise multiple regressions were run using Proc STEPWISE with the MAXR option in SAS. Both the best one-variable and the best multi-variable model were identified using Mallow's statistic. Moisture and temperature measurements were not included in these regression models due to the large amount of intercorrelation with litter and range site variables. As litter was the primary variable of interest for this study, an additional set of simple regressions were run between litter biomass and shoot and root biomass using Proc REG in SAS to determine the specific influence of litter on production.

4.2.5.8. Linking Litter, Microclimate, Range Site and Plant Production to Plant Community Composition

Measures of plant community structure (NMS axis scores, species richness, diversity and evenness) were analyzed only through bivariate correlations in this study as they were primarily used to help interpret patterns in plant production. Initial analyses examined the interrelationship between the different characterizations of the plant community, and then correlations were run with the plant production measurements. Finally, bivariate correlations were run between community structure parameters and all range site and microclimatic variables using Proc CORR in SAS.

4.3. Results

In the following analyses, correlation coefficients where $r > 0.36$ are significant at $P<0.05$. Further, $r > 0.46$ is significant at $P<0.01$, $r > 0.57$ is significant at $P<0.001$, and $r>0.64$ is significant at $P<0.0001$.

4.3.1. Variable Reductions

4.3.1.1. Litter

Mean litter cover, litter depth and May to July litter biomass were all correlated with one another ($P<0.05$), indicating that these different measures may be used as surrogates for each other. August litter biomass (mean=2684±1456 kg/ha) was only correlated with mean litter biomass of the other months (mean=1781±941 kg/ha). All litter parameters had a significant ($P<0.05$) positive correlation with landscape position (mean litter cover $r=0.51$, mean litter depth $r=0.51$, mean May to July litter biomass $r=0.49$; August litter biomass $r=0.37$). Litter depth was also positively correlated with soil organic matter content (OMC) ($r=0.57$) and negatively correlated with bulk density ($r=-0.38$). Litter biomass was primarily used in subsequent analyses.

4.3.1.2. Range Site

In the bivariate correlations run between soil and topographic variables, aspect was positively correlated with bulk density ($r=0.51$) and negatively correlated with soil OMC (-0.37) and sand (-0.37). Soil OMC was also negatively correlated ($P<0.0001$) with soil bulk density ($r=-0.67$). Soil texture measurements were all intercorrelated, with silt negatively correlated ($P<0.0001$) with both sand ($r=-0.93$) and clay ($r=-0.85$), and clay and sand showing a positive correlation ($r=0.60$). All other soil and topographic variables were uncorrelated ($P>0.05$).

The PCA analysis of soil bulk density, OMC, sand, silt and clay content, Ah depth, landscape position, slope and aspect accounted for 100% of the variance in the data with 8 principal components. The first five principal components cumulatively accounted for 89% of the variance in the soil moisture data (PC1=33%, PC2=25%, PC3=13%, PC4=10%, PC5=9% of variance) and were used in subsequent analyses. PC1 largely reflected soil texture influences, being positively associated with silt and negatively with the abundance of sand and clay (Table 4.2). In contrast, PC2 was negatively driven by bulk density and aspect, and positively affected by soil OMC. PC3 was positively linked to topographic position, PC4 to slope gradient, and PC5 to the depth of the Ah horizon.

4.3.1.3. Plant Community

The NMS analysis of August plant community data resulted in a two dimensional final ordination solution (Axis 1: P=0.01, Axis 2: P=0.02), with a final stress of 22.89. The proportion of variance represented by Axis 1 was 45.4%, and by Axis 2 was 23.1% based on the correlations between ordination distances and distances in the original n-dimensional space. Axis scores were not rotated as rotation resulted in little improvement in correlation with soil moisture. Correlation of plant species with the final axes indicated Axis 1 was associated closely with *Poa pratensis* (r=0.80), *Agrostis stolonifera*, (r=-0.51), *Stipa curtiseta* (r=-0.45), and *Symphoricarpos occidentalis* (r=0.43) (P<0.05). Axis 2 was also associated with *Poa pratensis* (r=-0.61), in addition to *Artemesia ludoviciana* (r=-0.56), *Solidago missouriensis* (r=0.49), and *Thermopsis rhombifolia* (r=0.46) (P<0.05) (see Appendix 5).

4.3.2. Observed Soil Moisture Patterns

Field moisture readings taken with the TDR probe were not well correlated to volumetric moisture measurements (R^2=0.20). The linear equation for the relationship between the two moisture readings was as follows: Volumetric moisture content = 0.173 + 17.21 (TDR moisture content) (see Appendix 2).

Near-surface soil moisture depletion patterns following rainfall over five days in each of May, June, July and August are shown in Fig. 4.1. May had the highest soil moisture levels, while July had the lowest. Total moisture depletion was greater in June (14.1±2.3%) and August (9.4±1.9%) than in May (4.5±2.3%) or July (2.6±1.2%). Additionally, plots with high litter tended to lose slightly less moisture (~1-2%) over the monitoring period, but only in June and August. Observed soil moisture values also showed a significant negative correlation with near-surface soil temperature in both June and July (Table 4.3).

4.3.3. Combined Litter and Range Site Influences on Soil Moisture and Temperature

4.3.3.1. Influences on Observed Soil Moisture (TDR Measurements)

Bivariate correlations linking observed soil moisture with litter showed that litter was most strongly related to soil moisture during the middle of the growing season (June and July), (Table 4.3). The total moisture depleted over the measurement period was also significantly correlated ($P<0.05$) with litter depth ($r=-0.36$) and litter biomass ($r=-0.42$) in June, and with litter biomass ($r=-0.37$) in August. Litter cover (%) was not significantly ($P>0.05$) correlated to moisture in any month.

Of the range site variables, soil texture, slope and topographic position were most strongly and consistently correlated to observed soil moisture over the growing season (Table 4.4). Bivariate correlations showed a slightly different pattern in May than other months, with aspect and soil bulk density related to soil moisture in the first half of the measurement sequence. Depth of the Ah horizon was also significantly correlated ($P<0.05$) to the total moisture lost over the sampling period in both May ($r=-0.37$) and July ($r=-0.41$). Finally, total moisture loss in June was positively correlated to soil bulk density ($r=0.39$). However, none of these correlations are significant at $P<0.01$.

Leading one-variable regression models determined through Mallows' statistic were able to explain 13-33% of the variance in measured soil moisture among plots, with models generally accounting for more of the variance in July compared to the other months (Table 4.5). Litter had an important influence in these models during June, July and August, particularly in the latter part of the sampling period (i.e. days 3-5). Notably, litter biomass was the single best predictor of total moisture loss during measurement in both May ($R^2=0.094$, $P=0.10$) and June ($R^2=0.173$, $P=0.02$). Conversely, PC5 (i.e. primarily Ah depth) had the most influence on total moisture loss in July ($R^2=0.083$, $P=0.12$), while PC4 (i.e. slope gradient) showed the strongest influence on moisture loss in August (R^2=0.085, P=0.12), although neither relationship was significant at $P<0.05$. PC1, representing soil texture, was also important as the single best predictor of daily soil moisture early in the sampling sequence after rainfall in most months (Table 4.5). Once again, May moisture showed a slightly different pattern of dependency than the other months, with PC2 (characterizing soil organic matter and bulk density) also showing important influences on soil moisture.

Stepwise multiple regression models for observed soil moisture generally explained 18-67% of the variance in moisture on the different days of measurement (Tables 4.6 – 4.9). Models for July tended to have the highest R^2 values, while those for August tended to have the lowest. Stepwise regression models for July were also the most complex, with 3-5 dependant variables, while August models generally had only one dependant variable. While models for May were limited to range site (i.e. PC) variables (Table 4.6), litter biomass was included in models for moisture content in June, July and August, particularly in the latter part of the sampling period. Litter was particularly important for models in July (Table 4.8), while shoot biomass was most important shortly after rainfall in June (Table 4.7). Litter was also included in multiple regression models for total moisture loss in both May [moisture loss = 2.3 + 0.0013(Litter Biomass) – 0.36(PC1) - 1.05(PC3); R^2=0.35] and June [moisture loss = 16 – 0.00095(Litter Biomass) + 0.77(PC4); R^2=0.28], but not in July [moisture loss = 2.6 - 0.39(PC5); R^2=0.08], or August [moisture loss = 12 – 0.0008(Shoot Biomass) - 0.68(PC4), R^2=0.18]. Among the range site variables, PC1 (texture) was included in almost all daily models and PC2 (soil OMC and bulk density) was again only important in those for moisture in May. Patterns in the other principal components were not as defined, although PC 3 (position) was important to June and July moisture models, while PC 4 (slope) appeared important in May and July.

4.3.3.2. Influences on Soil Temperature

Bivariate correlations showed that observed soil temperature was negatively associated ($P<0.05$) with litter depth (May r=-0.53, June r=-0.50, July r=-0.57, August r=--0.36) and mean May to July litter biomass (May r=-0.36, June r=-43, July r=-0.50, August r=-47). Temperature was also correlated with topographic position in May (r=-0.44), with soil organic matter in May (r=-0.42), June (r=-0.51) and July (r=0.41), and with slope in July (r=0.48).

Multiple regression models developed for soil temperature indicated that current-year above-ground production was generally more important than litter in regulating temperatures in May [temperature = 13+0.002(Shoot Biomass) – 0.25(Position); R^2=0.37], June [temperature = 24 -0.002(Shoot Biomass); R^2=0.27], and August [temperature =22 – 0.0006(Shoot Biomass); R^2=0.25]. In July, litter biomass and topography also showed significant influences in the soil temperature multiple regression model [temperature =28 -0.0006(Shoot Biomass) -0.0008(Litter Biomass) +0.14(Slope) +0.015(Aspect); R^2=0.50].

4.3.3.3. Influences on Moisture Content at Field Capacity and Permanent Wilting Point

Bivariate correlations showed that moisture content at field capacity and permanent wilting point were both strongly linked to soil organic matter in a positive direction, and to a lesser extent, soil bulk density and aspect, albeit negatively (Table 4.10). Conversely, plant available soil water was more strongly related to soil texture. Multiple regression models also reflected these influences, with models for moisture content at field capacity [=30– 0.7(PC1) +2.6(PC2); R^2=0.69] and permanent wilting point [=23 +2.7(PC2); R^2=0.65] explaining more of the variance in the data than the model for plant available soil moisture [=6.6- 0.3(PC1); R^2=0.19].

4.3.4. Combined Soil Moisture and Temperature Influences on Plant Production

Mean biomass values for the different plant functional groups over the growing season are shown in Figure 4.2. Bivariate correlation analysis showed that forb biomass demonstrated more significant correlations ($P<0.05$) with the observed soil moisture measures than other production variables (Table 4.11). Despite this, total aboveground shoot biomass was correlated with observed soil moisture only occasionally in June and July (i.e. 3 or 2 days after rainfall, respectively), and total vegetative cover was correlated with observed moisture in August as well as with the total moisture loss over the five days of measurement ($r = -0.36$) in July.

Biomass parameters were also positively correlated ($P<0.05$) with soil temperature in May, and negatively correlated with soil temperature in June, July and August (Table 4.11). Finally, plant biomass including roots, and to a lesser extent cover, were significantly correlated to soil moisture content at field capacity and permanent wilting point in the early to mid (May-July) part of the growing season (Table 4.12). Only cover was correlated with available soil water, and only in May. In contrast, cryptogam cover was uncorrelated ($P>0.05$) with any moisture or temperature measurement in any month.

Simple linear regression models between biomass and soil moisture parameters indicated that moisture content at field capacity and permanent wilting point had a consistently stronger influence on shoot and root production than did observed moisture measures (Table 4.13). These simple regression models also explained more variance in early growing season (May and June) biomass compared to biomass later in the growing season. Simple regressions with soil temperature showed a similar pattern to the bivariate correlations, with temperature positively influencing shoot biomass in May (R^2=0.24, P=0.006), and negatively influencing root and shoot biomass in June (R^2=0.27, P=0.003), July (shoot: R^2=0.32, P=0.0012, root: R^2=0.17, P=0.02), and August (R^2=0.25, P=0.005). In contrast, the root:shoot ratio was not associated with any moisture or temperature parameter.

Finally, the leading one-variable stepwise regression model developed to explain the predominant moisture or temperature influence on biomass also revealed that observed TDR soil moisture measurements were not as important. May shoot production was best explained by moisture content at field capacity, whereas June shoot biomass and July root biomass were both more affected by the permanent wilting point. Soil temperature exerted the strongest influence on shoot biomass in both July and August. The root:shoot ratio of vegetation was best explained by plant available soil moisture, although this relationship was not significant (R^2=0.06, P=0.20).

4.3.5. Combined Litter and Range Site Influences on Plant Production

Bivariate correlations between shoot biomass and litter showed positive linkages (<0.01) in both June (r=0.57) and July (r=0.53). Shoot production was also correlated with soil organic matter in both May (r=0.39) and June (r=0.54), and with slope angle in both June (r=-0.37) and July (r=-0.41). Other biomass parameters showed few significant correlations with range site variables. Nonetheless, total vegetation cover was positively correlated (P<0.01) with landscape position in June (r=0.46) and July (r=0.51). In addition, July root biomass was negatively correlated with aspect (r=0.41) and soil bulk density (r=40), and was positively correlated with soil organic matter content (r=0.41).

Simple linear regression analysis of shoot biomass with litter biomass also showed that litter positively influenced aboveground production in both June (R^2=0.32, P=0.001) and July (R^2=0.28, P=0.003). Litter had no significant influence on shoot biomass in May (R^2=0.0008, P=0.88) and August (R^2=0.003, P=0.76), and had no effect on July root biomass (R^2=0.08, P=0.13). The root:shoot ratio was also unrelated to litter biomass (R^2=0.02, P=0.44).

One-variable stepwise models determining the dominant litter or range site influence on shoot biomass (using Mallows' statistic) demonstrated that litter biomass was the best predictor of shoot biomass in both June (B=0.29, R^2=0.32, P=0.001) and July (B=0.53, R^2=0.28, P=0.003). In May, shoot biomass was most influenced by PC5 (Ah Depth) (B=106, R^2=0.10, P=0.09), and August shoot biomass was best explained by PC3 (plot position) (B=190, R^2=0.07, P=0.16). Similar to the pattern seen in the bivariate correlations, the best one-variable regression model for July root biomass was PC2 (OMC and bulk density) (B=12, R^2=0.26, P=0.004). Finally, the root:shoot ratio was best explained by PC4 (slope angle) (B=0.49, R^2=0.12, P=0.07).

Stepwise multiple regression models relating litter biomass and range site principle components to total shoot biomass accounted for anywhere from 18% to 53% of the variation in aboveground production (Table 4.14). Models were particularly poor early (May) and late (August) in the growing season (R^2<19%; P>0.05). Models for shoot biomass (July - 45%) were also generally stronger than those for root biomass (July - 26%). Litter was once again included as a key predictor of shoot biomass in both June and July when model fit peaked. PC2 and PC4 were also generally important in the multiple regression models.

4.3.6. Plant Community Responses

Bivariate correlations showed several intercorrelations between the different plant community summary measurements. NMS Axis 1 displayed a significant negative correlation ($P<0.05$) with species evenness ($r = -0.36$), whereas Axis 2 showed significant positive correlations ($P<0.001$) with species richness ($r = 0.58$) and diversity ($r = 0.59$). Species diversity ($r=0.44$) and evenness ($r=0.38$) were also positively correlated ($P<0.05$) with vegetation cover. Other measurements of plant production were uncorrelated with the plant community variables.

Community characteristics were also generally uncorrelated with observed soil moisture and temperature measurements (Table 4.15), although species richness was positively correlated to moisture at both field capacity and permanent wilting point. Moreover, plant community characteristics were generally uncorrelated ($P>0.05$) with soil and topographic variables, with the exception that species richness ($r=-0.39$), diversity ($r=-0.37$), and NMS Axis 2 ($r=-50$) were all negatively correlated with Ah horizon depth.

4.4. Discussion

4.4.1. Seasonal Soil Moisture Patterns

May soil moisture content was higher than in the other months, likely due to moisture recharge from recent snow melt. Soil moisture content in June, July and August reached levels well below those in May, indicating continuous removal of soil water stores under water deficit, and thus, greater moisture stress on plants as the summer progressed. Soil moisture content and total moisture depletion were generally lowest in July coincident with the highest air (and soil) temperatures, the most advanced plant growth and water use, and the lowest recent input of precipitation. Low moisture levels may well have diminished the capacity of plants to extract soil water as moisture approached the wilting point, resulting in reduced water loss through transpiration (Brutsaert and Chen 1995, Brutsaert and Chen 1996, Laio et al. 2001a). Greater moisture depletion seen in June and August may have been related to heavy recent input of water which was more prone to evaporation at the soil surface (Laio et al. 2001a, Viessman and Lewis 2003), as well as to movement into, through, and out of the soil due to greater hydraulic forces (Viessman and Lewis 2003).

August multiple regression models examining dependencies of soil moisture on litter and range site variables accounted for less variation in the data than in the other months. The poor fit of these models may be due in part to other unknown environmental variables not included in the models such as wind speed, relative humidity, intensity and duration of rainfall, frequency of past rainfall events, and air temperature fluctuations (Coupland 1961, Dix 1964, Facelli and Pickett 1991, Laio et al. 2001a, Schenk and Jackson 2002).

TDR moisture readings were not well correlated with volumetric moisture measurements in this study, which was possibly due to within-plot heterogeneity as the multiple TDR readings were not taken in the exact plot location as the single soil core used to determine volumetric soil moisture. Single soil cores are more prone to natural microsite variation within the plot, which in turn, would reduce the fit between TDR and volumetric moisture estimates. The lack of a strong correlation between the bulk density dependent volumetric moisture content and the field TDR moisture measurements may also have reduced the fit of some of the regression models involving the TDR derived moisture levels.

4.4.2. Litter and Its Influences on Soil Moisture and Temperature

Litter biomass was expected to be correlated with landscape position due to observations that upper slopes tended to have less above-ground plant production than toe-slopes (see also Coupland and Brayshaw 1953, Coupland 1961). The removal of litter from a third of the mid and lower slope plots prior to plant growth in April 2007 was an attempt to reduce the correlation between litter and landscape position. Nonetheless, all litter measurements remained significantly correlated to position, which may have confounded some of the relationships between litter and soil moisture in this study. Thus, significant litter effects in this study may actually partially represent topographic influences on soil moisture and plant production. Litter depth was also correlated to soil organic matter and bulk density, likely due to the relationship between production levels, litter breakdown and long-term incorporation of organic matter into the soil (Weaver and Rowland 1952).

Litter did appear to play a key role in regulating soil moisture content in this study. In the leading single-variable regression models for observed soil moisture content, litter biomass was the most influential variable in over half of the measurement days in June, July and August, indicating that it had a more consistent relationship with moisture than other measured range site variables. Litter also had more of an influence on soil moisture after larger precipitation events (E.g. June and August) or when the air temperature was higher (E.g. July), and had the strongest influence on maintaining high moisture levels for longer periods of time after rain. Consequently, the significant positive effects of litter were generally delayed in June and August for several days after rainfall, with litter also reducing total rates of moisture depletion. Further, because rainfall was so light prior to sampling in July, soils likely received little new input of soil moisture after substantial interception losses. In such a case, the significance of litter in influencing moisture on all measurement days in July may be more indicative of the ability of heavy litter loads to positively maintain moisture in the soil for extended time periods between major rainfall events. Finally, since litter was also correlated in general with soil temperature at this site, it appears that the influence of litter on soil moisture was likely through affects on evaporation rather than by reducing runoff and increasing water infiltration.

Shoot biomass had a similar relationship as litter on positively maintaining soil moisture levels during the mid-part of the growing season, and therefore probably augmented the shading influence of litter on reducing evaporation of soil water (as in Salve and Allen-Diaz 2001). As shoot biomass was also positively correlated with soil organic matter content, production influences on organic matter deposition may also account for increased soil water-holding capacity. Nonetheless, shoot biomass was not significantly correlated to soil moisture on most measurement days, which may have been due to the distinct tradeoff where reduced evaporation rates under a heavy canopy are balanced by increased water interception, and in particular, water use through uptake and transpiration (Naeth et al. 1991b).

The prominence of the effect of litter and shoot biomass on reducing evaporation rates is further evidenced in the apparent negative effect both of these variables had on soil temperature. Litter has been found to indirectly affect soil moisture by reducing temperatures in a number of studies (ex. McKinney 1929, Flory 1936, Weaver and Rowland 1952, Knapp and Seastedt 1986). Temperature was negatively correlated with observed soil moisture in June and July, the months where litter also exerted stronger influences on moisture levels. Temperature was also affected by landscape features including slope, aspect and position, which likely exerted influences on local microclimates by altering plot orientation to direct sunlight (Chapin et al. 2002).

4.4.3. Range Site Influences on Soil Moisture and Soil Water Holding Capacity

Soil texture had a strong association with soil moisture during most days in each sampling period and was important in the leading single-variable regression models, particularly in the first two days following rainfall before litter exerted a stronger influence on maintaining moisture levels. Despite a lower water holding capacity than clay, sand was positively correlated with soil moisture, and tended to have an influence in the first several days of each sampling period when sand would be expected to increase infiltration and percolation through the soil, as seen in other studies (Laio et al. 2001b, Chapin et al. 2002). However, clay content also demonstrated a strong positive correlation with soil moisture, suggesting a mix of sand and clay may be optimal for water entry, storage and retention in rangeland soils over time (Wilcox et al. 1988, Salve and Allen-Diaz 2001).

Topographic features of the site also significantly influenced soil moisture, although they did not appear as important in the leading single-variable regression models as litter biomass or soil characteristics. Slope can influence runoff and initial soil moisture levels (Meeuwig 1970), but may also influence the angle at which the sun hits the plot, thereby increasing evaporation (Chapin et al. 2002). As slope was most important in moisture models for May and July, months coinciding with lower rainfall and therefore lower runoff potential in this study, it is likely that slope more strongly influenced solar angle and evaporation in this investigation. Aspect can similarly affect evaporation by altering exposure to sunlight, as well as influencing orientation to prevailing wind directions, which are predominantly from the west in the Aspen Parkland (Coupland and Brayshaw 1953, Coupland 1961). Aspect did not appear as important in affecting soil moisture as most other variables examined in this study, but was negatively correlated to May moisture levels, indicating that moisture decreased with increased exposure to western winds.

Conversely, it is not surprising that topographic position demonstrated positive correlations with soil moisture in all measurement months, with more moisture available at lower slope positions. Lower plots receive water from surface and sub-surface runoff originating on upper slopes (Bork et al. 2001, Salve and Allen-Diaz 2001, Chanasyk et al. 2004). As this effect of runoff and seepage is time-delayed after rainfall input, it corresponds to patterns in soil moisture where correlations with position tended to be greater in the latter part of individual measurement periods. Lower slope grassland plots were also generally closer to small aspen groves common at lower topography in the Aspen Parkland (Moss 1932), and shading by aspen trees, particularly with low sun angles, may further explain the maintenance of greater moisture for longer periods at this location (Powell and Bork 2007). Nonetheless, correlations between landscape position and litter may represent a confounding influence of litter on these relationships.

Depth of the Ah horizon was generally less important in influencing soil moisture than the other variables measured in this study. Ah depth can influence the absolute amount of water that can be stored in a soil, as well as moisture depletion into lower soil layers, and may have important influences on moisture availability to plants (Laio et al. 2001b, Porporato et al. 2001). The Ah horizon did appear to influence total moisture loss during sampling in May and July, months when moisture depletion was relatively less pronounced. However, deeper Ah horizons resulted in greater moisture loss in May, whereas shallower soils had greater losses in July.

Soil organic matter content and bulk density exerted the greatest apparent influence on soil moisture in May. These variables appear important in influencing retention of soil moisture recharged from winter snowmelt. Organic matter is very effective at influencing both infiltration rates and the water-holding capacity of the soil (Wilcox et al. 1988, Naeth et al. 1991a, Dormaar and Carefoot 1996). The large amount of pore space in organic matter is particularly effective at holding water, thereby increasing the amount of moisture retained in the soil against gravity (Naeth et al. 1991a, Chapin et al. 2002). Bulk density may reflect the level of soil structure as well as soil composition (i.e. OM), and can also represent the soil's ability to hold water, as determined in large part by the soil texture effects discussed earlier (Meeuwig 1970, Wilcox et al. 1988). While it is surprising that organic matter and bulk density did not exert a stronger influence on soil moisture through the remainder of the growing season, this may be due to the relatively limited variation in organic matter and especially bulk density among plots across the landscape.

Along with soil structure, texture and organic matter strongly influence moisture absorption forces within the soil profile (Chapin et al. 2002). As such, it was not surprising that moisture content at field capacity was associated with soil texture, organic matter and bulk density, while moisture content at permanent wilting point appeared to depend on organic matter and bulk density. Plant available moisture was ultimately linked to soil texture, but had much less variance explained in the regression model. Clay tends to increase levels of moisture content at field capacity due to strong matric forces that prevent water from draining due to gravity, but also tend to have high moisture contents at permanent wilting point as moisture is held preventing extraction for use by plant roots (Laio et al. 2001a). Sandy soils, on the other hand, tend to drain fast with gravity resulting in lower moisture contents at field capacity and at permanent wilting point (Laio et al. 2001b). Organic matter may also bind water against the force of gravity, thereby increasing field capacity (Wilcox et al. 1988, Naeth et al. 1991a, Dormaar and Carefoot 1996) and, to a lesser extent, may bind water against use by plants, thereby increasing permanent wilting point (Hudson 1994, Olness and Archer 2005). Plant available soil moisture is therefore affected by complex combinations of soil characteristics that can either increase or decrease the range of soil moisture levels at which water is available for plant extraction.

4.4.4. Production Responses to Soil Moisture and Temperature

Most correlations between production and observed soil moisture in this study were not significant. This lack of significance may largely be due to the dual nature of the causal pathway between moisture and production, where increased moisture can augment growth, but increased growth in turn, depletes moisture faster through greater uptake and transpiration (Naeth et al. 1991b, Leriche et al. 2002, Donker et al. 2006). Nonetheless, regression models suggest that observed soil moisture levels were important in augmenting plant growth in June and July. During these months, moisture reached limiting levels for production, and the maintenance of high moisture in some plots likely had direct consequences for plant growth. Conversely, production parameters showed a trend of negative correlation with observed soil moisture in May. Although this relationship was not significant, it may indicate that excess moisture was limiting to plant establishment and growth in the early part of the growing season, possibly due to the effect of moisture on reducing soil temperatures (Wen et al. 2006, Wigneron 2008). By August, actual moisture levels may also have been less important to plant production as growth rates generally decline with senescence. Forb biomass exhibited stronger correlations to soil moisture than the other plant functional groups, particularly in July when moisture was most limiting and forb production had peaked, and it is possible that some forb species responded to moisture deficiencies with earlier senescence.

Soil moisture at both field capacity and permanent wilting point exhibited stronger relationships with plant production than actual moisture levels in the first part of the growing season. Field capacity and permanent wilting point were negatively correlated to production in May and positively correlated with production in June. Both measures were also positively correlated with production in July and August, although these relationships were not significant. A higher field capacity indicates that more water is retained in the soil against gravity, which can be important in reducing seepage losses after recharge from heavy rainfall (Laio et al. 2001a), as seen in June. Field capacity was also the single best predictor of shoot biomass in May, although the relationship was not as expected, with greater production in plots with lower field capacities. It is probable that too much moisture slowed plant growth after snow-melt, possibly through effects on soil temperature (Wen et al. 2006), and that better drained soils (ie with those less capability of holding water) therefore had greater early season production.

Moisture content at permanent wilting point was the single best predictor of shoot production in June, suggesting that shoot production was enhanced in plots that held water more tightly from extraction by plant roots. This relationship is counter-intuitive and not easily explained with the data. As actual permanent wilting points are plant species specific, it is possible that native plants at the study site were capable of extracting water at lower pressures than the measured 1/3 bars, and that variations in plant community composition accounted for patterns in soil water extraction (Chanasyk et al. 2004). It is also possible that the positive influence of the permanent wilting point may have been an artifact of an indirect pathway controlling plant production. For instance organic matter content was also positively correlated with permanent wilting point, and may have indirectly contributed to plant growth through greater nutrient availability (Berendse 1990, Facelli and Pickett 1991). In fact, shoot biomass was positively correlated to organic matter in May and June, and it is possible that the overriding influence of organic matter on production at this site was through nutrient cycling.

Finally, the two moisture content measures and plant available soil water had no significant association to production values in the latter half of the growing season. The relationship of plant production to both moisture content at permanent wilting point and plant available soil moisture was expected to increase in significance during months of greater moisture stress, with lower wilting points and higher ranges of available moisture leading to greater plant growth (Laio et al. 2001a, Porporato et al. 2001, Mapfumo et al. 2003). Although it is possible that plants at this site were never sufficiently moisture stressed for these variables to significantly hamper plant growth, this seems unlikely given the low moisture levels observed in July (direct assessments of when actual soil moisture levels were below the permanent wilting point were not examined due to the lack of correlation between TDR derived and volumetric soil moisture). Instead, moisture availability during the early growing season appears critical to maximizing production in this plant community.

Unlike any moisture measurement, soil temperature had a significant relationship with shoot production in all months of the growing season. Soil temperature appeared to positively influence production in May, indicating that higher temperatures were important for promoting early plant growth and potentially seed germination and plant establishment (Weaver and Rowland 1952, Penfound 1964, Thompson et al. 1977, Rice and Parenti 1978). During subsequent months, higher temperatures had a negative relationship with both shoot and root growth. Soil temperature can influence production directly by increasing photosynthetic rates (Chapin et al. 2002), but often influences plant growth indirectly through effects on evapotranspiration and soil moisture content (Sauer 1978, Dormaar and Carefoot 1996, Chapin et al. 2002). Negative temperatures later in the growing season corresponded to months where observed moisture levels were also more limiting, and it is likely that there was an interactive effect of these variables on increasing evaporation and water loss, and consequently decreasing production.

In general, regression models for moisture and temperature influences on plant biomass explained more of the variation in production in the early part of the growing season than in later months. Furthermore, moisture content at field capacity and permanent wilting point, and soil temperature seemed to explain patterns in plant production better than observed moisture levels using TDR readings. Nonetheless, all single-variable regression models were generally limited in effectiveness at explaining production patterns, indicating that moisture was not as limiting to plant growth as other variables, such as soil nutrient status, in this ecosystem (Burke et al. 1998, Chapin et al. 2002, Lamb et al. 2007).

4.4.5. Production Responses to Litter and Range Site

Of the measured vegetation and range site variables, litter appeared to be most strongly associated with production. Litter had an apparent positive influence on shoot biomass in June and July, and was also a better predictor of biomass than the topographic and soil variables in these months. June and July were the months when measured soil moisture had the greatest association with production, and where temperature had the greatest relationship to soil moisture. Because of these complex pathways, it is likely that increased shading under litter reduced temperatures, which then reduced evaporative losses of soil moisture, culminating in more water available for mid-season plant growth. Other studies have also found that litter can have positive influences on plant production through reducing evaporation and thereby increasing water available for plant growth (Hamrick and Lee 1987, Willms et al. 1993).

Organic matter content, depth of the Ah horizon, and slope angle influenced plant production in the regression models. Organic matter and Ah depth appeared more important in influencing moisture in the first half of the growing season, likely through important influences on soil water storage capacity, particularly as moisture content at field capacity and permanent wilting point also exerted strong influences on plant production in May and June. Organic matter may also have influenced production through effects on soil nutrient availability (Berendse 1990, Facelli and Pickett 1991). Slope angle was more important in the middle of the growing season, likely through influences on orientation to solar radiation and wind (Chapin et al. 2002, Coupland 1961). Nonetheless, range site variables were not able to account for as much variation in production as litter in this study. Therefore, it is likely that litter management can have a cascading effect on the soil microenvironment and associated production, although the strength of these relationships appear to depend on seasonal patterns of relative moisture deficits, which in turn, are at least partly dependent on range site characteristics, including soil and topographic properties.

4.4.6. Plant Community Responses

The plant community was generally unaffected by moisture and temperature parameters, and in turn, had little effect on vegetation production at this study site. Species diversity was negatively correlated to August soil temperature, indicating that plots with lower temperatures were more diverse. This is possibly due to the different temperature tolerances of plants (Berry and Bjorkman 1980), with species responding negatively to higher mid-growing season temperatures, and possibly to lower associated moisture levels. Species evenness showed a positive correlation with observed soil moisture on one day of measurement in August. It is possible that higher moisture levels reduced competition between plants, allowing a variety of species to more evenly dominate the plot (Chapin et al. 2002). Nonetheless, Lamb et al. (2007) found that soil water had little impact on plant competition at this study site. Richness was positively correlated with moisture content at both field capacity and permanent wilting point. Higher field capacities may represent better site potential with more moisture available earlier in the growing season, and may have positive effects on the establishment of multiple species. Generally, the lack of correlation between production and plant community characteristics indicates that the production potential of the area is more related to abiotic site factors than to the nature of the plant species assemblages.

4.5. Conclusions

This study demonstrates that natural litter loads do appear to have positive influences on maintaining soil moisture after rainfall in mesic grasslands of the Aspen Parkland. Range site characteristics, particularly soil properties including texture and organic matter content, had the strongest relationship to May soil moisture. Although range site continued to influence soil moisture in other months, plant and litter biomass exerted stronger associations with moisture than soil and topography in the second half of the growing season. Litter appears to have important effects on reducing evaporation and maintaining moisture in the soil for longer periods of time, particularly during drier mid-summer conditions. Despite the heavy use of empirical relationships in this investigation, and difficulty with establishing causality, these results do suggest that litter was one of the most influential of the measured range site variables in regulating plant production. Litter seems to augment growing-season production by reducing temperatures and evaporation rates, thereby increasing soil water levels for plant use. Other range site characteristics influencing the water-holding capacity of the soil also had important effects on plant production, particularly earlier in the growing season. Nonetheless, microclimatic, litter, and range site variables were not able explain the majority of variation in production in this study, and therefore other factors, including nutrient availability, are likely more limiting to plant growth in this system.

Table 4.1: Summary of the physical features of individual study plots across the research site in 2007.

Plot	Litter Removal	Topographic Position	Aspect (degrees)	Ah Depth (cm)	Slope (%)	Mean Litter Weight (kg/ha)
1	No	Upper	187	10.2	10	1253
2	No	Mid	92	13.1	13	1543
3	Yes	Low	129	18.2	10	843
4	No	Upper	166	11.5	5	637
5	Yes	Mid	136	12.5	12	490
6	No	Mid	180	8.5	16	1083
7	No	Low	176	8.1	12	3727
8	No	Very Low	156	7.5	8	1263
9	No	Very Low	194	9.4	7	2453
10	Yes	Very Low	106	10	6	2167
11	No	Low	166	11	6	3910
12	Yes	Low	180	13.2	3	897
13	No	Mid	178	10.2	8	3107
14	Yes	Mid	189	9.4	14.5	777
15	No	Mid	160	11	15	2377
16	Yes	Very Low	224	14.5	4.5	1673
17	No	Very Low	196	15.5	1	3627
18	No	Upper	164	10.8	3	1080
19	No	Mid	180	9.1	10	790
20	No	Upper	111	10.1	1.5	1797
21	Yes	Mid	202	9.8	2	1533
22	No	Low	174	25	3	2873
23	No	Mid	180	28	13	1557
24	Yes	Mid	190	10.5	13.5	1230
25	No	Upper	237	10.8	10.5	1467
26	No	Low	185	28	15.5	2703
27	Yes	Low	166	24.2	13.5	1693
28	Yes	Mid	139	11.5	12	1293
29	No	Upper	120	9.4	2	2123
30	No	Upper	192	12.5	11	1473

Table 4.2: Eigenvectors for soil and topographic variables for the first 5 principal components resulting from the PCA analysis. Eigenvectors are scaled to unit length.

Environmental Variable	1	2	3	4	5
Slope	0.20	0.05	-0.36	0.89	-0.10
Aspect	0.25	-0.40	0.40	0.12	-0.10
Position	0.01	0.21	0.78	0.24	-0.28
Ah Depth	0.25	0.22	0.27	0.17	0.85
Bulk density	0.03	-0.59	0.13	0.06	-0.08
OMC	-0.01	0.58	0.05	-0.10	-0.22
Sand	-0.53	0.11	0.08	0.24	-0.09
Clay	-0.49	-0.21	0.04	0.05	0.33
Silt	0.57	0.03	-0.07	-0.18	-0.09

Table 4.3: Bivariate correlation coefficients (*r*) of litter depth, litter biomass and soil temperature with soil moisture. Significant correlations (P<0.05) are in bold.

Soil Moisture Variables	Litter Depth	Litter Biomass[+]	Soil Temperature
May Day 1	0.34	0.20	-0.29
Day 2	0.29	0.16	-0.28
Day 3	0.23	0.07	-0.26
Day 4	0.22	0.12	-0.35
Day 5	0.18	0.02	-0.28
June Day 1	0.08	-0.01	-0.28
Day 2	**0.47****	**0.37***	**-0.55****
Day 3	**0.47****	**0.38***	**-0.61*****
Day 4	**0.40***	**0.38***	**-0.51****
Day 5	**0.47****	**0.42***	**-0.53****
July Day 1	**0.47****	**0.51****	**-0.50****
Day 2	**0.36***	**0.53****	**-0.53****
Day 3	**0.38***	**0.49****	**-0.58*****
Day 4	**0.39***	**0.57*****	**-0.58*****
Day 5	**0.54****	**0.52****	**-0.80******
Aug Day 1	0.28	0.06	-0.17
Day 2	**0.51****	0.12	-0.18
Day 3	0.31	0.33	0.03
Day 4	**0.50****	**0.50****	-0.22
Day 5	**0.54****	**0.44***	-0.27

+May, June and July analysis uses mean litter biomass for the period May to July, inclusive. August analysis uses ending August litter biomass.

*,**,***,**** Indicate significance at P≤0.05, P≤0.01, P<0.001and P≤0.0001, respectively.

Table 4.4: Bivariate correlation coefficients (*r*) for soil moisture with range site variables including topographic position and soil characteristics. Significant correlations (P<0.05) are in bold.

Soil Moisture	Slope	Aspect	Position	Ah	Bulk Density	% OMC	% Sand	% Clay	% Silt
May Day 1	0.11	**-0.40***	0.30	-0.09	**-0.37***	**0.38***	**0.52****	0.31	**-0.48****
Day 2	0.09	**-0.38***	0.26	-0.04	-0.35	**0.38***	**0.38***	0.23	**-0.36***
Day 3	0.11	**-0.37***	0.33	-0.03	-0.32	0.34	**0.40***	0.23	**-0.37***
Day 4	0.17	-0.32	**0.39***	0.03	-0.23	0.19	**0.39***	0.21	-0.35
Day 5	0.19	-0.31	**0.39***	0.11	-0.32	0.24	0.34	0.21	-0.32
June Day 1	-0.08	-0.19	0.00	-0.16	0.10	-0.02	**0.40***	**0.45***	**-0.47****
Day 2	**-0.42***	-0.06	**0.43***	-0.07	-0.23	0.33	**0.46****	0.36	**-0.48****
Day 3	-0.32	-0.16	0.29	0.02	-0.14	0.35	**0.45***	0.31	**-0.44***
Day 4	-0.33	-0.20	0.10	0.15	-0.30	0.28	0.30	0.32	-0.34
Day 5	**-0.46****	-0.12	0.34	0.00	-0.30	0.26	0.24	0.22	-0.26
July Day 1	**-0.56****	0.15	0.28	-0.28	-0.09	0.23	**0.40***	0.26	**-0.39***
Day 2	**-0.63*****	0.03	**0.50****	-0.09	0.12	0.11	0.32	0.13	-0.27
Day 3	**-0.52****	-0.13	**0.51****	-0.28	-0.13	0.29	**0.44***	0.22	**-0.39***
Day 4	**-0.48**	0.02	**0.42***	-0.23	-0.03	0.26	**0.37***	0.12	-0.29
Day 5	**-0.60**	-0.02	**0.42***	-0.01	-0.04	0.28	0.29	0.16	-0.27
Aug Day 1	-0.34	-0.11	0.09	-0.11	0.01	0.11	**0.40***	**0.38***	**-0.44***
Day 2	**-0.38***	-0.20	0.20	0.02	-0.19	0.20	**0.42***	0.18	-0.36
Day 3	-0.33	0.14	0.25	-0.16	0.09	-0.11	0.34	0.24	-0.33
Day 4	-0.14	0.17	**0.38***	-0.15	-0.11	0.10	0.29	0.08	-0.22
Day 5	-0.10	0.09	**0.38***	-0.12	-0.05	0.10	0.36	0.20	-0.33

*,**,***,**** Indicate significance at P≤0.05, P≤0.01, P<0.001and P≤0.0001, respectively.

Table 4.5: Results for the leading one-variable stepwise regression model, determined through Mallow's statistic, describing soil moisture on each day of monthly sampling in relation to range site principle components, shoot biomass and litter biomass.

Dependant Variable	Independent Variable	Relationship	Model R2	P-value
May Day 1	PC1	-	0.22	0.008
Day 2	PC2	+	0.17	0.02
Day 3	PC2	+	0.16	0.03
Day 4	PC4	+	0.13	0.05
Day 5	PC2	+	0.14	0.04
June Day 1	PC1	-	0.22	0.01
Day 2	PC1	-	0.23	0.007
Day 3	Shoot Biomass	+	0.24	0.006
Day 4	Litter Biomass	+	0.15	0.04
Day 5	Litter Biomass	+	0.18	0.02
July Day 1	Litter Biomass	+	0.26	0.004
Day 2	PC3	+	0.34	0.001
Day 3	Litter Biomass	+	0.24	0.006
Day 4	Litter Biomass	+	0.33	0.001
Day 5	Litter Biomass	+	0.27	0.003
Aug Day 1	PC1	-	0.20	0.01
Day 2	PC1	-	0.14	0.04
Day 3	Litter Biomass	+	0.18	0.02
Day 4	Litter Biomass	+	0.24	0.006
Day 5	Litter Biomass	+	0.18	0.02

Table 4.6: Multiple regression models developed for successive sampling days in May indicating soil moisture dependence on range site principal components, shoot biomass and litter biomass.

Variable	B	SEB	F	P-value
May Day 1				
Model			8.08	0.0006
Intercept	41.3	0.55	5652	<0.0001
PC1	-1.07	0.32	11.3	0.002
PC2	1.09	0.37	8.82	0.006
PC4	1.17	0.58	4.15	0.05
				$R^2 = 0.48$
May Day 2				
Model			5.81	0.008
Intercept	39.2	0.67	3440	<0.0001
PC1	-0.87	0.39	5.03	0.03
PC2	1.15	0.45	6.58	0.02
				$R^2 = 0.30$
May Day 3				
Model			4.88	0.008
Intercept	38.2	0.62	3827	<0.0001
PC1	-0.84	0.36	5.41	0.03
PC2	1.05	0.41	6.40	0.02
PC4	1.09	0.65	2.84	0.10
				$R^2 = 0.36$
May Day 4				
Model			4.30	0.01
Intercept	37.4	0.67	3132	<0.0001
PC1	-0.79	0.39	4.14	0.05
PC2	-0.87	0.45	3.74	0.06
PC4	1.57	0.70	5.01	0.03
				$R^2 = 0.33$
May Day 5				
Model			4.79	0.009
Intercept	36.7	0.70	2731	<0.0001
PC1	-0.74	0.41	3.23	0.08
PC2	1.11	0.47	5.57	0.03
PC4	1.74	0.74	5.56	0.03
				$R^2 = 0.36$

Table 4.7: Multiple regression models developed for successive sampling days in June indicating soil moisture dependence on range site principal components, shoot biomass and litter biomass.

Variable	B	SEB	F	P-value
June Day 1				
Model			7.67	0.01
Intercept	30.7	0.39	6212	<0.0001
PC1	-0.63	0.23	7.67	0.01
				R^2 = *0.22*
June Day 2				
Model			8.75	0.0004
Intercept	21.3	1.56	187	<0.0001
Shoot Biomass	0.001	0.001	3.90	0.06
PC1	-0.58	0.16	13.1	0.001
PC3	0.79	0.27	8.72	0.007
				R^2 = *0.50*
June Day 3				
Model			7.86	0.0007
Intercept	14.5	1.90	58.7	<0.0001
Shoot Biomass	0.002	0.001	10.8	0.003
PC1	-0.61	0.19	9.86	0.004
PC3	0.49	0.32	2.29	0.14
				R^2 = *0.48*
June Day 4				
Model			6.20	0.003
Intercept	15.6	0.69	516	<0.0001
Litter Biomass	0.001	0.0003	10.3	0.004
PC1	-0.46	0.18	6.57	0.02
PC5	0.85	0.36	5.70	0.02
				R^2 = *0.42*
June Day 5				
Model			4.04	0.01
Intercept	15.2	0.78	385	<0.0001
Litter Biomass	0.0007	0.0004	3.20	0.09
PC1	-0.41	0.19	4.39	0.05
PC3	0.53	0.36	2.19	0.15
PC4	-0.57	0.35	2.61	0.12
				R^2 = *0.39*

Table 4.8: Multiple regression models developed for successive sampling days in July indicating soil moisture dependence on range site principal components, shoot biomass and litter biomass.

Variable	B	SEB	F	P-value
July Day 1				
Model			9.94	0.0002
Intercept	9.75	0.54	329	<0.0001
Litter Biomass	0.001	0.0003	14.7	0.0007
PC1	-0.48	0.14	11.1	0.003
PC4	-0.54	0.26	4.37	0.05
				$R^2 = 0.53$
July Day 2				
Model			12.1	<0.0001
Intercept	10.1	0.37	762	<0.0001
Litter Biomass	0.0005	0.0002	6.43	0.02
PC1	-0.27	0.09	8.60	0.007
PC3	0.60	0.17	12.5	0.002
PC4	-0.46	0.17	7.68	0.01
				$R^2 = 0.66$
July Day 3				
Model			9.74	<0.0001
Intercept	10.4	0.83	157	<0.0001
Litter Biomass	0.001	0.0003	13.2	0.001
Shoot Biomass	-0.0007	0.0003	5.21	0.03
PC1	-0.48	0.12	15.3	0.0007
PC3	0.58	0.23	6.31	0.02
PC4	-0.66	0.24	7.41	0.01
				$R^2 = 0.67$
July Day 4				
Model			6.87	0.0004
Intercept	7.01	0.43	271	<0.0001
Litter Biomass	0.0006	0.0002	7.83	0.01
PC1	-0.29	0.10	7.99	0.009
PC3	0.33	0.19	2.86	0.10
PC4	-0.32	0.19	2.84	0.11
PC5	-0.32	0.21	2.43	0.13
				$R^2 = 0.59$
July Day 5				
Model			8.94	0.0001
Intercept	7.72	0.49	244	<0.0001
Litter Biomass	0.0007	0.0003	6.46	0.02
PC1	-0.33	0.12	6.88	0.01
PC3	0.58	0.23	6.32	0.02
PC4	-0.58	0.22	6.75	0.02
				$R^2 = 0.59$

Table 4.9: Multiple regression models developed for successive sampling days in August indicating soil moisture dependence on range site principal components, shoot biomass and litter biomass.

Variable	B	SEB	F	P-value
August Day 1				
Model			6.98	0.01
Intercept	23.0	0.34	4619	<0.0001
PC1	-0.52	0.20	6.98	0.01
				$R^2 = 0.20$
August Day 2				
Model			3.51	0.04
Intercept	20.3	0.29	4874	<0.0001
PC1	-0.38	0.17	5.00	0.03
PC3	0.42	0.28	2.27	0.14
				$R^2 = 0.21$
August Day 3				
Model			5.94	0.02
Intercept	9.48	3.39	7.80	0.009
Litter Biomass	2.45	1.00	5.94	0.02
				$R^2 = 0.18$
August Day 4				
Model			8.67	0.006
Intercept	4.61	3.67	1.57	0.22
Litter Biomass	3.20	1.09	8.67	0.006
				$R^2 = 0.24$
August Day 5				
Model			6.30	0.02
Intercept	1.79	4.70	0.14	0.30
Litter Biomass	3.49	1.39	6.30	0.02
				$R^2 = 0.18$

Table 4.10: Bivariate correlation coefficients (*r*) for soil moisture content at field capacity, permanent wilting point and plant available soil moisture with range site variables, including topographic and soil characteristics. Significant correlations ($P<0.05$) are in bold.

Soil Moisture	Slope	Aspect	Position	Ah Depth	Bulk Density	% OMC	% Sand	% Clay	% Silt
MC at FC	-0.11	**-0.42***	-0.32	-0.05	**-0.60*****	**0.92******	**0.39***	-0.10	-0.12
MC at PWP	-0.06	**-0.39***	0.30	0.02	**-0.62*****	**0.93******	0.29	-0.19	-0.10
PASM	-0.19	-0.06	0.05	-0.27	0.17	-0.15	**0.37***	**0.40***	**-0.42***

*,**,***,**** Indicate significance at $P\leq0.05$, $P\leq0.01$, $P<0.001$and $P\leq0.0001$, respectively.

Table 4.11: Correlation coefficients (*r*) for the vegetation biomass variables with near-surface observed soil moisture and soil temperature. Significant correlations ($P<0.05$) are in bold. Plant cover and biomass were re-sampled in each month.

Variable	% Vegetation Cover	Grass Biomass	Forb Biomass	Shrub Biomass	Shoot Biomass	Root Biomass	Root:Shoot
Moisture							
May Day 1	-0.11	-0.24	-0.17	-	-0.32	-	-
Day 2	-0.09	-0.23	-0.11	-	-0.28	-	-
Day 3	-0.06	-0.24	-0.12	-	-0.30	-	-
Day 4	-0.17	-0.19	-0.21	-	-0.27	-	-
Day 5	-0.15	-0.14	-0.25	-	-0.23	-	-
June Day 1	-0.27	-0.05	0.13	0.00	0.06	-	-
Day 2	-0.05	0.08	0.30	-0.12	0.31	-	-
Day 3	0.10	0.10	**0.42***	0.08	**0.49****	-	-
Day 4	-0.01	0.10	0.29	-0.07	0.35	-	-
Day 5	-0.07	0.16	0.26	-0.29	0.33	-	-
July Day 1	0.02	0.05	**0.44***	-0.29	0.23	0.15	0.01
Day 2	0.21	0.20	**0.50****	-0.19	**0.40***	0.06	-0.20
Day 3	0.22	-0.03	0.31	-0.24	0.11	0.18	0.09
Day 4	0.10	0.03	**0.38***	-0.24	0.20	0.16	0.02
Day 5	0.29	0.13	**0.46****	-0.07	0.35	0.24	-0.03
Aug Day 1	0.19	-0.14	0.15	-0.05	-0.01	-	-
Day 2	0.32	0.06	0.19	-0.15	0.14	-	-
Day 3	0.17	0.16	0.23	0.08	0.04	-	-
Day 4	**0.46****	-0.05	**0.40***	0.26	0.25	-	-
Day 5	**0.49****	-0.02	0.35	0.25	0.24	-	-
Temperature							
May	0.16	**0.45***	-0.03	-	**0.49****	-	-
June	-0.21	-0.26	-0.28	-0.08	**-0.52****	-	-
July	**-0.38***	-0.31	**-0.51****	-0.20	**-0.56****	**-0.41***	0.08
August	**-0.62*****	-0.17	**-0.56****	-0.15	**-0.50****	-	-

*,**,***,**** Indicate significance at $P\leq0.05$, $P\leq0.01$, $P<0.001$and $P\leq0.0001$, respectively.

Table 4.12: Correlation coefficients (*r*) of vegetative biomass with soil moisture content at field capacity and permanent wilting point, together with plant available soil moisture. Significant correlations (P<0.05) are in bold. Plant cover and biomass were re-measured in each month.

Variable		% Veg. Cover	Grass Biomass	Forb Biomass	Shrub Biomass	Shoot Biomass	Root Biomass	Root: Shoot
May	**MC at FC**	-0.33	**-0.45***	-0.08	-	**-0.52****	-	-
	MC at PWP	**-0.42***	**-0.43***	-0.06	-	**-0.49****	-	-
	PASM	**0.43***	-0.01	-0.08	-	-0.03	-	-
June	**MC at FC**	0.17	0.32	0.26	0.01	**0.56****	-	-
	MC at PWP	0.13	**0.37***	0.24	-0.06	**0.59*****	-	-
	PASM	0.15	-0.30	0.05	0.31	-0.18	-	-
July	**MC at FC**	**0.38***	0.20	0.14	-0.09	0.22	**0.49****	0.17
	MC at PWP	**0.38***	0.19	0.16	-0.12	0.21	**0.53****	0.22
	PASM	-0.06	0.04	-0.07	0.11	0.01	-0.26	-0.24
Aug	**MC at FC**	0.20	0.13	0.04	-0.03	0.12	-	-
	MC at PWP	0.25	0.13	0.11	-0.03	0.16	-	-
	PASM	-0.21	-0.05	-0.27	-0.02	-0.21	-	-

*,**,***,**** Indicate significance at P≤0.05, P≤0.01, P<0.001and P≤0.0001, respectively.

Table 4.13: Simple linear regression models relating soil moisture measurements (observed moisture and moisture content at field capacity and permanent wilting point) and soil temperature on above (shoot) and belowground (root) biomass.

Dependant Variable	Independent Variables	Relationship	Model R2	P-value
May Shoot	Moisture Day 1	-	0.10	0.09*
	Moisture Day 2	-	0.08	0.13
	Moisture Day 3	-	0.09	0.11
	Moisture Day 4	-	0.07	0.15
	Moisture Day 5	-	0.05	0.23
	Total Loss	-	0.01	0.60
	MC at FC	-	0.27	0.003**
	MC at PWP	-	0.24	0.006**
	PASM	-	0.001	0.86
June Shoot	Moisture Day 1	+	0.004	0.74
	Moisture Day 2	+	0.10	0.09*
	Moisture Day 3	+	0.24	0.006**
	Moisture Day 4	+	0.12	0.06*
	Moisture Day 5	+	0.11	0.07*
	Total Loss	-	0.06	0.18
	MC at FC	+	0.31	0.001**
	MC at PWP	+	0.34	0.0007**
	PASM	-	0.04	0.33
July Shoot	Moisture Day 1	+	0.05	0.22
	Moisture Day 2	+	0.16	0.03**
	Moisture Day 3	+	0.01	0.57
	Moisture Day 4	+	0.04	0.30
	Moisture Day 5	+	0.12	0.06*
	Total Loss	-	0.01	0.53
	MC at FC	+	0.05	0.25
	MC at PWP	+	0.04	0.27
	PASM	+	0.0001	0.95
August Shoot	Moisture Day 1	-	0.0001	0.95
	Moisture Day 2	+	0.02	0.45
	Moisture Day 3	+	0.002	0.83
	Moisture Day 4	+	0.06	0.19
	Moisture Day 5	+	0.06	0.21
	Total Loss	-	0.06	0.19
	MC at FC	+	0.01	0.54
	MC at PWP	+	0.03	0.39
	PASM	-	0.04	0.27
July Root	Moisture Day 1	+	0.02	0.42
	Moisture Day 2	+	0.003	0.76
	Moisture Day 3	+	0.03	0.34
	Moisture Day 4	+	0.02	0.41
	Moisture Day 5	+	0.06	0.20
	Total Loss	-	0.009	0.61
	MC at FC	+	0.24	0.006**
	MC at PWP	+	0.29	0.002**
	PASM	-	0.07	0.16

Table 4.14: Multiple regression models relating above and below-ground biomass to litter biomass and range site principle components.

Variable	B	SEB	F	P-value
May Shoot Biomass				
Model			3.0	0.06
Intercept	904	51	312	<0.0001
PC2	-57	34	2.7	0.11
PC5	106	57	3.4	0.08
			$R^2 = 0.18$	
June Shoot Biomass				
Model			9.7	0.0002
Intercept	2229	143	243	<0.0001
Litter Biomass	0.23	0.07	10	0.004
PC2	102	45	5.2	0.03
PC4	-169	67	6.38	0.02
			$R^2 = 0.53$	
July Shoot Biomass				
Model			7.2	0.001
Intercept	2115	302	49	<0.0001
Litter Biomass	0.58	0.15	15	0.0008
PC4	-306	143	4.6	0.04
PC5	300	156	3.7	0.07
			$R^2 = 0.45$	
August Shoot Biomass				
Model			1.7	0.20
Intercept	2891	134	463	<0.0001
PC2	103	90	1.3	0.26
PC3	181	130	2.0	0.17
			$R^2 = 0.11$	
July Root Biomass				
Model			10	0.004
Intercept	10261	560	335	<0.0001
PC2	1189	376	10	0.004
			$R^2 = 0.26$	

Table 4.15: Correlation coefficients (*r*) between August plant community variables and NMS axis plot scores for species composition with August soil moisture and temperature data. Significant correlations ($P<0.05$) are in bold.

Variable	Species Richness	Species Diversity	Species Evenness	NMS Axis 1	NMS Axis 2
Moisture Day 1	0.13	0.17	0.16	0.09	-0.10
Moisture Day 2	0.04	0.09	0.16	0.10	-0.21
Moisture Day 3	0.00	0.10	0.27	0.11	-0.17
Moisture Day 4	0.21	0.28	0.29	0.24	0.03
Moisture Day 5	0.16	0.27	**0.41***	0.20	0.06
Soil Temperature	-0.29	**-0.36***	-0.27	-0.07	-0.30
MC at FC	**0.40***	0.31	-0.09	0.20	0.20
MC at PWP	**0.37***	0.20	-0.09	0.25	0.13
Available Moisture	0.09	0.07	0.03	-0.22	0.28

*,**,***,**** Indicate significance at $P\leq0.05$, $P\leq0.01$, $P<0.001$ and $P\leq0.0001$, respectively.

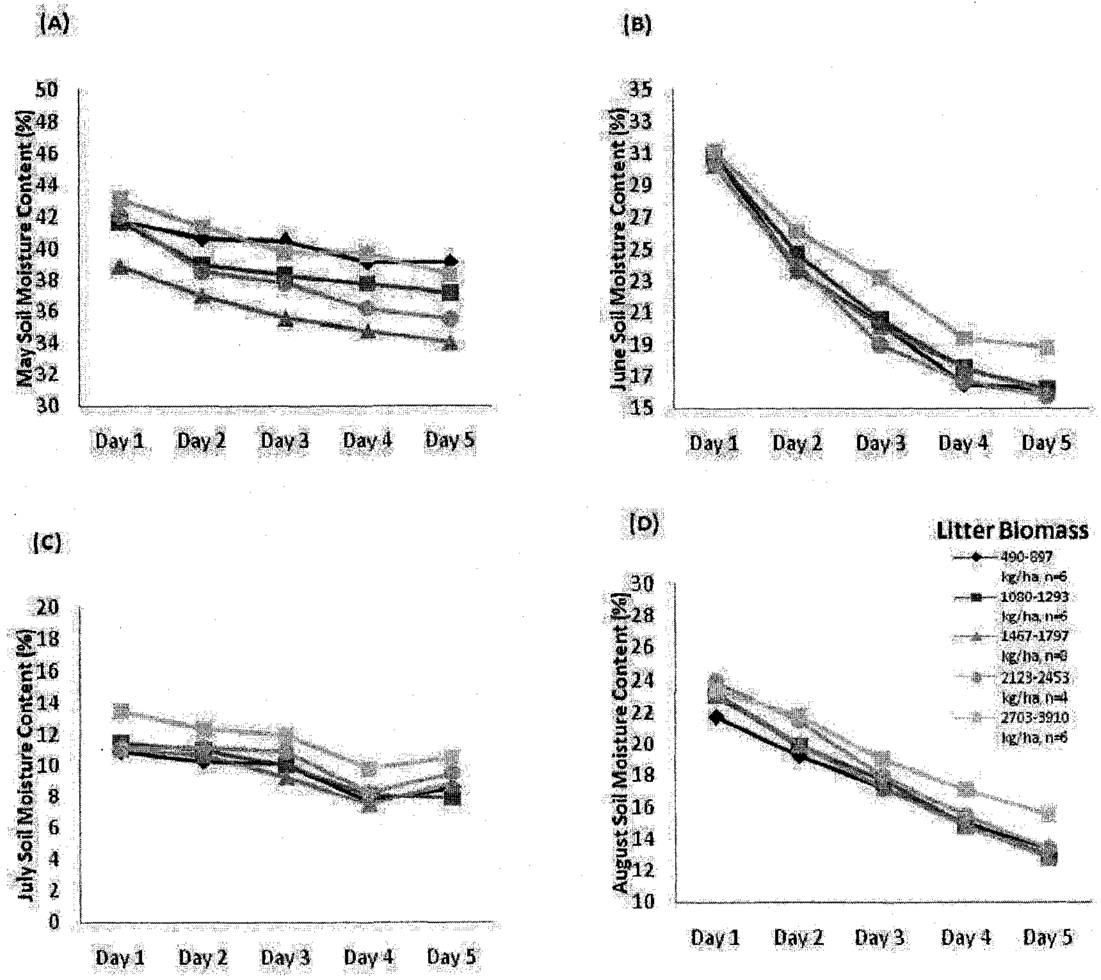

Figure 4.1: Patterns of soil moisture depletion over 5 days following rainfall in May (A), June (B), July (C) and August (D) of 2007 under 5 different catagories of litter biomass.

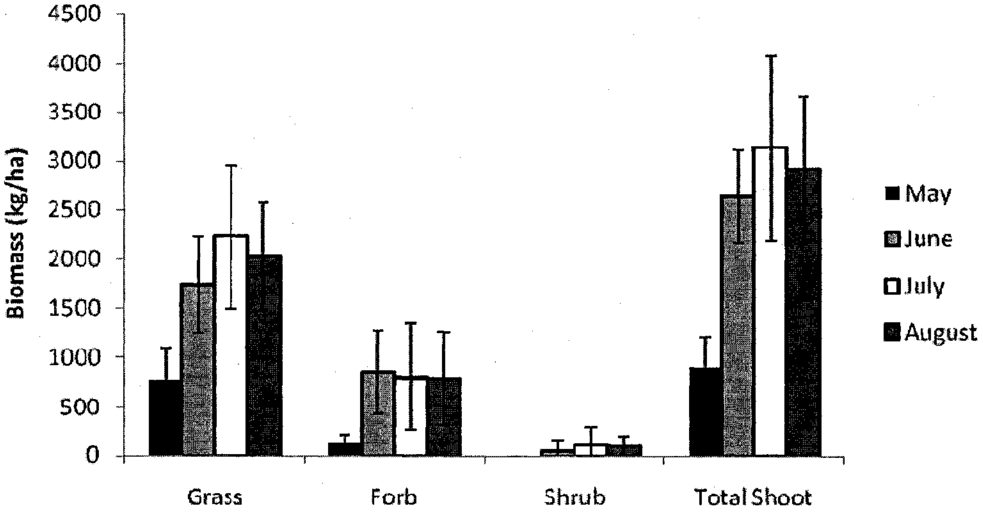

Figure 4.2: Mean (±SD) above ground biomass for each plant functional group as sampled in May, June, July or August of 2007.

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5. SYNTHESIS: LITTER AS AN INDICATOR OF RANGELAND HYDROLOGIC FUNCTION AND ECOSYSTEM HEALTH

With recent severe drought, and a likely increase in drought and moisture stress in the near future, management of soil moisture on northern rangelands will become increasingly important. Sustainable plant production for livestock grazing and other land uses will become ever more dependent on reducing localized evaporation of soil moisture, particularly under predicted global warming and climate change. Although managing levels of litter may provide a means to conserve soil moisture and promote water use efficiency, the importance of litter in mesic Parkland grasslands is not well understood. These studies attempted to evaluate the relationship between litter, soil moisture and plant production in various grasslands of the Alberta Parkland in order to provide information on the effectiveness of litter in ecosystems that have generally not experienced regular, severe moisture stress in the past.

Along with its effects on the hydrologic cycle and plant production, litter also has important influences on nutrient cycling and site and soil stability. As such, monitoring litter levels provides valuable information on overall function of key ecosystem processes. Further, recent changes to rangeland health assessments in both Canada and the United States have increasingly relied on litter as an indicator of important ecosystem attributes (Adams et al. 2004, Pellant et al. 2005). Overall, litter is recognized as an integral feature in sustaining healthy rangelands and improving the resistance and resilience of the entire system to both climate change and ongoing disturbance regimes.

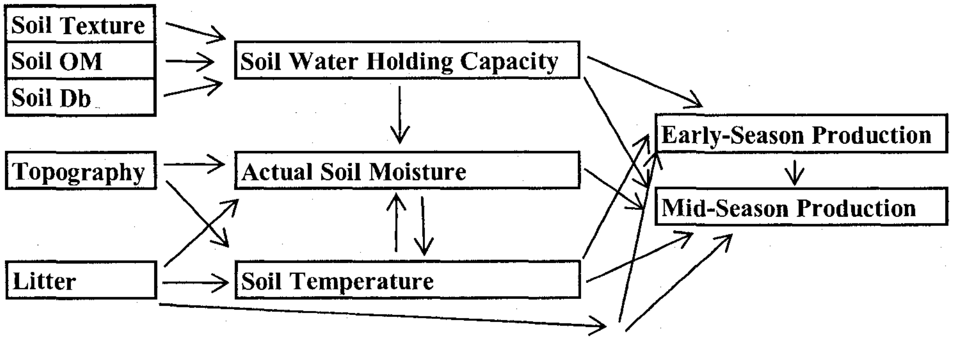
5.1. Litter Influences on Soil Microclimate and Production

In the first study (Chapter 3), litter demonstrated strong relationships both soil microclimate and plant production. Litter decreased light reaching the soil surface and surface soil temperatures, which together had significant negative impacts on early plant emergence, growth and development. Despite this, moderate to high litter loads did have a positive influence on maintaining soil moisture levels after rainfall, particularly in native grasslands, with differences between native and tame grasslands potentially tied to differences in absolute litter loads, the structural attributes of litter, or their associated range site characteristics. The positive influence of litter on moisture also appeared to result in improved grass re-growth following defoliation, indicating that litter can enhance plant production mid-season when moisture is limiting.

Overall, this study showed that litter can be used to manage soil moisture levels in mesic grasslands. Yet, the importance of litter also depended on the litter type and amount, the type of plant community, and the specific land-use prescriptions such as timing and severity of grazing. Additional research examining a wider range of litter loads on a greater variety of sites appears prudent to better outline specific litter threshold levels for managing moisture and optimizing season-long production in the Aspen Parkland, and in further isolating the specific mechanisms (i.e. microclimatic conditions) by which variable litter controls production. Furthermore, new research could examine how timing and frequency of defoliation would alter the impact of litter on plant re-growth, potentially leading to better recommendations for appropriate litter loads under different management scenarios. Ultimately, the importance of litter may depend more on the timing, frequency, intensity and duration of precipitation prior to and during the growing season.

The second study (Chapter 4), examined the importance of litter on soil moisture relative to key soil and topographic features of a typical Parkland landscape. Despite its reliance on empirical associations, this study demonstrated that litter can have important positive influences on both soil moisture and plant production, and thus may be used to effectively manage soil moisture in this grassland. Consistent with the previous study, litter had a more important positive relationship with production in the middle of the growing season rather than early on, when soil characteristics in particular dominated patterns of water availability, soil water holding capacity, and plant growth. Further, the positive influence of litter on production seemed to coincide with reduced soil surface temperatures, presumably leading to reduced evaporation.

Additional studies examining the spatial and temporal importance of litter may benefit from path analyses quantifying directional effects of various range site and litter characteristics on the soil microclimate and plant growth. These studies would require larger sample sizes to appropriately capture variability across the landscape and evaluate the significance of the alternative causal pathways between measured variables (McCune and Grace 2002). Further research should also replicate study designs on various range sites in the Aspen Parkland as the importance of litter impacts likely vary with local landscape features. A potential path model for the relationship of litter and range site with the soil microclimate and ultimately with plant production is shown below. This model could examine seasonal effects of litter and range site characteristics on production by emphasizing the importance of variables influencing soil water-holding capacity on early season production, while emphasizing litter and actual soil moisture levels on mid-season production.



In summary, these studies showed that the importance of litter on hydrologic and biotic processes varies temporally over the growing season, spatially with soil type and landscape position, and is also related to the type of plant community and range site present, and the local land-use and management regimes. Litter generally maintains higher mid-season soil moisture levels after precipitation, which can be important when mid-summer moisture deficits develop or when plants are additionally stressed by mid-season defoliation. In mesic Aspen Parkland grasslands, the importance of litter for improving production also appears to depend on the extent to which litter negatively influences early season plant growth by creating a microenvironment conducive to delayed plant emergence and establishment. With increasing drought conditions in the face of future climate change, litter will likely become increasingly important in mitigating summer moisture deficits in the Aspen Parkland, similar to patterns already recognized in the Dry Mixed Prairie to the south (Willms et al. 1986, Willms et al. 1993).

5.2. Litter as an Indicator of Rangeland Health

Given current drought and climate change concerns, the importance of litter on the sustainable management of a range site relates not only to the production potential of the site, but must ultimately be linked to the ability of litter to buffer changes in the whole ecosystem. Accounting for system complexity also matches a general change in thinking about rangeland management, where focus of rangeland monitoring protocols has shifted away from emphasizing solely plant production and community characteristics to stressing key ecosystem processes and attributes (Adams et al. 2004, Pellant et al. 2005). Traditionally, monitoring focused on vegetation or soil stability to characterize rangeland condition or livestock capacity, and relied on Clementsian successional models to explain deviation from the desired plant community. Current monitoring responds to concerns that traditional single attribute assessments cannot account for the complexity of ecological processes (Pellant et al. 2005), focuses away from structural characteristics of the rangeland, and instead emphasizes key ecosystem processes including the effective capture of solar energy, and nutrient and water cycling.

5.2.1. The Rangeland Health Concept

Range health is defined by Alberta Sustainable Resource Development as "the ability of rangelands to perform certain key functions," in particular "that all parts that make up the whole, are present and working together" (Adams et al. 2004), and by the US National Research Council as "the degree to which the integrity of the soil and ecological processes of the ecosystem are maintained" (NRC 1994). The health of an ecosystem is dependent on the diversity and complexity of pathways available for resource capture and energy flow, which in turn, increases the resistance and resilience of the system to disturbance. Resistance is defined as the capacity of ecological processes to continue to function with minimal change following a disturbance (Pellant et al. 2005). Resilience, on the other hand is the capacity of these processes to recover following a disturbance. Maintaining the resistance and resilience of a system to disturbance and change underlies the key aims of range health assessments (Pellant et al. 2005).

When sufficient disturbance does occur, the resulting deterioration in the health of the ecosystem can be manifested in compositional shifts of important structures and inefficiencies in important processes, and eventually in the simplification of resource and energy pathways (Brookes et al. 2005). Thus, managers must understand the complexity of the vegetation, soil and climatic conditions that drive the key ecosystem processes of energy, nutrient and water cycling (Pierson et al. 2002). Consequently, current range health assessments developed in the United States use a more encompassing view of ecosystem functioning and long-term sustainability within the context of multiple stable states and state and transition models (Pellant et al. 2005).

Ecological states include one or more biological communities that occur on a given range site, and that are similar in terms of plant functional groups, dynamic soil properties, ecosystem processes, and response to disturbance (Bestelmeyer et al. 2002, Stringham et al. 2001). Transitions are "threshold" shifts between stable states that are not reversible by simply altering the disturbance factors that initially caused changes in the system. Generally, transitions at a range site occur due to combined feedback mechanisms of disturbance on both soil and plant community dynamics (Schlesinger et al. 1990). The specific conditions at a site that are least resistant to and/or resilient following a particular disturbance are more likely to proceed through a transition to another alternative state.

Assessing ecosystem health within the context of state and transition models accounts for how interactions between soils and vegetation cause changes in the stability, biotic potential, and hydrologic and nutrient cycling at a site. Methods to do this have been developed in both Alberta (Adams et al. 2004) and the United States (Pellant et al.

2005), and both methods rely heavily on plant litter to characterize the ability of the system to function without irreversible state changes.

5.2.2. Range Health Assessment Methods

Range health assessments attempt to look at how well ecological processes on a site are functioning, and use biological and physical site characteristics to indicate the functional status of these ecological processes, including the water cycle (the capture, storage and release of precipitation), energy flow (the conversion of solar radiation into plant matter), and nutrient cycling (through the biotic and physical components of the system). The biological and physical potential of each site also has unique spatial and temporal qualities (Bestelmeyer et al. 2004), and maintaining a site within this natural range of variability depends on the resistance and resilience of the ecosystem. The purpose of the health assessment methods are to act as an early warning system to potential declines in rangeland condition and sustainability, and ultimately, in the resistance and resilience of a site.

5.2.3. The Role of Litter in Indicating Healthy Rangelands

In the Alberta health assessment, litter is used as the only direct measurement of hydrologic function and nutrient cycling. Litter normals were developed for this assessment from long-term benchmark monitoring of healthy and productive sites under light to moderate grazing. Litter is measured by a rough estimation of the amount of litter removed from a specified area of ground, and by the patchiness of its distribution. High litter loads and uniform distribution are often valued for conservation of soil moisture by increasing infiltration and reducing both evaporation and run-off. For nutrient cycling, litter influences the development of a soil by accumulating organic matter on the ground surface, which eventually becomes incorporated into the soil. The biochemical make-up of the litter can also control the rate of nutrient release into the soil (Facelli and Pickett 1991).

Other key indicators in the ASRD assessment could also be evaluated by examining the quantity and quality of litter at the site. For instance, healthy productivity levels occur when the plant community is highly efficient at using available energy and water resources in the production of optimal biomass (Chapin et al. 2002). In the two proceeding studies, as well as many others (Willms et al. 1986, Willms et al. 1993), the presence of plant litter has effectively increased the availability of water for plant growth. Additionally, site stability, representing the maintenance of the potential productivity of rangelands through stable soil resources, can be maintained by an effective litter layer (Weaver and Flory 1934, Dyksterhuis and Schmutz 1947). However, the degree to which litter mediates water, nutrient, energy and community compositional processes can vary depending on the climate, soil fertility, soil water retention, and species composition of an area (Facelli and Pickett 1991).

In the US assessment, litter is also directly assessed, but with more emphasis on nutrient than hydrologic processes. The amount of litter in contact with the soil surface is rated based on ecosite normals to provide information regarding on-site nutrient cycling via organic matter inputs into the soil and the provision of food for microorganisms. The US system also considers the direct ability of litter to moderate soil microclimate, as well as situations were excess litter may be a sign of defective energy pathways.

Nonetheless, the US system does not directly link litter abundance to site stability, although it does recognize the importance of litter in stabilizing the soil surface and increasing its resistance to runoff and erosion. Site stability is also directly linked to the lack of litter (i.e. bare ground) in the US assessment, which is reported as the most important contributor to soil stability relative to site potential. The US assessment emphasizes overland flow as an important indicator of site stability, a variable that has been found to be clearly regulated by litter in other studies (Weaver and Flory 1934, Dyksterhuis and Schmutz 1947,Rauzi 1960, Meeuwig 1970). Litter slows water movement and increases infiltration, thereby reducing sediment transport and increasing site stability (Dyksterhuis and Schmutz 1947, Dormaar and Carefoot 1996).

5.3. Conclusions

Altogether, it is clear that litter is one of the most prominent variables linking all key ecosystem processes at a given range site, and that it is an important bridge between vegetation and soil processes. The two preceding studies further confirm the importance of litter in regulating the hydrologic cycle and biotic potential at the site. Yet, as litter can have both positive and negative effects on soil water, plant production and plant community characteristics, it is also apparent that there are site-specific upper and lower litter threshold levels for the optimal function of different ecosystem processes. The Alberta health assessment recommends 1680 kg/ha as a healthy litter load for native rangelands on loamy sites of the Aspen Parkland. The preceding studies indicate that litter levels of 10,000 kg/ha may still be important for improving hydrologic function, with values up to 5,500 kg/ha still having positive influences on plant production. Further studies specifically examining litter effects on site stability and nutrient cycling in the Aspen Parkland will be important for ultimately justifying recommended upper threshold levels in the ASRD range health assessment, as well as potentially redefining lower threshold levels. In the US protocol, although specific thresholds are not recommended, the inclusion of direct litter measurements in assessments of site stability and increasing the emphasis on litter impacts on hydrologic processes would be important for evaluating runoff, infiltration and evaporation at each range site. In general, monitoring litter can provide important information not only on hydrologic functioning and associated plant production, but on overall ecosystem health.

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APPENDIX 1: Weather Data for Sampling Periods

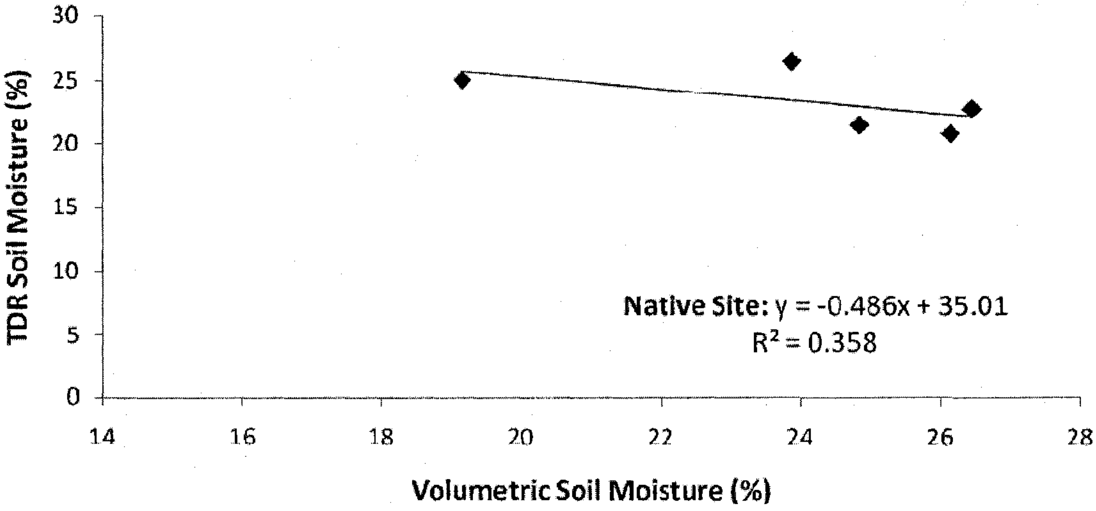
Appendix 1.1.: Weather data from Kinsella, Alberta for the individual monthly soil moisture sampling periods during 2007. Highlighted day is date of rainfall that initiated sampling, while the 5 (or 4 in June) days following are dates of soil moisture depletion sampling. Antecedent conditions for 5 days prior to rainfall are also shown (in italics).

Month	Date	Maximum Air Temperature (°C)	Minimum Air Temperature (°C)	Average RH (%)	Wind Speed (Scalar) (m/sec)	Total Rain (mm)
April	*29*	*11.64*	*0.35*	*58.23*	*2.74*	*6.5**
	30	*12.57*	*0.02*	*61.41*	*2.69*	*0**
May	*1*	*11.51*	*0.95*	*60.23*	*4.60*	*1**
	2	*13.63*	*5.60*	*79.00*	*3.54*	*3**
	3	*16.62*	*5.60*	*87.60*	*4.32*	*6.5**
	4	10.65	1.88	95.30	4.57	9.5*
	6	18.27	3.68	44.65	3.03	0*
	7	19.53	7.72	47.12	3.36	0*
	8	22.78	5.94	52.67	2.39	0*
	9	13.63	3.08	72.30	4.39	0*
	10	13.37	1.35	63.11	4.41	0*
	31	*23.97*	*6.80*	*64.77*	*2.64*	*0**
June	*1*	*27.29*	*10.18*	*52.51*	*2.06*	*0**
	2	*29.48*	*12.57*	*46.96*	*1.74*	*1**
	3	*27.35*	*14.56*	*54.99*	*2.73*	*0**
	4	*26.10*	*10.92*	*53.65*	*3.03*	*0**
	5	25.17	12.17	69.22	4.99	22.5*
	6	16.55	7.46	67.99	3.79	0*
	7	18.14	3.02	49.78	2.86	0*
	8	19.8	9.65	53.72	4.65	0*
	9	19.53	7.26	67.20	2.84	2*

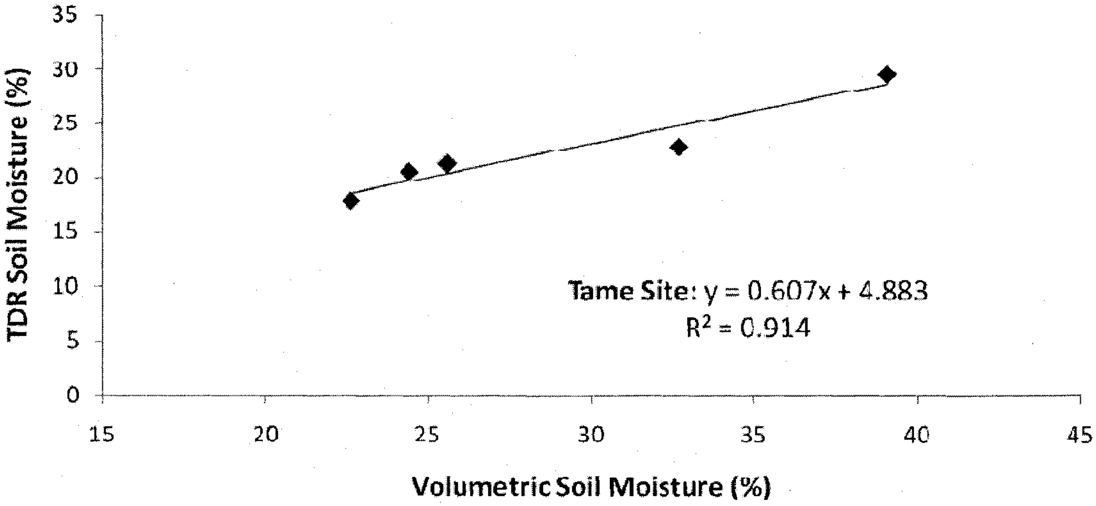
Month	Date	Maximum Air Temperature (°C)	Minimum Air Temperature (°C)	Average RH (%)	Wind Speed (Scalar) (m/sec)	Total Rain (mm)
July	*4*	*25.5**	*11**	-	-	*0**
	5	*30**	*13**	-	-	*0**
	6	*24**	*14**	-	-	*1**
	7	*22**	*11.5**	-	-	*0**
	8	*22.5**	*5**	-	-	*1**
	9	18*	10.5*	-	-	2*
	10	22*	5.5*	-	-	2*
	11	22.5*	11.5*	-	-	0*
	12	28.5*	13.5*	-	-	0*
	13	30.5*	14*	-	-	0*
	14	32.5*	14.5*	-	-	0*
August	*5*	*25**	*8.5**	-	-	*0**
	6	*25.5**	*9**	-	-	*0**
	7	*30.5**	*12**	-	-	*0**
	8	*20**	*9**	-	-	*3**
	9	*15.16*	*9.85*	*72.10*	*1.25*	*1.3*
	10	10.58	4.94	91.6	2.63	13.5
	11	20.00	3.75	72.10	2.14	0.3
	12	23.65	8.52	68.77	3.57	0
	13	15.76	8.39	81.30	3.51	0
	14	20.86	4.34	66.85	2.53	0
	15	20.13	7.53	65.16	2.48	0

* Indicates data taken from Viking, Alberta weather station due to Kinsella datalogger failure. Total rainfall may not accurately represent precipitation at Kinsella.

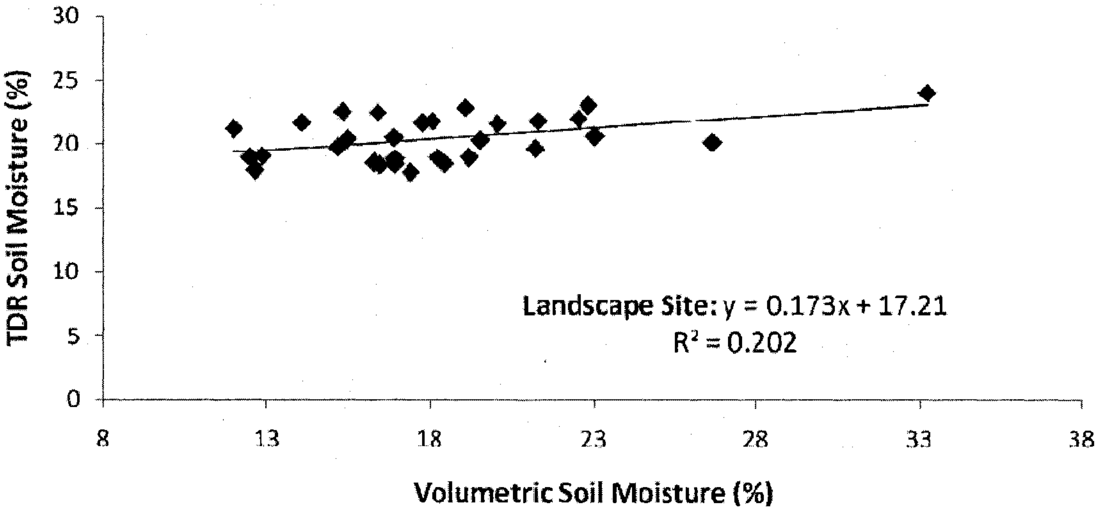
APPENDIX 2: Validation of TDR Moisture Measures



Appendix 2.1.: Relationship between volumetric moisture and observed moisture at the Native Site in Chapter 3.



Appendix 2.2.: Relationship between volumetric moisture and observed moisture at the Tame Site in Chapter 3.



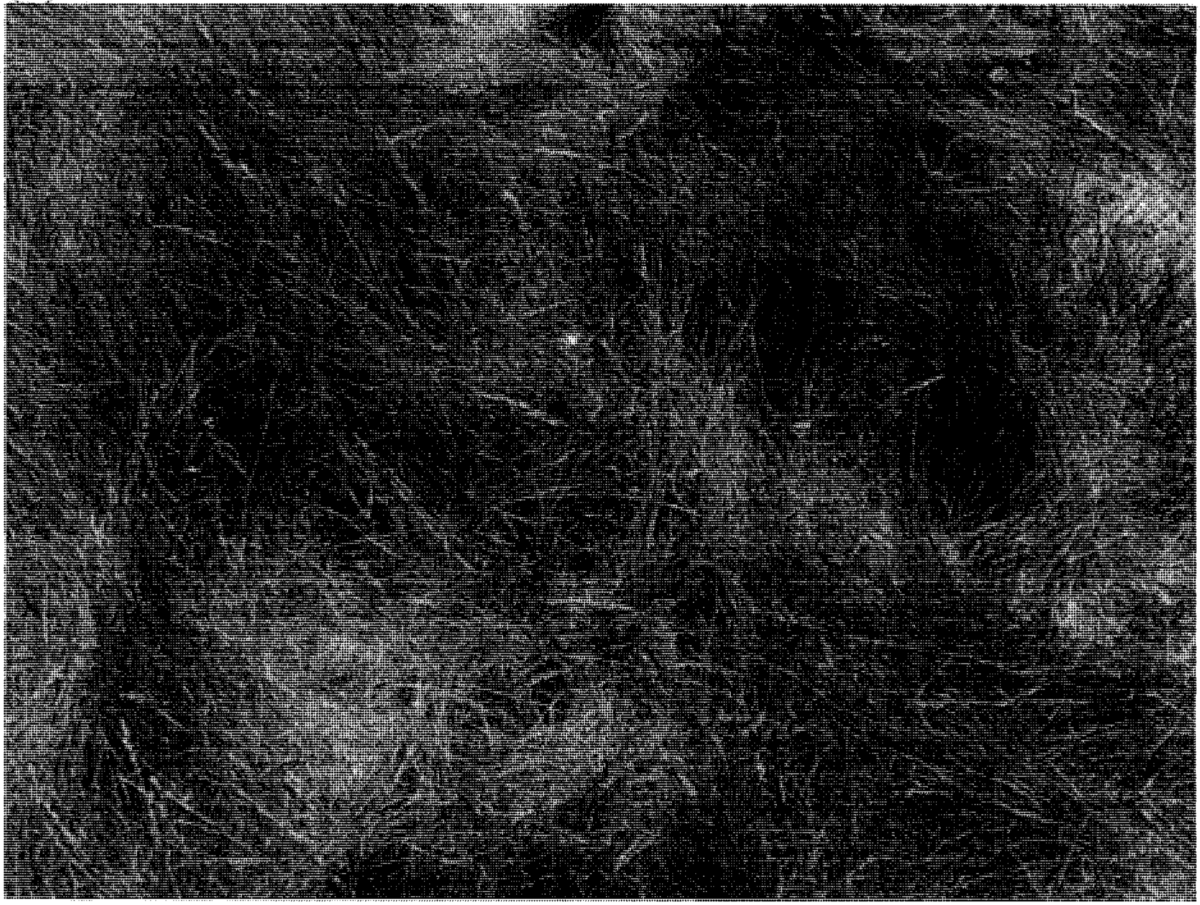
Appendix 2.3.: Relationship between volumetric moisture and observed moisture at the Landscape Site in Chapter 4.

APPENDIX 3: Native and Tame Site Photos

Appendix 3.1. Pictures showing the effect of the litter treatments, including (A) Double, (B) *In Situ* and (C) Litter Removal, on vascular plant cover at the Native Site in July 2007.

(A) Double Litter

(B) *In Situ* Litter



(C) Litter Removal

Appendix 3.2. Pictures showing the effect of the litter treatments, including (A) Double, (B) *In Situ* and (C) Litter Removal, on vascular plant cover at the Tame Site in July 2007.

(A) Double Litter

(B) *In Situ* Litter

(C) Litter Removal

APPENDIX 4: Overview of Landscape Study Site

Appendix 4.1. Picture showing the south-facing slope used in the landscape experiment of Chapter 4.

APPENDIX 5: Result of the NMS Ordination of Plant Community Data in Chapter 4.

Appendix 5.1.: Summary of Pearson correlations of NMS axis scores with local plant species.

Species	NMS Axis 1 r	NMS Axis 2 r
Astragalus spp.	0.186	-0.009
Achillea millefolium	-0.021	-0.045
Agropyron spp.	0.095	0.141
Agrostis stolonifera	-0.508	-0.169
Anemone patens	-0.182	0.124
Antennaria parvifolia	0.052	-0.041
Antennaria spp.	0.278	-0.036
Artemisia frigida	-0.029	0.182
Artemisia ludoviciana	-0.115	-0.555
Aster falcatus	-0.097	-0.301
Aster laevis	0.011	0.116
Bouteloua gracilis	-0.232	-0.335
Campanula rotundifolia	0.167	0.299
Carex spp.	0.186	0.051
Cerastium arvense	-0.137	0.168
Comandra umbellata	0.116	0.242
Erigeron philadelphicus	0.188	0.085
Festuca hallii	-0.142	0.380
Festuca idahoensis	0.090	0.382
Festuca saximontana	-0.029	0.027
Galium boreale	0.291	0.375
Geum triflorum	0.188	0.085
Helictotrichon hookeri	0.126	0.242
Koeleria macrantha	-0.285	0.208
Lathyrus ochroleucus	0.138	-0.055
Orthocarpus luteus	0.015	0.174
Oxytropis spp.	0.122	0.301
Penstemon procerus	-0.154	0.080
Poa pratensis	0.803	-0.614
Potentilla anserina	0.139	0.362
Rosa arkansana	0.012	0.218
Sisyrinchium montanum	-0.025	-0.002
Solidago missouriensis	0.135	0.493
Stipa curtiseta	-0.451	0.183
Symphoricarpos occidentalis	0.429	-0.114
Thermopsis rhombifolia	-0.069	0.464
Viola spp.	0.024	0.035

Appendix 5.2.: Ordination of plots in species space with overlay of local plant species.