University of Alberta

Clipping and Watering Effects on Caespitose and Rhizomatous Grasses: Implications for Grazing Management

by

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Abstract

Recent experimental evidence suggests that rotational grazing, despite strong perceptions to the contrary, does not promote plant community productivity relative to continuous grazing on rangelands. However, clipping studies from tame pastures of Alberta's Aspen Parkland show clear plant community production benefits and compensatory yielding under defoliation regimes associated with rotational grazing (*i.e.*, high intensity low frequency [HILF] defoliation). Unlike relatively mesic tame pastures that are often dominated by rhizomatous grasses, rangelands are generally semiarid native grasslands with a preponderance of caespitose grasses. This suggests that grass growth form may mediate plant community production potential. This study used a greenhouse and field experiment to compare growth dynamics of phylogenetically similar and co-occuring grasses of contrasting growth form (caespitose vs. rhizomatous) to test (1) whether caespitose grasses, compared to rhizomatous grasses, grow more determinately, and (2) if this in turn constrains compensatory yielding under some combination of defoliation frequency and intensity. Plant community productivity and composition were also assessed. Treatments included variable clipping and watering regimes, and the field experiment encompassed both a mesic lowland and drier upland mixedgrass prairie site. In the greenhouse, compensatory growth occurred in 3 rhizomatous grasses and 1 caespitose grass. However, this was not corroborated by the field experiment, where the caespitose grass (*Hesperostipa comata*) compensated under HILF defoliation and the rhizomatous grass (*Pascopyrum smithii*) did not—the opposite was observed in the greenhouse for both grasses. Although defoliation increased plant growth rates, compensatory growth was limited by declining tiller populations, especially in *P. smithii*. Compensatory yielding within the plant community at the mesic lowland site was similarly limited by declining *P. smithii* populations because this grass was the dominant contributor to yield. In contrast, compensatory yielding was common at the drier upland site where *P. smithii* was markedly less dominant. Results suggest that (1) determinate growth is not characteristic of caespitose grasses, but rather (2) compensatory responses depend on plant ability to maintain tiller populations under defoliation. Further, compensatory yielding under HILF defoliation within mixedgrass prairie plant communities may be limited to drier sites where more defoliation tolerant (but less productive) grasses are dominant.

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Chapter 1. Production ecology of North American rangelands: the potential role of graminoid growth form and implications for rotational grazing

1.1. Impetus for Research

Currently there is dissension among producers, managers, and scientists regarding the role of rotational cattle grazing on North America's rangelands because of recent and past reviews of experimental evidence indicating rotational grazing does not consistently enhance livestock and plant community productivity to continuous grazing (Briske *et al*. 2008; Holecheck *et al*. 2000). Rotational grazing is a strategy that includes multiple so-called grazing systems that all involve subdividing a management unit into smaller paddocks, in which livestock are concentrated and rotated through on a scheduled basis. This contrasts continuous grazing that involves season-long use of a contiguous area. A benefit of rotational grazing is that it allows for annual deferment and control over the season of grazing. However, this grazing strategy most differs from continuous grazing when livestock are concentrated at high enough densities to promote more even utilization, and grazing periods are sufficiently short to prevent re-utilization of plant regrowth, such as under short-duration rotational grazing or the so-called Savory grazing method (Savory 1999). Rotatonal grazing, as defined here, represents this form of grazing management.

Rotational grazing is commonly perceived to maximize plant community productivity (i.e., aboveground phytomass yield or standing crop), presumably due to intermittent defoliation and rest. Although this premise invariably depends on the nature of grazing (*i.e.,* intensity, frequency, and season of occurrence), plant community response to herbivory is regulated by a complexity of factors, which can be both intrinsic and extrinsic (McNaughton 1983). Intrinsic factors are those that relate to specific physiological plant responses induced by grazing and include such things as increased growth rates through leaf elongation and tillering, increased nutrient uptake, as well as improved water and nutrient status and increased photosynthesis in remaining leaves. Extrinsic factors influence plant responses through subsidiary effects on abiotic conditions and include such things as enhanced nutrient availability via nutrient cycling induced by consumption and dung deposition; increased soil water availability through reduced plant transpirational surfaces; modification of light availability through litter and upper canopy leaf removal which subsequently affects soil temperatures and microbial mineralization; and increased light penetration to younger leaves with potentially greater photosynthetic capacity relative to upper canopy older leaves. The potential for any of these mechanisms, and their interaction, to promote compensatory plant responses that lead to overcompensation in plant communities likely varies under a continuum of environmental and ecological conditions (Maschinski and Whitham 1989). Compensatory responses include growth responses that ameolorate defoliation effects, and overcompensation occurs when accumulated yields of defoliated shoots exceed that of the overall yield of undefoliated shoots.

Given the complexity of factors that regulate plant responses to defoliation, there is ambiguity regarding the conditions under which and/or the potential for grazing to increase plant community productivity in various plant communities despite extensive research on the subject (see Belsky 1986; Huntly 1991; Milchunas and Lauenroth 1993; Hawks and Sullivan 2001; Heitschmidt *et al*. 2005). This has equated to a corresponding uncertainty surrounding the suitability of grazing management practices designed to capitalize on potential synergistic complementary/compensatory adaptations between plants and herbivores. Indeed, grazing system recommendations by range scientists have been limited to moderate to light grazing through the use of conservative stocking rates (see Holecheck *et al*. 2004). The first step to reconciliation of this dilemma for rangelands of the northwestern Great Plains and Aspen Parkland is obtaining a mechanistic understanding of plant responses under given defoliation regimes and environmental conditions to ascertain whether defoliation can potentially increase productivity of dominant range plants.

1.2. Overarching Factors Influencing Graminoid Response to Defoliation

Graminoids account for the vast majority of forage biomass in grasslands and a small number of species typically dominate a given grassland community

(Coupland 1961). Cattle show some selection for forbs and shrubs but graminoids provide the bulk of their diet on rangelands (Schwartz and Ellis 1981). Forage yields under rotational cattle grazing consequently depend largely on how the dominant graminoid species respond to grazing. At the ecosystem level, moisture regime and prior evolutionary history of grazing by large herbivores are two overarching factors hypothesized to influence plant community response to grazing (Milchunas *et al*. 1988). Alberta's native rangeland plants coevolved with the presence of large herbivores and this may have led to plant traits that confer tolerance to at least moderate levels of herbivory. However, plant adaptation would likely be constrained to historical herbivory patterns (*e.g*., frequency and intensity) and herbivory is not the only ecosystem driver affecting plant communities.

The inability of contemporary grazing practices to adequately emulate historical grazing regimes may be an impediment to their ability to stimulate increases in plant community productivity. For example, Milchunas and Lauenroth (1993) reported that only 20% of studies found grazing increased plant community productivity, and insufficient rest following grazing was suspected as the primary reason for this. Indeed, the grazing pattern of native ungulates, whereby herds sought out actively growing vegetation, was that of intense defoliation during periods of rapid growth followed by extensive rest (Douglas and McNaughton 1993). Other evidence suggests that plants need at least an entire growing season to recover from intense defoliation (Briske *et al*. 2011).

The temporal scale at which production responses to grazing are assessed may also be important. For instance, grazing can increase production in the short-term if photosynthate is preferentially allocated to regrowth instead of root system maintenance and resource acquisition; however, persistent defoliation without rest reduces plant vigor when root systems and reserve pools become insufficient to supply resource demands (Turner *et al. 1*993). Defoliation of *Bouteloua gracilis*, for instance, has been found to induce allocation of photosynthate to leaf regrowth with a corresponding decrease in root growth (Detling *et al*. 1979).

Finally, the overarching effects of climate, especially as they relate to moisture regime, asynchronous resource availability, and drought, ultimately regulate ecosystems (Milchunas *et al*. 1988; Fuhlendorf *et al*. 2001) and associated plant community dynamics (Briske and Hendrickson 1998). Both drought and herbivory are two important factors affecting plant community dynamics and their relative importance varies with the rangeland in question. In semiarid rangelands of North America with a long evolutionary history of grazing by large herbivores, plant adaptations conferring grazing and drought tolerance are convergent (Milchunas *et al*. 1988), which is expressed through characteristics such as basal meristems, small stature, high shot density, substantive belowground nutrient reserves and rapid growth (Coughenour 1985). Moderate to heavy grazing in these systems tends to increase the density and cover of grazing tolerant, dominant graminoids. In contrast, plants of relatively more mesic rangelands with similar evolutionary history, exhibit divergent selection for canopy dominance or grazing tolerance, which entails that grazing has a greater influence on plant community composition and physiognomy. In these systems, grazing generally replaces taller, late-seral, canopy dominant species with those that are more prostrate and grazing tolerant.

1.3. Ecosystem Drivers and Plant Morpho-physiology of Alberta's Rangelands

Alberta's rangelands encompass an west-east and south-north gradient of increasing precipitation (Coupland 1961). The relative importance of drought and herbivory likely varied across this gradient, and, thus, plant community responses to grazing systems may also vary correspondingly (see Willms *et al*. 1986). Over a gradient of increasing aridity, the caespitose (bunchgrass) growth form tends to predominate over rhizomatous (Sims *et al*. 1978) and caespitose graminoids are common within Alberta's native rangelands (Moss 1952). Two characteristics of this growth form contribute to its adaptation to semi-arid, seasonal environments. The first of which is expressed in the aggregate canopy and erect culm characteristics of caespitose grasses, which have microhabitat influences because robust canopies inhibit heat and water vapour transfer and erect culms trap insulating snow in winter (Mack and Thompson 1982). The caespitose growth form also promotes soil heat fluxes and earlier spring thaw, which are advantageous when growth must take place within a relatively short growing season (Chapin *et al*. 1979).

The nature of resource competition amongst plants also varies with increasing aridity, such that relative competition switches from aboveground resources (*e.g.*, light and space) to belowground resources (*e.g.* water and nutrients) across this gradient (Burke *et al.* 1998). Intense competition for belowground resources in arid environments increases the allocation of biomass belowground in perennial grasses (Sims *et al.* 1978). The second key characteristic of bunchgrasses is that they spatially concentrate root biomass and act as resource islands by accumulating resources through various mechanisms (Hook *et al.* 1991; Vinton and Burke 1995; Derner *et al.* 1997; Burke *et al.* 1998). Indeed, greater accumulation of carbon and nitrogen within root and soil complexes of caespitose grasses relative to rhizomatous competitors in semiarid environments has been attributed to their greater competitive ability and fitness in these resource-limited environments (Derner and Briske 2001). Although the rhizomes of rhizomatous species in these environments contain relatively large concentrations of nitrogen and non-structural carbohydrates, total below ground resource pools are markedly less than those of caespitose grasses and this likely explains the general tendency for rhizomatous grasses to be restricted to microsites with higher soil organic carbon and nitrogen in semi-arid environments (Derner and Briske 2001).

The nature of resource storage also varies between the rhizomatous and caespitose growth form. Although caespitose grasses typically accumulate larger resource pools than rhizomatous species (Derner and Briske 2001), predicting regrowth capacity is confounded because in some cases plants seemingly utilize only a small portion of their available resource pool to replace photosynthetic tissue following defoliation (Chapin *et al*. 1990; White 1973). Stem bases are a primary soluble carbohydrate storage area for all grasses and rhizomes are essentially underground stems that also provide a labile source of non-structural carbohydrates readily available for plant growth whereas roots, despite comprising a significant carbon pool, contain low non-structural carbohydrate concentrations (White 1973; Chapin *et al*. 1990; Suzuki and Stuefer 1999; Derner and Briske 2001). This entails that although caespitose grasses contain more overall carbohydrate resources, labile reserves may be greater in rhizomatous grasses.

Consequently, these characteristics combined may enable a more continuous growth pattern in rhizomatous grasses in response to repeated defoliation and rest. Indeed, Busso *et al*. (2001) found circumstantial evidence that nutrient retention confers greater defoliation tolerance in semi-arid environments whereas increasing humidity enables comparatively rapid and prolonged growth, leading to widespread nutrient and resource exploitation. This begs the question of whether increasing humidity (*i.e.,* rainfall) favours the rhizomatous growth form because it enables more rapid and continuous nutrient and carbon assimilation (*i.e.,* growth), whereas caespitose grasses predominate where severe moisture and soil fertility limitations entail that resource accumulation and slow growth are more advantageous. Furthermore, if indeed caespitose and rhizomatous grasses conform to these respective theories, what bearing does herbivory have on mediating the adaptations of these growth forms and, ultimately, how does this effect forage responses to rotational grazing systems that seek to capitalize on overcompensation incurred through defoliation and rest?

1.4. Plant Growth Characteristics Conferring Grazing Tolerance

Environmental conditions aside, grazing tolerance in perennial grasses appears most dependent upon plant ability to replace photosynthetic tissues through tillering and leaf growth (Caldwell *et al*. 1981; Detling and Painter 1983; Hodgkinson *et al*. 1989), whereas reserve carbon pool size and physiological changes that confer greater photosynthetic efficiency are seemingly less important (Nowak and Caldwell 1984; Richards and Caldwell 1985). Apical meristem loss (usually due to grazing following culm elongation), development of an inflorescence, and senescence eliminates intercalary meristem growth potential (*i.e*., leaf elongation) and entails that further photosynthetic organ replacement occurs through the outgrowth of axillary buds and production of new tillers (*i.e*., tillering). Tillering thus depends on axillary bud and labile carbohydrate availability as well as the appropriate allocation of the limited labile carbon pool. Plant ability to rapidly activate axillary buds, curtail other physiological processes, and preferentially allocate reserves to recruitment of tillers thus affects both regrowth potential following defoliation and tolerance to herbivory. For instance, in a comparison of bunchgrasses with similar growth form and resource pool size, a greater ability to mobilize and allocate resources to tiller formation was thought to enhance both the grazing tolerance and competitive ability of *Agropyron desertorum* over *Agropyron spicatum*; the grazing tolerant *A. desertorum* produced 13 – 18 times more tillers than the grazing intolerant *A. spicatum* (Caldwell *et al*. 1981).

However, the work of Hodgkinson *et al*. 1989 on two Australian bunchgrasses, *Cenchrus ciliaris* and *Themeda triandra,* of contrasting grazing tolerances contradicts the notion that differential tillering capacity following defoliation primarily determines grazing tolerance as both grasses in this study displayed similar tillering rates. These authors attributed superior grazing tolerance of *C. ciliaris* to its morphological plasticity as related to its ability to produce decumbent, lateral spreading tillers with a greater number of leaves and greater photosynthetic area, which subsequently contributed to greater photosynthesis rates and labile carbon availability. This suggests that any morphological response to defoliation, be it increased tillering or the ability to produce tillers with greater leaf area, that increases photosynthesis potential facilitates plant recovery following defoliation, which contributes to grazing tolerance and also promotes subsequent forage yields.

Decumbent morphology also seems to contribute to grazing tolerance because it is also associated with relatively more rapid growth and tillering rates. Even within species of plants and over a relatively short timeframe, grazing can select for more prostrate phenotypes that better tolerate grazing through relatively more rapid tillering and leaf replacement following defoliation (Peterson 1962; Detling and Painter 1983; Carman 1992). Indeed, Oesterheld and McNaughton

(1988) found that *Themeda triandra* clones from short ecotypes countered defoliation by exhibiting relatively higher growth rates and producing greater numbers of smaller tillers with lower leaf specific weights as compared to clones from mid and taller ecotypes that receive less grazing pressure. Detling and Painter (1983) found that *Agropyron smithii* genotypes from heavily grazed prairie dog (*Cynomys spp*.) colonies showed morpho-physiological adaptation; these plants were shorter but also had relatively more rapid tillering, greater overall leaf areas and leaf replacement rates than genotypes selected outside of prairie dog colonies.

1.5. Defoliation's Influence on Tiller Recruitment, Mortality, and Longevity

Although tillering is a fundamental plant process with important implications on forage yields and plant persistence, we currently have an incomplete understanding of the mechanisms controlling it (Murphy and Briske 1992; Tomlinson and O'Connor 2004). The traditional theory that the plant hormone auxin produced in young leaves and the apical meristem primarily controls tillering through what is known as apical dominance has been challenged by experimental evidence indicating that another plant hormone, cytokinin, is also involved and resource availability, axillary bud exposure to light, and interplant competition also influences tillering. This confounds interpretation of defoliation's effect on tiller recruitment, mortality, and longevity. And, indeed, these responses are not ubiquitous under all conditions. Despite this, commonly reported factors reported to influence defoliation effect on tillering include plant phenological stage at the time of defoliation as well as the frequency and intensity of defoliation (Jameson and Huss 1959; Vogel and Bjugstad 1968; Olson and Richards 1988). Tiller capacity to withstand defoliation is also species and, perhaps, growth form dependent. For instance, defoliation has reduced tiller recruitment and longevity in numerous bunchgrasses (Butler and Briske 1988), while promoting it in rhizomatous grasses (Zhang and Romo 1995).

1.6. Growth Form's Influence on Plant Growth and Grazing Tolerance

Given that grazing tolerance is strongly related to regrowth capacity following defoliation, this suggests that rhizomatous forages have potentially greater tolerance to herbivory under environmental conditions favourable for growth, considering that they generally have greater regrowth capacity (Mack and Thompson 1982). Rhizomatous grasses are also more resistant to defoliation and trampling damage given that population persistence can be maintained solely through vegetative reproduction, and severed rhizomes can regenerate into independent ramets (Mack and Thompson 1982). Rhizomatous species are disadvantaged in semiarid environments, however, with a trade-off existing between resource accumulation (as expressed by caespitose grasses' ability to act as resource islands) and rapid growth (which may be more characteristic of rhizomatous grasses). Indeed, although the caespitose growth form predominates with increasing aridity, rhizomatous and stoloniferous characteristics are more associated with areas of long-evolutionary grazing history (Mack and Thompson 1982).

The corollary of this entails that the potential for grazing to elicit compensatory responses and yield overcompensation may be mediated not only by edaphic conditions and moisture availability throughout the growing season but also by plant adaptations, as primarily expressed in growth form, that govern resource allocation patterns and growth responses. If the caespitose growth form counters seasonality in resource availability by sacrificing rapid growth for resource accumulation (*i.e.*, their growth is more determinate), these inherent limitations may entail that repeated defoliation and rest cannot stimulate compensatory growth in caespitose species to the same extent that it can in rhizomatous species. This would consequently prevent realization of overcompensation and question the merits of controlling defoliation frequency and intensity in more intensively managed rotational grazing systems in plant communities dominated by caespitose grasses.

1.7. Compensatory Growth

A dichotomy currently exists in theories outlining conditions under which compensatory growth is most likely realized. Based on the sigmoidal plant growth curve, where vegetation attains maximum growth rate during a certain period of phenological development, Voisin (1961) proposed overall pasture forage yields could increase through periodic defoliation. The premise being that intermittent defoliation, because it stimulates plant regrowth, prolongs rapid growth and thereby increases plant productivity. For this theory to hold true, however, plants must have adequate regrowth potential following defoliation, meaning that plant growth cannot be overly constrained by extrinsic factors (*e.g.*, moisture and nutrient availability) and intrinsic characteristics (*e.g.*, grazing tolerance). Although this theory provided impetus for rotational grazing and conceptually illustrated the basis by which rotational grazing could increase plant community productivity, its application may only hold true in the mesic pasture systems, consisting predominantly of rhizomatous sod grasses, from which it was first conceived and implemented upon.

Hilbert *et al.* (1981) further proposed that compensatory growth depends on the relative growth rate of plants at the time of defoliation (*i.e.*, their stage of growth on the sigmoid curve) relative to their maximum potential growth rate in the absence of defoliation and compensatory growth is realized only when defoliation elicits an increase in plant growth rate. This entails that, in order to increase production, slower growing plants require less increase in growth rate through grazing than rapidly growing plants (*i.e.*, plants with a steeper sigmoid growth curve). Milchunas and Lauenroth (1993) provide evidence supporting this theory given they found that grazing was most likely to increase productivity in plant communities of low productivity and long coevolutionary history with herbivory, provided grazing was moderate-light. This corresponds with evidence that grazing in these ecosystems enhances the growth and cover of grazing tolerant, dominant graminoids (Milchunas *et al.* 1988). Models of Hilbert *et al.* (1981) also revealed that for plants growing below their maximum growth rate, less stimulation in growth is required to increase productivity. This is consistent with the observation that grazing tends to increase forage production in mesic grasslands that receive over 450 mm of annual rainfall because it reduces litter build-up that would otherwise limit productivity, suggesting that grazing can theoretically stimulate plant growth when aboveground factors (*i.e.*, light and growing space) limit plant growth and plant community productivity (see Knapp and Seastedt 1986).

Given that caespitose grasses may generally have slower growth rates relative to rhizomatous grasses (see Hartvigsen and McNaughton 1995), the theories developed by Hilbert *et al.* (1981) suggest that less of an increase in their growth rate is required to yield a compensatory response. Early spring grazing, which is a period when moisture conditions are favourable and growth is most rapid, has been found to increase the growth rate of *Agropyron desertorum*, a Eurasian C_3 perennial bunchgrass extremely tolerant to defoliation, relative to ungrazed plants (Olson and Richards 1988). Initially grazed plants thus overcompensated; however, their productivity declined relative to ungrazed plants as temperature increased and moisture availability decreased through the growing season; overall yield was thus less in grazed plants relative to ungrazed plants presumably because defoliation early in the growing season exacerbated moisture stress later in the summer. As there is a general paucity of documented overcompensation in bunchgrasses (see also Dyer and Bokhari 1976), ambiguity consequently exists regarding the potential for grazing to increase plant community productivity in semiarid grasslands dominated by graminoids of this growth form.

In contrast, rhizomatous communities, often comprised of introduced tame forages, have yielded an indeterminate growth response to defoliation regimes corresponding to rotational grazing patterns in Alberta's mesic Aspen Parkland natural subregion, where infrequent and intense defoliation was found to increase forage production relative to more frequent but less intensive defoliation (De Bruijn *et al.* 2010). This contradicts the notion that utilization should not exceed 50% in order to retain adequate leaf area for plant recovery. Moreover, overcompensation has been documented in greenhouse grown verds (*i.e.,* sods) of introduced perennial rhizomatous forages of *Poa pratensis* and *Bromus inermis*, species common in mesic pastures of the Aspen Parkland in central Alberta (Donkor *et al.* 2002). And Eneboe *et al.* (2002) found that grazing could increase relative growth rates of *B. gracilis* and *A. smithii* under adequate moisture conditions.

In contrast, the capacity of caespitose grasses to respond similarly may be confounded by the aforementioned characteristics and potential adaptations of this growth form, although whether this is a function of environmental conditions under which plant response is studied or the caespitose growth form itself is unclear. Given that most studies fail to manipulate growing conditions and implement defoliation or grazing regimes that correspond with grazing systems, ambiguity exists regarding the potential for caespitose grasses to yield favourably under certain defoliation frequencies and intensities. It is therefore necessary to examine how grass growth form relates to tolerance and response to defoliation. Further to this, perceived benefits of grazing systems should be reconciled with a mechanistic understanding of plant growth potential and response under given environmental and ecological conditions.

1.8. Research Objectives and Hypotheses

The objective of this research is to assess whether grass growth form (*i.e.*, caespitose vs. rhizomatous) influences regrowth potential under defoliation regimes associated with rotational grazing (*e.g.*, high intensity defoliation at low frequency) and if this, in turn, limits compensatory plant and plant community production responses to defoliation. Tested hypotheses are that caespitose and rhizomatous grasses have determinate and indeterminate growth, respectively. Determinate growth, defined here, represents growth that is decoupled from resource availability (Brooker and Callaghan 1998; Chapin 1991). Plants said to have determinate growth have relatively low growth rates regardless of ambient resource conditions. If true, determinate growth in caespitose grasses may constrain beneficial plant community responses to intermittent defoliation in more semiarid rangelands, whereas indeterminate growth in rhizomatous grasses may explain compensatory regrowth observed in plants of more mesic, tame pastures. This mechanism may explain why grazing systems largely fail to differentially influence plant community productivity on rangelands.

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Chapter 2. Greenhouse grown caespitose and rhizomatous grasses under variable clipping and watering: implications for forage yield under rotational and continuous grazing

2.1. Abstract

Rotational grazing's potential to promote plant community productivity on rangelands is uncertain. This may be because rangelands are typically semiarid grasslands with a predominance of caespitose grasses, for which determinate growth may constrain compensatory grass re-growth. This experiment examined re-growth responses of co-occuring or phylogenetically similar caespitose and rhizomatous grasses in order to test the hypotheses that (1) grass re-growth responses are more determinate in caespitose compared to rhizomatous grasses and (2) accumulated plant biomass will vary between growth forms in response to different intensities and frequencies of defoliation. A total of eight grasses (4 caespitose and 4 rhizomatous) were grown from seed in the greenhouse. Over a 3-month period, treatments of high intensity-low frequency (HILF), high intensity-high frequency (HIHF), low intensity-high frequency (LIHF), or deferred (*i.e.*, control) defoliation, were combined with high and low moisture in a full-factorial, randomized complete block design. Defoliation responses were inconsistent among species and moisture conditions also altered defoliation effects, with high

moisture leading to more pronounced defoliation effects. Accumulated shoot biomass was consistently greatest in the deferred treatment, which in turn, remained similar to LIHF defoliation. No species overcompensated in terms of biomass in response to defoliation and high intensity defoliation reduced biomass in all grasses except one. Under high moisture conditions, 3 of the 4 rhizomatous grasses and only 1 caespitose species produced greater biomass under HILF compared to HIHF defoliation. Caespitose grasses generally maintained more consistent root:shoot ratios and tiller numbers regardless of defoliation regime. Plant water-use efficiency appeared unrelated to growth form, but instead corresponded with moisture regime adaptation. Finally, our findings potentially indicate the specific conditions under which intermittent defoliation regimes, such as those used under rotational grazing, may benefit overall biomass production in pastures dominated by various grass species.

2.2. Introduction

Recent publications question rotational grazing's (RG) potential to promote plant community productivity relative to continuous grazing (CG) (Briske *et al.* 2008; Holechek *et al.* 2000). RG involves subdividing a management unit and grazing pastures intermittently, temporarily increasing stocking densities and controlling defoliation timing and frequency (Bailey and Brown 2011). In theory, this would maximize forage yields if defoliation induces compensatory re-growth responses that either prolong growth (delay senescence) or increase growth rates (Voisin 1961; Hilbert *et al.* 1981), by some physiological mechanism or physical/environmental effect (see McNaughton 1983). Hence, RG would be beneficial if compensatory plant responses to defoliation can be capitalized on through re-grazing, or at a minimum, if accumulated plant production under RG exceed those of CG. Although overcompensation (increased aboveground plant production under defoliation) is uncommon (Belsky 1986; Hawkes and Sullivan 2001), combinations of given intensities and frequencies of defoliation mediate yield responses, such that high intensity defoliation at low frequencies can maintain yields relative to low intensity and deferred defoliation regimes, particularly under high resource conditions (De Bruijn and Bork 2010; De Bruijn *et al.* 2003; Donkor *et al.* 2003; Donkor *et al.* 2002; Turner *et al.* 1993). This suggests that RG may have merit under given conditions.

However, these studies encompassed predominantly mesic, productive swards of rhizomatous grasses whereas North American rangelands are typically marginal lands remaining uncultivated because of climatic and edaphic constraints on productivity (Burke *et al.* 1994). Plant community physiognomy also varies across North America, with caespitose grasses more abundant relative to rhizomatous grasses in arid western grasslands (Sims *et al.* 1978; Mack and Thompson 1982). This suggests that grass morphology (growth form) and environmental conditions (moisture) may regulate forage yield under repeated defoliation.

Indeed, the growth potential of caespitose grasses may be influenced by the unique ecology and morphology of this growth form. Caespitose grass genets (*i.e.*, tussocks) consist of a collection of ramets (*i.e.*, tillers) that are usually spatially clustered and largely physiologically independent (Derner and Briske 1998). Given that contiguity and longevity promote genet fitness (Burke *et al.* 1998), the benefits of being caespitose must exceed adverse effects of intra-specific competition among ramets (see de Kroon 1993). Competition among ramets may be ameliorated by determinate growth (Knapp 1984; Brooker and Callaghan 1998; Grime 2001; Fitter and Hay 2002), which describes a phenomenon common in resource stressed environments where plants grow slowly regardless of resource availability (see Grime 1977; Chapin 1980; Chapin 1991; Chapin *et al.* 1993). Determinate growth generally occurs with relatively exclusive resource access, such as evergreen shrubs that exploit deep soil moisture and succulents that store water (Noy-Meir 1973). Although grasses typically avoid resource limitations by growing rapidly when conditions are favourable (and thereby avoid resource limitations), determinate growth may occur in caespitose grasses because concentrated root biomass beneath genets creates edaphic resource islands of enhanced soil carbon and fertility (Hook *et al.* 1991; Burke *et al.* 1998) and potentially excludes adjacent plants from accessing these edaphic resource pools, thereby extending and enhancing resource availability for prolonged growth.

In contrast, rhizomatous grasses may have indeterminate growth. Not only are rhizomatous grasses more prevalent in mesic grasslands (Sims *et al.* 1978), but their presence in semiarid grasslands is restricted to micro-sites of higher fertility (Derner and Briske 2001), and over 70% of major agronomic forage grasses used worldwide are of this growth form (Mack and Thompson 1982). Moreover, tillering propensity, which influences grazing tolerance and forage yields (Caldwell *et al.* 1981), may be facilitated in rhizomatous grasses by tiller autonomy, extravaginal tillering, and readily mobile carbohydrate and nutrient reserves in rhizomes (Mack and Thompson 1982; Suzuki and Stuefer 1999). Clonal integration, facilitated by rhizome connectivity, may also promote defoliation tolerance in rhizomatous grasses (Liu *et al.* 2009). In contrast, tillering in caespitose grasses is constrained intravaginally within leaf sheaths (Sosebee *et al.* 1988), recruitment is primarily limited to genet peripheries (Derner and Briske 1998), and genets seemingly avoid tiller mortality by limiting excess tiller recruitment (Briske and Butler 1989).

Determinate growth may be a mechanism limiting positive productivity responses to repeated defoliation given that growth plasticity is necessary for compensatory re-growth (*i.e.*, defoliation must increase plant growth rate or prolong growth). If caespitose grasses grow determinately, then defoliation's potential to increase plant community productivity in semiarid environments may be constrained regardless of ambient growing conditions. The objectives of this study were twofold. The first was to elucidate whether, or the degree to which, caespitose grasses grow determinately by comparing the growth dynamics of greenhouse-grown grasses of contrasting growth form (*i.e.*, caespitose vs. rhizomatous). Second was to examine yields under contrasting moisture conditions combined with various intensities and frequencies of defoliation in order to study plant growth potential under different environmental conditions and grazing systems. Although individual plant responses are not perfect proxies for that of plant communities, a relatively small number of dominant graminoids often constitute the majority of biomass in grasslands (Coupland 1961). Thus grasses that are considered desirable, key forage species were selected, and as such, most were late-seral decreasers. In order to assess the influence of moisture regime adaptation, grasses were selected from all major grassland subregions within Alberta, Canada, encompassing a moisture regime gradient of 343 to 430 mm annual precipitation.

Research hypotheses included that determinate growth in caespitose grasses would manifest as, in comparison to rhizomatous grasses, (1) relatively more conservative production increases under high moisture compared to low moisture, (2) greater relative allocation of biomass to roots compared to shoots, (3) relatively more stable tiller number responses, and (4) greater water-use efficiency. I further hypothesized that these responses would be more prominent in caespitose grasses from arid environments (*i.e.*, of lower moisture adaptation).

In contrast, rhizomatous grasses were predicted to have more indeterminate growth regardless of moisture adaptation, and that this would manifest as more positive and negative yield responses to defoliation under high and low moisture, respectively. Thus, rhizomatous grasses were hypothesized to compensate (and potentially overcompensate) to defoliation, but only under high moisture conditions.

2.3. Materials and Methods

2.3.1. Species Selection

The intent was to compare grasses that were similar in most respects (*i.e.*, grazing response and ecological niche), but differed in their growth form. Pairs of caespitose and rhizomatous grasses were thus based on either sympatric occurrence (*i.e.*, co-dominants) or phylogenetic similarity (*i.e.*, the same genus). Paired species therefore shared a common moisture regime adaptation given either their co-occurrence in the same natural subregion or occurrence in areas of similar moisture regime (*i.e.*, annual precipitation). Resulting pairs encompassed a gradient from relatively low to high moisture regime (Table 2-1). From the semiarid Dry Mixedgrass and more mesic Mixedgrass Prairie natural subregions of Alberta, Canada, caespitose-rhizomatous pairs included *Hesperostipa comata* (Trin. & Rupr.) Barkw. – *Pascopyrum smithii* (Rydb.) A. Love, as well as *Hesperostipa curtiseta* (Hitchc.) Barkw. – *Elymus lanceolatus* (Scribn. & J.G. Sm.), respectively. The phylogenetically similar *Festuca campestris* Rydb. –

Festuca hallii (Vasey) Piper pair were included from the western Foothills Fescue and Northern Fescue natural subregions, respectively. Although these species are similar, a key morphological difference is that *F. hallii* has short rhizomes and a more contiguous growth pattern whereas *F. campestris* is strongly caespitose (Pavlick and Looman 1984). The caespitose *Bromus riparius* Rehm. and rhizomatous *Bromus inermis* Leyss. pair are also phylogenetically similar and are common in the Central Parkland (Kupsch *et al*. 2012). Most of these grasses are late-seral, native dominants within their aforementioned subregions, thus sharing similar ecological niches and inherent grazing tolerances (Adams *et al*. 2004; Adams *et al*. 2005; Adams *et al*. 2003; Burkinshaw *et al*. 2009). The exceptions include both brome grasses (*i.e*., *B. inermis* and *B. riparius*), which are introduced agronomics with high grazing tolerance (Harrison and Romo 1994; Olge *et al*. 2002).

2.3.2. Plant Establishment

Grass plants were grown from commercial seed in tray plugs (4 cm wide and 6 cm deep) with standard potting soil on June 10, 2010. Emerging seedlings were hand thinned to a single seedling in each cell. Established seedlings were allowed to freely tiller to form genets that were subsequently transplanted into pots (hexagonal in profile, 46 cm deep, and 18 cm wide, tapering to 13 cm at the bottom) of mechanically mixed 1:1 potting soil (Sun Gro© Sunshine Mix LA#4:

60 – 75 % sphagnum peat with perlite and dolomite limestone) and sand. Inclusion of sand ensured sufficient drainage to avoid water logging.

Five genets were planted equidistantly in every pot, with the exception of the needle grasses (i.e., *H. comata* and *H. curtiseta*), for which 4 genets were used because of lower germination and limited availability of these grasses. Multiple genets were planted in each pot to simulate a monoculture and impose intraspecific competitive limitations on lateral plant growth. And relatively deep pots were used to minimize limitations of pot volume on root growth. Due to differences in germination and establishment rate among species, transplanting occurred in mid-August for bromes, early-September for wheat grasses (*P. smithii* and *E. lanceolatus*), early-October for needle grasses, and mid-October for fescues (*Festuca spp.*).

Greenhouse photoperiod was 16:8 hrs (light:dark), and temperature between 21 and 26°C. Pots were watered weekly and fertilized with Plant Prod© 20N–20P–20K solution in 250 mL doses at a 2.88 g/L rate to ensure nutrients were never limiting to growth. To standardize growth stage among grasses and prevent senescence in rapidly developing brome and wheat grass plants, all pots received a conditioning clip to a 5 cm stubble height on December 20.

2.3.3. Experimental Design and Treatments

Pots were arranged, with 10 cm spacing, in a randomized complete block design. Treatments included defoliation and moisture in a full (4 x 2) factorial with 5 replicates. Defoliation treatments were control, low intensity-high frequency (LIHF), high intensity-low frequency (HILF), and high intensity-high frequency (HIHF) defoliation. HILF and HIHF defoliation pots were clipped at 3 cm stubble heights every 3 and 6 weeks, respectively, whereas LIHF pots were clipped at a 15 cm stubble height at 3-week intervals. Defoliation treatments were implemented between January 29, 2011 and April 23, 2011 simulating a 3-month growing season and allowing 3 and 5 defoliations for low and high frequency treatments, respectively. Final harvests of all pots, including the controls, were to a 1 cm stubble height. HILF and LIHF defoliation were intended to emulate two types of short-duration rotational grazing. HIHF approximates defoliation under continuous grazing in recurrently grazed patches (Ring *et al.* 1985). Controls represent maximum plant growth potential in the absence of prior defoliation, and provided a comparison with other defoliation treatments on overall plant productivity.

Gravimetric techniques were used for moisture treatments, which established a relationship between measured soil moisture and volumetric moisture. Soil moisture content of randomly selected pots with varying moisture levels (n = 90) was measured with a Delta-T Devices© theta probe soil moisture sensor; three readings were taken and averaged. Volumetric water content was estimated as the difference of pot weight relative to the average weight of dry pots (mean=11039 g, SE=105.5). Probe readings were subsequently correlated with volumetric water content and a second-order polynomial trend-line best fitted these data ($r^2=0.55$). This relationship was used to convert probed moisture readings to an estimate of volumetric soil moisture.

Pots at field capacity had an average of 26% volumetric soil moisture, which was estimated by saturating pots and weighing 24 hr later (mean=13612 g, SE=135.7). High and low moisture treatment pots were watered weekly to field capacity and 10% volumetric moisture content, respectively. Water addition volume was determined based on volumetric moisture content estimates from single moisture probe readings. To acclimate plants, moisture treatments commenced 14 d prior to the first defoliation treatments. For the high moisture treatment, the objective was to water as much as possible in order to avoid water limitations, although this was not entirely possible for brome and wheat grasses due to their superior productivity. This was especially evident late in the experiment under the control treatment. For the low moisture treatment the intention was to water as little as possible to ensure plants were moisture stressed at some point between the watering interval.

2.3.4. Vegetation Measurements

Tiller counts were done on plants prior to the first, third, and last defoliations. Due to the absence of extravaginal tillering, tillers were counted repeatedly on one genet per pot for caespitose grasses and *F. hallii*, whereas all tillers within pots were counted on rhizomatous grasses (*i.e.*, *B. inermis*, *P. smithii*, and *E. lanceolatus*). Root biomass was extracted by dry sieving soil through a 6 mm sieve; roots were then washed over a 2 mm sieve. 'Root' material included plant crowns and all belowground organs (*e.g.*, rhizomes). Harvested shoots and roots were dried at 60°C for 48 hrs and weighed.

2.3.5. Data Analysis

Response parameters included shoot and root yield, root:shoot ratio, tiller number, and water-use efficiency. Shoot yield included biomass accrual over the experiment, excluding the conditioning clip. Relative root:shoot allocation dynamics were assessed as the ratio of root biomass relative to that of shoots. Water-use efficiency was calculated as total (root+shoot) yield relative to total water addition from the first defoliation to the final harvest.

Data were checked for homogeneity of variance and normality with Levene's and Shapiro-Wilk tests, respectively (SAS 9.2—SAS Institute, 1989). All response variables were analyzed with ANOVA using mixed model procedures and LSmeans. Significance was assessed at $P \leq 0.05$ and post-hoc mean comparisons for significant main effects and interactions were Tukey's adjusted. Species were analyzed independently for shoot and root yields, with defoliation and moisture as fixed factors and replicate block as random. Species were analyzed both combined (with species as a fixed factor) and independently (due to interactions of species with defoliation and moisture) in ANOVA models for root:shoot ratio and water-use efficiency.

Tiller counts of individual species were analyzed using repeated measure ANOVAs with time as a fixed factor. Covariance structure models were selected based on the best-fit AIC statistic. However, interactions of time and defoliation as well as time and moisture, indicated that mean separation occurred primarily in the last tiller count for most grasses (Figure 2-5). Thus final tiller numbers were also analyzed with the covariate of initial tiller number (prior to the first defoliation) to account for initial differences in tiller number among plants. Finally, to compare tillering among species, the relative change in tiller number (*i.e.*, overall change in tiller numbers relative to the first tiller count) was analyzed with species as a fixed factor.

2.4. Results

2.4.1. Root and Shoot Biomass Yield

Defoliation and moisture treatments, as well as their interaction influenced shoot yield in all species (Table 2-2 and 2-3). Treatment interactions were attributed to greater separation among defoliation means under high moisture compared to low moisture (Figures 2-1 – 2-4). No grasses overcompensated under LIHF, HILF, or HIHF defoliation given shoot yields under these treatments never exceeded controls, irrespective of moisture regime (Figures 2-1 – 2-4). Under high moisture, control and LIHF shoot yields were similar within each species, but response patterns varied for the HILF treatment. HILF defoliation reduced shoot yield relative to the control and LIHF in all species except *B. inermis*, for which all three treatments yielded similarly (Figures 2-1 – 2-4). *B. riparius* displayed a similar pattern, with HILF shoot yield lower than that of the control but similar to LIHF (Figure 2-1). Only in the wheat grasses and brome grasses did HIHF further reduce shoot yields relative to HILF defoliation (Figures 2-2, 2-3, 2-4).

High moisture failed to promote productivity in rhizomatous grasses relative to that observed in caespitose grasses, and low moisture reduced yield by 23-37% among species (data not shown). Increases in shoot yield under high moisture relative to low moisture occurred in control and LIHF treatments for all species, but also for HILF in *P. smithii* and *B. inermis* (Figures 2-1, 2-4).

Relatively little separation occurred among defoliation treatments under low moisture compared to high moisture. Under low moisture, shoot yields were similar among control, LIHF, and HILF in all species except *F. hallii* and *H. comata*. Shoot yield under HILF was less than the control in *F. hallii*, and both the control and LIHF in *H. comata* (Figures 2-2, 2-4). Also evident under low moisture, HILF and HIHF shoot yields were similar among all species except *F. campestris*, for which HIHF further reduced shoot yield relative to HILF (Figure 2-2).

Root yield was affected by moisture, defoliation, and their interaction in all grasses except the two needle grasses (Table 2-2 and 2-3). For *H. curtiseta*, moisture did not affect root yield (P = 0.09), while neither moisture (P = 0.53), nor the interaction of moisture and defoliation (P = 0.16) were significant in *H. comata*. Otherwise, compared to high moisture, root yields were always less under low moisture (Figures 2-1 – 2-4). Interactions were again attributed to greater separation among defoliation treatments under high moisture conditions compared to low moisture.

Under high moisture, all defoliation treatments reduced root yields relative to controls in *B. inermis* and the wheat grasses, whereas only HILF and HIHF reduced yields in *H. comata* and both fescues (Figures 2-1 – 2-4). Root yields under high moisture in *H. curtiseta* peaked under LIHF; however, this increase was likely due to two outliers, and LIHF remained statistically similar to the control, which was also similar to HILF and HIHF (Figure 2-3). For *B. riparius* under high moisture, root yield was reduced only by HIHF defoliation. Also under high moisture, HIHF defoliation further reduced root yields relative to HILF in *B. inermis* only (Figure 2-1). Under low moisture, HILF defoliation reduced root yield in *F. hallii*, *P. smithii*, and *H. comata*, whereas only HIHF reduced root yield in *B. riparius*, *F. campestris*, and *E. lanceolatus* (Figures 2-1, 2-2, 2-3). Defoliation did not reduce root yield in *B. inermis* and *H. curtiseta* under low moisture (Figures 2-1, 2-3).

2.4.2. Root:Shoot Ratios

Root:shoot ratios differed among species and were also influenced by defoliation and moisture, as well as the interactions of species by moisture, species by defoliation, and a three-way between all fixed factors (Table 2-4). However, independent ANOVAs for each species showed no significant defoliation by moisture interactions (Table 2-2 and 2-3), indicating the three-way interaction was due to variable defoliation and moisture effects among, rather than within, individual species. Root:shoot ratios mostly exceeded 0.8 and were similar among the brome, fescue, and needle grasses, but were lower in *A. dasystachyum*, and lowest in *P. smithii*, at 0.62 and 0.44, respectively (Table 2-7).

Overall, root:shoot ratios were greater under low moisture, but this was significant in only 3 species, all of which were caespitose, including *F. campestris*, *H. curtiseta*, and *H. comata* (Table 2-7). Only in the caespitose *B. riparius* was root:shoot ratio reduced under low moisture. Overall root:shoot ratios peaked under no defoliation (control), and were progressively reduced by LIHF, HILF, and HIHF defoliation treatments (Table 2-7), indicating proportionally larger reductions in root than shoot biomass. However, only in the wheat grasses did LIHF reduce root:shoot ratios relative to the controls, while HILF reduced root:shoot ratios in almost all species except *H. curtiseta* and *F. campestris*, for which defoliation did not affect root:shoot ratios, and *B. riparius*, for which only HIHF reduced root:shoot ratios.

2.4.3. Water-Use Efficiency

Water-use efficiency varied among species and was also influenced by moisture and defoliation, as well as the interactions of species by moisture, and species by defoliation (Table 2-4). Water-use efficiencies were similar between grasses within moisture regime adaptations, and greatest in both *Bromus* species

(Table 2-9). Grasses from the Mixedgrass and Dry Mixedgrass Prairies (i.e., the wheat grasses and needle grasses), had similar overall water-use efficiencies. Water-use efficiencies in the fescues were similar to those species of the Dry Mixedgrass Prairie (*i.e.*, *P. smithii* and *H. comata*), but lower than those species of the Mixedgrass Prairie (*i.e.*, *E. lanceolatus* and *H. curtiseta*) (Table 2-9).

Water-use efficiencies were greater under low moisture for all species (Table 2-9), meaning the species by moisture interaction is presumably due to different mean separation patterns among species and within moisture regime treatments (Table 2-6). LIHF, HILF, and HIHF defoliation progressively reduced overall water-use efficiency relative to non-defoliated controls. However, water-use efficiency under control and LIHF treatments remained similar in all species, while HILF reduced water-use efficiency in all grasses except the bromes. Water-use efficiency was similarly low under HIHF and HILF defoliation in the needle grasses only (Table 2-9).

2.4.4. Tiller Dynamics

Tiller counts responded to time of sampling in all species ($P < 0.001$) (Table 2-5 and 2-6), with tiller numbers increasing 30–123% over the experiment (Table 2-9). Defoliation influenced final tiller numbers in all species except *B. riparius* (Table 2-2 and 2-3), while moisture influenced final tiller numbers in all species except *B. riparius* and *H. comata* (Table 2-2 and 2-3). Only rhizomatous species had moisture by defoliation interactions, which were attributed to greater separation among defoliation treatment means under high compared to low moisture. High moisture conditions increased tiller number in all species for which this effect was significant (Table 2-9). Tiller numbers were similar between control and LIHF defoliation treatments for all species except *B. inermis*, where LIHF defoliation reduced tillers (Table 2-9). HILF defoliation universally reduced tiller numbers relative to controls (except in *B. riparius*), and only in *F. hallii* and the wheat grasses were tiller numbers further reduced by HIHF defoliation (Table 2-9).

Relative changes in tiller numbers varied among species, and was also affected by defoliation and moisture treatments (Table 2-4). Species by defoliation, and defoliation by moisture interactions were also significant. The defoliation by moisture interaction was attributed to greater separation among defoliation means under high compared to low moisture. Under high moisture and across all species, tiller numbers increased by over 134% over the experiment for control and LIHF defoliation, but increases were reduced almost 3-fold under HILF defoliation, and were non-existent under HIHF defoliation (Table 2-9). Under low moisture, tiller increases were 30% less and defoliation effects remained similar, except that relative tillering did not differ between HILF and HIHF defoliation (Table 2-9). Relative tillering rates were greatest in *H. comata*, *F. campestris*, and *F. hallii*, which increased tiller number over the experiment by 123, 103, and 96%, respectively (Table 2-9). Overall, high moisture increased tiller numbers by over 30% (Table 2-9).

Tiller number changes over time indicate that defoliation and moisture effects predominantly manifested in the latter half of the experiment for all but two grasses (*B. riparius* and *H. curtiseta*) (Table 2-5 and 2-6, Figure 2-5). Tiller numbers tended to increase over the experiment under no- and lenient-defoliation (control and LIHF), especially under high moisture for the rhizomatous grasses (Figure 2-5). The exception to this was *B. inermis* and *P. smithii*, for which no overall tiller number increases occurred under LIHF defoliation under low moisture conditions; and *B. inermis* and *F. hallii*, for which tiller numbers increased under HILF defoliation under high moisture conditions (Figure 2-5). Defoliation effects were perhaps most pronounced in *P. smithii* given that HIHF defoliation reduced tiller numbers in this species. For the caespitose *H. comata* and *F. campestris*, only HIHF prevented overall increases in tiller number, and tiller numbers increased under both high and low moisture.

2.5. Discussion

2.5.1. Shoot and Root Yield

It was hypothized that compensatory growth would occur only in rhizomatous grasses, and only under high moisture conditions. Select shoot yield responses to defoliation and moisture were consistent among growth forms, but these did not manifest as hypothesized. First, high moisture promoted similar production increases between caespitose and rhizomatous grasses, thereby rejecting the hypothesis that rhizomatous grasses would be more responsive to increased moisture availability. Similarly, rhizomatous grasses did not overcompensate under any defoliation regime regardless of moisture conditions. However, rhizomatous grass yields were more resilient to defoliation under high moisture. Most rhizomatous grasses (all except *F. hallii*) yielded higher under HILF relative to HIHF defoliation; whereas HILF defoliation suppressed yields in most caespitose grasses (all but *B. riparius*). Given that moisture influenced this response, it suggests rhizomatous grasses may have superior defoliation tolerance under conditions favourable for growth. Shoot yields under the various defoliation treatments were more similar in all grasses under low moisture, and may reflect the fact that suppressed plant growth with limited moisture is likely to prevent a clear stress response to variation in defoliation intensity and frequency. These results are similar to those of van Staalduinen and Anten (2005), who compared greenhouse growth responses of respective rhizomatous and caespitose grasses *Leymus chinensis* and *Stipa krylovii*, and found compensatory growth for the former was dependent on high moisture conditions, whereas compensatory growth for the caespitose *S. krylovii* was limited to low moisture conditions.

Root yield responses were not always consistent with those of shoots, but some were consistent among growth forms. For example, unlike shoots, low moisture failed to reduce root yield in all grasses. Caespitose grasses of the mixedgrass prairies (*i.e.*, both needle grasses) maintained similar root yields (relative to that of shoots) under high and low moisture. While, like shoot yields, defoliation effects on roots were more prominent under high moisture, with even low intensity defoliation reducing root biomass in most rhizomatous grasses (except *F. hallii*). However, this pattern was not observed under low moisture, indicating root growth in rhizomatous grasses may be more sensitive to defoliation, but only under high moisture, where root:shoot allocation is generally lower (Wijk 2011).

The second objective of this study was to examine grass yield under various defoliation and moisture regimes. In theory, RG involves redistributing grazing pressure to control defoliation timing and frequency on individual plants, thereby creating opportunities to re-graze plants in a single growing season. Utilizing plant re-growth would be advantageous if defoliation induces compensatory growth. Although overcompensation was not observed, defoliation did not unanimously reduce yields, as evidenced by similar shoot yields in all grasses between the LIHF and control defoliation treatments. In contrast, HILF defoliation had a variable effect, reducing yield in all grasses except *B. inermis*. Nevertheless, yields were also relatively high under HILF defoliation in *B. riparius*, and to a lesser extent in the wheat grasses. The bromes are unique among the other grasses examined here in that both are introduced cultivars with high defoliation tolerance (Harrison and Romo 1994; Jensen *et al.* 2001).

Compensatory yielding under HILF defoliation in the brome grasses is consistent with other studies (*e.g.,* Donkor *et al.* 2002, 2003, De Bruijn and Bork 2006, De Bruijn *et al.* 2010) finding introduced grasses within the Aspen Parkland, including smooth brome grass (*Bromus inermis* Leyss.), Kentucky bluegrass (*Poa pratensis* L.) and timothy (*Phleum pratense* L.), can sustain high intensity defoliation and yield similarly to low intensity and even deferred defoliation regimes. Moreover, increased shoot biomass in 3 of the 4 rhizomatous species tested here under HILF compared to HIHF defoliation indicates that improved re-growth under intense but infrequent defoliation may be tied to the presence of rhizomes (see Liu *et al.* 2009). Collectively, this suggests that grasses with high grazing tolerance and re-growth potential may be better able to maintain productivity under intense but infrequent defoliation. Indeed, grazing tolerance *is* a function of plant re-growth potential, which manifests as preferential growth to rapid photosynthetic tissue regeneration (Peterson 1962; Caldwell *et al* 1981; Detling and Painter 1983). Conversely, high intensity defoliation, regardless of frequency, reduced yields in all native grasses, which corroborates numerous field and greenhouse studies finding compromised plant yield under defoliation for those grasses examined in this experiment (Peterson 1962; Wright 1967; Polley and Detling 1988; Zhang and Romo 1994; Willms 1991; Pantel *et al.* 2010; Pantel *et al.* 2011), and supports the common management recommendation of conservative stocking and utilization on native grasslands (Holechek *et al.* 2004).

Unlike all other defoliation treatments, HIHF defoliation consistently resulted in the lowest grass biomass, indicating that simultaneously increasing the severity and frequency of defoliation had additive negative impacts on growth, even in the defoliation tolerant bromes. These results are again consistent with other studies highlighting the potential for management strategies striving to either limit biomass removal and/or provide lengthy rest periods to improve plant vigour and overall yield (Holechek *et al.* 2004; Briske *et al.* 2008).

Grass yield differences in response to defoliation can also be interpreted in the context of grazing systems (*i.e.*, RG vs. CG), assuming they are applied at the same stocking rate. As both RG and CG involve variations of the defoliation regimes tested here, our findings indicate that either grazing system will largely fail to promote compensatory plant responses and increase re-grazing opportunities. Nevertheless, one purported benefit of RG is the ability for more uniform utilization within pastures (Derner *et al.* 1994), whereas CG can promote selection of re-growth over time, leading to so-called patch grazing from repeated use of previously grazed patches, interspersed with ungrazed or lightly grazed areas (Willms *et al.* 1988; Ring *et al.* 1985). Under these conditions, repeated, intense defoliation of patches is likely to reduce herbage yield at these locations, similar to that observed under HIHF defoliation in this study. However, remaining un-grazed patches, yielding similar to controls, could offset this and maintain overall pasture productivity (see Figure 2-6). In contrast, under homogenous, intense use at low frequencies associated with some rotational systems (*e.g.*, short-duration grazing), pasture yields may approximate those observed here under HILF defoliation. Thus, RG's potential to promote community productivity over CG may depend on (1) whether the yield from uniformly impacted areas of the RG (*i.e.*, HILF or LIHF) pasture are sufficient to overcome the average biomass observed from the combination of less productive HIHF defoliation patches together with the highly productive counterparts comprised of ungrazed or lightly grazed areas, as well as (2) the relative contribution of re-currently grazed and unused areas in the CG treatment, and the degree to which this differential use is ameliorated by RG (see Figure 2.6).

In this context, our results suggest that the trade-offs associated with (1) are more favourable in brome grasses and to a lesser extent *E. lanceolatus* (Figure 2-6), potentially due to greater re-growth potential and defoliation tolerance in these species. This may account for why RG has increased plant community production over CG in pastures dominated by defoliation tolerant species (DeBruijn *et al*. 2010). Uniform pasture use under high stocking densities, accompanied by favourable re-growth during long rest periods, is likely to capitalize on yield increases possible with HILF compared to HIHF grazing in swards comprised of grazing tolerant forage species. Only under low utilization levels, such that if only 10-25% of the pasture were heavily utilized and the remainder of the area avoided, would plant community productivity of *B. inermis* and *B. riparius* swards be greater under continuous grazing (Figures 2-7 and 2-9). In contrast, given the apparent lack of compensatory re-growth to high intensity defoliation for both needle grasses and fescues, as well as *P. smithii*, uniform use under RG may 'uniformly' lower plant yields in fescue and mixedgrass grasslands (Figure 2-6). This may account for why the majority of rotational and continuous grazing trials produce similar residual standing crops in native grasslands of North America (*e.g.*, Briske *et al*. 2008; Holechek *et al*. 2000). Rotational grazing may only maximize plant community productivity in native grass swards if avoided areas under continuous grazing make up less than 10-25% of the pasture (Figures

2-8 and 2-10), albeit stocking rates associated with this level of use would likely be unsustainable regardless of grazing system.

2.5.2. Root:Shoot Ratio Dynamics

Caespitose grasses were hypothesized to allocate more biomass to roots than shoots. Instead, defoliation and moisture mediated root:shoot ratio responses, and some of these effects were consistent among growth forms. First, defoliation reduced root allocation in all rhizomatous grasses whereas caespitose grasses had more similar root:shoot ratios under increasing intensity and frequency and defoliation. Two caespitose grasses (*F. campestris* and *H. curtiseta*) maintained similar root:shoot ratios under all defoliation regimes, and *B. riparius* reduced root:shoot allocation only under HIHF defoliation. Continued root growth in response to defoliation has been associated with grazing intolerance in the caespitose *Agropyron spicatum* (Caldwell *et al*. 1981), perhaps indicating that potentially lower grazing tolerance in caespitose grasses (*e.g.*, see Milchunas and Lauenroth 1993) may be due to greater biomass allocation to roots under defoliation. Conversely, determinate root allocation may enable caespitose grasses to better cope with aridity and maintain resource islands of enhanced fertility (Burke *et al*. 1998; Hook *et al*. 1991).

Moisture conditions influenced root:shoot ratios in caespitose grasses only, with most having greater root:shoot ratios under low moisture conditions. Indeed, plants generally allocate a greater proportion of biomass belowground under increasing aridity (Wijk 2011), a response that could be advantageous when belowground resources (*e.g.*, water and soil nutrients) are more limiting than aboveground resources (*e.g.*, space and light) (Burke *et al.* 1998). In contrast, *B. riparius* allocated more biomass to roots under high moisture. Reasons for the latter are unknown, but could stem from *B. riparius* being the only introduced caespitose grass examined here. As a forage cultivar, *B. riparius* is selected for high shoot production and is adapted to relatively mesic conditions (Olge *et al.* 2002).

Defoliation and moisture effects aside, overall root:shoot ratios were similar among most grasses, but were markedly lower in the rhizomatous wheat grasses: *E. lanceolatus* and *P. smithii*. Derner and Briske (2001) found that in more arid environments rhizomatous grasses exploit micro-sites of enhanced fertility and store greater nutrient concentrations in rhizomes. As *E. lanceolatus* and *P. smithii* are of the lowest moisture regime adaptation examined, these grasses may reduce allocation to root growth for preferential resource storage, in turn compromising growth (see Chapin *et al.* 1990).

2.5.3. Water-use Efficiency

Water-use efficiency was hypothesized to be greater in caespitose grasses, but this was not observed. Instead, water-use efficiencies varied among species of different moisture regime, and remained similar among grasses of the same moisture adaptation. However, water-use was not restricted to plant utilization through transpiration, but could also include evaporation and percolation water losses. Consequently, a more comparable metric would be precipitation-use efficiency, which represents annual net primary production relative to average annual precipitation (Paruelo *et al*. 1999).

Across a precipitation gradient, precipitation-use efficiency of grassland ecosystems tends to be unimodal, peaking under intermediate precipitation and declining under xeric and mesic extremes (Yang *et al*. 2010; Paruelo *et al*. 1999). For the Great Plains of North America, Paruelo *et al*. (1999) found this peak occurred around 475 mm annual precipitation. Of the natural subregions from which grasses were selected, this corresponds most closely with the Aspen Parkland, which on average has 430 mm precipitation (Burkinshaw *et al*. 2009). Indeed, the brome grasses selected from this region had the greatest water-use efficiencies. The same was not true for the fescues, despite also being adapted to a relatively mesic environment.

Paruelo *et al*. (1999) hypothesized that precipitation-use efficiency is lower in more arid environments because determinate growth characteristics of xerophytic vegetation constrain positive productivity responses to precipitation. This is consistent with the definition of determinate growth used here and defined by Chapin *et al*. (1993) and Grime (2001). Indeed, low water-use efficiencies in fescues may have been due to determinate growth, manifested as inherently low growth rates, slow establishment, and low productivity. In contrast, productivity was high in both bromes, especially under high moisture. This suggests that precipitation-use efficiency peaks in mesic grasslands because mesophytic plants can better utilize rainfall for biomass production, thus minimizing evaporation and percolation water losses.

2.5.4. Tiller Dynamics

Our hypothesis that defoliation and moisture effects would be less pronounced in caespitose grasses received some support in this investigation. For example, high moisture promoted tillering in all rhizomatous grasses but only two bunchgrasses (*F. campestris* and *H. curtiseta*), and only in rhizomatous grasses did moisture conditions alter defoliation effects. Together this indicates that tiller production or survival may be contingent on moisture conditions for rhizomatous grasses. In addition, although defoliation generally reduced tiller numbers (except in *B. riparius*), further reductions under HIHF compared to HILF defoliation were not observed in caespitose grasses, presumably because of sensitivity to intense defoliation regardless of frequency in this growth form (*e.g.*, see Milchunas and Lauenroth 1993).

Tiller numbers increased over the duration of the experiment in all grasses, especially for both fescues and *H. comata*. Although this could be interpreted as an indeterminate response, this may occur because of delayed development in these grasses, as the fescues and needle grasses were the last to germinate and establish. Apical dominance is regarded as the primary mechanism regulating tillering (Murphy and Briske 1992), though light penetration (Casal *et al.* 1990; Deregibus *et al.* 1985) and resource availability (Olson and Richards 1989) can also play a role, which suggests that grasses modulate tillering relative to perceived resource availability. Therefore, more pronounced tillering in slower developing grasses could have resulted from their inability to saturate pot rhizospheres and come under density dependent constraints.

For most grasses, defoliation and moisture effects appeared to be cumulative, manifesting predominantly in the latter half of the experiment. During this time, tiller recruitment in rhizomatous grasses was pronounced under deferred and low-intensity defoliation, especially under high moisture conditions. Low intensity and deferred defoliation also promoted tillering in two bunchgrasses (*H. comata* and *F. hallii*) in the latter stages of the study, although high moisture did not modify recruitment in these grasses. This further highlights the potentially greater dependency of growth processes on moisture conditions in rhizomatous grasses. In contrast, the effects of high intensity defoliation were not to reduce tiller numbers *per se* (except in *P. smithii*), but rather to prevent tiller recruitment over the duration of the experiment. Low-intensity defoliation did not suppress tillering and may even have allowed continued production of tillers in rhizomatous grasses under conditions favourable for growth (high moisture). This may be a mechanism of more indeterminate growth in this growth form, and may explain why yielding was similarly high to controls under this treatment.

2.6. Summary

All hypotheses predicting determinate growth responses in caespitose grasses were rejected, suggesting that caespitose grasses do not grow determinately in response to defoliation and moisture. However, some defoliation and moisture effects were *generally* consistent among rhizomatous and caespitose grasses, respectively, suggesting potential influences of growth form on re-growth responses. These include that the majority of rhizomatous grasses yielded more favourably to HILF relative to HIHF defoliation, whereas caespitose grasses maintained more consistent tiller numbers and root:shoot ratios under defoliation. However, as this study examined only a limited number of grasses, more empirical evidence is necessary to evaluate potential characteristics associated with growth form and whether caespitose grasses consistently demonstrate determinate growth.

It is tenuous to assume that clipping treatments emulate herbivory (Bryant and Blaser 1968), especially under different grazing systems. Nevertheless, this experiment shows that there are trade-offs associated with defoliation frequency and intensity; and these trade-offs vary depending on species and growing conditions. Plant community yields under contrasting grazing systems may depend on the contribution of areas repeatedly defoliated relative to those avoided, and the degree to which uniform, intense defoliation compromises productivity. Grasses in this experiment maintained yields under low intensity defoliation, but effects of high intensity defoliation were variable. Compensatory growth under HILF occurred only in the rhizomatous *B. inermis*; *B. riparius* nearly compensated, and the rhizomatous wheat grasses also showed more favourable yield under HILF relative to HIHF defoliation. Consequently, rotational systems that encourage high utilization in order to homogenize grazing pressure may have greater potential to promote community productivity within grazing tolerant introduced and/or predominantly rhizomatous grasslands. Future research on grazing systems should examine defoliation patterns under different grazing systems and ascertain how these, in turn, affect plant community productivity. Moreover, meta-analyses investigating plant community productivity under different grazing systems should include studies from a diversity of ecosystems, including both native grasslands and non-native pasturelands.

Table 2-1. Caespitose and rhizomatous grass pairs and their respective natural subregions and associated mean annual precipitation levels.

Natural subregion	Caespitose grass	Rhizomatous grass	Annual precipitation (mm)
Dry Mixedgrass	*Hesperostipa comata*	*Pascopyrum smithii*	343
Mixedgrass	*Hesperostipa curtiseta*	*Elymus lanceolatus*	419
Northern Fescue	-	*Festuca hallii*	383
Foothills Fesuce	*Festuca campestris*	-	416
Central Parkland	*Bromus riparius*	*Bromus inermis*	430

Table 2-2. Shoot and root biomass, root:shoot ratios, water-use, and tiller number ANOVA *F*-values for 4 graminoid species relative to the fixed factors of moisture (moist), defoliation (defol.), and their interaction as well as the covariate (initial tiller number) for tiller numbers.

	df	Shoot	Root	Ratio	Water-use	Tiller number
Bromus inermis^{R}[1]						
Moisture	1	57.9^{***}[2]	29.6^{***}	0.6	103.5^{***}	37.3^{***}
Defoliation	3	25.1^{***}	23.0^{***}	7.9^{***}	15.1^{***}	19.7^{***}
Moist x defol.	3	8.9^{***}	7.3^{***}	1.1	0.9	8.8^{***}
Covariate						6.1^{*}
Bromus riparius^{C}						
Moisture	1	40.0^{***}	39.9^{***}	5.7^{*}	88.2^{***}	0.3
Defoliation	3	35.1^{***}	30.2^{***}	12.3^{***}	13.3^{***}	0.5
Moist x defol.	3	4.9^{**}	5.1^{**}	1.7	0.1	0.6
Covariate						28.8^{***}
Festuca hallii^{R}						
Moisture	1	55.2^{***}	27.6^{***}	3.6	360.9^{***}	32.6^{***}
Defoliation	3	74.4^{***}	78.5^{***}	7.1^{**}	41.3^{***}	43.4^{***}
Moist x defol.	3	7.3^{***}	8.8^{***}	1.0	3.8^{*}	4.7^{***}
Covariate						20.5^{***}
Festuca campestris^{C}						
Moisture	1	39.3^{***}	5.9^{*}	10.5^{**}	200.9^{***}	19.0^{***}
Defoliation	3	45.9^{***}	20.8^{***}	0.60	27.5^{***}	38.5^{***}
Moist x defol.	3	8.01^{***}	3.9^{*}	1.5	4.2^{*}	2.2
Covariate						31.4^{***}

[1] Rhizomatous and caespitose grasses denoted with ^{R} and ^{C}, respectively.

[2] *, **, *** Indicates significance at $P < 0.05$, $P < 0.01$, and $P < 0.001$, respectively.

Table 2-3. Shoot and root biomass, root:shoot ratios, water-use, and tiller number ANOVA *F*-values for 4 graminoid species relative to the fixed factors of moisture (moist), defoliation (defol.), and their interaction as well as the covariate (initial tiller number) for tiller numbers.

	df	Shoot	Root	Ratio	Water-use	Tiller number
Elymus lanceolatus ^{R} [1]						
Moisture	1	55.6***[2]	26.8***	3.7	38.0***	9.0**
Defoliation	3	50.8***	30.8***	18.6***	20.5***	64.5***
Moist x defol.	3	7.5***	6.5***	1.2	0.3	6.9***
Covariate						66.5***
Hesperostipa curtiseta ^{C}						
Moisture	1	20.9***	3.0	4.5*	58.4***	5.9*
Defoliation	3	17.9***	8.2***	2.0	7.1**	5.1**
Moist x defol.	3	4.0*	3.5*	2.1	1.3	1.2
Covariate						71.0***
Pascopyrum smithii ^{R}						
Moisture	1	25.1***	19.9***	0.0	65.2***	17.4***
Defoliation	3	44.3***	64.2***	11.7***	23.2***	97.1***
Moist x defol.	3	0.7**	10.9***	1.1	0.3	14.0***
Covariate						39.3***
Hesperostipa comata ^{C}						
Moisture	1	32.9***	0.4	24.5***	253.2***	2.8
Defoliation	3	118.2***	66.5***	10.6***	45.6***	21.0***
Moist x defol.	3	17.8***	1.9	1.6	0.1	1.7
Covariate						31.0***

[1] Rhizomatous and caespitose grasses denoted with ^{R} and ^{C}, respectively.

[2] *, **, *** Indicates significance at $P < 0.05$, $P < 0.01$, and $P < 0.001$, respectively.

Table 2-4. Root-shoot ratio, water-use, and relative tiller number change ANOVA *F*-values for fixed factors of species (spp), moisture (moist), defoliation (defol), and interactions thereof.

	df	Root-shoot ratio	Water-use	Tiller number
Spp	7	30.7^{***1}	90.4^{***}	24.9^{***}
Moist	1	6.1^{*}	689.5^{***}	40.0^{***}
Spp x moist	7	6.5^{***}	5.2^{***}	1.9
Defol	3	35.4^{***}	119.2^{***}	134.5^{***}
Spp x defol	21	3.8^{***}	2.3^{**}	6.9^{***}
Defol x moist	3	0.6	0.7	6.1^{***}
Spp x defol x moist	21	1.7^{*}	0.7	1.2

[1] *, **, *** Indicates significance at $P < 0.05$, $P < 0.01$, and $P < 0.001$, respectively.

Table 2-5. Tiller number ANOVA *F*-values for all species relative to fixed effects of defoliation (defol.), moisture (moist), time, and interactions thereof for 4 graminoid species.

	df	F-value			
		Bromus inermis^R[1]	*Bromus riparius*^{C}	*Festuca hallii*^{R}	*Festuca campestris*^{C}
Defol	3	5.8**[2]	0.4	9.3***	11.5***
Moist	1	5.0*	0.8	12.1**	5.4*
Defol x Moist	3	6.3**	0.1	1.9	2.5
Time	2	61.9***	14.4***	109.6***	99.5***
Defol x Time	6	13.4***	0.6	22.4***	16.1***
Moist x Time	2	22.1***	2.4	17.4***	9.7***
Defol x Moist x Time	6	3.0*	2.1	2.5*	1.6

[1] Rhizomatous and caespitose grasses denoted with ^{R} and ^{C}, respectively.

[2] *, **, *** Indicates significance at $P < 0.05$, $P < 0.01$, and $P < 0.001$, respectively.

Table 2-6. Tiller number ANOVA *F*-values for all species relative to fixed effects of defoliation (defol.), moisture (moist), time, and interactions thereof for 4 graminoid species.

	df	F-value			
		Elymus lanceolatus$^{R\ 1}$	*Hesperostipa curtiseta*^{C}	*Pascopyrum smithii*^{R}	*Hesperostipa comata*^{C}
Defol	3	10.4^{***2}	0.1	22.5***	3.3*
Moist	1	0.9	0.6	4.4*	0.1
Defol x Moist	3	0.4	2.1	2.1	2.4
Time	2	56.9***	21.7***	62.7***	117.3***
Defol x Time	6	38.0***	1.4	35.1***	13.5***
Moist x Time	2	6.1**	1.4	6.1**	3.6*
Defol x Moist x Time	6	3.8**	1.8	5.5***	1.7

[1] Rhizomatous and caespitose grasses denoted with ^{R} and ^{C}, respectively.

[2] *,**,*** Indicates significance at $P < 0.05$, $P < 0.01$, and $P < 0.001$, respectively.

Table 2-7. Root:shoot ratio means (standard error in parentheses) for eight grasses relative to treatments of high and low moisture, as well as control, low intensity high frequency (LIHF), high intensity low frequency (HILF), and high intensity high frequency (HIHF) defoliation. Mean comparisons are Tukey's adjusted ($P < 0.05$) and means with the same letter are not significantly different.

	Overall	Moisture			Defoliation				
		High	Low		Control	LIHF	HILF	HIHF	
Bromus inermis$^{R\,1}$	0.81^{a2}	0.84^{A3}	0.79^{A}	(0.04)	1.04^{A}	0.82^{AB}	0.77^{B}	0.63^{B}	(0.06)
Bromus riparius^{C}	0.81^{a}	0.88^{A}	0.74^{B}	(0.05)	0.96^{A}	0.77^{A}	0.96^{A}	0.55^{B}	(0.06)
Festuca hallii^{R}	0.84^{a}	0.81^{A}	0.88^{A}	(0.04)	0.89^{A}	0.94^{A}	0.71^{B}	0.83^{AB}	(0.05)
Festuca campestris^{C}	0.84^{a}	0.76^{B}	0.91^{A}	(0.04)	0.86^{A}	0.87^{A}	0.79^{A}	0.83^{A}	(0.05)
Elymus lanceolatus^{R}	0.62^{b}	0.68^{A}	0.57^{A}	(0.04)	0.95^{A}	0.61^{B}	0.52^{B}	0.42^{B}	(0.05)
Hesperostipa curtiseta^{C}	0.92^{a}	0.83^{B}	1.01^{A}	(0.06)	0.94^{A}	1.06^{A}	0.77^{A}	0.90^{A}	(0.08)
Pascopyrum smithii^{R}	0.44^{c}	0.43^{A}	0.44^{A}	(0.03)	0.62^{A}	0.41^{B}	0.40^{B}	0.32^{B}	(0.04)
Hesperostipa comata^{C}	0.82^{a} (0.04)	0.69^{B}	0.96^{A}	(0.06)	1.03^{A}	0.91^{A}	0.69^{B}	0.67^{B}	(0.07)
All species		0.74^{a}	0.79^{b}	(0.03)	0.91^{a}	0.80^{b}	0.70^{c}	0.64^{c}	(0.03)

[1] Rhizomatous and caespitose grasses denoted with ^{R} and ^{C}, respectively.

[2] Lowercase superscript represents vertical mean separation comparisons within columns and among species.

[3] Uppercase superscript represents horizontal mean separation comparisons within rows and independent fixed factors.

Table 2-8. Water-use (g biomass/L water addition) means (standard error in parentheses) for eight grasses relative to treatments of high and low moisture, as well as control, low intensity high frequency (LIHF), high intensity low frequency (HILF), and high intensity high frequency (HIHF) defoliation. Mean comparisons are Tukey's adjusted ($P < 0.05$) and means with the same letter are not significantly different.

	Overall	Moisture			Defoliation				
		High	Low		Control	LIHF	HILF	HIHF	
Bromus inermis^{R}[1]	2.86^{a}[2]	2.10^{B}[3]	3.63^{A}	(0.11)	3.48^{A}	2.93^{A}	2.98^{A}	2.07^{B}	(0.15)
Bromus riparius^{C}	2.73^{a}	1.94^{B}	3.51^{A}	(0.12)	3.16^{A}	2.96^{A}	2.96^{A}	1.83^{B}	(0.17)
Festuca hallii^{R}	1.43^{c}	0.93^{B}	1.92^{A}	(0.04)	1.73^{A}	1.67^{A}	1.30^{B}	1.01^{C}	(0.06)
Festuca campestris^{C}	1.36^{c}	0.90^{B}	1.81^{A}	(0.06)	1.67^{A}	1.57^{A}	1.26^{B}	0.93^{C}	(0.07)
Elymus lanceolatus^{R}	1.75^{b}	1.34^{B}	2.15^{A}	(0.10)	2.40^{A}	1.98^{AB}	1.63^{B}	0.98^{C}	(0.14)
Hesperostipa curtiseta^{C}	1.83^{b}	1.27^{B}	2.40^{A}	(0.10)	2.15^{AB}	2.19^{A}	1.58^{BC}	1.42^{C}	(0.15)
Pascopyrum smithii^{R}	1.59^{bc}	1.11^{B}	2.08^{A}	(0.12)	2.21^{A}	1.87^{AB}	1.41^{B}	0.88^{C}	(0.14)
Hesperostipa comata^{C}	1.51^{bc}	0.89^{B}	2.13^{A}	(0.10)	2.01^{A}	1.91^{A}	1.16^{B}	0.97^{B}	(0.11)
	(0.07)								
All species combined		1.31^{b}	2.46^{a}	(0.04)	2.35^{a}	2.14^{b}	1.79^{c}	1.26^{d}	(0.05)

[1] Rhizomatous and caespitose grasses denoted with ^{R} and ^{C}, respectively.

[2] Lowercase superscript represents vertical mean separation comparisons within columns and among species.

[3] Uppercase superscript represents horizontal mean separation comparisons within rows and independent fixed factors.

Table 2-9. Mean tiller number (adjusted with initial tiller number as a covariate) [standard error in brackets] and percent change (in parentheses) for eight grasses relative to treatments of high and low moisture, as well as control, low intensity high frequency (LIHF), high intensity low frequency (HILF), and high intensity high frequency (HIHF) defoliation. Mean comparisons are Tukey's adjusted ($P < 0.05$) and means with the same letter are not significantly different.

	Overall	Moist			Defoliation				
		High	Low		Control	LIHF	HILF	HIHF	
Bromus inermis^{R}[1]	(46.4)^{b}[2]	72.2^{A}[3]	52.1^{B}	[2.3]	81.4^{A}	63.0^{B}	57.8^{BC}	46.5^{C}	[3.3]
Bromus riparius^{C}	(29.7)^{b}	24.6^{A}	23.5^{A}	[1.5]	25.8^{A}	24.5^{A}	23.1^{A}	22.8^{A}	[2.0]
Festuca hallii^{R}	(95.5)^{a}	68.4^{A}	47.6^{B}	[2.8]	74.7^{A}	81.2^{A}	47.6^{B}	28.5^{C}	[3.8]
Festuca campestris^{C}	(103.1)^{a}	59.2^{A}	44.4^{B}	[2.4]	66.5^{A}	72.5^{A}	40.0^{B}	28.2^{B}	[3.4]
Elymus lanceolatus^{R}	(42.8)^{b}	68.7^{A}	58.3^{B}	[2.5]	91.1^{A}	81.1^{A}	51.4^{B}	30.1^{C}	[3.6]
Hesperostipa curtiseta^{C}	(41.9)^{b}	54.5^{A}	46.6^{B}	[4.2]	50.5^{AB}	60.8^{A}	46.8^{B}	44.2^{B}	[4.8]
Pascopyrum smithii^{R}	(45.8)^{b}	58.2^{A}	45.5^{B}	[2.8]	80.6^{A}	71.5^{A}	41.0^{B}	14.4^{C}	[3.5]
Hesperostipa comata^{C}	(122.7)^{a}	39.0^{A}	34.8^{A}	[1.8]	49.9^{A}	43.9^{A}	29.6^{B}	24.0^{B}	[2.5]
	[7.8]								
All species combined									
High moisture	(81.8)^{a}				(145.6)^{A*}[4]	(134.3)^{A*}	(47.4)^{B}	(-0.1)^{C}	[7.8]
Low moisture	(50.2)^{b}				(96.6)^{A*}	(80.1)^{A*}	(25.9)^{B}	(-1.8)^{B}	[7.8]
	[4.9]								
All moisture					(121.1)^{A}	(107.2)^{A}	(36.7)^{B}	(-1.0)^{C}	[6.0]

[1] Rhizomatous and caespitose grasses denoted with ^{R} and ^{C}, respectively.

[2] Lowercase superscript represents vertical mean separation comparisons within columns.

[3] Capital superscript represents horizontal mean separation comparisons within rows and independent fixed factors.

[4] Asterisks indicate a difference between the same defoliaton treatment across moisture regimes.

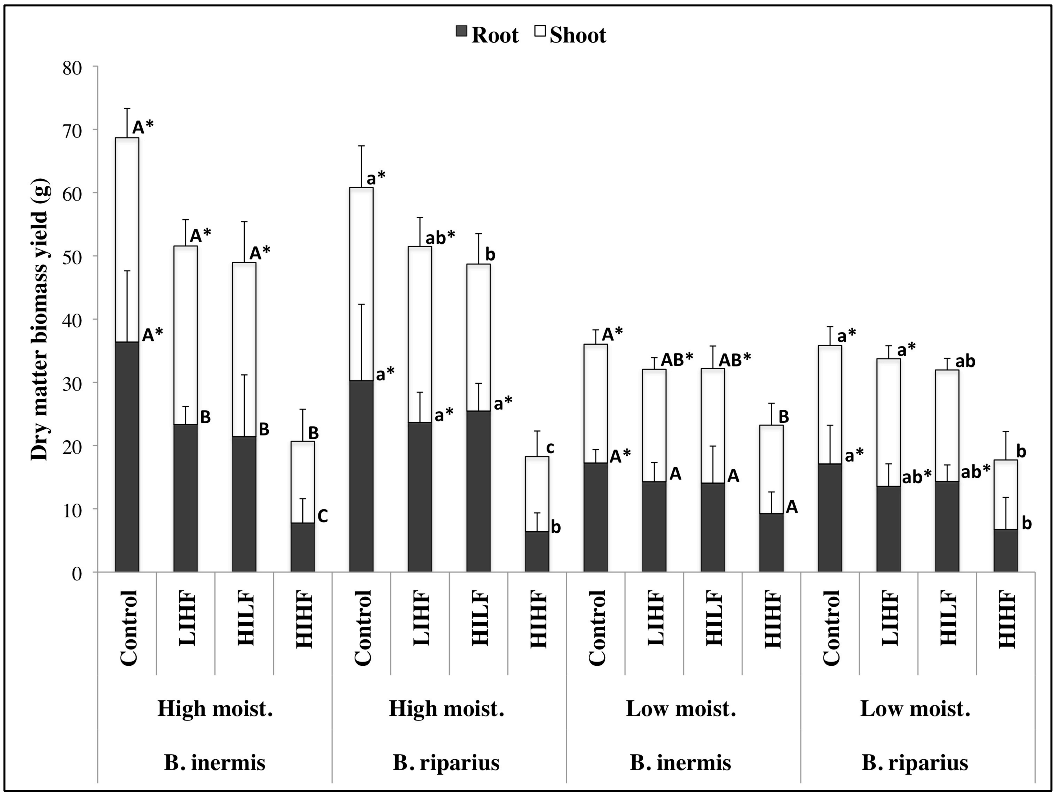


Figure 2-1. Accumulated mean shoot and root yield in *Bromus inermis* (rhizomatous) and *Bromus riparius* (caespitose) relative to high and low moisture, and control, low intensity high frequency (LIHF), high intensity low frequency (HILF), and high intensity high frequency (HIHF) defoliation. Error bars represent 95% confidence intervals. Upper- and lower-case letters denote mean separation among defoliation treatments within moisture regimes, while asterisks represent differences between high and low moisture within the same defoliation treatment. Mean comparisons are Tukey's adjusted ($P < 0.05$).

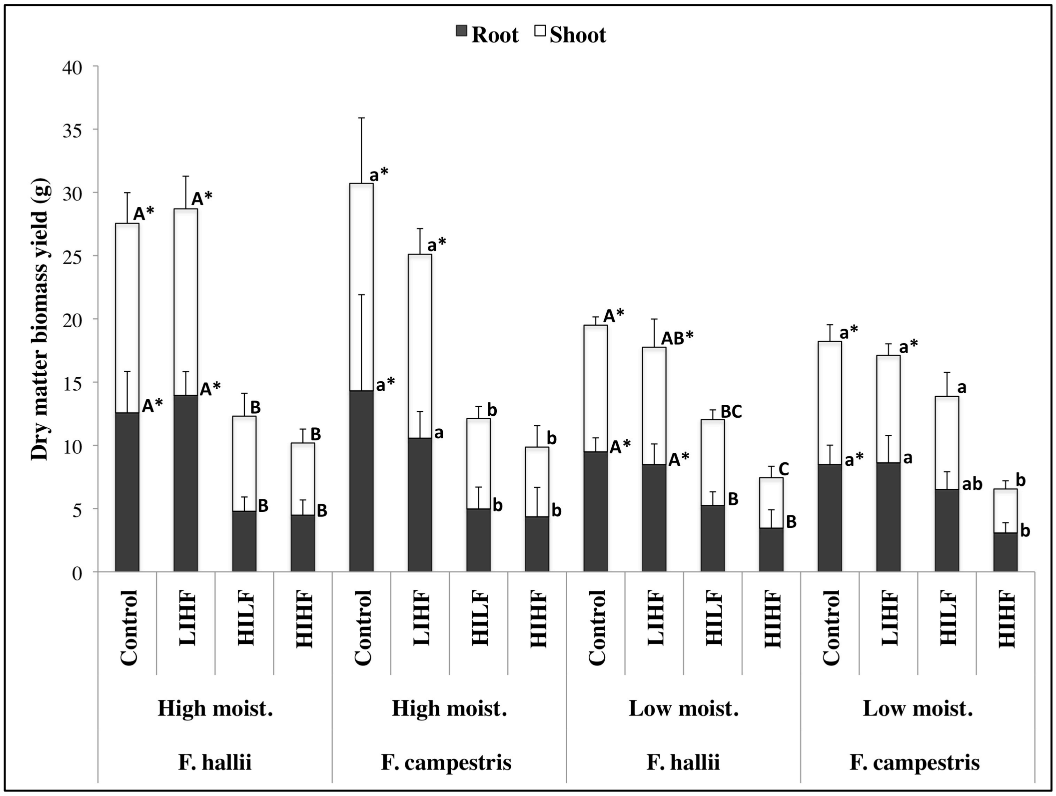


Figure 2-2. Accumulated mean shoot and root biomass in *Festuca hallii* (rhizomatous) and *Festuca campestris* (caespitose) relative to high and low moisture, and control, low intensity-high frequency (LIHF), high intensity-low frequency (HILF), and high intensity-high frequency (HIHF) defoliation. Error bars represent 95% confidence intervals. Upper- and lower-case letters denote mean separation among defoliation treatments within moisture regimes for *F. hallii* and *F. campestris*, respectively, while asterisks represent differences between high and low moisture within the same defoliation treatment. Mean comparisons are Tukey's adjusted ($p < 0.05$).

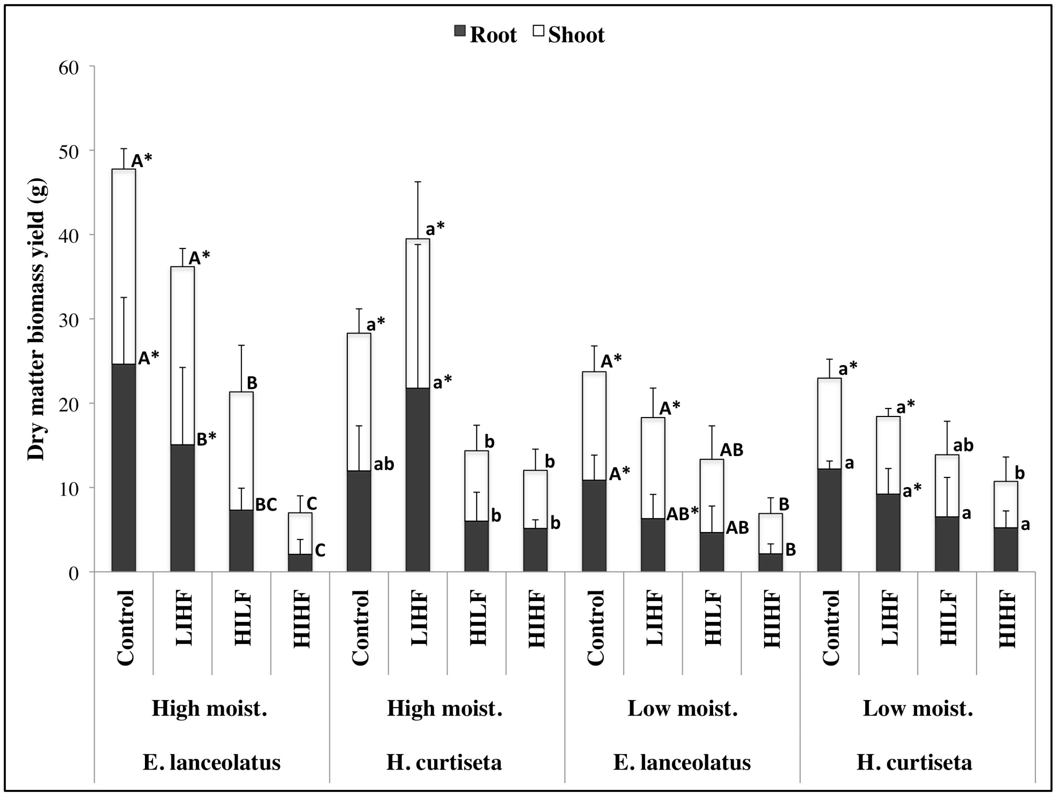


Figure 2-3. Accumulated mean shoot and root biomass in *Elymus lanceolatus* (rhizomatous) and *Hesperostipa curtiseta* (caespitose) relative to high and low moisture, and control, low intensity-high frequency (LIHF), high intensity-low frequency (HILF), and high intensity-high frequency (HIHF) defoliation. Error bars represent 95% confidence intervals. Upper- and lower-case letters denote mean separation among defoliation treatments within moisture regimes for *E. lanceolatus* and *H. curtiseta*, respectively, while asterisks represent differences between high and low moisture within the same defoliation treatment. Mean comparisons are Tukey's adjusted ($p < 0.05$).

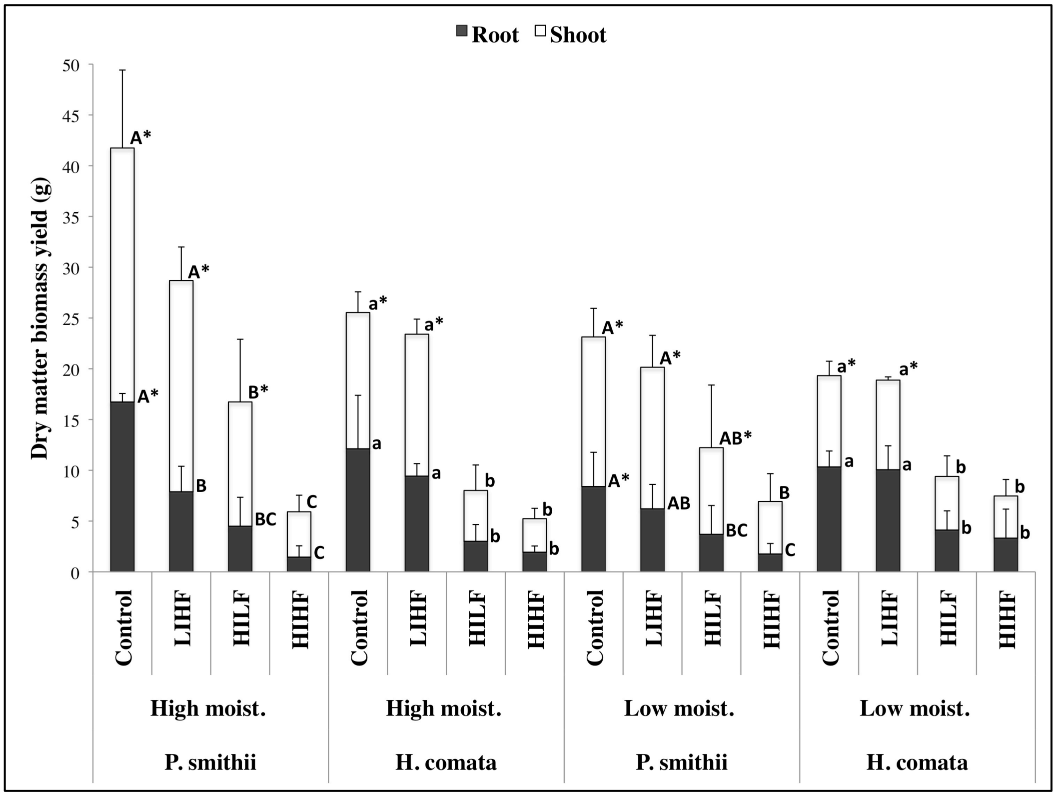


Figure 2-4. Accumulated mean shoot and root biomass in *Pascopyrum smithii* (rhizomatous) and *Hesperostipa comata* (caespitose) relative to high and low moisture, and control, low intensity-high frequency (LIHF), high intensity-low frequency (HILF), and high intensity-high frequency (HIHF) defoliation. Error bars represent 95% confidence intervals. Upper- and lower-case letters denote mean separation among defoliation treatments within moisture regimes for *P. smithii* and *H. comata*, respectively, while asterisks represent differences between high and low moisture within the same defoliation treatment. Mean comparisons are Tukey's adjusted ($p < 0.05$).

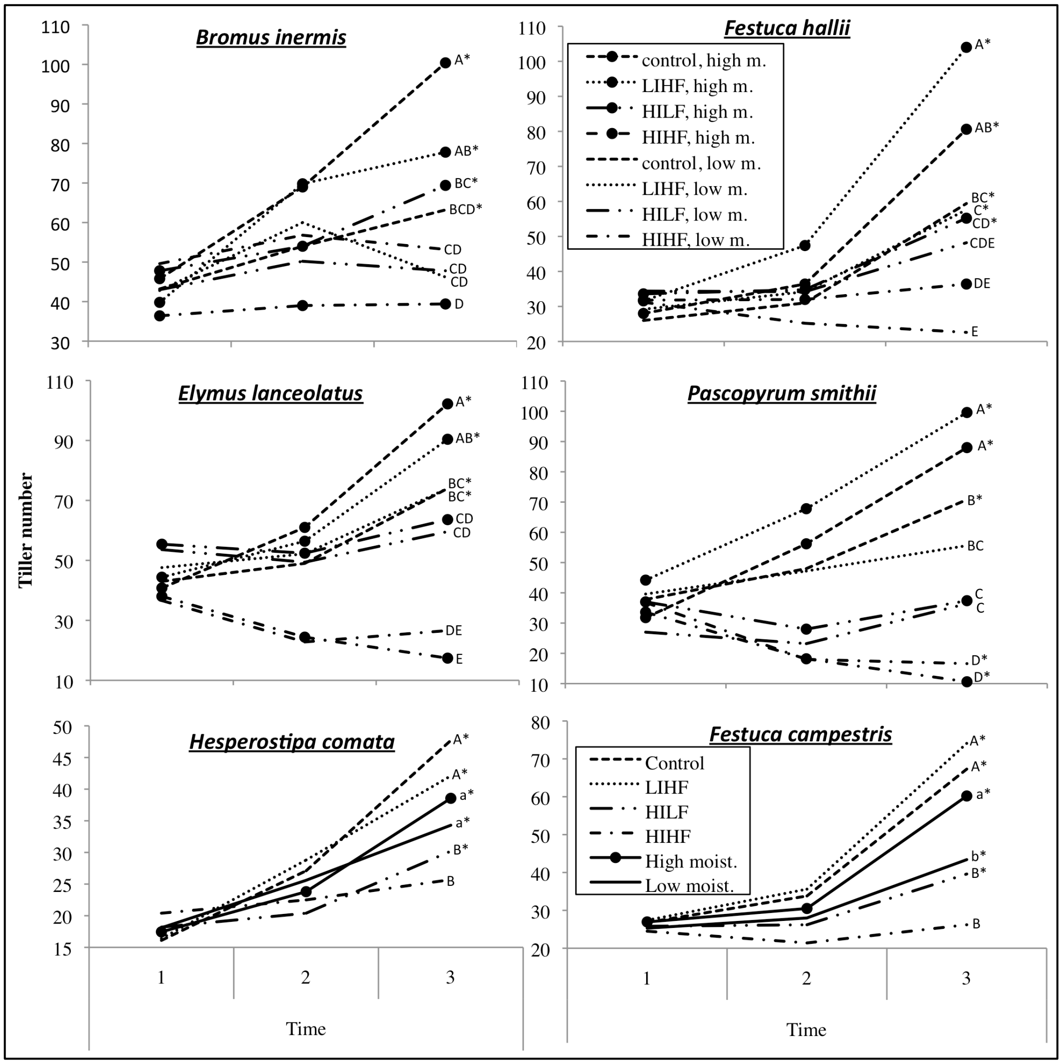


Figure 2-5. Tiller number changes from the beginning (time 1) to the end of the experiment (time 3) relative to defoliation treatments (control, low-intensity high-frequency [LIHF], high-intensity low-frequency [HILF], high-intensity high-frequency [HIHF]) under both high and low moisture for 6 graminoid species (top 4 are rhizomatous and bottom 2 are caespitose). Letters represent Tukey's adjusted differences ($P < 0.05$) in final tiller number, with initial tiller number used as a covariate; means with the same letter are not significantly different. Asterisks denote a significant change in tiller number from the beginning of the experiment. Lowercase letters represent mean comparisons among moisture treatments.

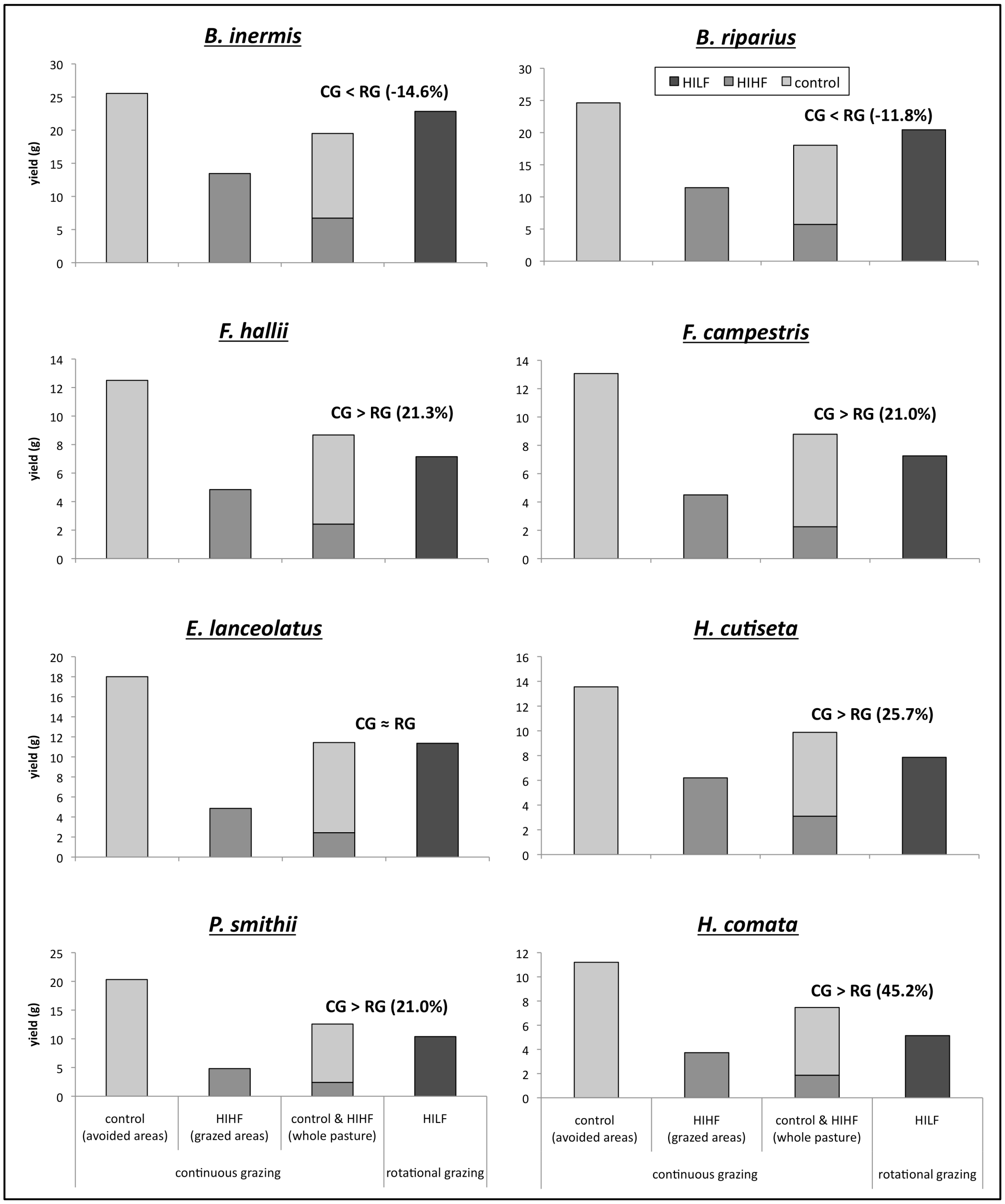


Figure 2-6. Conceptual model predicting rotational and continuous grazing (CG and RG) plant community yields (rhizomatous grasses on the left and caespitose grasses on the right) based on means (high and low moisture combined), assuming continuously grazed pastures consist of equal parts avoided (control) and intensively, recurrently grazed (HIHF) portions and rotational grazing involves homogenous, intense, and infrequent grazing (HILF). Percent differences between theoretical continuous whole pasture and rotational grazing yields (relative to RG) are in parentheses.

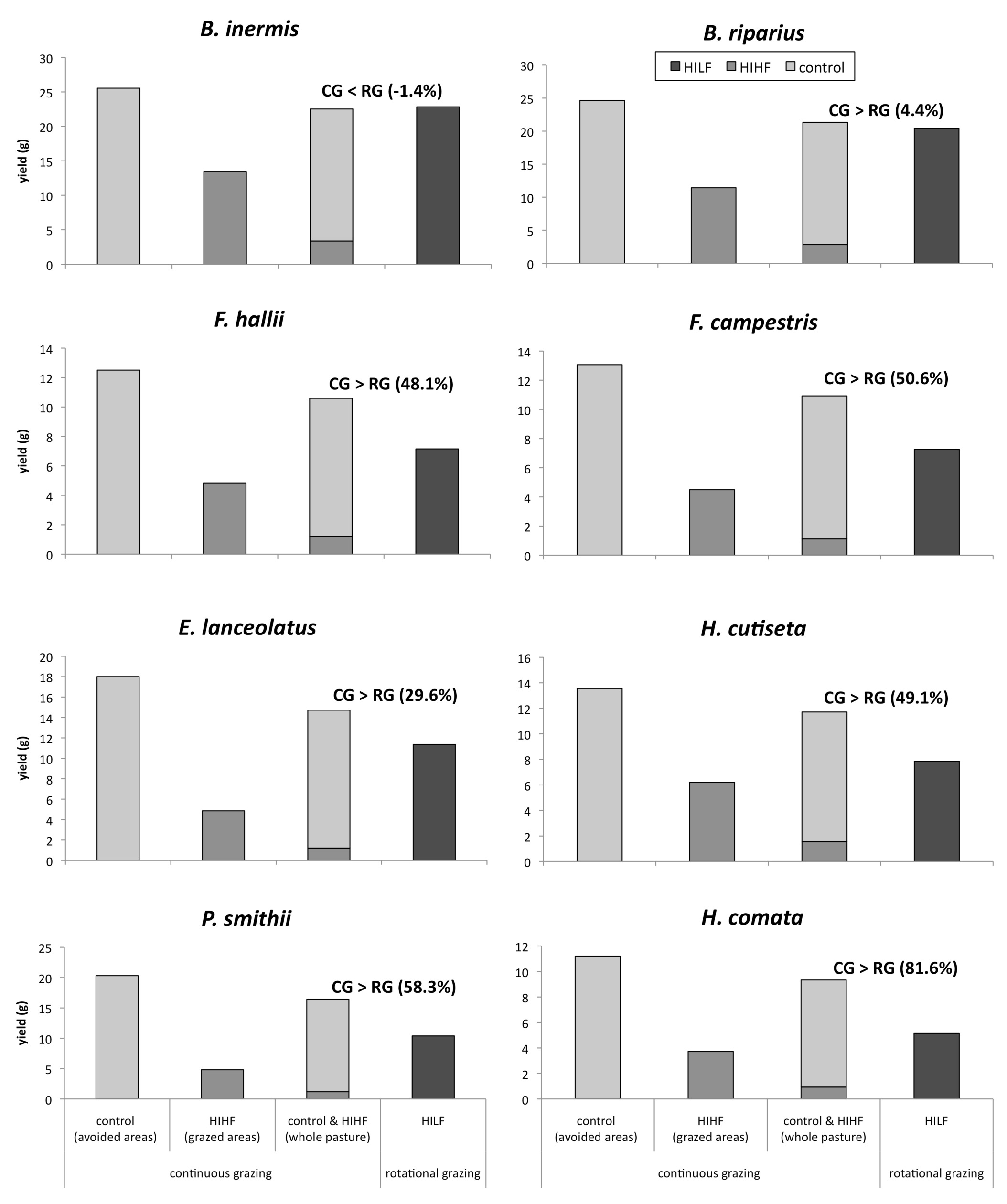


Figure 2-7. Conceptual model predicting rotational and continuous grazing (CG and RG) plant community yields (rhizomatous grasses on the left and caespitose grasses on the right) based on means (high and low moisture combined), assuming continuously grazed pastures consist of 75% avoided (control) and 25% intensively, recurrently grazed (HIHF) portions and rotational grazing involves homogenous, intense, and infrequent grazing (HILF). Percent differences between theoretical continuous whole pasture and rotational grazing yields (relative to RG) are in parentheses.

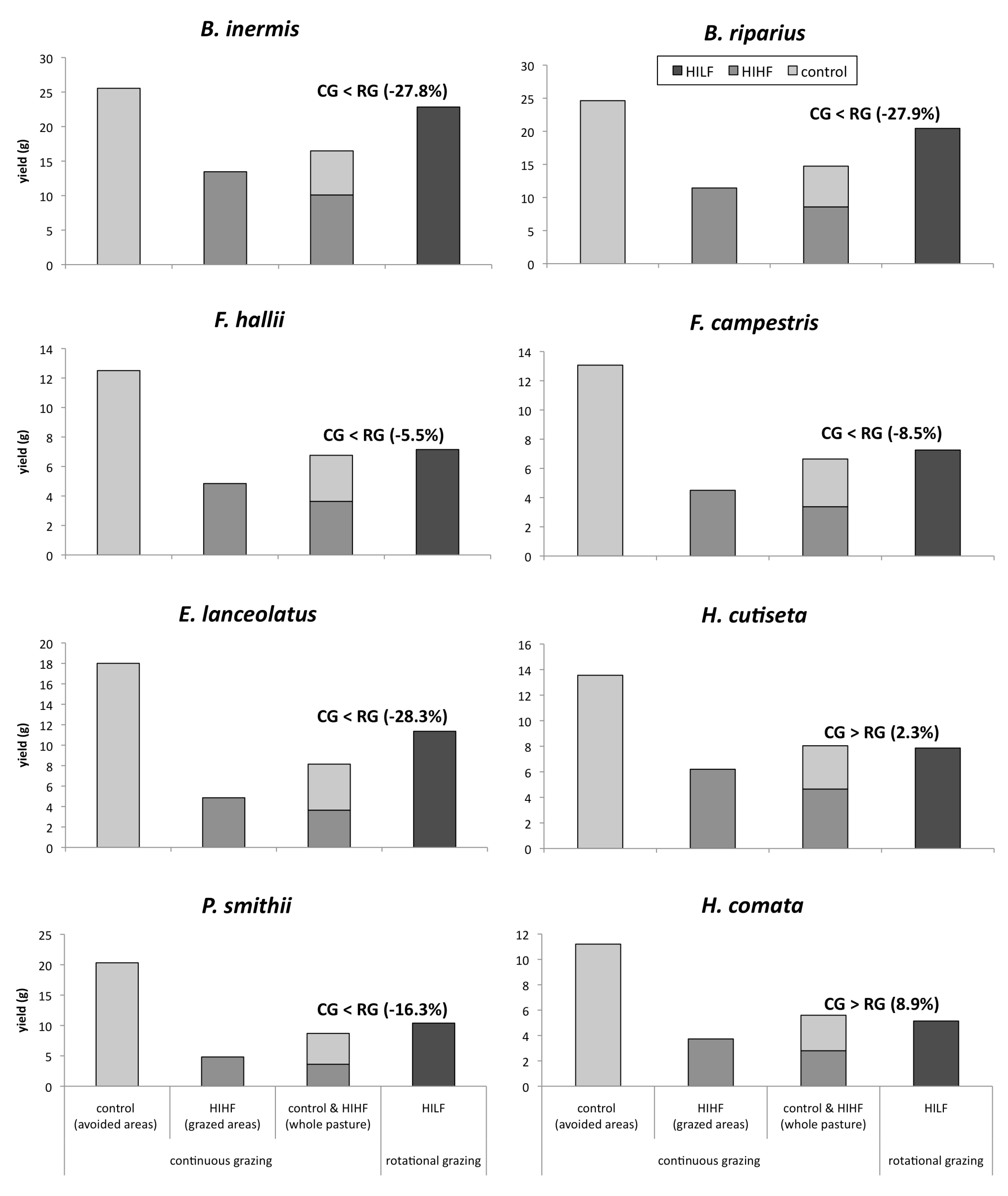


Figure 2-8. Conceptual model predicting rotational and continuous grazing (CG and RG) plant community yields (rhizomatous grasses on the left and caespitose grasses on the right) based on means (high and low moisture combined), assuming continuously grazed pastures consist of 25% avoided (control) and 75% intensively, recurrently grazed (HIHF) portions and rotational grazing involves homogenous, intense, and infrequent grazing (HILF). Percent differences between theoretical continuous whole pasture and rotational grazing yields (relative to RG) are in parentheses.

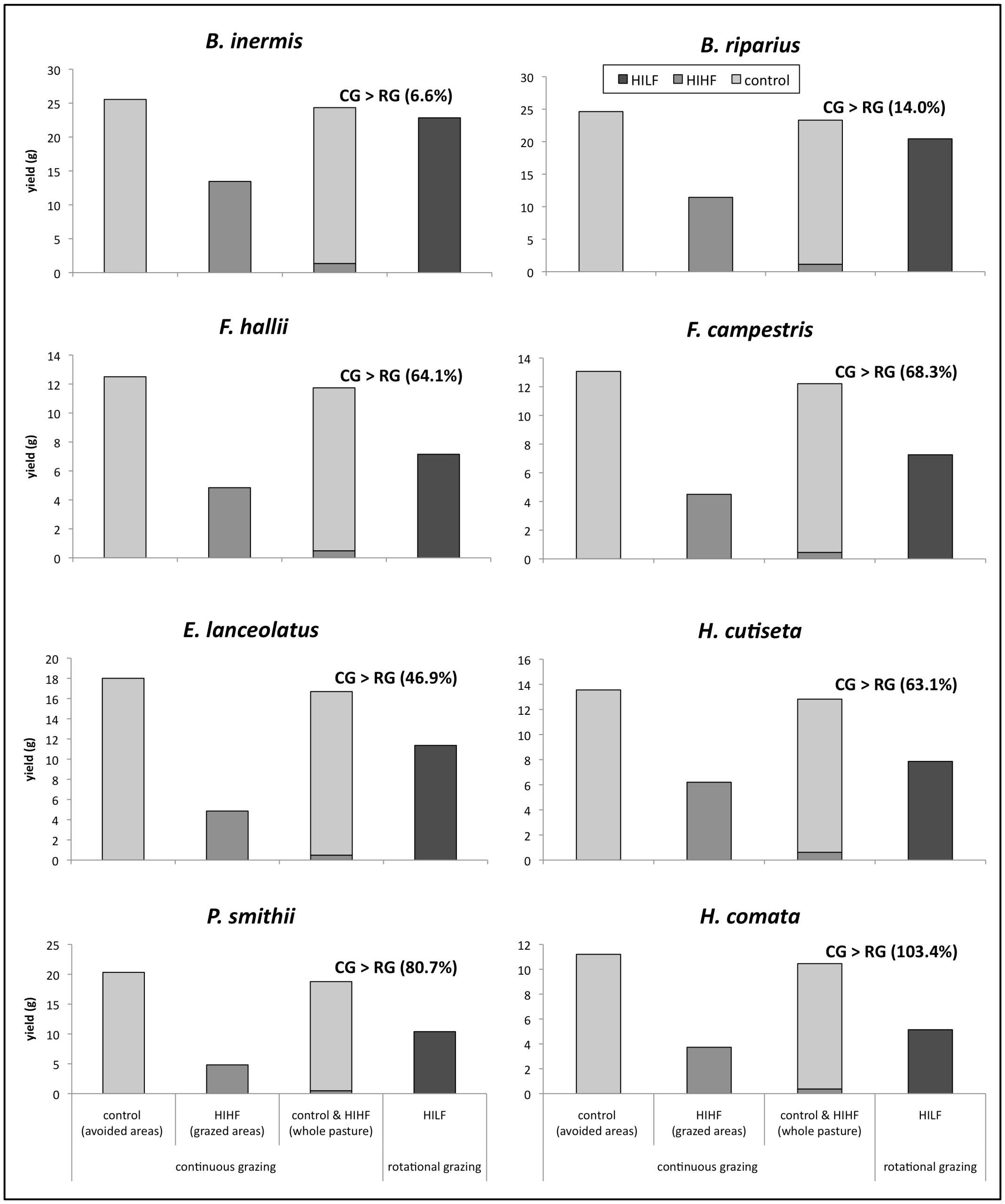


Figure 2-9. Conceptual model predicting rotational and continuous grazing (CG and RG) plant community yields (rhizomatous grasses on the left and caespitose grasses on the right) based on means (high and low moisture combined), assuming continuously grazed pastures consist of 10% avoided (control) and 90% intensively, recurrently grazed (HIHF) portions and rotational grazing involves homogenous, intense, and infrequent grazing (HILF). Percent differences between theoretical continuous whole pasture and rotational grazing yields (relative to RG) are in parentheses.

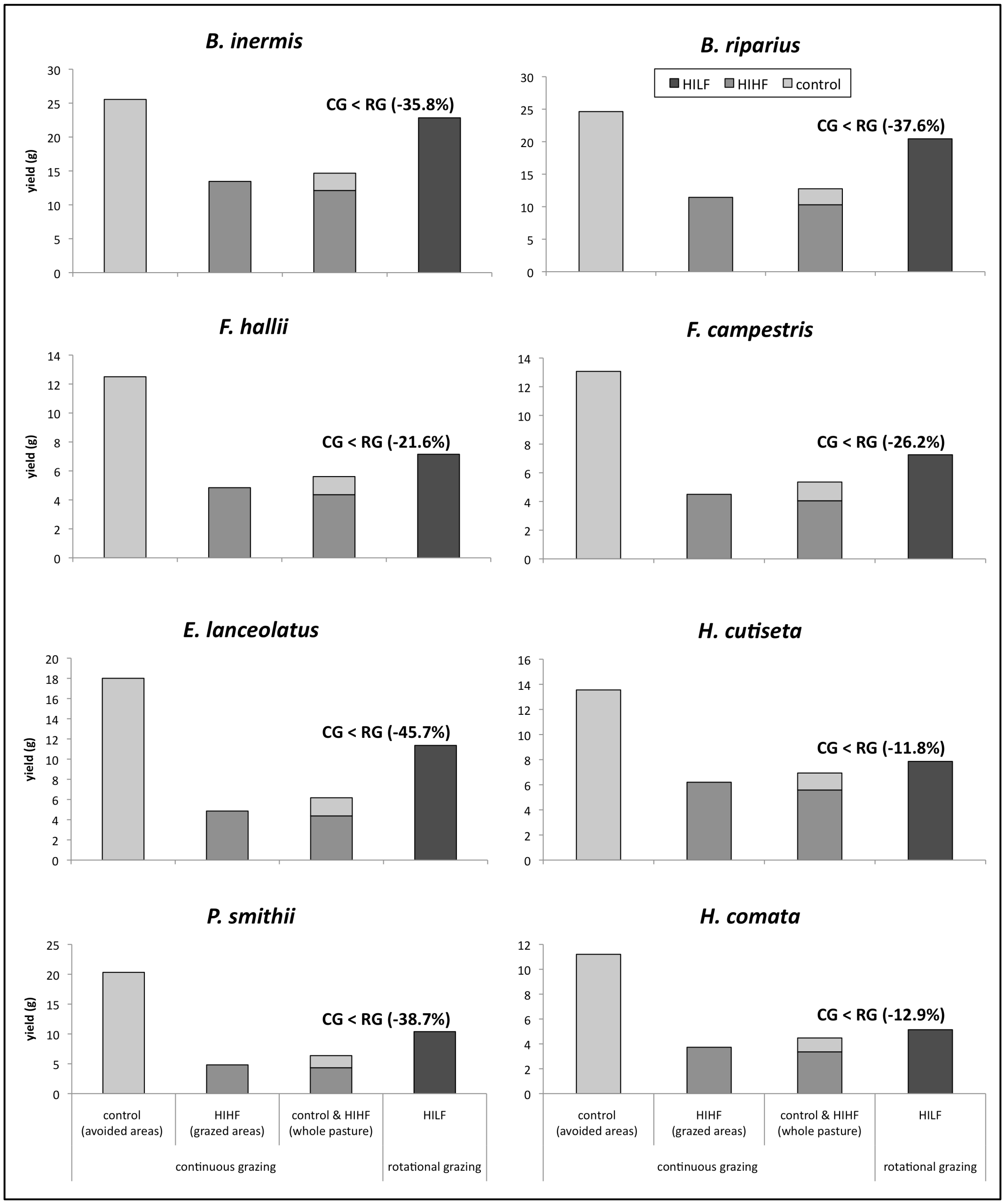
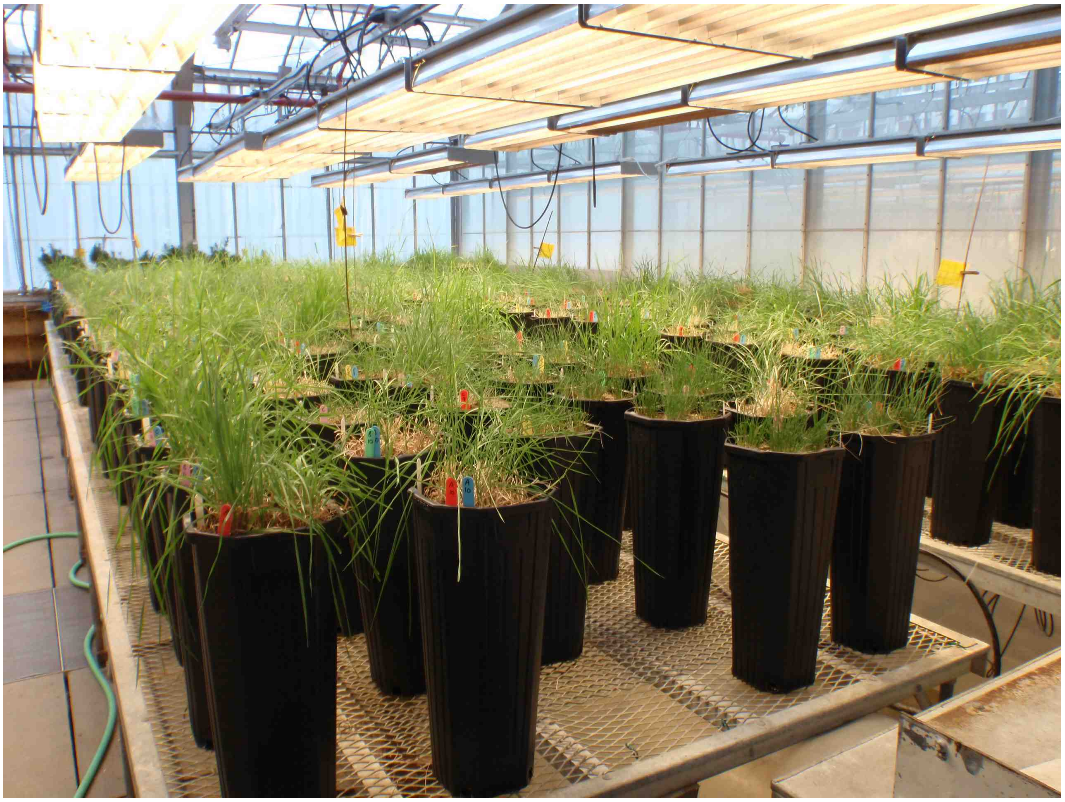
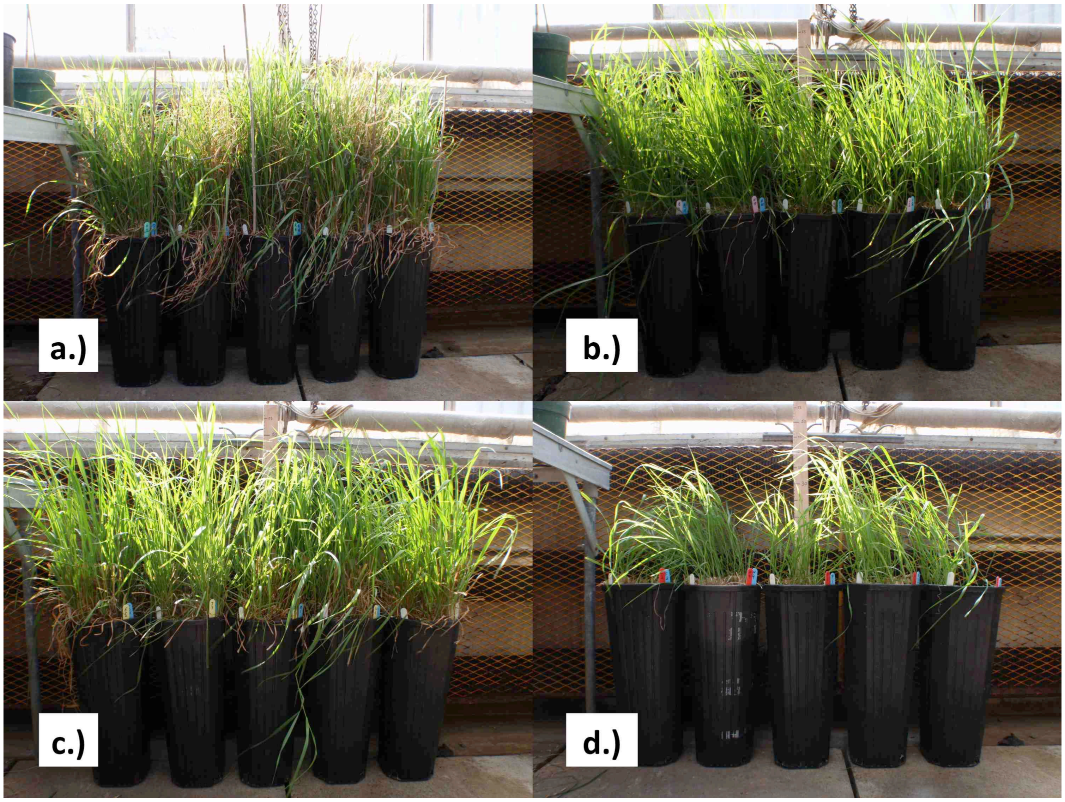


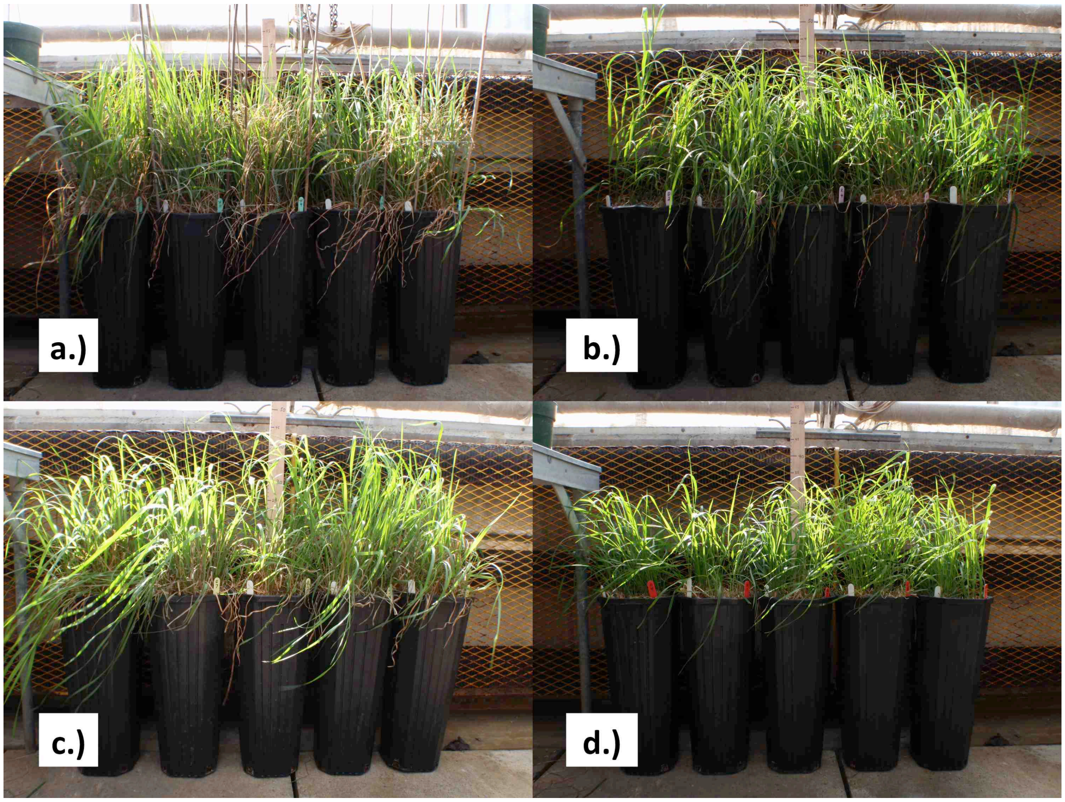
Figure 2-10. Conceptual model predicting rotational and continuous grazing (CG and RG) plant community yields (rhizomatous grasses on the left and caespitose grasses on the right) based on means (high and low moisture combined), assuming continuously grazed pastures consist of 90% avoided (control) and 10% intensively, recurrently grazed (HIHF) portions and rotational grazing involves homogenous, intense, and infrequent grazing (HILF). Percent differences between theoretical continuous whole pasture and rotational grazing yields (relative to RG) are in parentheses.



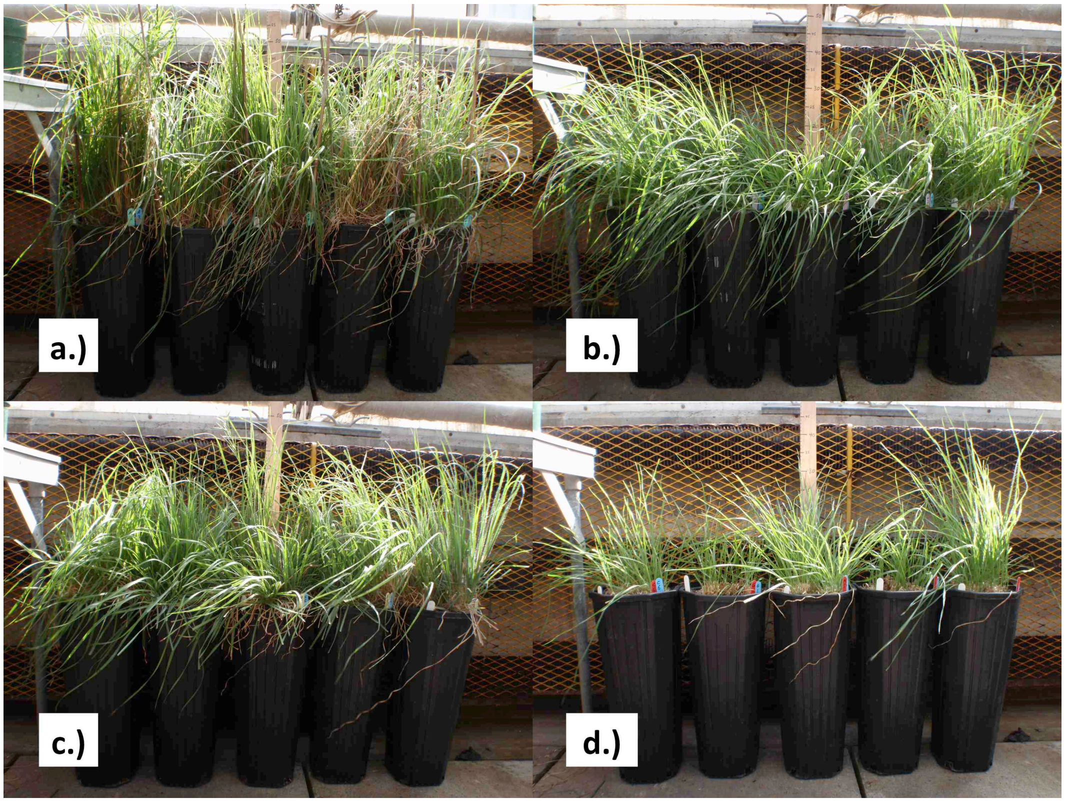
Photograph 2-1. Greenhouse experiment pot arrangement.



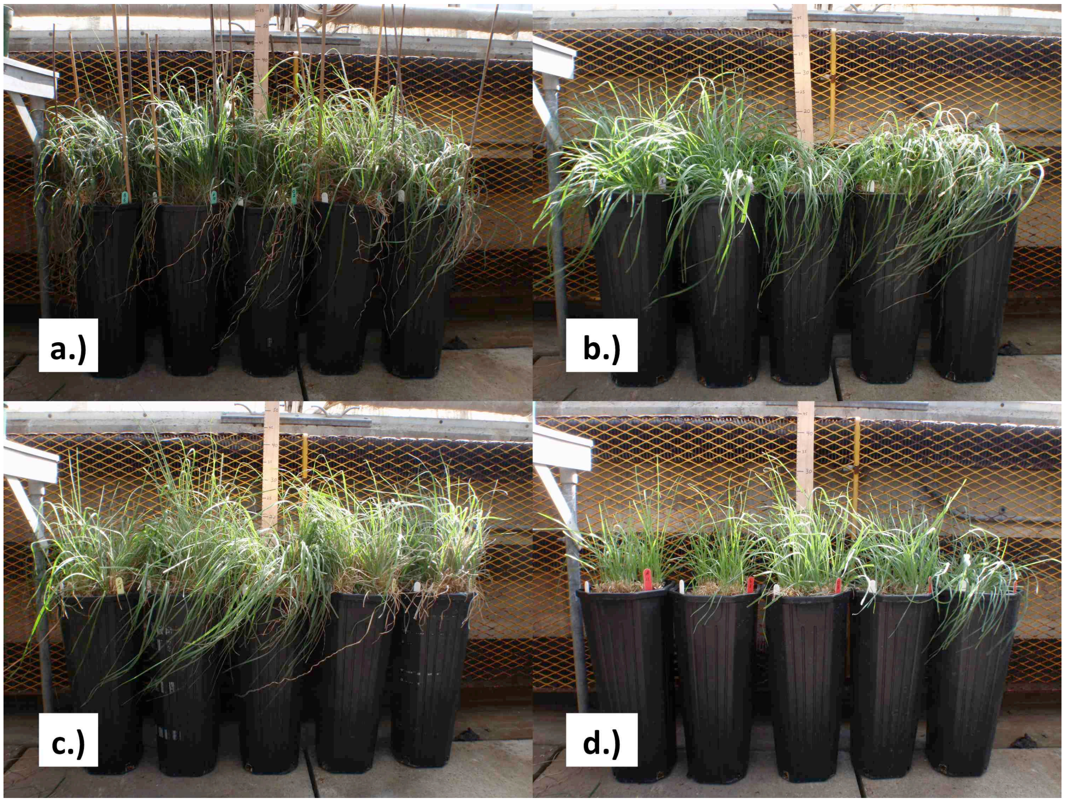
Photograph 2-2. *Bromus inermis* pots at the end of the experiment under high moisture and control (a.), HILF (b.), LIHF (c.), and HIHF (d.) defoliation.



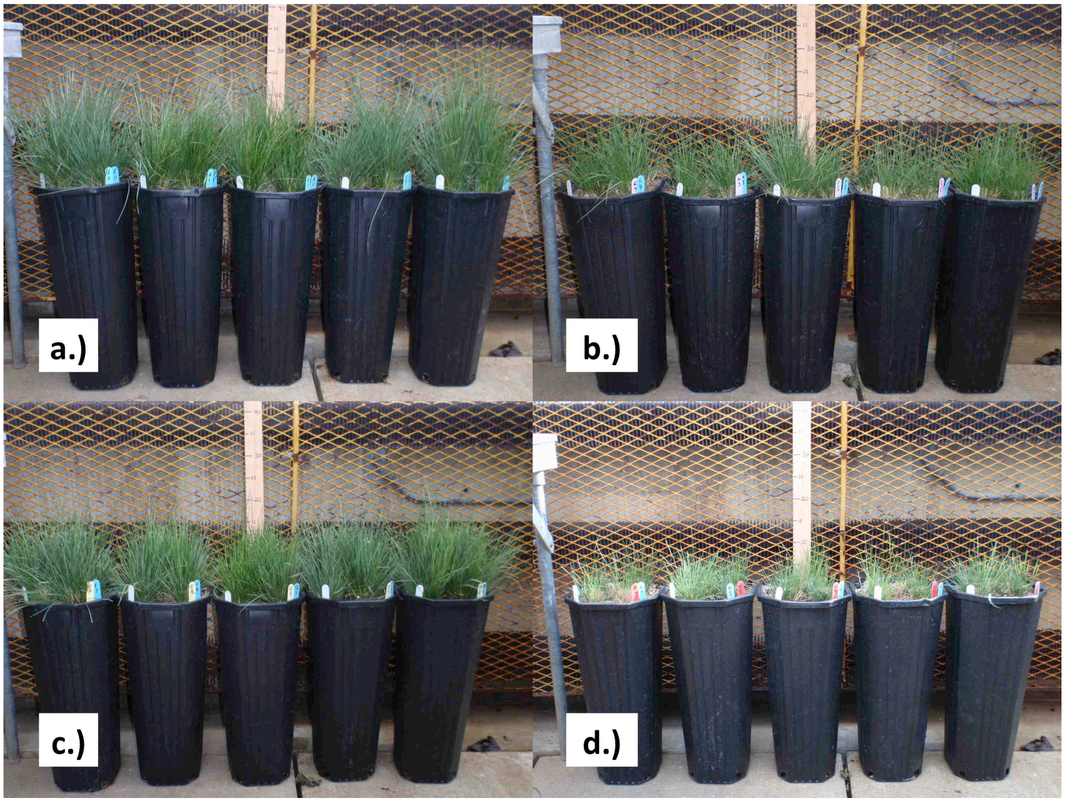
Photograph 2-3. *Bromus inermis* pots at the end of the experiment under low moisture and control (a.), HILF (b.), LIHF (c.), and HIHF (d.) defoliation.



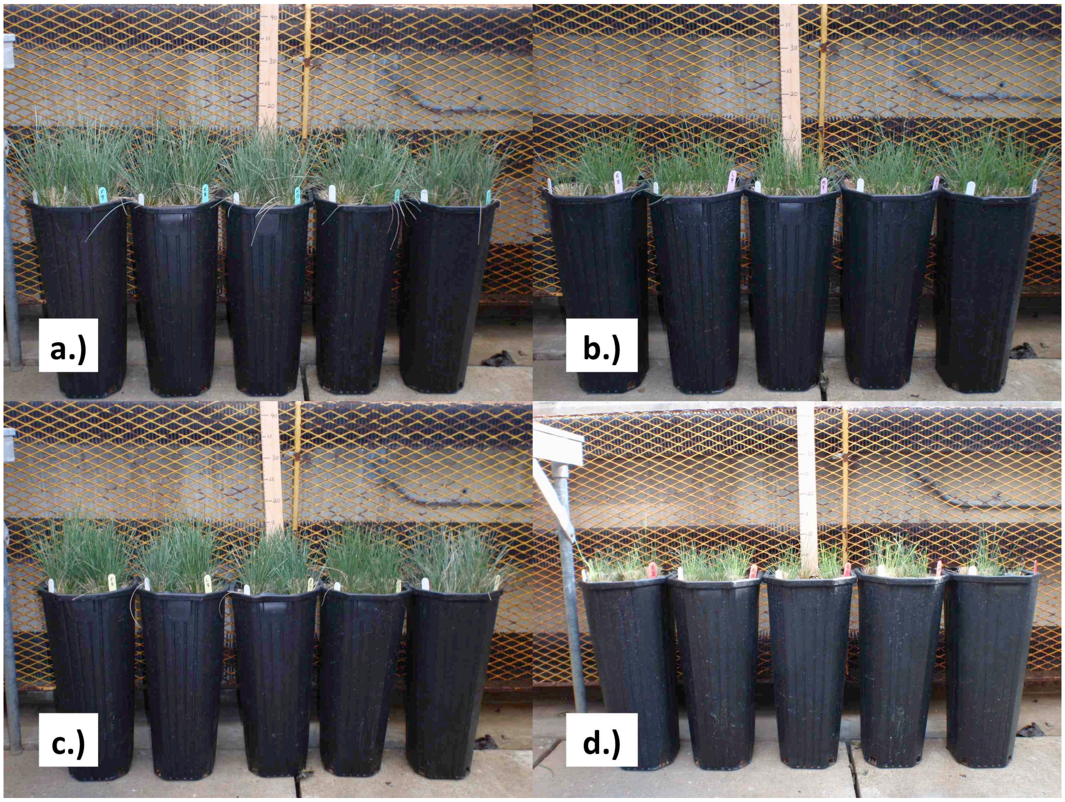
Photograph 2-4. *Bromus riparius* pots at the end of the experiment under high moisture and control (a.), HILF (b.), LIHF (c.), and HIHF (d.) defoliation.



Photograph 2-5. *Bromus riparius* pots at the end of the experiment under low moisture and control (a.), HILF (b.), LIHF (c.), and HIHF (d.) defoliation.

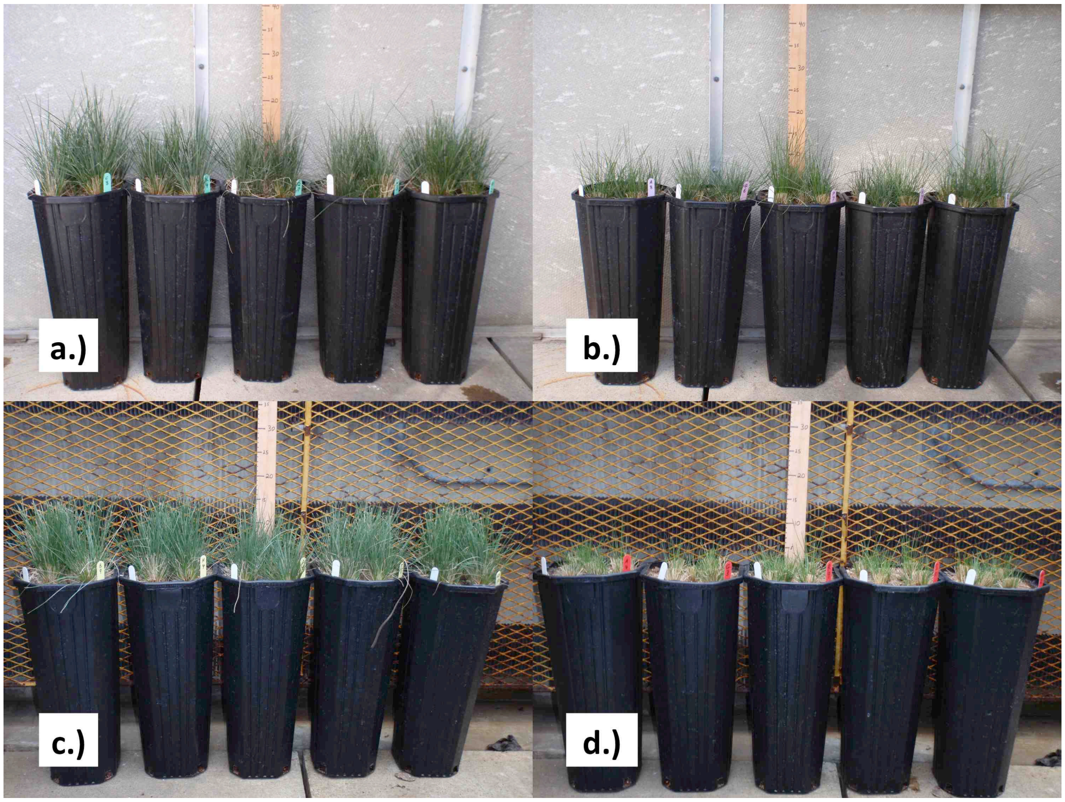


Photograph 2-6. *Festuca hallii* pots at the end of the experiment under high moisture and control (a.), HILF (b.), LIHF (c.), and HIHF (d.) defoliation.

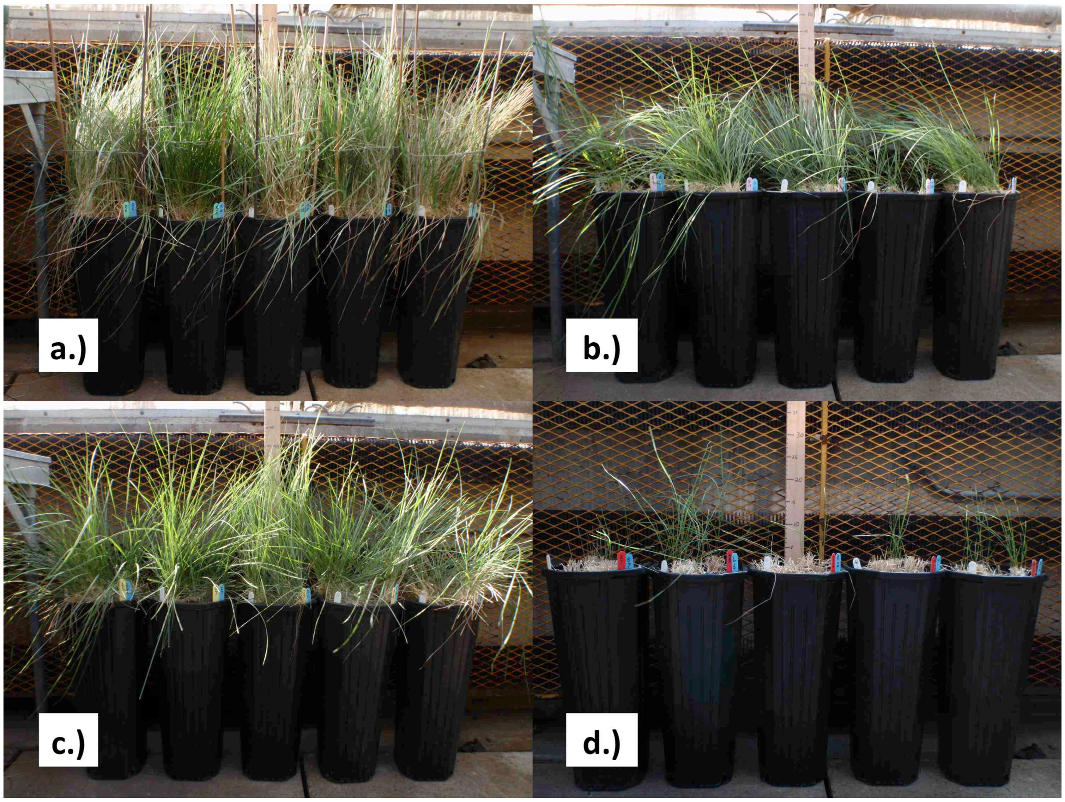


Photograph 2-7. *Festuca hallii* pots at the end of the experiment under low moisture and control (a.), HILF (b.), LIHF (c.), and HIHF (d.) defoliation.

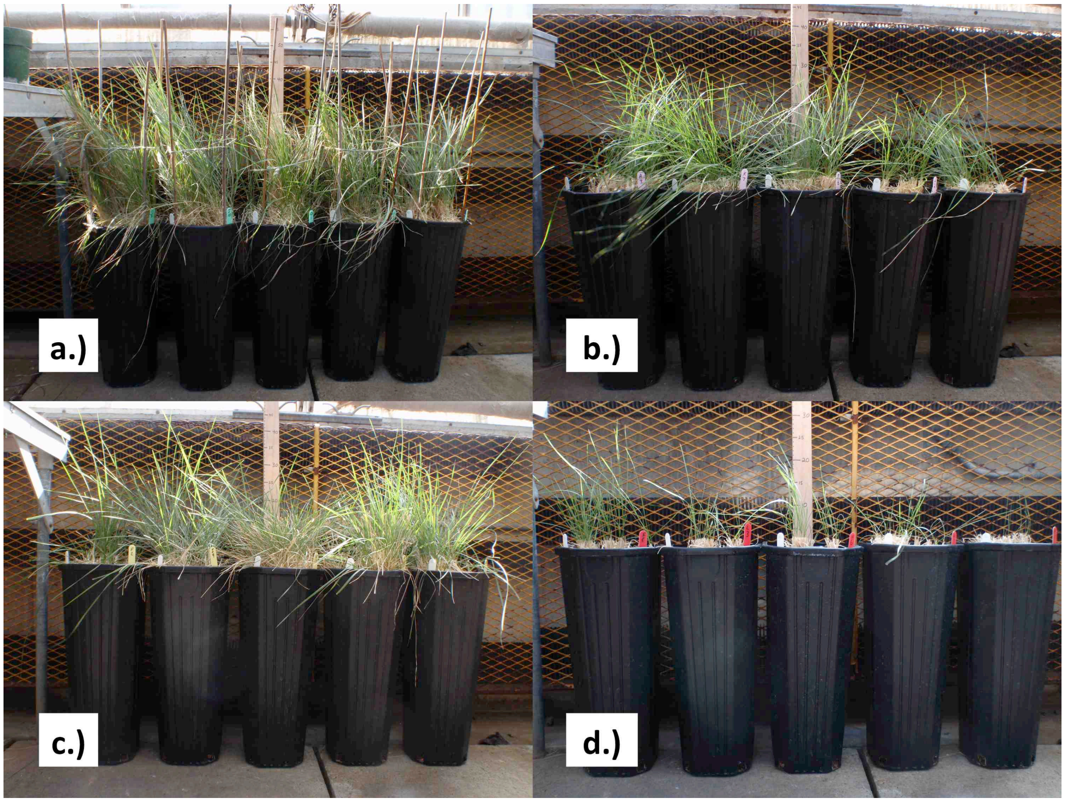
Photograph 2-8. *Festuca campestris* pots at the end of the experiment under high moisture and control (a.), HILF (b.), LIHF (c.), and HIHF (d.) defoliation.



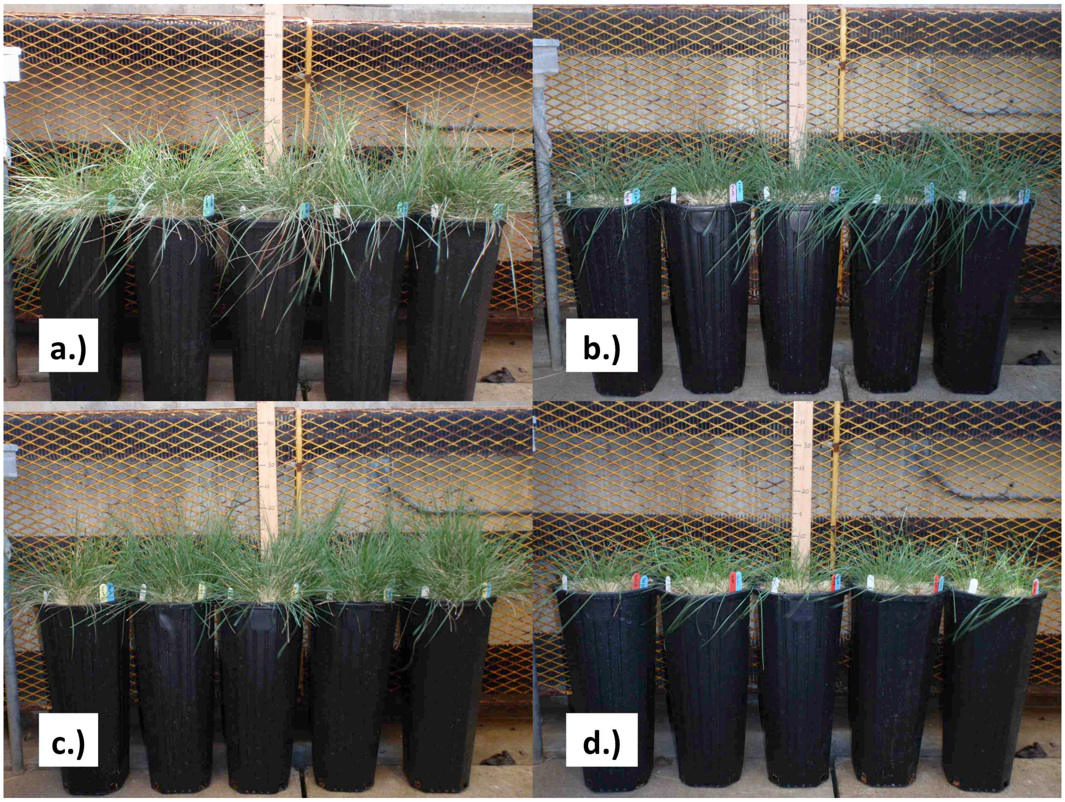
Photograph 2-9. *Festuca campestris* pots at the end of the experiment under low moisture and control (a.), HILF (b.), LIHF (c.), and HIHF (d.) defoliation.



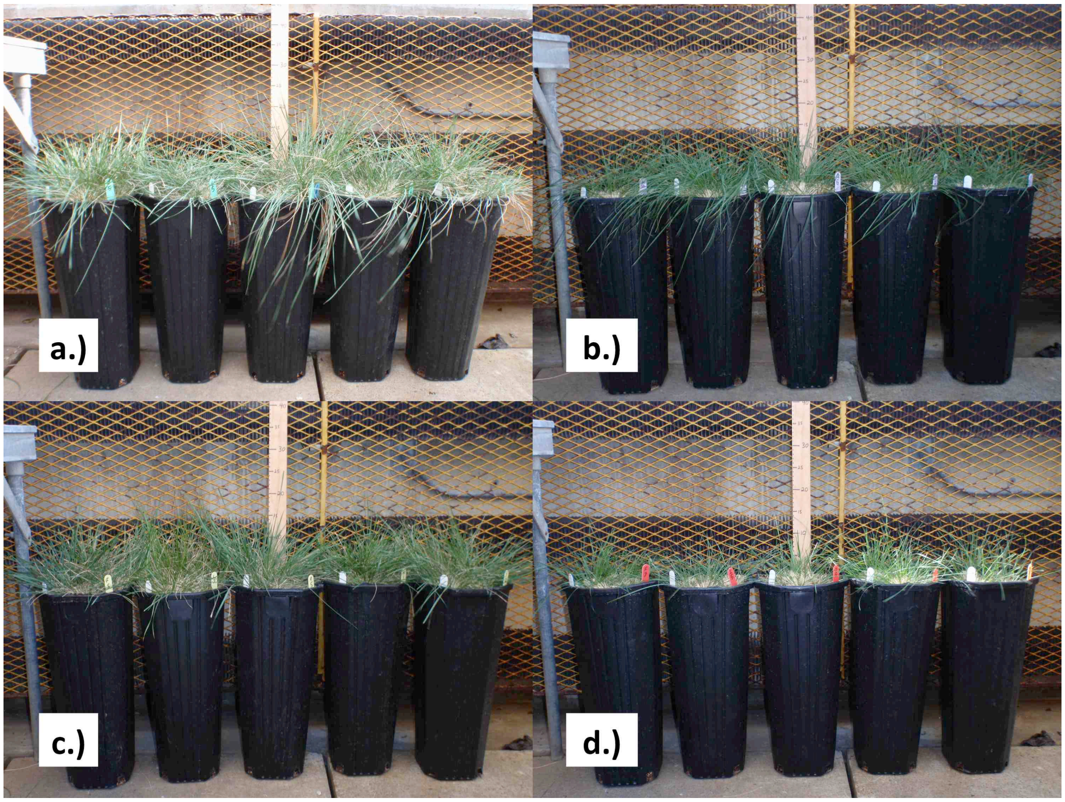
Photograph 2-10. *Elymus lanceolatus* pots at the end of the experiment under high moisture and control (a.), HILF (b.), LIHF (c.), and HIHF (d.) defoliation.



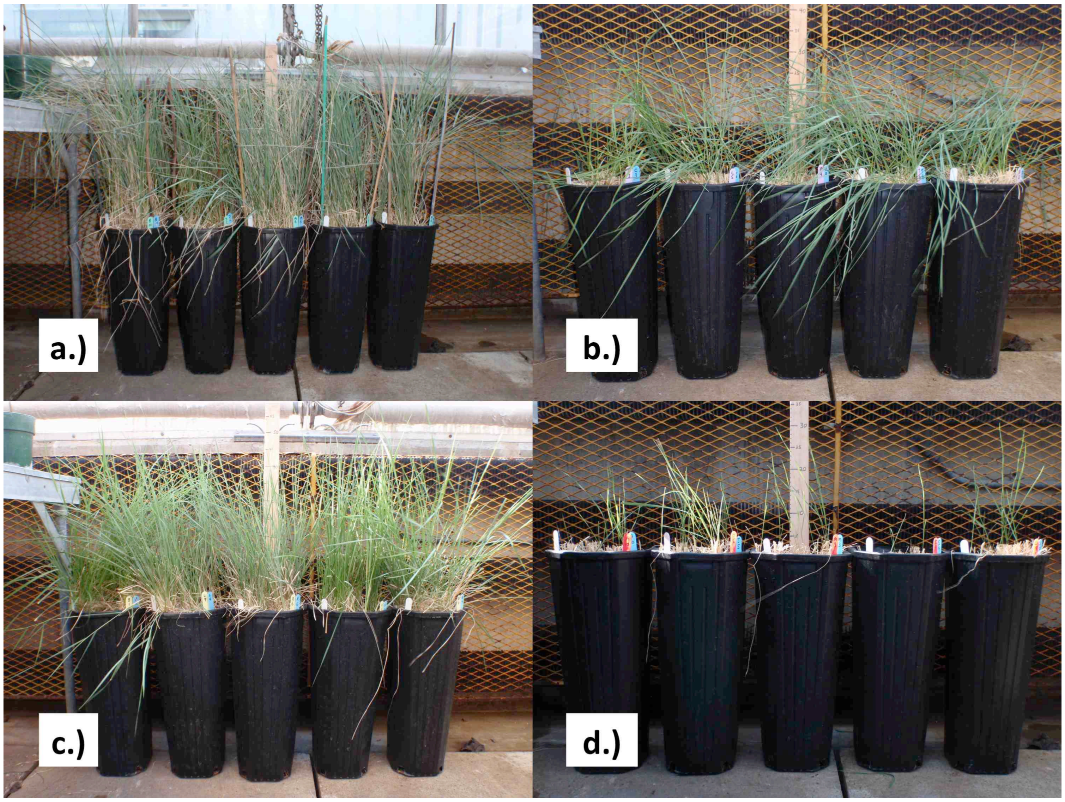
Photograph 2-11. *Elymus lanceolatus* pots at the end of the experiment under low moisture and control (a.), HILF (b.), LIHF (c.), and HIHF (d.) defoliation.



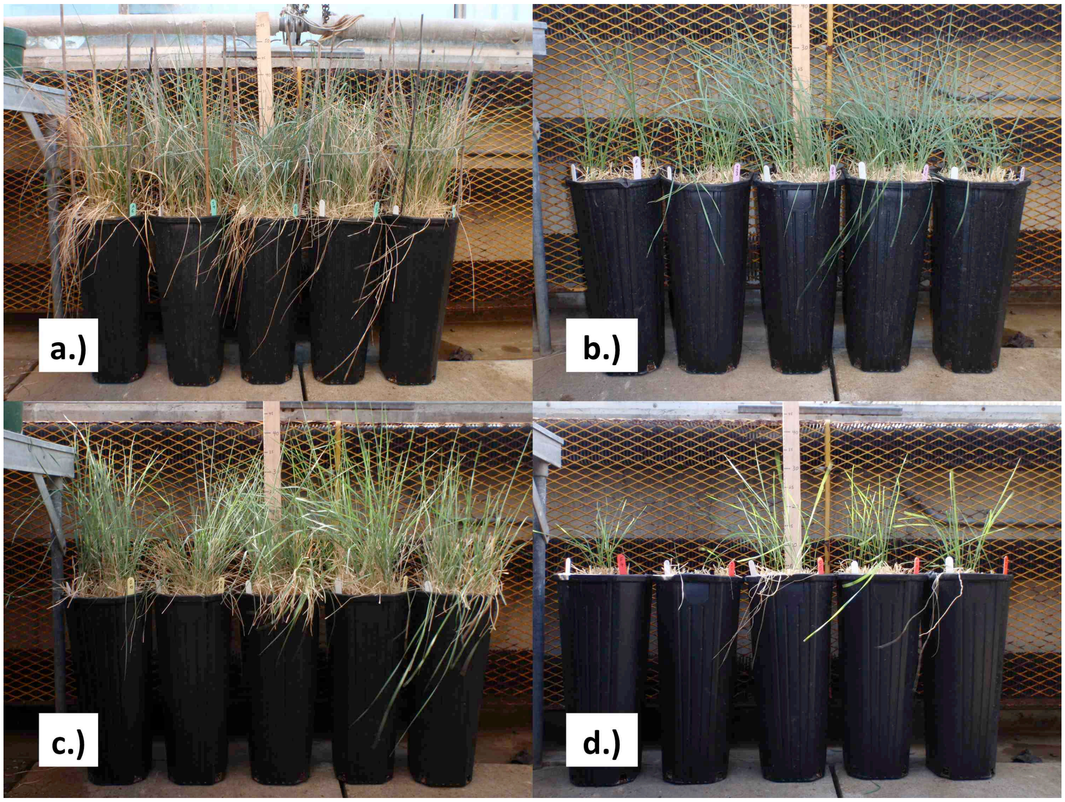
Photograph 2-12. *Hesperostipa curtiseta* pots at the end of the experiment under high moisture and control (a.), HILF (b.), LIHF (c.), and HIHF (d.) defoliation.



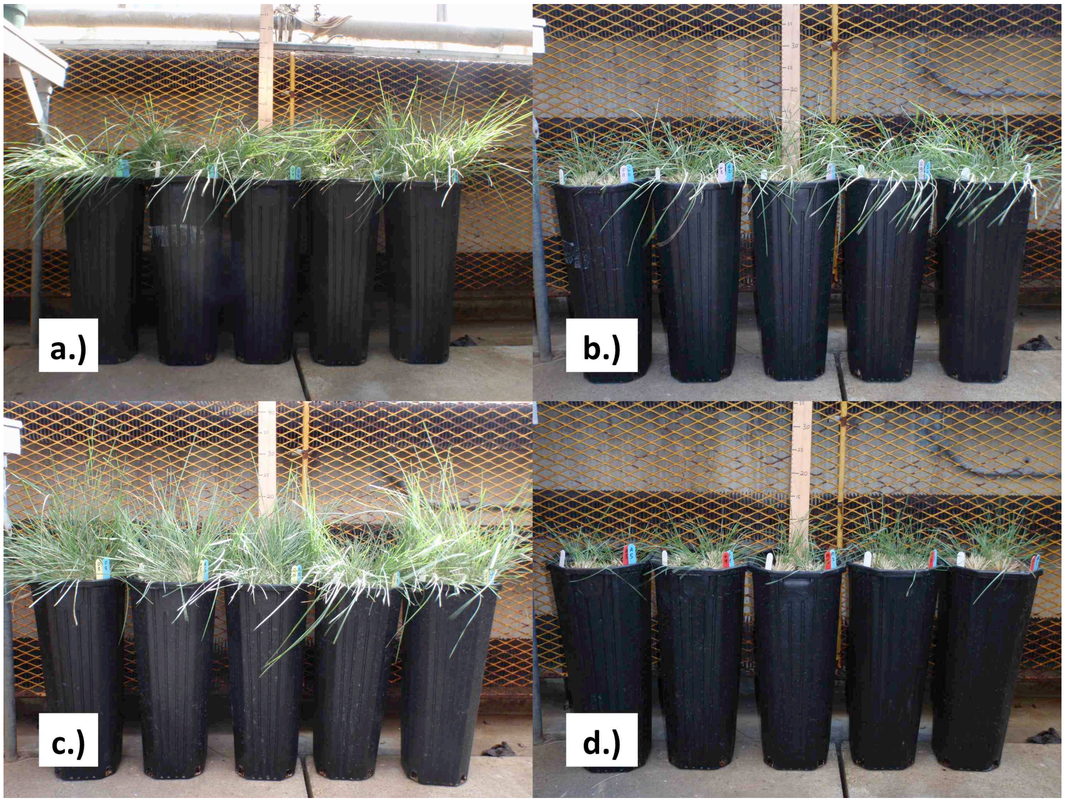
Photograph 2-13. *Hesperostipa curtiseta* pots at the end of the experiment under low moisture and control (a.), HILF (b.), LIHF (c.), and HIHF (d.) defoliation.



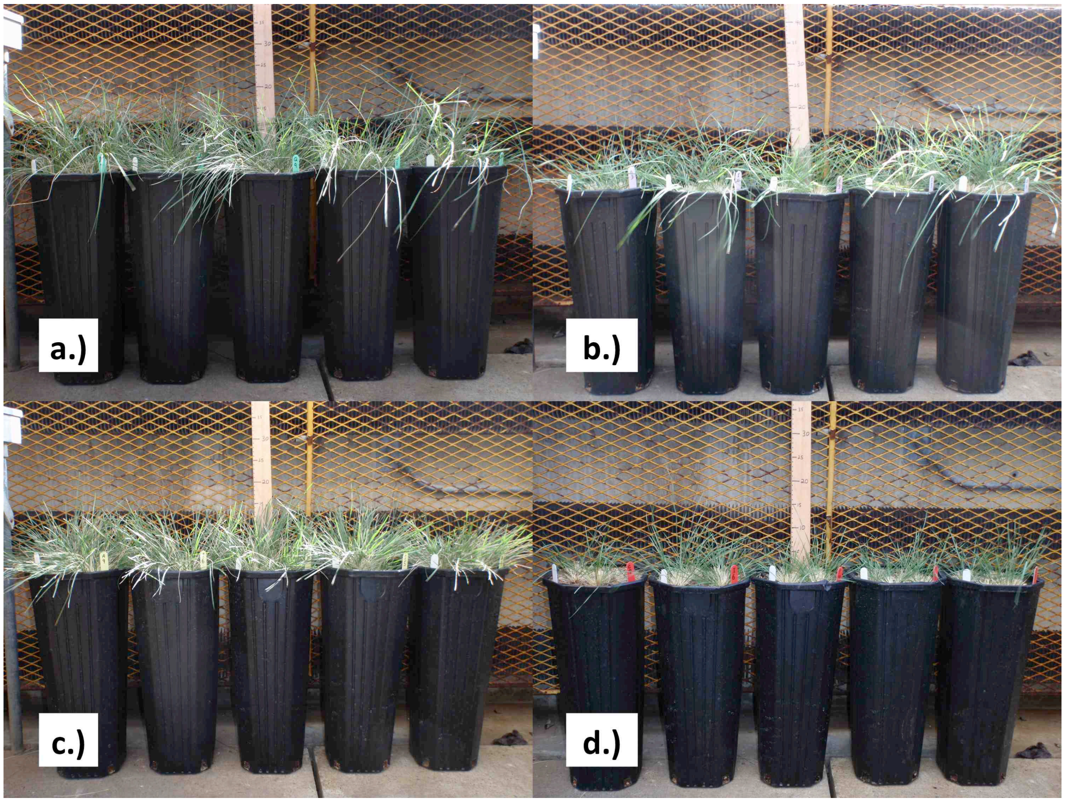
Photograph 2-14. *Pascopyrum smithii* pots at the end of the experiment under high moisture and control (a.), HILF (b.), LIHF (c.), and HIHF (d.) defoliation.



Photograph 2-15. *Pascopyrum smithii* pots at the end of the experiment under low moisture and control (a.), HILF (b.), LIHF (c.), and HIHF (d.) defoliation.



Photograph 2-16. *Hesperostipa comata* pots at the end of the experiment under high moisture and control (a.), HILF (b.), LIHF (c.), and HIHF (d.) defoliation.



Photograph 2-17. *Hesperostipa comata* pots at the end of the experiment under low moisture and control (a.), HILF (b.), LIHF (c.), and HIHF (d.) defoliation.

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Chapter 3. *Pascopyrum smithii* and *Hesperostipa comata* shoot growth and yield under three years of clipping and watering in the Dry Mixedgrass Prairie: A test of determinate growth

3.1. Abstract

One benefit of rotational grazing may be that plant compensatory re-growth responses can be capitalized on through re-grazing of pastures. However, determinate growth in xeriphytic vegetation may limit compensatory growth potential. Moreover, determinate growth may be more associated with caespitose, compared to rhizomatous, grasses. This study compared tiller growth rates, tiller population dynamics, and ultimately plant yield in two dominant grasses of the Mixedgrass Prairie that are of contrasting growth form: *Hesperostipa comata* (caespitose) and *Pascopyrum smithii* (rhizomatous), which were hypothesized to have more determinate and indeterminate growth, respectively. Treatments included defoliation (deferred [control]; high intensity low frequency [HILF], low intensity high frequency [LIHF], and high intensity high frequency [HIHF]) and moisture (ambient and addition), applied in both a relatively drier and more mesic, lowland and upland site, respectively. Growth responses were site specific for *P. smithii*, such that all defoliation regimes increased tiller growth rates (relative to controls) in the upland site, whereas HILF and LIHF defoliation

reduced growth rates in the lowland site. Moisture addition increased growth rates, and there was little evidence that there were seasonal differences in plant growth under either defoliation or moisture for *P. smithii*. In contrast, all defoliation regimes, but especially HIHF, increased tiller growth rates for *H. comata*, primarily in the latter part of the growing season when control plants were senescing, and moisture did not influence growth rates. Defoliation effects on seasonal tiller population dynamics for both grasses differed among growing seasons and moisture treatments. Generally, repeated growing season defoliation at high intensity reduced tiller populations, especially in the latter years of the experiment. And only for *P. smithii* did tiller populations increase under deferred (control) defoliation. Plant yield largely reflected defoliation and moisture effects on final tiller numbers, with high frequency defoliation, regardless of intensity, reducing plant yield relative to the controls for both grasses. Results suggest that neither grass may grow determinately under varied defoliation, whereas moisture conditions may promote more determinate and indeterminate growth in *H. comata* and *P. smithii*, respectively.

3.2. Introduction

Recent literature reviews suggest that rotational grazing (RG), despite strong perceptions to the contrary, does not promote plant community productivity or standing crop relative to continuous grazing (CG) on rangelands (Holechek *et al.* 2000; Briske *et al.* 2008). RG involves subdividing a management unit into smaller paddocks, which are then grazed intermittently in a single growing season. Often high stocking densities are used to limit animal selectivity and control the frequency and uniformity of vegetation defoliation (Derner *et al.* 1994; Volesky 1994). Nevertheless, defoliation under this system can vary from intense events followed by long rest periods (Savory 1999), to low intensity defoliation at higher frequencies with shorter rest periods.

In contrast, CG involves season-long use of a contiguous area. Defoliation regimes under CG can be variable, with some areas intensively utilized at the expense of other areas being avoided or lightly utilized (Ring *et al.* 1985; Willms *et al.* 1988). Although the degree to which this occurs may depend on moisture conditions, pasture heterogeneity, and plant community characteristics (Bailey and Brown 2011). It is thus unclear exactly what defoliation regimes actually occur across various grazing systems, which makes inferences regarding why RG does not enhance plant community productivity difficult.

Nevertheless, understanding how frequency and intensity of defoliation regulate plant growth and forage yield is necessary to evaluate the merits of RG. RG entails that opportunities exist to re-graze pastures, which would be beneficial if grazing/defoliation stimulates compensatory plant responses (McNaughton 1983) that can be capitalized on through re-grazing. Indeed, although defoliation tolerance varies widely among grasses (Caldwell *et al.* 1981), defoliation does not universally compromise grass productivity (Donkor *et al.* 2002; De Bruijn *et al.* 2003; Donkor *et al.* 2003; De Bruijn and Bork 2010), and in some cases may maximize it at some intermittent frequency and intensity (Turner *et al.* 1993). Thus, defoliation at given frequencies under RG may be beneficial if plants can both cope and re-grow vigorously.

Grasses have various mechanisms to cope with defoliation, including basal buds from which new ramets (*i.e.*, tillers) originate, culmless shoots that maintain apical meristems near the ground surface, and intercalary meristems from which additional leaf material can be produced (Coughenour 1985). Plant re-growth can thus occur laterally through the activation of basal buds and recruitment of new tillers, or vertically through the production of additional phytomers via the apical meristem or the extension of existing leaves via the intercalary meristem (Sharman 1945). Defoliation can increase shoot growth and forage yields (*i.e.*, overcompensate) if the rate of these re-growth processes exceeds the rate at which undefoliated plants grow (Hilbert *et al.* 1981), or if it prolongs active growth by delaying senescence (Voisin 1961). Re-growth potential also depends on grass morphology (Peterson 1962; Etherington 1984; Polley and Detling 1988), resource allocation traits (Caldwell *et al.* 1981), growing conditions (Dyer *et al.* 1993), and meristem availability (N'Guessan and Hartnett 2011).

In addition, some evidence suggests that grass growth form—*i.e.*, whether a plant is caespitose vs. rhizomatous—may also influence re-growth potential. According to Mack and Thompson (1982), the majority of agronomic grasses are rhizomatous and a dominance of rhizomatous grasses often destinguishes grasslands that are resilient to (and evolved under) large ungulate herbivory. Indeed, some evidence suggest that rhizomes are associated with grazing tolerance (Benot *et al.* 2013), perhaps because tiller recruitment may be facilitated by rhizome meristems and readily mobile carbohydrate and nutrient reserves in rhizomes (Suzuki and Stuefer 1999). In contrast tillering in caespitose grasses is constrained intravaginally within leaf sheaths (Sosebee *et al.* 1988), recruitment is limited to genet peripheries (Derner and Briske 1998), and genets seemingly avoid tiller mortality by limiting excess tiller recruitment (Briske and Butler 1989). Given that tillering can be an important regrowth process (Caldwell *et al.* 1983), these characteristics may limit grazing tolerance in caespitose grasses, for which some evidence indicates may be the case (Milchunas and Lauenroth 1993).

The biology of caespitose and rhizomatous grasses also differs. Within the Great Plains, caespitose grasses are more common in the western, more arid portion (Sims *et al.* 1978), presumably because this growth form ameliorates environmental stress by accumulating soil organic carbon and nitrogen beneath genets, creating so-called resource islands of fertility (Hook *et al.* 1991; Burke *et al.* 1998; Derner and Briske 2001). In contrast, rhizomatous grasses in these environments appear restricted to micro-sites of higher fertility and store more resources endogenously within rhizomes (Derner and Briske 2001). This suggests that caespitose grasses are potentially better adapted to aridity and resource stress.

Plants adapted to resource stress commonly have what is termed determinate growth, which in this context is a phenomenon whereby plant growth is relatively fixed for the growing season, regardless of environmental conditions (Grime 1977; Chapin 1980; Chapin *et al.* 1993), and this may be the case for caespitose grasses. Determinate growth is particularly common among plants with relatively exclusive resource access, such as evergreen shrubs with deep tap roots and succulents that store water (Noy-Meir 1973). Nevertheless, determinate growth may occur in caespitose grasses because concentration of roots beneath genets can monopolize access to these belowground resource islands and maintain growing conditions longer throughout the growing season (Chapin *et al.* 1979). Determinate growth may also ameliorate competition among tillers within caespitose grass tussocks/genets (Brooker and Callaghan 1998), given that physiological connectivity and resource sharing between parent and daughter tillers is limited to only a few generations (Derner and Briske 1998).

The objective of this study was to examine trade-offs associated with various intensities and frequencies of defoliation under different environmental conditions (moisture) on the growth dynamics of two dominant grasses of the Dry Mixedgrass Prairie that are of contrasting growth form: *Hesperostipa comata* (Trin. & Rupr.) Barkw. (caespitose) and *Pascopyrum smithii* (Rydb.) Á. Löve (rhizomatous). These species are co-dominant and constitute the majority of biomass production in the Mixedgrass Prairie (Coupland 1961). As such, plant community productivity is often determined by how these species respond to grazing management (Smoliak 1965) and a central consideration of grazing management is to maintain these late-seral grasses (Willms and Jefferson 1993; Reece *et al*. 2001). Tested hypotheses include that *H. comata* would have greater determinate growth compared to *P. smithii*, which would manifest as relatively fixed growth rates and tiller population dynamics regardless of defoliation regime and moisture conditions, thereby constraining positive yield responses. More indeterminate growth in *P. smithii* was hypothesized to manifest as positive and negative tiller growth rate and population dynamics under high and low moisture conditions, respectively. Should this be the case, *P. smithii* could demonstrate greater tiller growth and reproduction (and thus overcompensate) under repeated defoliation at some optimal intensity or frequency, but only under high, rather than low, moisture conditions.

3.3. Methods

3.3.1. Site Description

Two study sites were located in the Brooks Plain within the Dry Mixedgrass Prairie Natural Sub-region of Alberta, Canada (Adams *et al*. 2005). Mean annual precipitation and daily temperature in this area are 354 mm and 4.2°C, respectively (Adams *et al*. 2005). Sites were chosen based on uniformity of topography and plant community composition, with consistent presence of *P. smithii* and *H. comata*, and contrasting edaphic conditions (dry vs. wet). Site 1

(50° 53’ 40.2” N; 111° 52’ 26.3” W) was a relatively mesic, lowland range site with a Gleyed Eluviated Brown Chernozemic soil (Soil Classification Working Group [SCWG] 1998) of sandy loam texture (pH=6.3, EC=37µs/cm, organic matter content=2.5%). Vegetation composition consisted mostly of *Pascopyrum smithii*, with *Koeleria macrantha* (Ledeb.) J.A. Schultes and *Hesperostipa comata* as sub-dominants. Site 2 (50° 52’ 23.8” N; 111° 52’ 26.2” W) was a relatively xeric, upland range site with a Rego Brown Chernozemic soil (SCWG 1998) of loamy sand texture (pH=6.7, EC=27µs/cm, organic matter content=1.3%). Dominant vegetation at this site included *P. smithii*, *H. comata*, and *Bouteloua gracilis* (Willd. *ex* Kunth) Lag. *ex* Griffiths. Both sites had range health assessment scores of 80%, or healthy (Adams *et al.* 2003), and were previously grazed for the long-term at light-moderate stocking rates.

3.3.2. Treatments and Experimental Design

Treatments of defoliation and moisture were combined in a fully randomized factorial (4 x 2) design, with 6 replicates per site, and applied to 1 x 1 m plots, separated by at least 0.5 m. Plots were located by visual assessment for the presence of both *H. comata* and *P. smithii* tillers. Defoliation treatments imposed included control, high intensity at low frequency (HILF), high intensity at high frequency (HIHF), and low intensity at high frequency (LIHF). Control plots were clipped to a 2 cm stubble height in late August, and thus represented deferred defoliation to the end of the growing season. HILF and HIHF defoliation plots were clipped at 2 cm stubble heights every 3 and 6 weeks, respectively. And LIHF plots were clipped at a 5 cm stubble height every 3 weeks. Low intensity clipping heights of 5 cm were used to prevent shorter statured species (e.g., *Bouteloua gracilis*) from escaping defoliation, thereby preventing confounding competitive interactions. High intensity clipping heights of 2 cm were used to ensure complete removal of leaf material. Moisture treatments included not watering (*i.e.*, ambient rainfall) and watering of plots to augment rainfall and maintain an equivalent of over 150 mm of monthly precipitation throughout the growing season; this is double the average precipitation level for June, which is the month of highest rainfall. The objective here was to remove moisture availability as a constraint for plant growth. Watering occurred at approximately 10 d intervals and all treatments commenced and terminated in early June and late August, respectively, in 2010-2012. Prior to initiating treatments in April 2010, plots were hand-raked to remove coarse standing litter. This was done to help separate previous years' standing dead tillers from current years' growth.

3.3.3. Response Parameters

Within the centre 0.5 x 0.5 m portion of plots, a focal *H. comata* bunchgrass was delineated using a wire ring for ongoing monitoring. Due to its rhizomatous habit, *P. smithii* tillers were assessed in a fixed area subplot of 0.2 x 0.2 m dimension in the lowland, and 0.25 x 0.25 m in the upland site. A larger subplot was used in the upland site because *P. smithii* was less abundant. Tiller numbers for focal *H. comata* genets ranged between 9-41 and 14-91 in the lowland and upland sites, respectively (means were 25 and 30, respectively). Basal areas of *H. comata* ranged between 3.1-41.3 and 6.6-62.9 cm^2 in the lowland and upland sites, respectively (means were 17.6 and 21.1 cm^2, respectively). Tiller numbers of *P. smithii* ramets within subplots ranged between 9-29 and 7-28 in the lowland and upland sites, respectively (means were 16 and 15, respectively). Every 3-weeks (prior to defoliation), tillers were counted and up to 5 vegetative tillers were randomly selected and measured to the highest extended leaf or sheath. Senescent leaf tips were not measured in order to account for biomass losses associated with senescence and leaf abscission. Different focal plants were selected in subsequent years if full mortality of tillers was observed in early June (this occurred rarely, and only for *H. comata*). In order to establish a relationship between tiller height and weight, 15 tillers were randomly selected, measured, and harvested at ground level from within plots, but outside the centre 0.5 x 0.5 m portion. This was done after the first defoliation and prior to each subsequent defoliation event in the first growing season. Harvested tillers and accumulated herbage yield from focal plants were dried at 60°C for 48 hrs, and weighed. In the first year of study, the previous year’s standing dead tillers were removed from focal plants prior to weighing in order to ensure yield estimates consisted of only the current year’s growth.

3.3.4. Data Analysis

Height-weight correlations were developed from vegetative tillers harvested outside the centre 0.5 x 0.5 m portion of plots for each defoliation treatment (Figures 3-1 and 3-2). Trend-lines were fitted to these data (r^2=0.85-0.72, n≈180) and used to convert all tiller measurements from vegetative tillers inside plots into non-destructive estimates of biomass. Given that tiller heights on focal plants were obtained at 3-week intervals and prior to defoliation, biomass accrual relative to time was estimated non-destructively as a measure of the average growth rate over each successive 21 d period for vegetative tillers. Plants declining to 0 tillers within a growing season were precluded from this analysis. Tiller dynamics were assessed as the relative change in tiller numbers over each growing season (year), as well as the final tiller number at the end of the experiment. Lastly, focal plant yield represented accumulated herbage from all defoliation events. Given that tillers were counted prior to each defoliation event, yields were analyzed for both the entire genet/focal plant and on a per-tiller basis, using a tiller number average from the 5 counts. This was done in order to examine changes in tiller morphology that are often associated with defoliation, such as declines in tiller specific mass (Peterson 1962; Detling and Painter 1983).

All data were checked for homogeneity of variance and normality with Levene's and Shapiro-Wilk tests (SAS 9.2—SAS Institute, 1989), respectively, and focal plant yields were log-transformed to normalize these data. Mixed model, repeated measure ANOVA were used, with covariance structures modelled based on the best fit AIC statistic. Fixed effects included defoliation, moisture, and year of sampling, which was also the repeated measure. When defoliation or moisture effects were inconsistent among sites ($P \leq 0.05$), sites were analyzed independently. Otherwise site was treated as a random effect. Significance of model effects were assessed at an alpha of 0.05 and post-hoc mean comparisons were performed using a least significant difference (LSD) test for all significant main effects and interactions. Comparisons were unadjusted to minimize the risk of type II errors. Tiller growth rate dynamics within growing seasons were analyzed by independent ANOVAs for each growing season, using time period within each growing season as the repeated measure. These data were summarized and examined by pooling means and standard errors across all growing seasons for given periods from within each growing season. This was done for significant interactions of fixed effects (defoliation and moisture) with the repeated measure (time period within growing season).

3.4. Results

3.4.1. Tiller Growth Rates

Tiller growth rates were influenced by defoliation ($P<0.05$) in both *H. comata* and *P. smithii* (Table 3-2), although the relative effects of defoliation differed among sampling years for *H. comata* ($P<0.001$) and between sites for *P. smithii* ($P<0.001$) (Table 3-2). Tiller growth rates in *H. comata* were greatest under HIHF, followed by LIHF and HILF defoliation (Table 3-3), but these differences were most pronounced in 2010 (Table 3-4), when growth rates were markedly higher compared to 2011 and 2012 (Table 3-5). Defoliation, especially LIHF and HIHF, markedly increased growth rates for *P. smithii* in the upland site, whereas growth rates were similarly high for controls and HIHF in the lowland site (Table 3-5). Moisture addition did not influence tiller growth rates in *H. comata* (P=0.15); whereas it did increase growth rates in *P. smithii* by 21 and 37% in the lowland and upland sites, respectively (P<0.001) (Tables 3-2 and 3-3).

Seasonal dynamics of tiller growth were largely influenced by defoliation, with defoliation by sampling time (within each growing season) interactions significant for both species (P≤0.023), except for *P. smithii* in the lowland site in 2012 (P=0.212) (data not shown). Regardless of defoliation treatment, tiller growth rates for both grasses steadily declined throughout the growing season (Figure 3-3). However, defoliation effects on seasonal growth rate dynamics differed slightly between the two grasses. For *H. comata*, growth rates were negative (likely due to senescence) under control defoliation over the period of early to late August; and defoliation (*i.e.*, HILF, LIHF, and HIHF) effects primarily manifested by increasing tiller growth rates relative to controls during this period (Figure 3-3). In contrast, there were few seasonal differences among individual tiller growth rates under different defoliation regimes for *P. smithii*, especially in the lowland site (Figure 3-3). The same was generally true for moisture effects given that the only defoliation by moisture interaction occurred in 2010 (P=0.022; P>0.22 for 2011 and 2012), at which time moisture addition increased tiller growth rates in the latter part of the growing season (data not shown).

3.4.2. Tiller Dynamics

Tiller population dynamics (*i.e.*, the relative change in tiller numbers in each growing season) in both *H. comata* and *P. smithii* responded to defoliation ($P<0.001$), but not moisture ($P>0.05$) (Table 3-2). Defoliation (HILF, LIHF, HIHF, vs. control) tended to reduce tiller numbers for *P. smithii* at both sites, with declines under LIHF defoliation less pronounced in the lowland site (Table 3-6). In contrast, LIHF defoliation did not reduce tiller numbers relative to the control in *H. comata* (Table 3-6). Defoliation effects further differed among years of study for *P. smithii* in the lowland site ($P=0.022$) and *H. comata* ($P<0.001$) (Table 3-2). For example, high intensity defoliation (HILF, HIHF), regardless of frequency, reduced tiller numbers the most in both species, but this was especially pronounced in later years of the experiment for *P. smithii* at the lowland site, as well as in *H. comata* (Table 3-6). In contrast, tiller numbers increased under deferred defoliation (control) in *P. smithii*, especially in the lowland site.

Although moisture alone did not influence tiller population dynamics, it altered defoliation effects for *P. smithii* in the lowland site and *H. comata* (Table 3-2). In both cases, tiller number declines under HILF defoliation were more pronounced when under ambient moisture conditions.

Finally, overall changes in tiller population dynamics varied among years for both *H. comata* and *P. smithii* ($P<0.001$) (Table 3-2). This reflected the much greater tiller population declines in 2011 and 2012 compared to 2010, although tiller numbers actually increased slightly during 2010 for *P. smithii* at the lowland site and *H. comata* (Table 3-6). However, tiller numbers declined in 2010 for *P. smithii* at the upland site, especially under ambient moisture conditions (Table 3-7).

Along with tiller population dynamics (relative change in tiller number) for each growing season, final tiller numbers were also assessed. Final tiller numbers generally reflected the net effects of seasonal tiller dynamics, although there were some inconsistencies. Similar responses include that defoliation effects on *P. smithii* were again inconsistent among sites ($P<0.001$), with final tiller numbers reduced the most under high intensity defoliation, regardless of frequency, in the lowland site and under all defoliation regimes in the upland site (Table 3-8). Indeed, for *P. smithii* in the lowland site, final tiller numbers were up to 88% less under high intensity, and 63% less under low intensity, defoliation compared to controls, whereas in the upland site tiller numbers were at least 66% less than controls under all defoliation regimes (Table 3-8). Moreover, the defoliation by moisture interaction for *P. smithii* in the lowland site was due to different relative effects of LIHF defoliation under contrasting moisture regimes. Under ambient moisture conditions, tiller numbers were similar under both LIHF defoliation and controls, whereas under moisture addition, LIHF defoliation reduced tiller numbers by 87% compared to controls; and LIHF plants had similarly low tiller numbers compared to those under HIHF and HILF defoliation (Table 3-8).

An inconsistency arose for *P. smithii*, such that although moisture did not influence seasonal tiller population dynamics, it did affect final tiller numbers in the upland site (Table 3-2). Overall, plants under moisture addition had 64% more tillers than those under ambient moisture (Table 3-8). Inconsistencies for *H. comata* included that although high intensity defoliation at low frequency reduced tiller populations by at least 20% in both 2011 and 2012 (Table 3-6), plants under this treatment ended the experiment with similar tiller numbers to the controls (Table 3-8). And although LIHF defoliation did not reduce tiller populations over each growing season (Table 3-6), plants under this treatment ended the experiment with 53% less tillers compared to controls (Table 3-8).

3.4.3. Tiller Specific Mass

Tiller specific mass (*i.e.*, season-long plant yield relative to tiller number) responses were consistent among sites for both both grasses (P>0.44), but differed between years (P<0.001). For *P. smithii*, specific mass was 11.7 and 23.0% lower in 2011 and 2012, respectively, compared to 2010. This same trend was observed under all defoliation treatments except HIHF, for which specific tiller mass was relatively similar among all years (Table 3-10). For *H. comata*, tiller specific mass was almost 50 and 67% lower in 2011 and 2012, respectively, compared to 2010 (Table 3-10). Moisture increased specific tiller mass in *P. smithii* by 21.2% (P<0.001), but did so only in 2010 (by 18.7%) for *H. comata* (Table 3-10). Specific tiller mass was greater under control and HILF defoliation compared to

LIHF and HIHF (by at least 16.1 and 18.7% in *P. smithii* and *H. comata*, respectively), although the control remained similar to the LIHF (*P*=0.56) and HIHF (*P*=0.064) defoliation treatments for *H. comata* (Table 3-10).

3.4.4. Overall Plant Yield

Accumulated yield responses for focal plants were consistent among sites for both grasses (*P*>0.17) (Data not shown), but yields (*P*<0.001), as well as defoliation (*P*≤0.041) and moisture (*P*≤0.008) effects, varied among years of sampling (Table 3-9). Defoliation effects (*P*<0.001) largely mirrored final tiller number responses, with high frequency defoliation (LIHF, HIHF) generally reducing total plant yields relative to controls in both grass species, except in 2010 for *H. comata* (Table 3-11). Additionally, similar to tiller number responses, the relative effect of HILF defoliation on plant yield differed between *H. comata* and *P. smithii*. For *H. comata*, overall plant yields were similar under HILF and control defoliation, and HILF yielded greater than LIHF and HIHF defoliation by 60.6%, although controls yielded similarly to LIHF and HIHF defoliation in 2010 (Table 3-11). In the case of *P. smithii*, plant yields under HILF were similar to the controls in 2010, but declined in 2011 and 2012, such that, overall, control treatment yields were 53.2% higher than HILF yields, which in turn, were 31.2% greater than LIHF and HIHF yields (Table 3-11).

Plant yield was strongly influenced by moisture for *P. smithii* (*P*<0.001), but not for *H. comata* (*P*=0.13) (Table 3-9). And although *P. smithii* yields were

48% greater under moisture addition, this treatment did not increase yields in 2010 (*P*=0.42), whereas in the driest growing season (*i.e.*, 2011), moisture addition increased *H. comata* yields by 44% (Table 3-11). Moreover, similar to specific tiller mass, plant yields in both grasses declined over successive years of the experiment, especially in *H. comata*. Indeed, plant yield in *H. comata* declined by 80% from 2010 through 2012, whereas *P. smithii* yield declined 30% over the same period.

3.5. Discussion

3.5.1. Tiller Growth Rates

It is difficult for controlled defoliation studies to test why RG apparently fails to enhance aboveground plant community productivity because it is uncertain what defoliation regimes actually occur under various grazing systems (*e.g.*, Hart *et al.* 1993; Derner *et al.* 1994). Defoliation studies can, however, address the assumptions by which RG may influence plant growth, and thereby confer production benefits through compensatory plant responses (McNaughton 1983). Two such assumptions are that controlling defoliation frequency and timing can maintain either more rapid growth, or prolong plant growth during the growing season (Voisin 1961; Dobarro *et al.* 2012). In mesic grasslands where light and space predominantly limit plant community productivity for most of the growing season (Burke *et al.* 1998), it is conceivable that this would be beneficial in order to capitalize on grazing induced productivity increases that accrue through the reduction in standing dead plant material (litter) and mobilization of nitrogen (Knapp and Seastedt 1986; Hik *et al.* 1991). However, in drier grasslands such as the Mixedgrass Prairie, where current annual precipitation (Manley *et al.* 1997) and litter (Willms *et al.* 1986; Willms *et al.* 1993) heavily influence productivity, repeated defoliation may fail to maintain rapid growth throughout the growing season. Moreover, determinate growth in dominant grasses of the Mixedgrass Prairie may even constrain production under high moisture conditions (Chapin 1980; Chapin *et al.* 1983). In particular, I hypothesized this would be the case for the caespitose *H. comata*, but not the rhizomatous *P. smithii*.

In terms of growth processes that increase tiller height and biomass (*e.g.*, leaf elongation and phytomer production), and subsequent individual tiller growth rate, both *H. comata* and *P. smithii* demonstrated determinate and indeterminate growth characteristics. Contrary to my hypothesis, tiller growth rates in *H. comata* responded positively to repeated defoliation, especially later in the growing season. This contradicts results of Olson and Richards (1988) who found that grazing early in the growing season increased tiller growth rates relative to undefoliated plants in the caespitose *Agropyron desertorum*, but tiller growth rates subsequently declined to below that of ungrazed tussocks later in the growing season. The authors attributed this response to an exacerbation of moisture stress later in the growing season from earlier-season grazing, presumably because grazing reduced litter and stressed plants. In contrast, above normal precipitation that occurred throughout this study may have allowed continued tiller growth, albeit at a low rate, later in the growing season. Indeed, repeated defoliation, especially under HIHF, maintained continued tiller growth and apparently prevented senescence in *H. comata*, suggesting that individual tiller growth may not be determinate in this species. Although overcompensation is rare, other studies have documented increased growth rates under defoliation in caespitose grasses (Busso and Richards 1985; Gold and Caldwell 1989; Becker *et al.* 1997; Enedoe *et al.* 2002) and other graminoids (Coughenour *et al.* 1985; Enedoe *et al.* 2002).

Tiller growth rate responses under different defoliation regimes for *P. smithii* were site specific and varied, with some evidence for and against indeterminate growth. For example, similar to *H. comata*, in the drier upland site, *P. smithii* tiller growth rates were greater under repeated defoliation, which is consistent with our hypothesis of indeterminate growth for this rhizomatous grass. However, *P. smithii* plants in the lowland site under deferred defoliation maintained greater growth rates than those under two of the three repeated defoliation treatments (HILF and LIHF) and had a similar overall growth rate to plants under HIHF defoliation. Additionally, in contrast to *H. comata*, there were no pronounced seasonal differences in plant growth rates among varied defoliation treatments, suggesting that defoliation did not delay senescence or prolong rapid growth in *P. smithii*. Thus, although it appears that defoliation may promote tiller growth in drier ecosites, the mechanism for this is not clear. This contradicts my hypothesis that *P. smithii* would respond more favourably to defoliation under high moisture conditions. Moreover, given these site-based discrepancies, it is perplexing that moisture conditions did not influence defoliation effects. For example, if these contrasting effects of defoliation were because mesic conditions in the lowland site maintained growth under deferred defoliation (*i.e.*, controls), then moisture addition in the upland site should have produced the same result. As this did not occur, it suggests that local edaphic conditions may influence growth plasticity in *P. smithii*; but contrary to my hypothesis, it appears that growth rate plasticity is more characteristic of *P. smithii* in drier range sites, regardless of moisture conditions.

Although defoliation effects were mixed, moisture effects on tiller growth rates showed clear evidence of determinate and indeterminate growth for *H. comata* and *P. smithii*, respectively. For example, despite more than doubling June precipitation throughout the growing season, there was no affect on growth rates of *H. comata*, which is consistent with my hypothesis of determinate growth in this species. In contrast, *P. smithii* growth rates were markedly greater under moisture addition, especially in the drier upland site. Although, given there were essentially no clear seasonal differences for *P. smithii* tiller growth rates under contrasting moisture regimes, mechanisms for this response are unclear. Consequently, instead of prolonging growth or delaying senescence, moisture addition may simply increase tiller vigour and growth. Nevertheless, this suggests that *P. smithii* tiller growth is more responsive (*i.e.*, indeterminate) to moisture availability, whereas *H. comata* may have more determinate (*i.e.*, fixed) growth.

3.5.2. Tiller Population Dynamics

Plant growth is not only a function of individual tiller growth given that tiller population dynamics strongly influence plant productivity (Reichmann *et al.* 2013) and persistence (Peterson 1962; Caldwell *et al.* 1981; Detling and Painter 1983). Plant growth determinacy under varied defoliation regimes and moisture conditions is thus also influenced by tiller reproduction and longevity/persistence. Tillering allows annual regeneration of perennial grasses (Langer 1956; Hendrickson and Briske 1997), but its contribution to plant regrowth following defoliation may depend on defoliation timing (Hendon and Briske 1997), environmental conditions (Deregibus *et al.* 1985; Olson and Richards 1989) and intrinsic allocation characteristics (Caldwell *et al.* 1981). In this case, specific hypotheses were (1) that tiller populations in *H. comata* would be more stable (*i.e.*, less responsive) to varied defoliation regimes and moisture conditions; and (2) for *P. smithii*, tiller population dynamics in response to varied defoliation would depend on moisture conditions, such that populations would increase under some level of defoliation and high moisture availability, whereas defoliation under moisture stress would reduce tiller populations. However, tiller population sensitivity to defoliation largely constrained compensatory responses, especially in *P. smithii*. This is not surprising given that both grasses studied here are canopy dominant, which is a characteristic that generally confers low tolerance to defoliation in mixed-canopy grasslands (Peterson 1962; Detling and Painter 1983; Milchunas *et al.* 1988). Moreover, defoliation effects on tiller populations were small in the first year, but increased in the second and third years of the experiment, suggesting that repeated defoliation had an additive affect in reducing the capacity of tillers to regenerate.

Nevertheless, tiller population dynamics were not consistent among all defoliation regimes, and trade-offs between frequency and intensity were apparent. For example, at least within each growing season, high intensity defoliation, regardless of frequency, reduced tiller populations for both grasses. This suggests that intensity, rather than frequency, of defoliation largely influences tiller populations, although it is unclear whether it is a lack of tiller persistence and/or regeneration that is responsible for these changes. Moreover, these divergent responses occurred despite the fact that the difference between high and low intensity defoliation was only 3 cm (2 vs 5 cm) and both treatments resulted in almost complete removal of leaf material. Given that observed regrowth was entirely due to additional phytomer emergence within enclosed but previously clipped leaf sheaths, apical meristems were likely left intact (except if clipping followed the boot stage for reproductive tillers). Thus, variation in tiller survival between the two intensities of clipping may have resulted from different energetic requirements for plant regrowth, which presumably would have been greater in more intensively clipped plants, or that remaining sheaths were an important source of photosynthetic material needed to facilitate recovery (*e.g.*, Nowak and Caldwell 1984).

While HILF defoliation consistently reduced tiller populations in all growing seasons, *H. comata* plants under this treatment ended the experiment with similar tiller numbers as controls. This suggests that *H. comata* was able to offset seasonal tiller declines with higher recruitment between growing seasons. Harrison and Romo (1999) observed a similar response in crested wheatgrass, in which defoliation did not increase tiller populations until the following growing season. It is possible that intensively clipped tillers avoided senescence prior to the end of the growing season, but maintained meristem (*i.e.*, basal bud) viability until the following growing season. This suggests that tillering as a mechanism of regrowth may indeed be more determinate in *H. comata*, particular within growing seasons.

There was also evidence of more indeterminate growth in *P. smithii*, particularly with regard to moisture effects and plant responses to deferred defoliation. Although not significant in any growing season alone, by the end of the experiment adding moisture increased tiller numbers for *P. smithii* in the drier upland site, whereas moisture conditions did not influence tiller populations in *H. comata*. Moreover, under control (deferred) defoliation, *P. smithii* plants in the lowland site consistently recruited, on average, an additional 30% more tillers in every year of the experiment in the mesic lowland site. In contrast, for *H. comata*, tiller populations under control defoliation increased only initially and then declined thereafter. These results suggest that *P. smithii* may have greater propensity to recruit tillers under deferred defoliation and high moisture conditions. In contrast, Hendrickson and Berdahl (2002) found that tiller populations in other rhizomatous grasses (*Thinopyrum intermedium* and *Psathyrostachys juncea*) of the same tribe as *P. smithii* (*Triticeae*) were not reduced by low moisture conditions, although defoliation similarly reduced tiller populations. Similarly, Lauenroth *et al.* (1985) found that *P. smithii* tiller populations could tolerate intense defoliation at low, but not high, frequency.

Tillers arise from basal buds, primarily in early spring, from the previous year's standing tillers (Dalgleish and Hartnett 2006). Longevity of tillers seemingly does not exceed two years (Langer 1956, Hendrickson and Briske 1997), and recruitment from seed is minimal in perennial grasses (Benson and Hartnett 2006), suggesting that annual tillering allows regeneration of tiller populations, giving rise to the perennial nature of grasses that reproduce vegetatively. Following the initial flush of new tillers early in the growing season, meristem availability for the production of new tillers seemingly depends on grassland moisture regime, with drier grasslands being under a meristem limitation and more mesic grasslands producing additional meristems for continued tiller recruitment throughout the growing season (Dalgleish and Hartnett 2006). Meristem limitation may be one mechanism causing determinate grass growth in more xeric, resource limited environments, such that drier grasslands fail to increase productivity in wetter years to the same extent that more mesic grasslands can respond to differences in inter-annual moisture availability (Paruelo *et al.* 1999; Knapp and Smith 2001). Results from this experiment suggest that meristem limitation may be of greater importance in *H. comata* compared to *P. smithii*. This indeed would suggest that the former species is more determinate in terms of tillering propensity in the absence of growing season defoliation and provided moisture is abundant.

3.5.3. Overall Plant Yield

Both individual tiller growth and recruitment of new tillers contributes to total herbage yield in grasses (Sharman 1945). However, *H. comata* and *P. smithii* yields in this experiment largely mirrored defoliation and moisture effects on final tiller numbers, as opposed to tiller growth rates. N'Guessan and Hartnett (2011) also found that plant yields corresponded with tiller population size. This suggests that tiller survival and recruitment, as opposed to individual tiller growth, was the principal determinant of plant yield under varied defoliation. For example, although repeated growing season defoliation promoted tiller growth rates, in most cases it also simultaneously reduced tiller populations, thereby nullifying initial compensatory responses. Similar yields occurred under control (deferred) and HILF defoliation for *H. comata*, but tiller populations were also similar between these treatments: all other defoliation treatments reduced tiller numbers and yields relative to controls. Some compensatory yielding also occurred under HILF defoliation for *P. smithii*, but primarily in the first growing season. Productivity in this treatment declined in subsequent growing seasons, but overall yields were above that of LIHF and HIHF defoliation. Similarly, Lauenroth *et al.* (1985) found that *P. smithii* demonstrated compensatory yielding when defoliation occurred, regardless of intensity, once during the growing season, whereas two defoliations during a single growing season inevitably reduced yields further. Despite the fact that other studies document reduced yields of *P. smithii* under increasing defoliation intensity (Branson 1953; Everson 1966; Eneboe *et al.* 2002), *P. smithii* may cope with high intensity defoliation at appropriate frequencies (*i.e.*, once during the growing season). Although moisture conditions did not alter defoliation effects on plant yield, moisture addition did increase yields, tiller populations, and growth rates in *P. smithii*, but not *H. comata*.

In addition to defoliation effects, plant yields also varied among the growing seasons. While some compensatory responses were observed, overall plant yields of each species declined as the experiment progressed, especially in *H. comata*. This corresponds with a simultaneous decline in the specific mass of tillers. For example, *H. comata* and *P. smithii* overall yields declined by 80 and 28% from 2010-2012, respectively, and specific tiller mass correspondingly declined by 66 and 23%. This suggests that the reduction in grass yield over time can be explained by a reduction in specific tiller mass.

Defoliation tolerant grasses can cope with defoliation by producing tillers with leaves of lower specific mass (biomass relative to leaf area) (Caldwell *et al.* 1981, Detling and Painter 1983). Defoliation also selects for genotypes that produce many small, as opposed to fewer large, tillers (Peterson 1962; Bogen *et al.* 2002; Cullen *et al.* 2005). Indeed, repeated defoliation has been found to both increase tiller number and reduce tiller weight of *H. comata* (Reece *et al.* 1988). These responses likely facilitate rapid re-establishment of photosynthetic tissue and ramets (Caldwell *et al.* 1981), which is the underlying characteristic associated with defoliation tolerance (Belsky *et al.* 1993). Consequently, *H. comata's* caespitose architecture of a cluster of relatively small tillers, may have facilitated defoliation tolerance, and thus compensatory regrowth, in this grass. In contrast, specific tiller mass was 3-fold greater in *P. smithii* compared to *H.*

comata, suggesting that regrowth of the former constitutes a much greater bioenergetic investment. This contradicts the notion that defoliation tolerance is an intrinsic property of rhizomatous grasses (Mack and Thompson 1982). Small shoot stature is also associated with aridity (Brooker and Callaghan 1998), suggesting this trait evolved convergently to cope with both defoliation and moisture stress (Milchunas *et al*. 1988). Similarly, Eneboe *et al*. (2002) found that grazing did not reduce plant yield in *Bouteloua gracilis*, which is also a caespitose grass with small shoot stature, but did so in *P. smithii*. Grazing tolerance in *H. comata* may have also been facilitated by greater nutrient status in this grass (Chapin *et al*. 1979; Burke *et al*. 1998). Finally, annual declines in plant yield under even the controls, suggests that a single deferred defoliation event late in the growing season is sufficient to alter plant growth.

3.6. Management Implications and Conclusion

RG encompasses many variations of livestock management, but generally the objective is to use high animal densities to limit selectivity, and, as such, grazing tends to be homogenous and intense, with relatively long periods of deferment, such as under short-duration rotational grazing. In this experiment HILF defoliation probably best approximates the defoliation regime under management intensive RG. This experiment shows that compensatory plant yields under this frequency and intensity of defoliation are possible, particularly for *H. comata*. Therefore, plant community yields under short-duration RG may depend on the relative contribution of these two species to the overall yield of the plant community. Defoliation regimes under CG are not known (Bailey and Brown 2011), but under some circumstances CG can result in patch-grazing, where some areas are recurrently grazed at the expense of other areas being avoided (Ring *et al*. 1985; Willms *et al*. 1988). In this situation HIHF defoliation may approximate defoliation regimes of recurrently grazed patches whereas controls may approximate those of avoided areas. Plant community yield under CG may thus depend on the relative contribution of these areas. If both were equally represented in a pasture, *H. comata* and *P. smithii* plant yields would be higher and lower under RG, respectively, relative to CG (Figure 3.4). *P. smithii* may only yield higher under RG compared to CG when avoided areas under CG make up a small proportion of the landscape (Figure 3.4).

This contrasts my initial hypothesis, where *P. smithii* was expected to respond more favourably to recurrent defoliation under high moisture conditions. It is also inconsistent with results of a similar experiment under greenhouse conditions, where *P. smithii* showed compensatory responses under high moisture while *H. comata* did not (Chapter 2). Greenhouse experiments may better expose innate characteristics and growth potential of plants (Grime 2001), but differing growth responses of *H. comata* and *P. smithii* in field and greenhouse conditions indicate that other factors in the environment, such as competing vegetation, nutrients, temperature, or light, may also limit indeterminate regrowth responses. Moreover, other ecological factors may also play a role, such as mycorrhizae, or endophytes.

Although I hypothesized that *H. comata* would express determinate growth and thereby constrain compensatory plant responses to defoliation, this was not the case. Instead, compensatory yielding occurred under HILF defoliation for *H. comata*, and this was due to defoliation tolerance and plasticity in tiller growth rate. In contrast, compensatory responses were constrained in *P. smithii* because of tiller population sensitivity to defoliation. As a result, determinate growth may not be characteristic of caespitose grasses. Nevertheless, *H. comata* did show much more determinate growth responses to moisture addition, given that this treatment did not increase tiller growth rates, populations, or yield, whereas the opposite was observed in the rhizomatous *P. smithii*. This indeed suggests that *H. comata*, and perhaps caespitose grasses, have more determinate growth in response to variation in environmental conditions, although a paucity of studies test this empirically. Further studies are warranted to understand the tiller growth and population dynamic mechanisms that regulate overall plant yield for grasses of contrasting growth form, including their response to defoliation and environmental variation.

Table 3-1. Ambient growing season precipitation (mm) and recent long-term averages for the Brooks area of Alberta, Canada.

	Year				Average[1]
	2009	2010	2011	2012	1971-2000
June	54	123	77	135	63
July	137	52	36	48	42
August	39	20	23	29	36
Total (June-Aug.)	230	195	135	212	141

[1] Environment Canada climate normals.

Table 3-2. ANOVA *F* and *P* values for *Hesperostipa comata* and *Pascopyrum smithii* for tiller growth rate, change in tiller number, and final tiller number relative to fixed effects of defoliation, moisture, and year of study.

	H. comata		*P. smithii*			
			Lowland site		Upland site	
	F value	*P* value	*F* value	*P* value	*F* value	*P* value
Tiller growth rate						
Defoliation	$27.6_{(3, 96)}$[1]	**<0.001**	$3.20_{(3, 40)}$	**0.034**	$16.6_{(3, 48)}$	**<0.001**
Moisture	$2.10_{(1, 96)}$	0.15	$15.1_{(1, 40)}$	**0.001**	$60.4_{(1, 48)}$	**<0.001**
Defol. x moist.	$0.68_{(3, 96)}$	0.56	$0.96_{(3, 40)}$	0.42	$1.47_{(3, 48)}$	0.23
Year	$78.5_{(2, 178)}$	**<0.001**	$15.3_{(2, 66)}$	**<0.001**	$26.5_{(2, 87)}$	**<0.001**
Year x defol.	$5.46_{(6, 178)}$	**<0.001**	$1.35_{(6, 66)}$	0.25	$0.55_{(6, 87)}$	0.77
Year x moist.	$0.18_{(2, 178)}$	0.83	$0.79_{(2, 66)}$	0.46	$0.23_{(2, 87)}$	0.79
Year x defol. x moist.	$0.34_{(6, 178)}$	0.91	$0.54_{(6, 66)}$	0.78	$0.84_{(6, 87)}$	0.55
Relative change in tiller number						
Defoliation	$15.8_{(3, 96)}$	**<0.001**	$46.4_{(3, 40)}$	**<0.001**	$59.7_{(3, 48)}$	**<0.001**
Moisture	$0.00_{(1, 96)}$	0.97	$3.97_{(1, 40)}$	0.053	$3.40_{(1, 48)}$	0.071
Defol. x moist.	$6.94_{(3, 96)}$	**<0.001**	$3.59_{(3, 40)}$	**0.022**	$0.91_{(3, 48)}$	0.44
Year	$27.8_{(2, 96)}$	**<0.001**	$27.7_{(2, 40)}$	**<0.001**	$17.2_{(2, 48)}$	**<0.001**
Year x defol.	$2.48_{(6, 96)}$	**0.028**	$2.91_{(6, 40)}$	**0.019**	$2.26_{(6, 48)}$	0.053
Year x moist.	$1.77_{(2, 96)}$	0.18	$1.23_{(2, 40)}$	0.30	$3.96_{(2, 48)}$	**0.026**
Year x defol. x moist.	$0.36_{(6, 96)}$	0.90	$2.00_{(6, 40)}$	0.088	$0.98_{(6, 48)}$	0.45
Final tiller number						
Defoliation	$15.2_{(3, 95)}$	**<0.001**	$47.5_{(3, 40)}$	**<0.001**	$18.7_{(3, 48)}$	**<0.001**
Moisture	$0.01_{(1, 95)}$	0.93	$1.84_{(1, 40)}$	0.18	$6.85_{(1, 48)}$	**0.012**
Defol. x moist.	$1.67_{(3, 95)}$	0.18	$10.1_{(3, 40)}$	**<0.001**	$1.91_{(3, 48)}$	0.14

[1] Numerator and denominator degrees of freedom, respectively.

Table 3-3. ANOVA growth rate means (mg/tiller/day) and standard errors (in parentheses) for *Hesperostipa comata* and *Pascopyrum smithii* under defoliation treatments of deferred (control), high intensity low frequency (HILF), low intensity high frequency (LIHF), and high intensity high frequency (HIHF), as well as moisture treatments of ambient and addition.

	Defoliation					Moisture		
	Control	HILF	LIHF	HIHF		Addition	Ambient	
H. comata	0.37^{C1}	0.60^{B}	0.67^{AB}	0.74^{A}	(0.03)	-	-	-
P. smithii								
Lowland site	2.51^{A}	2.08^{B}	2.16^{B}	2.40^{AB}	(0.12)	2.51^{X}	2.06^{Y}	(0.08)
Upland site	1.51^{C}	1.73^{B}	2.13^{A}	2.13^{A}	(0.08)	2.17^{X}	1.58^{Y}	(0.06)

[1] Means with the same letter within rows are not significantly different ($P \leq 0.05$).

Table 3-4. Growth rate means (mg/tiller/day) and standard errors (in parentheses) for *Hesperostipa comata* under deferred (control), high intensity low frequency (HILF), low intensity high frequency (LIHF), and high intensity high frequency (HIHF) defoliation for 2010-2012.

Year	Defoliation				
	Control	HILF	LIHF	HIHF	
2010	^{C}[1] 0.45 ^{a}[2]	^{B} 0.89 ^{a}	^{B} 0.88 ^{a}	^{A} 1.14 ^{a}	(0.05)
2011	^{B} 0.44 ^{a}	^{AB} 0.53 ^{b}	^{A} 0.64 ^{b}	^{A} 0.66 ^{b}	(0.05)
2012	^{B} 0.24 ^{b}	^{AB} 0.37 ^{c}	^{A} 0.50 ^{b}	^{A} 0.42 ^{c}	(0.05)

[1] Uppercase letters denote mean separation within rows ($P \leq 0.05$).

[2] Lowercase letters denote mean separation within columns ($P \leq 0.05$).

Table 3-5. ANOVA growth rate means (mg/tiller/day) and standard errors (in parentheses) for *Hesperostipa comata* and *Pascopyrum smithii* for the 2010-2012 growing season.

	Year			
	2010	2011	2012	
H. comata	0.84[a1]	0.57[b]	0.38[c]	(0.03)
P. smithii				
Lowland site	2.78[a]	2.24[b]	1.84[c]	(0.11)
Upland site	2.46[a]	1.73[b]	1.44[c]	(0.10)

[1] Means with the same letter are not significantly different ($P \leq 0.05$).

Table 3-6. Relative change in tiller number ANOVA means and standard errors (in parentheses) for *Hesperostipa comata* and *Pascopyrum smithii* under defoliation treatments of deferred (control), high intensity low frequency (HILF), low intensity high frequency (LIHF), high intensity high frequency (HIHF), and moisture treatments of addition and ambient for the 2010-2012 growing seasons. Negative values indicate a net loss of tillers.

	Defoliation					Overall	
	Control	HILF	LIHF	HIHF			
H. comata							
Moisture addition	^{A1} -0.08 ^{b2}	^{A} -0.10 ^{a}	^{A} -0.12 ^{a}	^{A} -0.20 ^{a}	(0.05)	-	-
Ambient moisture	^{A} 0.08 ^{a}	^{B} -0.20 ^{a}	^{A} 0.01 ^{a}	^{C} -0.39 ^{b}	(0.05)	-	-
2010	^{A} 0.22 ^{a}	^{B} 0.01 ^{a}	^{B} -0.03 ^{a}	^{B} -0.06 ^{a}	(0.07)	0.04 ^{a}	(0.03)
2011	^{A} -0.10 ^{b}	^{B} -0.26 ^{b}	^{A} -0.12 ^{a}	^{C} -0.46 ^{b}	(0.05)	-0.24 ^{b}	(0.02)
2012	^{AB} -0.12 ^{b}	^{B} -0.197 ^{b}	^{A} -0.01 ^{a}	^{C} -0.37 ^{b}	(0.05)	-0.18 ^{b}	(0.02)
Overall	^{A} 0.00	^{B} -0.15	^{A} -0.05	^{C} -0.30	(0.03)	-	-
***P. smithii* (lowland site)**							
Moisture addition	^{A} 0.38 ^{a}	^{B} -0.26 ^{a}	^{B} -0.24 ^{a}	^{C} -0.54 ^{a}	(0.08)	-	-
Ambient moisture	^{A} 0.23 ^{a}	^{C} -0.59 ^{b}	^{B} -0.06 ^{a}	^{C} -0.72 ^{a}	(0.08)	-	-
2010	^{A} 0.44 ^{a}	^{B} 0.06 ^{a}	^{BC} -0.02 ^{a}	^{C} -0.29 ^{a}	(0.10)	0.05 ^{a}	(0.05)
2011	^{A} 0.25 ^{a}	^{C} -0.60 ^{b}	^{B} -0.17 ^{a}	^{C} -0.75 ^{b}	(0.10)	-0.32 ^{b}	(0.05)
2012	^{A} 0.23 ^{a}	^{C} -0.75 ^{b}	^{B} -0.27 ^{a}	^{C} -0.86 ^{b}	(0.06)	-0.41 ^{b}	(0.03)
Overall	^{A} 0.31	^{C} -0.43	^{B} -0.15	^{D} -0.63	(0.06)	-	-
***P. smithii* (upland site)**							
Overall	^{A} 0.06	^{B} -0.48	^{B} -0.49	^{C} -0.71	(0.04)	-	-

[1] Uppercase letters denote mean separation within rows ($P \leq 0.05$).

[2] Lowercase letters denote mean separation within columns ($P \leq 0.05$).

Table 3-7. Relative change in tiller number ANOVA means and standard errors (in parentheses) for *Pascopyrum smithii* in the upland site for 2010-2012 under moisture treatments.

	Year		
	2010	2011	2012
Moisture addition	^{A1} -0.12 ^{a2}	^{B} -0.49 ^{a}	^{B} -0.48 ^{a}
Ambient moisture	^{A} -0.37 ^{b}	^{B} -0.54 ^{a}	^{AB} -0.42 ^{a}
	(0.06)	(0.04)	(0.05)
Overall	^{A} -0.25	^{B} -0.51	^{B} -0.45
	(0.04)	(0.03)	(0.03)

[1] Uppercase letters denote mean separation within rows ($P \leq 0.05$).

[2] Lowercase letters denote mean separation within columns ($P \leq 0.05$).

Table 3-8. Final tiller number ANOVA means and standard errors (in parentheses) for *Hesperostipa comata* and *Pascopyrum smithii* under deferred (control), high intensity low frequency (HILF), low intensity high frequency (LIHF), and high intensity high frequency (HIHF) defoliation.

	Defoliation					Overall	
	Control	HILF	LIHF	HIHF			
H. comata							
Overall	^{A1} 21.8	^{A} 20.1	^{B} 10.2	^{B} 9.3	(3.2)	-	-
***P. smithii* (lowland site)**							
Moisture addition	^{A} 46.3 ^{a2}	^{B} 6.8 ^{a}	^{B} 6.0 ^{b}	^{B} 3.0 ^{a}	(3.2)	-	-
Ambient moisture	^{A} 26.2 ^{b}	^{B} 2.0 ^{a}	^{A} 21.2 ^{a}	^{B} 0.5 ^{a}	(3.2)	-	-
Overall	^{A} 36.3	^{C} 4.4	^{B} 13.6	^{C} 1.8	(2.3)	-	-
***P. smithii* (upland site)**							
Moisture addition	-	-	-	-	-	9.0 ^{a}	(0.9)
Ambient moisture	-	-	-	-	-	5.5 ^{b}	(0.9)
Overall	^{A} 15.8	^{B} 4.5	^{B} 5.4	^{B} 3.1	(1.3)	-	-

[1] Uppercase letters denote mean separation within rows ($P \leq 0.05$).

[2] Lowercase letters denote mean separation within columns ($P \leq 0.05$)

Table 3-9. ANOVA *F* and *P* values for *Hesperostipa comata* and *Pascopyrum smithii* for plant yield relative to fixed factors of defoliation, moisture, and year of sampling.

	H. comata		*P. smithii*	
	F value	*P* value	*F* value	*P* value
Yield-per-tiller				
Defoliation	$3.02_{(3, 96)}$[1]	**0.034**	$16.6_{(3, 96)}$	**<0.001**
Moisture	$3.89_{(1, 96)}$	0.052	$25.5_{(1, 96)}$	**<0.001**
Defol. x moist.	$1.78_{(3, 96)}$	0.16	$0.65_{(3, 96)}$	0.59
Year	$157.9_{(2, 184)}$	**<0.001**	$45.1_{(2, 188)}$	**<0.001**
Year x defol.	$0.91_{(6, 184)}$	0.49	$6.23_{(6, 188)}$	**<0.001**
Year x moist.	$3.93_{(2, 184)}$	**0.021**	$1.78_{(2, 188)}$	0.17
Year x defol. x moist.	$1.35_{(6, 184)}$	0.24	$1.40_{(6, 188)}$	0.22
Total plant yield				
Defoliation	$13.1_{(3, 96)}$	**<0.001**	$16.9_{(3, 96)}$	**<0.001**
Moisture	$2.37_{(1, 96)}$	0.13	$20.8_{(1, 96)}$	**<0.001**
Defol. x moist.	$1.29_{(3, 96)}$	0.28	$1.48_{(3, 96)}$	0.23
Year	$263.1_{(2, 184)}$	**<0.001**	$48.4_{(2, 188)}$	**<0.001**
Year x defol.	$2.24_{(6, 184)}$	**0.041**	$4.92_{(6, 188)}$	**<0.001**
Year x moist.	$6.05_{(2, 184)}$	**0.003**	$13.0_{(2, 188)}$	**<0.001**
Year x defol. x moist.	$1.32_{(6, 184)}$	0.25	$1.25_{(6, 188)}$	0.28

[1] Numerator and denominator degrees of freedom, respectively.

Table 3-10. ANOVA means and standard errors (in parentheses) for *Hesperostipa comata* and *Pascopyrum smithii* tiller specific mass (mg of yield/tiller) under defoliation treatments of deferred (control), high intensity low frequency (HILF), low intensity high frequency (LIHF), and high intensity high frequency (HIHF), and moisture treatments of addition and ambient in the 2010-2012 growing seasons.

	Year			Overall
	2010	2011	2012	
H. comata				
Control	-	-	-	84.8 ^{ab2}
HILF	-	-	-	90.2 ^{a}
LIHF	-	-	-	76.0 ^{b}
HIHF	-	-	-	72.3 ^{b}
	-	-	-	(4.7)
Moisture addition	^{A1} 142.4 ^{a}	^{B} 71.3 ^{a}	^{C} 42.7 ^{a}	-
Ambient moisture	^{A} 119.3 ^{b}	^{B} 64.1 ^{a}	^{C} 45.2 ^{a}	-
	(7.1)	(3.6)	(1.9)	-
Overall	^{A} 130.9	^{B} 67.7	^{C} 43.9	-
	(5.0)	(2.6)	(1.4)	-
P. smithii				
Control	^{A} 325.8 ^{a}	^{B} 287.1 ^{a}	^{C} 218.1 ^{a}	277.0 ^{a}
HILF	^{A} 302.7 ^{a}	^{B} 271.4 ^{a}	^{C} 242.7 ^{a}	272.3 ^{a}
LIHF	^{A} 231.5 ^{b}	^{B} 200.4 ^{b}	^{C} 155.4 ^{b}	195.8 ^{c}
HIHF	^{A} 247.5 ^{b}	^{A} 219.6 ^{b}	^{A} 236.5 ^{a}	234.5 ^{b}
	(13.9)	(11.9)	(10.2)	(9.3)
Moisture addition	-	-	-	268.4 ^{a}
Ambient moisture	-	-	-	221.4 ^{b}
	-	-	-	(6.6)
Overall	^{A} 276.9	^{B} 244.6	^{C} 213.2	-
	(7.0)	(6.0)	(5.1)	-

[1] Uppercase letters denote mean separation within rows ($P \leq 0.05$).

[2] Lowercase letters denote mean separation within columns ($P \leq 0.05$).

Table 3-11. Plant yield ANOVA means (g) (untransformed) and standard errors (in parentheses) for *Hesperostipa comata* and *Pascopyrum smithii* for the 2010-2012 growing seasons under defoliation treatments of deferred (control), high intensity low frequency (HILF), low intensity high frequency (LIHF), and high intensity high frequency (HIHF) and moisture treatments of addition and ambient.

	Year			Overall
	2010	2011	2012	
H. comata				
Control	^{A1} 4.17 ^{ab2}	^{B} 2.34 ^{a}	^{C} 1.28 ^{a}	2.59 ^{a}
HILF	^{A} 5.06 ^{a}	^{B} 2.32 ^{a}	^{C} 1.05 ^{a}	2.81 ^{a}
LIHF	^{A} 3.90 ^{b}	^{B} 0.91 ^{b}	^{C} 0.45 ^{b}	1.75 ^{b}
HIHF	^{A} 3.04 ^{b}	^{B} 0.93 ^{b}	^{C} 0.50 ^{b}	1.49 ^{b}
	(0.49)	(0.25)	(0.12)	(0.23)
Moisture addition	^{A} 4.24 ^{a}	^{B} 1.92 ^{a}	^{C} 0.80 ^{a}	-
Ambient moisture	^{A} 3.85 ^{a}	^{B} 1.33 ^{b}	^{C} 0.84 ^{a}	-
	(0.35)	(0.18)	(0.08)	-
Overall	^{A} 4.04	^{B} 1.63	^{C} 0.82	-
	(0.25)	(0.13)	(0.06)	-
P. smithii				
Control	^{A} 5.61 ^{a}	^{A} 6.17 ^{a}	^{B} 5.39 ^{a}	5.73 ^{a}
HILF	^{A} 4.64 ^{a}	^{B} 3.88 ^{b}	^{C} 2.71 ^{b}	3.74 ^{b}
LIHF	^{A} 3.53 ^{b}	^{B} 2.78 ^{c}	^{C} 2.24 ^{bc}	2.85 ^{c}
HIHF	^{A} 3.39 ^{b}	^{B} 2.34 ^{c}	^{B} 2.00 ^{c}	2.58 ^{c}
	(0.35)	(0.39)	(0.42)	(0.33)
Moisture addition	^{A} 4.65 ^{a}	^{B} 4.48 ^{a}	^{C} 4.20 ^{a}	4.44 ^{a}
Ambient moisture	^{A} 3.94 ^{a}	^{B} 3.10 ^{b}	^{C} 1.97 ^{b}	3.00 ^{b}
	(0.25)	(0.28)	(0.30)	(0.24)
Overall	^{A} 4.29	^{B} 3.79	^{C} 3.09	-
	(0.17)	(0.20)	(0.21)	-

[1] Uppercase letters denote mean separation within rows ($P \leq 0.05$).

[2] Lowercase letters denote mean separation within columns ($P \leq 0.05$).

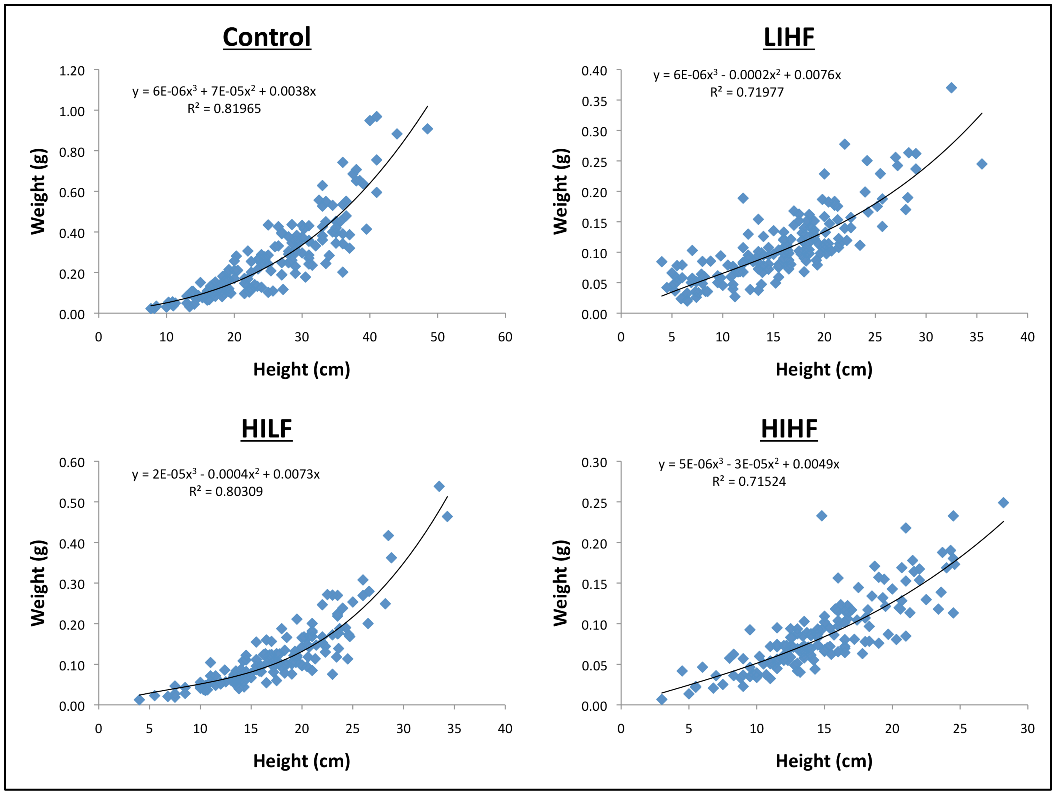

Figure 3-1. Tiller height-weight relationships for *Pascopyrum smithii*, as modeled for plants exposed to each of the control, low intensity high frequency (LIHF), high intensity low frequency (HILF), and high intensity high frequency (HIHF) defoliation treatments.

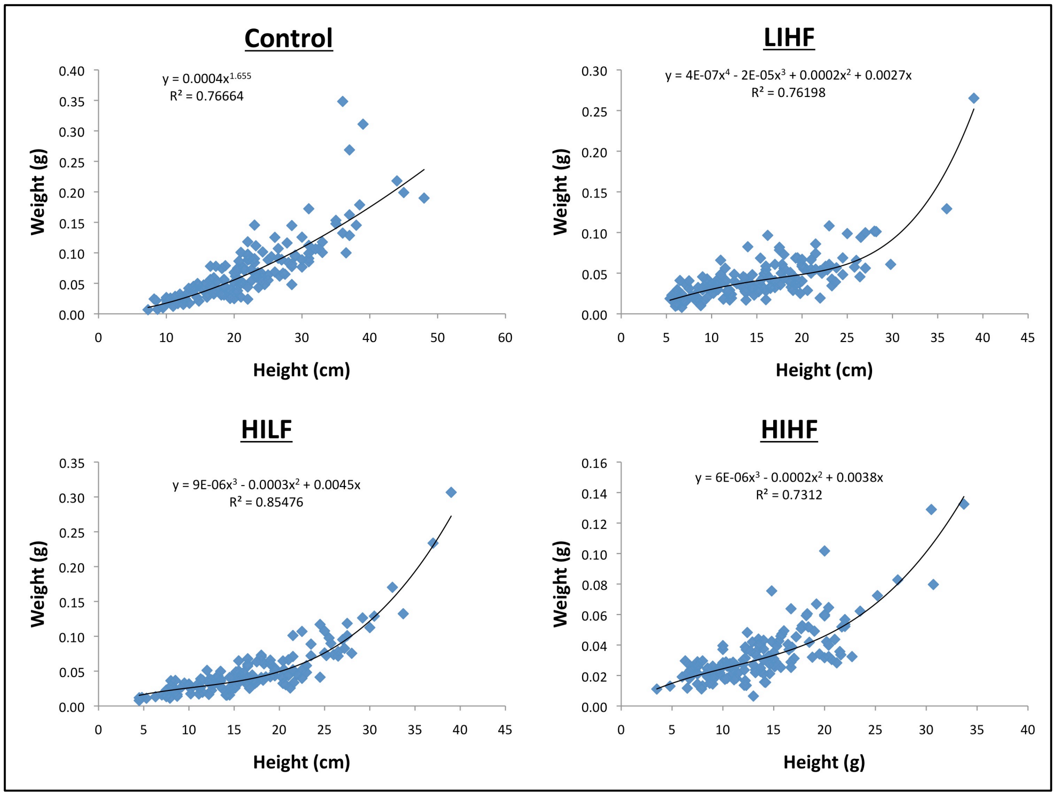

Figure 3-2. Tiller height-weight relationships for *Hesperostipa comata*, as modeled for plants exposed to each of the control, low intensity high frequency (LIHF), high intensity low frequency (HILF), and high intensity high frequency (HIHF) defoliation treatments.

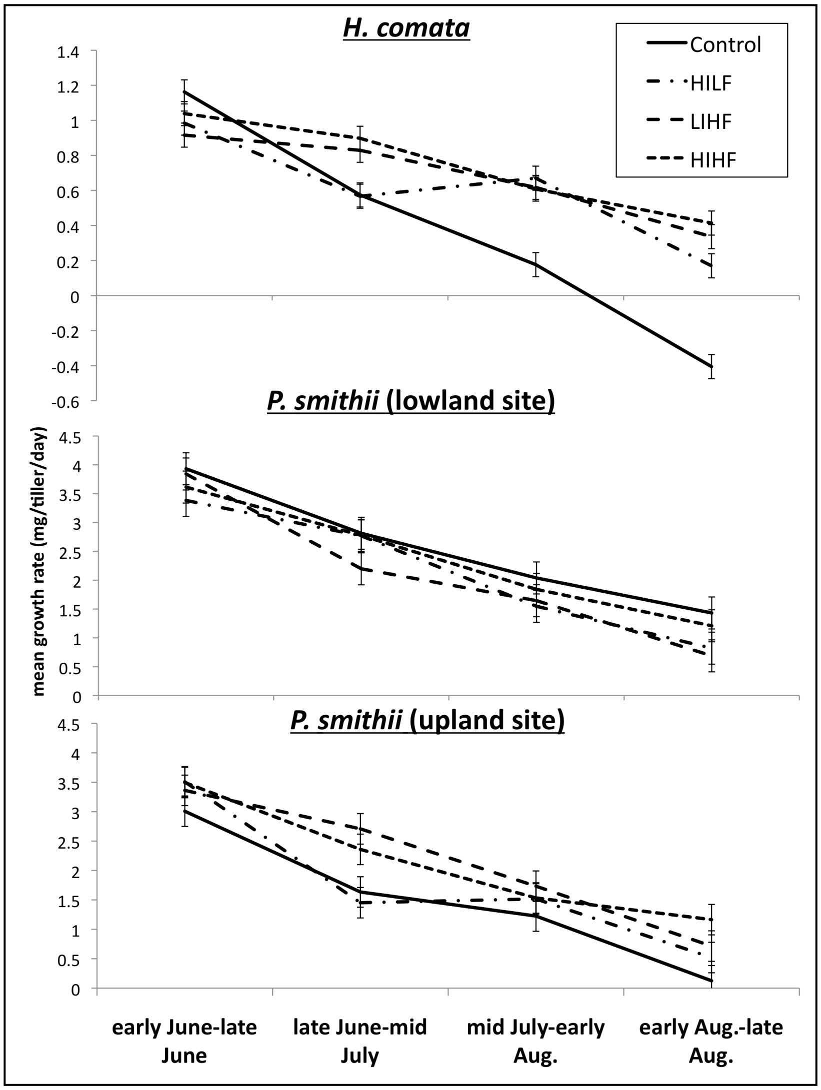

Figure 3-3. Seasonal tiller growth rate means (2010-2012 combined) for *Hesperostipa comata* and *Pascopyrum smithii* relative to deferred (control), high intensity low frequency (HILF), low intensity high frequency (LIHF), and high intensity high frequency (HIHF) defoliation.

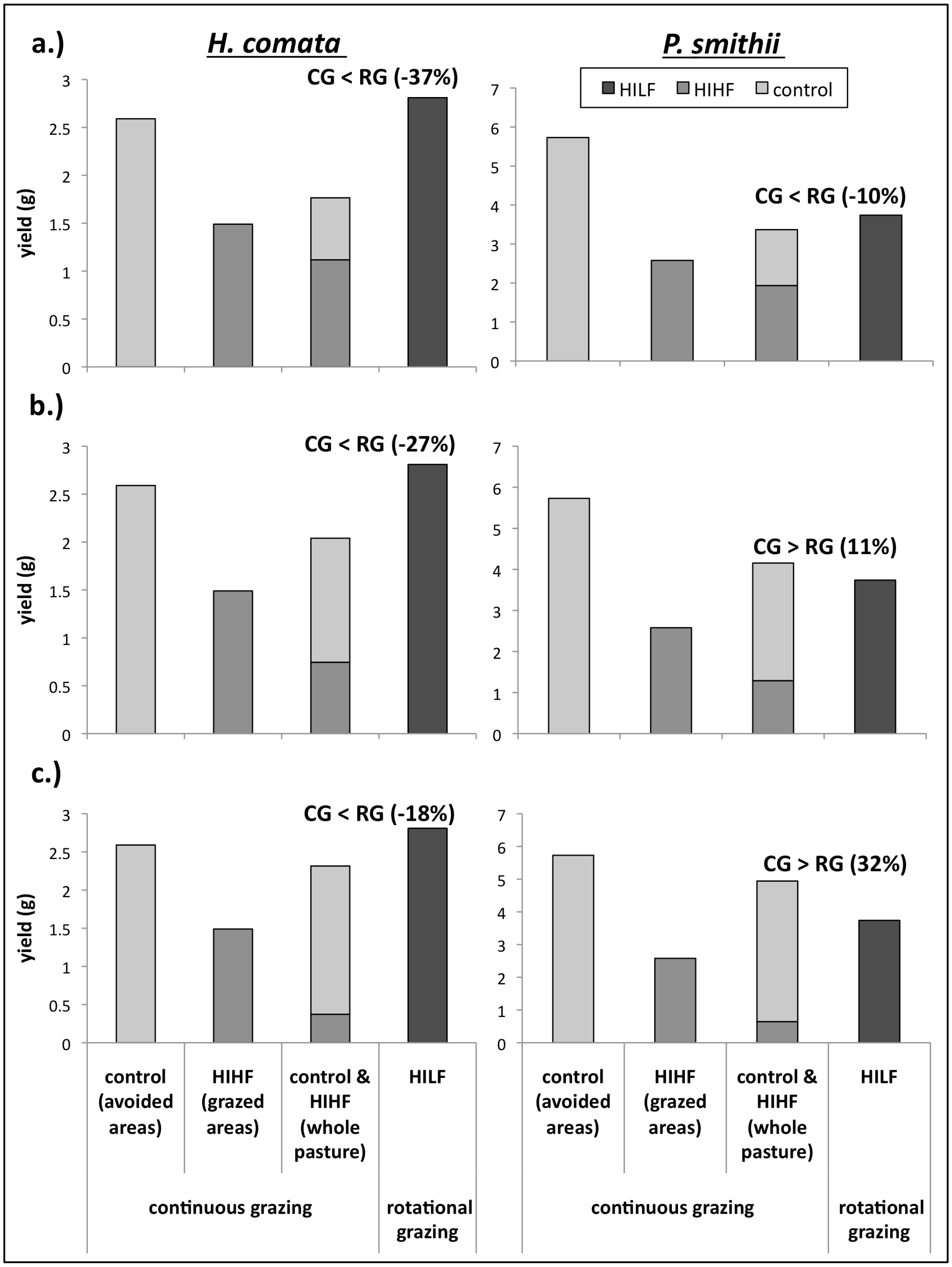

Figure 3-4. Conceptual model predicting plant production under continuous grazing (CG) and rotational grazing (RG) for *Hesperostipa comata* and *Pascopyrum smithii*. CG represents yield based on different proportions of control and high intensity defoliation at high frequency (HIHF) [a.) 25% control and 75% HIHF, b.) 50% of both, c.) 75% control and 25% HIHF], whereas RG represents yields under high intensity defoliation at low frequency.

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Chapter 4. A three year clipping and watering experiment in the dry mixedgrass prairie: Can rotational grazing maximize plant community productivity?

4.1. Abstract

Recent literature reviews suggest that rotational grazing (RG) may not increase plant community productivity relative to continuous grazing (CG) on rangelands. Rangelands are commonly native grasslands and these differ from introduced pasture systems, which generally have more suitable conditions for plant growth and are comprised of grazing tolerant forages that can compensate (and sometimes overcompensate) under high intensity defoliation. However, whether these same benefits confer to native grasslands is not well understood. This study examined plant community productivity in the Mixedgrass Prairie under treatments that included hand-clipping plots over three growing seasons at high intensity and low frequency (HILF), low intensity and high frequency (LIHF), high intensity and high frequency (HIHF), and the end of the growing season (control), combined with moisture treatments of ambient rainfall or water addition (4 defoliation x 2 moisture factorial). The study was conducted in a drier upland and more mesic lowland site. Yield was measured as accumulated aboveground phytomass, and for HILF and control treatments, yield was also compiled for the forb component and all major graminoids. Changes in the phenology (*i.e.*, timing)

of production, assessed here as the proportion of yield accumulating over different periods of the growing season, was examined for the HILF and HIHF defoliation treatments, as well as for forbs and graminoids within the HILF treatment. Moisture addition markedly increased accumulated aboveground phytomass, especially in the upland site, but had little influence on defoliation effects. For the lowland site, plant community productivity was greatest in the controls, followed by the HILF and then the HIHF and LIHF treatments. While yields under HILF defoliation were initially high, they declined in successive years of the experiment. Defoliation did not influence plant community productivity in the upland site, although there were minor defoliation effects under high moisture. Relative to the control defoliation treatment, HILF consistently increased yields of *Bouteloua gracilis* but reduced yields of *Pascopyrum smithii* in the more mesic lowland site and increased yields of *Carex spp*. in the upland site. Regardless of defoliation and moisture treatments, the majority of plant yield accrued by mid-July, with the exception of the warm season grass *B. gracilis*. Relative to HILF defoliation, HIHF defoliation accumulated more yield later in the growing season. Collectively, these results suggest that compensatory forage yielding within mixedgrass swards, regardless of moisture conditions, may be constrained by (1) defoliation sensitivity in key decreaser grasses, particularly *P. smithii*; and (2), the low regrowth potential of these same forages during the latter part of the growing season. In contrast, compensatory yields may be more common where short-statured, increaser grasses with greater regrowth potential dominate.

4.2. Introduction

Compelling arguments have been made regarding the superiority of rotational grazing (RG) over more conventional season-long continuous grazing (CG) (Voisin 1961; Savory 1999). There are many variations of RG, but the general premise is to subdivide a management unit into smaller paddocks, where livestock grazing is concentrated for shorter periods. RG can differ from CG if animal density is used to limit selectivity and thereby promote greater uniformity of grazing within pastures. This can promote managerial control over defoliation timing and frequency (Derner *et al*. 1994; Volesky 1994), and allows for extended rest periods between grazing events. Perhaps because sward productivity is often maximized at some optimal level of defoliation intensity, frequency, and timing (McNaughton 1983), RG is also commonly thought to maximize plant community productivity (*i.e.*, aboveground herbage yield). However, the majority of experiments suggest that RG may not increase plant community productivity relative to CG on rangelands (Holechek *et al*. 2000; Briske *et al*. 2008), although no definitive explanations exist for why it does not. To reconcile this it may be necessary to understand the tradeoffs associated with defoliation intensity, timing, and frequency on plant community productivity.

Rangelands mostly consist of native grasslands, but RG may be better suited to tame pasture and relatively mesic grasslands. Indeed, tame pastures in Alberta's Aspen Parkland have been found to tolerate intense and infrequent defoliation, and yield similarly, or in some cases, more than, low intensity defoliation regimes conducted at higher frequencies and deferred defoliation regimes (Donkor *et al*. 2002; De Bruijn *et al*. 2003; Donkor *et al*. 2003; De Bruijn and Bork 2010). Similar responses have been documented for native grasslands in the Tallgrass Prairie (Turner *et al*. 1993) and saltmarsh grasslands (Hik *et al*. 1991). Moreover, Dyer *et al*. (1991) found that mowing markedly increased yields in swards of the introduced agronomic grass, *Bromus inermis*, in the Tallgrass Prairie. Unifying characteristics among these plant communities appear to be that their dominant plants have high grazing tolerance and conditions are favourable for regrowth (*e.g.*, high moisture and fertility) for much of the growing season. Under these conditions, the primary constraints on plant community productivity may be light availability and space for growth (Burke *et al*. 1998), which in turn may enable increases in overall aboveground net primary productivity to accrue from recurrent growing season defoliation through reduced litter accumulation (Knapp and Seastedt 1986), or increased nutrient cycling (Hik *et al*. 1991).

In contrast, productivity may be more constrained by such things as limited soil moisture and nutrients for grasslands of greater aridity (Burke *et al*. 1998). Under these conditions, plant communities may not yield consistently high under intermittent defoliation within a single growing season given that the time required for plant recovery may exceed the length of the growing season (Bailey and Brown 2011). Even in the Great Plains of North America where vegetation evolved under relatively high grazing pressure from large ungulates (Mack and Thompson 1982), historical grazing regimes likely involved long ‘rest’ periods between grazing events. Nevertheless, herbivores may historically have tracked wildfire and rainfall, and preferentially grazed previously defoliated and burned areas to capitalize on lush regrowth (Vinton *et al*. 1993; Fuhlendorf and Engle 2001). Thus, although intensive mob grazing occurred, it was likely seldom recurrent in a given location within a single growing season (McNaughton 1993). This defoliation regime of intense defoliation followed by long recovery may maximize plant community productivity (Douglas and McNaughton 1993), and lack of adequate rest following grazing may limit plant community productivity under recurrent grazing (Milchunas and Lauenroth 1993; Pantel *et al*. 2010). This questions the ability of semiarid grasslands within the Great Plains to maintain aboveground yield under multiple bouts of intense and uniform defoliation within a single growing season.

For the Mixedgrass Prairies of the Great Plains in particular, plant community productivity may decline under periodic grazing because this in turn alters plant community composition. The Mixedgrass Prairie is named so because both taller mid- and shorter short- grasses coexist (Coupland 1961). Generally these mid- and short-grasses are differentially adapted to either canopy dominance or defoliation tolerance, respectively (Milchunas *et al*. 1988). Consequently, under increasing grazing pressure the late-seral midgrasses are replaced by more defoliation tolerant shortgrass species (Weaver 1954). This compositional change is accompanied by a decrease in community productivity given that shortgrass species, such as *Bouteloua gracilis*, are less productive than canopy dominant midgrasses, including *Hesperostipa comata* and *Pascopyrum smithii* (Coupland 1961; Smoliak 1965; Willms and Jefferson 1993).

This study examined plant community yield within the mixedgrass prairie under treatments of different intensities and frequencies of defoliation, combined with different moisture and edaphic conditions. The premise being that if plant communities can tolerate high intensity defoliation and yield similarly to low intensity and perhaps deferred defoliation regimes (*i.e.*, have compensatory regrowth), then RG may have merit in increasing forage yields. However, if compensatory regrowth doesn't occur, this would support the notion that conservative stocking and any grazing system that favours the retention of decreaser grasses will maximize plant community productivity (Bartolome 1993). Research objectives were to (1) determine whether compensatory growth responses are possible under given combinations of defoliation intensity and frequency, and (2) investigate whether moisture conditions mitigate yield responses. I hypothesized that defoliation at low frequency would produce plant community yields that are similar to those under deferred defoliation, but only under high moisture and/or edaphically favourable conditions.

4.3. Methods

4.3.1. Site Description

Two study sites were investigated, both located in the Brooks Plain within the Dry Mixedgrass Prairie natural subregion of Alberta, Canada (Adams *et al.* 2005). Mean annual precipitation and daily temperature in this area are 354 mm and 4.2°C, respectively (Adams *et al.* 2005). Sites were chosen based on uniformity of topography and plant community composition, with consistent presence of *P. smithii* and *H. comata*, and contrasting edaphic conditions (dry *vs.* wet). Site 1 (50° 53’ 40.2” N; 111° 52’ 26.3” W) was a relatively mesic, lowland range site with a Gleyed Eluviated Brown Chernozemic soil (Soil Classification Working Group [SCWG] 1998) of sandy loam texture (pH=6.3, EC=37µs/cm, organic matter content=2.5%). Vegetation composition consisted mostly of *Pascopyrum smithii*, with *Koeleria macrantha* (Ledeb.) J.A. Schultes and *Hesperostipa comata* as sub-dominants. Site 2 (50° 52’ 23.8” N; 111° 52’ 26.2” W) was a relatively xeric, upland range site with a Rego Brown Chernozemic soil (SCWG 1998) of loamy sand texture (pH=6.7, EC=27µs/cm, organic matter content=1.3%). Dominant vegetation at this site included *P. smithii*, *H. comata*, and *Bouteloua gracilis* (Willd. *ex* Kunth) Lag. *ex* Griffiths. Both sites had range health assessment scores of 80%, or healthy (Adams et al. 2003), and were previously grazed for the long-term at light-moderate stocking rates.

4.3.2. Treatments and Experimental Design

Treatments of defoliation and moisture were combined in a fully randomized factorial (4 x 2) design, with 6 replicates per site, and applied to 1 x 1 m plots, separated by at least 0.5 m. Defoliation treatments included hand clipping at high intensity and low frequency (HILF), high intensity and high frequency (HIHF), low intensity and high frequency (LIHF), and a deferred control. HILF and HIHF defoliation plots were clipped at 2 cm stubble heights every 3 and 6 weeks, respectively. LIHF plots were clipped at a 5 cm stubble height every 3 weeks. And control plots were clipped to a 2 cm stubble height in late August. Low intensity clipping heights of 5 cm were used to prevent shorter statured species (e.g., *Bouteloua gracilis*) from escaping defoliation, thereby preventing confounding competitive interactions. High intensity clipping heights of 2 cm were used to ensure complete removal of leaf material. Moisture treatments included not watering (*i.e*., ambient moisture conditions) and watering plots to augment rainfall and maintain an equivalent of over 150 mm of monthly precipitation throughout the growing season; this is double the average precipitation in June, the month of greatest rainfall. The objective here was to remove moisture availability as a constraint for plant growth. Watering occurred at approximately 10 d intervals and all treatments commenced and terminated in early June and late August, respectively, in 2010-2012. Prior to initiating treatments, plots were hand-raked to remove litter, and after the first clipping, green plant material was separated from senescent material in order to separate previous years' standing dead tillers from current year's growth. Plots were hand raked of litter to prevent confounding effects given that litter would largely be eliminated under high intensity clipping, but not under low intensity and deferred defoliation.

4.3.3. Response Parameters and Data Analyses

Within the centre 0.5 x 0.5 m portion of plots, clipped plant material was harvested, dried at 60°C for 48 hr, and weighed. Non-vascular plants and succulents were not harvested because these were rare and generally below harvest heights (*e.g.*, *Selaginella densa* and *Coryphantha vivipara*). For the HILF and control treatments in 2012, forbs (together as one component) and each species within the graminoid component were harvested separately. This was done to better understand how defoliation influenced plant community composition and assist in interpreting yield responses among sites.

Plot yield (*i.e.*, plant community productivity) represented accumulated aboveground phytomass. These data were checked for normality and homogeneity of variance with Shapiro-Wilk and Levene's tests, respectively, and analyzed with a repeated measures two-way ANOVA, using defoliation, moisture, and year of sampling as fixed factors (SAS 9.2—SAS Institute, 1989); year of sampling was also a repeated measure. Sites were analyzed independently because defoliation effects differed among sites, as evidenced by defoliation x site interactions ($P<0.001$) under a preliminary ANOVA that treated site as a fixed factor. To minimize the probability of a type II error, mean separation tests for significant main effects and interactions were based on least-significant differences (LSD).

The relative contribution of each species to plot yield was determined, including the proportion of yield that accrued over various intervals during the growing season, both for individual species and overall community yield. For the 2012 data, the percentage that forbs and each graminoid species contributed to overall plot yield was determined for the control and HILF defoliation treatments. The phenology of each species yield was also determined for the HILF defoliation treatment by calculating the percentage of total yield accruing for three consecutive periods of the growing season: prior to early-June, early-June to mid-July, and mid-July to late-August. The same was also done for total community yield for the HILF and HIHF defoliation treatments. ANOVA could not be performed on these data because they violated the assumption that all residuals were free to vary from 0 to infinity, so data were summarized using Proc Means (SAS 9.2) to obtain means and associated confidence intervals. Significant effects were assessed based on whether the 95% confidence intervals failed to overlap. Mean comparisons were made within defoliation and moisture treatments, but interactions were not investigated.

4.4. Results

4.4.1. Growing Conditions

Precipitation over the period of the experiment was high in both 2010 and 2012, with ambient rainfall exceeding average precipitation levels by 38 and 50%, respectively (Table 4-1). However, this was mostly due to heavy rains in June, while July and August precipitation levels were close to average. Precipitation during 2011 (135 mm) was relatively close to average (140.9 mm), but June was again relatively wet, whereas July and August were relatively dry. The preceding growing season (2009) was relatively dry in June, but very wet in July (Table 4-1).

4.4.2. Plant Community Yield

Overall, the effect of defoliation was significant in the lowland ($P < 0.001$), but not the upland ($P = 0.33$) (Table 4-2), site. However, in both sites, defoliation effects varied among moisture regimes and years of sampling ($P < 0.02$) (Table 4-2), but trends were again dissimilar. In the lowland site HILF defoliation initially yielded similar to controls, and then declined markedly to yield similarly to the LIHF and HIHF treatments (Table 4-3). However, HILF yielded more favourably relative to LIHF and HIHF when under high moisture conditions in 2011, as compared to low moisture conditions in that same year (Table 4-3). The net effect was that HILF reduced yield relative to controls by 21%, and high frequency defoliation (regardless of intensity) reduced yield by 32%. In the upland site there were no consistent defoliation effects among years (Table 4-4). Initially, HILF defoliation out-yielded controls by 21%, but both treatments yielded similarly high in 2011, and there was no differentiation among defoliation treatments in 2012 and overall (Table 4-4). Moisture conditions influenced this by promoting greater mean segregation among defoliation treatments under moisture addition in 2010 and 2011 (Table 4-4). And in contrast to the lowland site, overall community yield in the upland did not decline as the study progressed (Table 4-4).

Despite relatively high ambient rainfall in all growing seasons, moisture addition still markedly increased herbage yield ($P < 0.001$), especially in the drier, upland site. However, the principle effect of moisture addition was to maintain plant community productivity at a consistent level; whereas under ambient moisture conditions, plant community productivity progressively declined in each growing season. Nevertheless, moisture addition increased overall yields by 37 and 73% in the lowland and upland sites, respectively (Tables 4-3 and 4-4).

Total mean productivity (across years and treatments) for the lowland and upland site was 2602 and 1733 kg/ha, respectively (data not shown), suggesting the lowland site was, on average, 50% more productive. Maximum productivity at both sites occurred under the combination of moisture addition and deferred defoliation in 2011, with production peaking for the lowland and upland sites at 4056 and 2540 kg/ha (Tables 4-3 and 4-4). In contrast, productivity reached its lowest under high frequency defoliation and ambient growing conditions, with lowland and upland sites yielding only 1644 and 988 kg/ha, respectively (Tables 4-3 and 4-4).

4.4.3. Yield Composition and Phenology

In comparison to controls, HILF defoliation increased the relative contribution of *Bouteloua gracilis* to forage yields by 2.9 and 1.7 fold in the lowland and upland sites, respectively (Table 4-5). The only other notable alterations to the relative contribution of major plant species to plot yield included a 43% decrease in *Pascopyrum smithii*, and a 2-fold increase in upland *Carex* species under HILF defoliation within the lowland and upland sites, respectively (Table 4-5). Moisture influences were limited to *Hesperostipa comata* in the lowland, where the relative contribution of this species to plot yield was 3-fold greater under ambient moisture (Table 4-5).

The majority of yield for plots originated from the three dominant graminoid species, especially in the lowland site, and defoliation influenced which species were dominant contributors to yield. The top 3 plants that accounted for 84% of plot yield under control defoliation in the lowland site included, from greatest to least, *P. smithii*, *Koeleria macrantha*, and *H. comata*. In contrast, under HILF defoliation, 65% of plot yield originated from *P. smithii*, *B. gracilis*, and *K. macrantha*, respectively. Although *P. smithii* contributed the most to forage plot yield under both these defoliation treatments, this value remained markedly lower under HILF defoliation, which explains why all these species contributed more similarly to plot yield under HILF defoliation, and the lower amount that these 3 species contributed together to plot yield (*i.e.*, 65 *vs.* 84%) (see Table 4-5). *P. smithii* in general, was not as dominant in the upland site, especially under HILF defoliation, where *B. gracilis*, *Carex spp.*, and *P. smithii* made up 75% of plot yield, whereas 73% of yield for the controls consisted of *P. smithii*, *H. comata*, and *B. gracilis*.

Of all the dominant forage species, on average 90% of plant yield accrued within the first half of the growing season (Table 4-6). This was especially evident for *P. smithii* and *K. macrantha*, for which 96 and 93% of yield accrued by this period, respectively. In contrast, *Bouteloua gracilis* accumulated only 67% of its yield by mid-July. Production phenology also varied between defoliation treatments, with HILF defoliation accruing more yield earlier in the growing season compared to HIHF defoliation (*e.g.*, 82 *vs*. 66%). Moisture conditions, however, did not alter production phenology (Table 4-6).

4.5. Discussion

4.5.1. Plant Community Yield

RG systems strive to balance defoliation and recovery to maintain livestock and plant community productivity (Briske *et al*. 2011). Thus, understanding how defoliation frequency, intensity, and timing regulate productivity may help evaluate the merits of RG for semiarid plant communities. Given that RG allows managerial control over the timing of defoliation, compensatory plant growth responses may be capitalized on through regrazing of pastures later in the growing season. This may increase yield if plant communities maintain productivity under recurrent grazing through compensatory regrowth. However, RG may not increase productivity in semiarid plant communities given that vegetation may need an entire growing season to recover (*i.e.*, compensate) (Bailey and Brown 2011), albeit this can depend on defoliation timing (Pantel *et al*. 2010). Results here do not refute or support this presumption given that community productivity responses to defoliation were not consistent among sites.

At the drier upland site, HILF defoliation initially maximized community productivity under moisture addition, but this was not sustained. Interestingly, no defoliation regime consistently reduced or promoted plant community yield relative to the controls. This suggests that grazing management may have little influence on plant community productivity in these environments, and perhaps accounts for why the majority of grazing system studies on rangelands document this (Holechek *et al.* 2000; Briske *et al.* 2008). It may also be because compensatory plant responses may be more common in slower growing vegetation in edaphically stressful environments. For example, Hilbert *et al.* (1981), demonstrated that compensatory growth is more likely to occur for slow, rather than rapidly, growing plants. This is because slow growing plants in low resource environments are likely growing below their potential maximum growth rate, and therefore require less of an increase in growth rate to compensate for defoliation effects. Milchunas and Lauenroth (1993) also found that grazing was most likely to increase productivity in plant communities of low productivity and long co-evolutionary history with large herbivores, provided grazing was light-moderate. However, this contradicts other studies that have found overcompensation in grasslands of higher productivity, such as the Tallgrass Prairie (Turner *et al.* 1993) and Aspen Parkland (Donkor *et al.* 2003). Moreover, Belsky (1986) recognized that most cases of overcompensation are limited to situations of high productivity and low competition for resources, such as in cropland and greenhouse experiments. Similarly, Hawks and Sullivan (2001), found that compensatory responses are more common among basal meristem monocots (*e.g.*, graminoids) under high resource conditions, compared to under low resource conditions for dicotelydenous herbs.

Consequently, there is a dichotomy of ideas regarding the conditions necessary for compensatory regrowth to occur. I hypothesized that compensatory growth would occur under elevated moisture conditions, either in the more mesic lowland site or in the upland site under moisture addition. Results of this experiment both support and reject this notion. First, the lowland community was found to sustain HILF defoliation with 3 intense defoliations and initially yield similarly to controls, but this trend was not sustained beyond the first or second growing season (depending on moisture conditions). These results are similar to those of the more mesic Northern Mixedgrass Prairie, where Zhang and Romo (1994) found higher yields under less frequent defoliation; but similar to our results, any growing season defoliation decreased yield relative to deferred defoliation. Second, although moisture addition markedly increased plant community productivity, especially in the drier upland site, this treatment failed to consistently mitigate HILF defoliation effects on plant community production. The only evidence for this occurred during the first year at the upland site, where HILF defoliation and moisture addition maximized yields, and in the second year at the lowland site, where moisture addition promoted yields under HILF defoliation above that of the high frequency defoliation regimes. However, both of these effects did not persist into year three. Therefore, it appears that moisture conditions can increase mixedgrass prairie resiliency to HILF defoliation to some degree, but only in the short-tem.

Declining productivity under HILF is notable given that this treatment probably best approximates the defoliation regime of short-duration RG. In contrast, CG can result in ‘patch grazing’, where previously grazed patches are recurrently utilized and other areas are avoided (Ring *et al*. 1985; Willms *et al*. 1988). Under this paradigm, control and HIHF defoliation treatments here may represent plant yield in recurrently grazed and avoided patches, respectively. Assuming that HIHF pasture productivity consists of similar contributions of both patch types, then overall productivity would be highest under continuous and rotational grazing in the lowland and upland sites, respectively (Figure 4-1).

Higher yielding under modelled CG for the lowland site was due to the relatively high yield of controls, which compensated for lower yields under HIHF defoliation. This is especially evident when avoided areas make up a greater proportion of the pasture (Figure 4-1). This suggests that although recurrent grazing in grazed patches markedly reduces plant community productivity, the avoided patches may compensate for any overall reduction in productivity associated with HIHF defoliation. This may account for the similar plant community productivity observed under various grazing systems on rangelands (Holechek *et al*. 2000; Briske *et al*. 2008), although this assumes patch grazing indeed occurs under grazing trials of relatively small spatial and temporal scales (Norton 1998). In contrast, relatively similar yields under all defoliation regimes in the upland site accounts for similar modelled yields in both avoided and recurrently grazed patches. Although not significant, plant community yield at this site was slightly higher under HILF compared to HIHF and deferred (control) defoliation combined. This suggests that RG systems that use high animal densities to promote more uniform utilization may help maximize overall plant community productivity in more arid sites of the mixedgrass prairie.

4.5.2. Yield Composition and Phenology

Differences in plant community composition, along with how dominant grasses respond to defoliation, may account for the divergent effects of defoliation on community productivity observed between sites. *P. smithii* was initially dominant in the lowland site, and under HILF defoliation the less productive *B. gracilis* and upland *Carex* species increased at the expense of *P. smithii* and other mid-grasses. In contrast, community changes under HILF defoliation were not as pronounced in the upland site (see Chapter 5). *P. smithii* was not as dominant and *B. gracilis* was relatively more abundant at this location, especially in controls. Given that *P. smithii* is a very productive grass in the Mixedgrass Prairie (Coupland 1961; Willms *et al.* 2002), this would account for the decline in productivity under HILF defoliation in the lowland site. In contrast, *P. smithii* was markedly less dominant in the upland site, meaning that its decline in the community would have a relatively smaller impact on overall community productivity.

These results are generally consistent with plant community physiognomy changes associated with grazing in the tallgrass and shortgrass prairies (Milchunas *et al.* 1988). In tallgrass communities grazing causes composition to change from grasses that are canopy dominant in favour of those that are decumbent and grazing tolerant, whereas in shortgrass communities grazing tends to increase the cover and density of the already dominant shortgrasses. This suggests that more mesic and xeric areas of the mixedgrass prairie may be functionally more similar to the tallgrass and shortgrass prairies, respectively (see Chapter 5). *B. gracilis* was the dominant shortgrass species in the upland site, and indeed this plant has demonstrated compensatory responses elsewhere due to its high growth rate and grazing tolerance to defoliation under conditions of sufficient moisture (Alward and Joern 1993). Moreover, given *B. gracilis'* dominance in the upland site, compensatory responses (and perhaps overcompensation) in this graminoid may have compensated for the minor reduction in yield from canopy dominant decreaser grasses.

RG may also promote compensatory responses by maintaining consistent community production throughout the growing season. However, the sigmoidal growth pattern of plants entails that growth is generally very rapid for only a short period within the growing season (Lauenroth and Whitman 1977). Voisin (1961) postulated that intermittent defoliation combined with appropriate rest periods can counter this by recurrently promoting rapid regrowth. This was tested here by examining production phenology as the percentage of yield accruing during given periods of the growing season. However, this could only be done for the HILF and HIHF defoliation regimes given that destructive sampling to a common intensity is necessary to test this. Moreover, because each species was harvested independently within HILF plots, production phenology could also be examined on a species basis.

This study showed that under HILF defoliation, greater than 80% of plant community biomass accrues by the middle of July, regardless of moisture conditions. This is the case for the forb component and all major graminoids except *B. gracilis*, which accumulated only 66% of its biomass by this period. This difference in production phenology is likely because *B. gracilis* is the only warm-season graminoid dominant within plots (*Calamovilfa longifolia* was rare). This corroborates findings that spring precipitation largely determines productivity in the Mixedgrass Prairie (Milchunas *et al.* 1994; Schellenberg *et al.* 1999; Derner and Hart 2007; Derner *et al.* 2008) because mid-grasses such as *P. smithii* and *H. comata*, which contribute the most to sward yield and are cool-season, grow mostly early in the growing season (Manley *et al.* 1997; Pantel *et al.* 2010). Consequently, although a comparison cannot be made to deferred defoliation (controls), anecdotally it appears that HILF does not dramatically alter the sigmoidal growth pattern of plants. This suggests that regrowth potential and opportunity for grazing induced compensatory regrowth later in the growing season is low for cool-season midgrasses.

Consequently, plant phenology appears to correspond with the region's precipitation pattern given that the majority of growing season precipitation in the Dry Mixedgrass Prairie falls within the month of June (Singh *et al.* 1983), and spring growth is also driven by accumulated fall and winter precipitation (Smoliak 1986; Heitschmidt *et al.* 2005). Thus, cool season midgrasses of the Dry

Mixedgrass Prairie exploit these dependable mesic conditions by concentrating growth relatively early in the growing season. Given that moisture conditions in this experiment failed to alter growth phenology, Mixedgrass Prairie vegetation may lack the plasticity to respond to later growing season precipitation. This finding may be because higher temperatures limit stomatal conductance and photosynthesis in cool-season grasses, especially in *P. smithii* (Kemp and Williams 1980). However, even the warm-season grass, *B. gracilis*, failed to accumulate relatively more biomass in the latter portion of the growing season under moisture addition. Nevertheless, perhaps cool-season plants are better suited to more mesic areas of the Mixedgrass Prairie because, despite being a relatively dry environment (Ode *et al.* 1980), these grasses can pre-emptively exploit fall, winter, and early spring moisture by growing rapidly and completing their growth early in the growing season when temperatures have not reached those optimal for warm-season plant growth (Epstein *et al.* 1997).

In terms of comparative phenology of production for HILF and HIHF, the latter accumulated relatively more yield later in the growing season. Two mechanisms may explain this. First, HIHF defoliation may have prolonged regrowth during the growing season. Alternatively, and more likely, HIHF defoliation may favour *B. gracilis*, which was corroborated by an ordination of cover values (Chapter 5). Having greater abundance of *B. gracilis* would shift production to later within the growing season (Derner and Hart 2007). This suggests that recurrently grazed patches that occur under CG may be important for maintaining sources of higher quality forage later in the growing season

(Mack and Thompson 1982). However, if the same defoliation regime was applied across pastures using RG, then overall plant community productivity may decline where tall-statured decreaser grasses are more abundant.

4.6. Conclusion and Management Implications

Recent literature reviews suggest that RG does not enhance plant community productivity relative to CG (Holechek *et al*. 2000; Briske *et al*. 2008; Briske *et al*. 2011). For RG to enhance plant community productivity, uniform intense defoliation at given frequencies must promote compensatory regrowth. I hypothesized that compensatory responses would depend on moisture conditions, and be more likely at the mesic lowland site or under moisture addition. Contrary to this, moisture conditions had little influence on compensatory regrowth, and, surprisingly, growing season defoliation did not affect plant community productivity in the upland site, at least not overall. In contrast, defoliation, especially at high frequency, reduced productivity in the lowland site. These varying responses to defoliation may have resulted from differences in plant composition between sites. For example, declining productivity under defoliation in the lowland may be associated with the reduction of *P. smithii*, which is a highly productive, canopy dominant species. In contrast, the upland site consisted of more defoliation tolerant, shortgrasses, such as *B. gracilis* and upland sedges. Phenology of production was also examined to determine whether repeated defoliation may prolong growth, which is one mechanism for compensatory growth. Surprisingly, regardless of moisture conditions and even under repeated defoliation, the majority of yield accumulated early in the growing season. This is true for all dominant graminoids except the warm-season *B. gracilis*, which accumulates relatively more biomass in the latter portion of the growing season.

These results suggest that compensatory responses, and therefore RG's ability to enhance plant community productivity, may be limited by more than just ambient moisture conditions in the Mixedgrass Prairie. First, defoliation sensitivity of canopy dominant, productive grasses entails that recurrent utilization will invariably limit plant community productivity potential in more mesic mixedgrass sites where canopy dominant, tall grasses are more dominant (Chapter 5). In contrast, within drier areas where more defoliation tolerant shortgrasses may be dominant, plant communities appear more resilient to different intensities and frequencies of defoliation (see Milchunas *et al*. 1988). Second, plant phenology may also limit compensatory growth given that the majority of biomass accrues relatively early in the growing season, meaning opportunities for regrowth and plant recovery are low. Together, defoliation sensitivity of key decreasers and a relatively short growing season may limit compensatory growth potential in the Mixedgrass Prairie. The corollary of this may be that for plant communities to respond favourably to uniformly intense defoliation at some frequency (*e.g.*, short-duration RG), dominant plants may have to possess both high grazing tolerance and regrowth potential.

Table 4-1. Ambient growing season precipitation (mm) and recent long-term averages for the Brooks area of Alberta, Canada.

	Year				Average[1]
	2009	2010	2011	2012	1971-2000
June	54	123	77	135	63
July	137	52	36	48	42
August	39	20	23	29	36
Total (June-Aug.)	230	195	135	212	141

[1] Environment Canada climate normals.

Table 4-2. Plot yield ANOVA *F* and *P* values for fixed factors of defoliation, moisture, and year of sampling within both a lowland and upland site of the Mixedgrass Prairie.

Effect	Lowland site		Upland site	
	F value	*P* value	*F* value	*P* value
Defoliation	$15.9_{(3, 40)}$[1]	**< 0.001**	$1.2_{(3, 48)}$	0.33
Moisture	$48.4_{(1, 40)}$	**< 0.001**	$137.5_{(1, 48)}$	**< 0.001**
Defol. x moist.	$1.5_{(3, 40)}$	0.23	$1.3_{(3, 38)}$	0.29
Year	$39.7_{(2, 80)}$	**< 0.001**	$5.8_{(2, 96)}$	**0.004**
Defol. x year	$3.8_{(6, 80)}$	**0.002**	$6.6_{(6, 96)}$	**< 0.001**
Moist. x year	$21.9_{(2, 80)}$	**< 0.001**	$11.9_{(2, 96)}$	**< 0.001**
Defol. x moist. x year	$2.9_{(6, 80)}$	**0.013**	$4.0_{(6, 96)}$	**0.001**

[1] *F*-ratio numerator and denominator degrees of freedom, respectively.

Table 4-3. Herbage yield (g) means (standard errors in parentheses) for the lowland site in relation to all significant ($P < 0.05$) fixed effects and interactions of defoliation, moisture, and year of sampling. Defoliation treatments included deferred (control), high intensity at low frequency (HILF), low intensity at high frequency (LIHF), and high intensity at high frequency (HIHF).

	Year			Overall
	2010	2011	2012	
Defoliation				
Control	^{A}[1] 87.3 ^{a}[2]	^{A} 84.4 ^{a}	^{B} 73.7 ^{a}	81.8 ^{a}
HILF	^{A} 78.0 ^{a}	^{B} 63.1 ^{b}	^{C} 53.0 ^{b}	64.7 ^{b}
LIHF	^{A} 63.5 ^{b}	^{AB} 56.6 ^{b}	^{B} 53.0 ^{b}	57.7 ^{bc}
HIHF	^{A} 62.7 ^{b}	^{B} 53.1 ^{b}	^{B} 52.3 ^{b}	56.0 ^{c}
	(3.93)[3]	(3.66)	(2.73)	(2.95)
Moisture				
Addition	^{A} 77.2 ^{a}	^{A} 75.3 ^{a}	^{A} 73.5 ^{a}	75.3 ^{a}
Ambient	^{A} 68.6 ^{b}	^{B} 53.2 ^{b}	^{C} 42.5 ^{b}	54.8 ^{b}
	(2.78)	(2.59)	(1.93)	(2.09)
Defol. x moist.				
Control, added moist.	^{B} 89.0 ^{a}	^{A} 101.4 ^{a*}[3]	^{AB} 96.8 ^{a*}	
HILF, added moist.	^{A} 83.6 ^{ab}	^{A} 78.7 ^{b*}	^{B} 69.5 ^{b*}	
LIHF, added moist.	^{A} 69.5 ^{bc}	^{A} 64.4 ^{c*}	^{A} 64.8 ^{b*}	
HIHF, added moist.	^{A} 66.6 ^{c}	^{A} 56.9 ^{c}	^{A} 62.8 ^{b*}	
Control, ambient moist.	^{A} 85.7 ^{a}	^{B} 67.4 ^{a*}	^{C} 50.5 ^{a*}	
HILF, ambient moist.	^{A} 72.5 ^{ab}	^{B} 47.5 ^{b*}	^{C} 36.5 ^{b*}	
LIHF, ambient moist.	^{A} 57.5 ^{b}	^{A} 48.7 ^{b*}	^{B} 41.1 ^{ab*}	
HIHF, ambient moist.	^{A} 58.8 ^{b}	^{A} 49.4 ^{b}	^{B} 41.7 ^{ab*}	
	(5.56)	(5.18)	(3.85)	
Overall	^{A} 72.9	^{B} 64.3	^{C} 58.0	
	(1.97)	(1.83)	(1.36)	

[1] Uppercase letters denote mean separation within rows ($P \leq 0.05$).

[2] Lowercase letters denote mean separation within columns ($P \leq 0.05$).

[3] Asterisks denote mean separation between different moisture treatments within the same defoliation treatment ($P \leq 0.05$).

Table 4-4. Herbage yield (g) means (standard errors in parentheses) for the upland site in relation to all significant ($P < 0.05$) fixed effects and interactions of defoliation, moisture, and year of sampling. Defoliation treatments included deferred (control), high intensity at low frequency (HILF), low intensity at high frequency (LIHF), and high intensity at high frequency (HIHF).

	Year			Overall
	2010	2011	2012	
Defoliation				
Control	^{B1} 41.7 ^{b2}	^{A} 46.6 ^{a}	^{AB} 45.3 ^{a}	
HILF	^{A} 50.3 ^{a}	^{A} 46.4 ^{a}	^{B} 40.5 ^{a}	
LIHF	^{A} 44.4 ^{ab}	^{B} 37.3 ^{b}	^{A} 42.2 ^{a}	
HIHF	^{A} 46.6 ^{ab}	^{B} 36.6 ^{b}	^{A} 42.3 ^{a}	
	(2.85)	(1.94)	(2.59)	
Moisture				
Addition	^{A} 53.6 ^{a}	^{A} 55.4 ^{a}	^{A} 55.7 ^{a}	54.9 ^{a}
Ambient	^{A} 37.9 ^{b}	^{B} 28.1 ^{b}	^{B} 29.4 ^{b}	31.8 ^{b}
	(2.01)	(1.37)	(1.83)	(1.39)
Defol. x moist.				
Control, added moist.	^{B} 48.5 ^{b*3}	^{A} 63.5 ^{a*}	^{B} 55.8 ^{a*}	
HILF, added moist.	^{A} 65.1 ^{a*}	^{A} 62.4 ^{a*}	^{B} 53.5 ^{a*}	
LIHF, added moist.	^{B} 48.9 ^{b}	^{B} 49.8 ^{b*}	^{A} 58.3 ^{a*}	
HIHF, added moist.	^{A} 51.8 ^{b}	^{B} 45.8 ^{b*}	^{A} 55.4 ^{a*}	
Control, ambient moist.	^{A} 34.8 ^{a*}	^{A} 29.7 ^{a*}	^{A} 34.8 ^{a*}	
HILF, ambient moist.	^{A} 35.6 ^{a*}	^{A} 30.5 ^{a*}	^{A} 27.5 ^{a*}	
LIHF, ambient moist.	^{A} 40.0 ^{a}	^{B} 24.7 ^{a*}	^{B} 26.2 ^{a*}	
HIHF, ambient moist.	^{A} 41.3 ^{a}	^{B} 27.5 ^{a*}	^{B} 29.2 ^{a*}	
	(4.02)	(2.74)	(3.66)	
Overall	^{A} 45.7	^{B} 41.7	^{AB} 42.6	
	(1.42)	(0.97)	(1.29)	

[1] Uppercase letters denote mean separation within rows ($P \leq 0.05$).

[2] Lowercase letters denote mean separation within columns ($P \leq 0.05$).

[3] Asterisks denote mean separation between different moisture treatments within the same defoliation treatment ($P \leq 0.05$).

Table 4-5. Grass species mean percent (with 95% confidence intervals in parentheses) contribution to herbage yield in relation to two defoliation (deferred [control] and high intensity low frequency [HILF]) and two moisture (addition and ambient) treatments.

	Defoliation		Moisture	
	Control	HILF[1]	Addition	Ambient
Lowland site				
Hesperostipa comata	13.5 $^{(21.3-5.7)}$	8.5 $^{(13.2-3.9)}$	5.7 $^{(8.4-3.1)}$	16.3 $^{(23.4-9.2)}$
Pascopyrum smithii	54.0 $^{(67.1-40.9)}$	30.6 $^{(39.2-22.0)}$	50.2 $^{(65.6-34.8)}$	34.4 $^{(44.1-24.8)}$
Bouteloua gracilis	6.9 $^{(9.5-4.2)}$	20.0 $^{(26.6-13.4)}$	14.9 $^{(23.0-6.9)}$	12.0 $^{(17.6-6.3)}$
Koeleria macrantha	16.3 $^{(24.7-7.9)}$	14.4 $^{(21.3-7.5)}$	13.9 $^{(19.9-8.0)}$	16.7 $^{(25.8-7.7)}$
Carex spp.	6.3 $^{(9.6-3.1)}$	14.1 $^{(19.4-8.8)}$	8.1 $^{(13.2-2.9)}$	12.4 $^{(17.3-7.4)}$
Other graminoids	0.0	1.1 $^{(2.3-0.0)}$	0.7 $^{(1.5-0.0)}$	0.4 $^{(1.4-0.0)}$
Forb spp	2.9 $^{(5.6-0.3)}$	11.3 $^{(15.9-6.7)}$	6.5 $^{(11.7-1.3)}$	7.7 $^{(12.2-3.2)}$
Upland site				
Hesperostipa comata	23.8 $^{(31.3-16.3)}$	18.3 $^{(25.0-11.6)}$	22.0 $^{(29.9-14.1)}$	20.1 $^{(26.8-13.4)}$
Pascopyrum smithii	26.4 $^{(35.9-16.8)}$	18.4 $^{(23.6-13.3)}$	27.7 $^{(36.6-18.7)}$	17.2 $^{(22.5-11.8)}$
Bouteloua gracilis	22.5 $^{(29.3-15.6)}$	37.8 $^{(41.8-33.9)}$	32.6 $^{(40.3-25.0)}$	27.7 $^{(34.8-20.6)}$
Koeleria macrantha	1.7 $^{(4.3-0.0)}$	0.6 $^{(1.7-0.0)}$	0.6 $^{(1.7-0.0)}$	1.7 $^{(4.3-0.9)}$
Carex spp.	9.5 $^{(11.6-7.4)}$	19.1 $^{(21.8-16.4)}$	14.4 $^{(17.7-11.0)}$	14.3 $^{(18.8-9.7)}$
Other graminoids	0.0	0.5 $^{(1.0-0.0)}$	0.3 $^{(0.7-0.0)}$	0.2 $^{(0.6-0.0)}$
Forb spp	16.1 $^{(31.9-0.3)}$	5.3 $^{(8.5-2.0)}$	2.5 $^{(4.5-0.5)}$	18.8 $^{(33.8-3.9)}$

Table 4-6. Mean percent of total herbage yield (95% confidence intervals in parentheses) accruing at different times during the growing season for different plant species, as well as different defoliation and moisture treatments.

	Prior to June	Early-June to mid-July	Mid-July to late-Aug.
Species			
Hesperostipa comata	38.6 (43.2-34.0)	43.9 (48.1-39.6)	17.6 (19.8-15.3)
Pascopyrum smithii	40.1 (43.0-37.3)	55.4 (58.9-51.9)	4.5 (5.6-3.3)
Bouteloua gracilis	13.6 (15.7-11.6)	53.0 (55.2-50.8)	33.4 (36.7-30.0)
Koeleria macrantha	57.3 (61.9-52.6)	36.0 (39.0-33.1)	6.7 (10.0-3.4)
Carex spp.	53.0 (58.6-47.5)	36.0 (39.7-32.3)	11.0 (13.6-8.4)
Forb spp.	27.1 (36.1-18.2)	57.8 (66.9-48.6)	15.1 (20.2-9.9)
Treatments			
HIHF[1] defoliation	27.5 (28.9-26.2)	38.6 (39.8-37.5)	33.8 (35.5-32.2)
HILF[2] defoliation	33.1 (34.9-31.4)	48.5 (50.0-47.0)	18.3 (20.6-16.1)
Moisture addition	29.3 (31.1-27.5)	43.3 (45.5-41.1)	27.4 (30.8-24.0)
Ambient moisture	31.4 (33.3-29.4)	43.8 (46.3-41.3)	24.8 (28.6-21.0)

[1] High Intensity High Frequency.

[2] High Intensity Low Frequency.

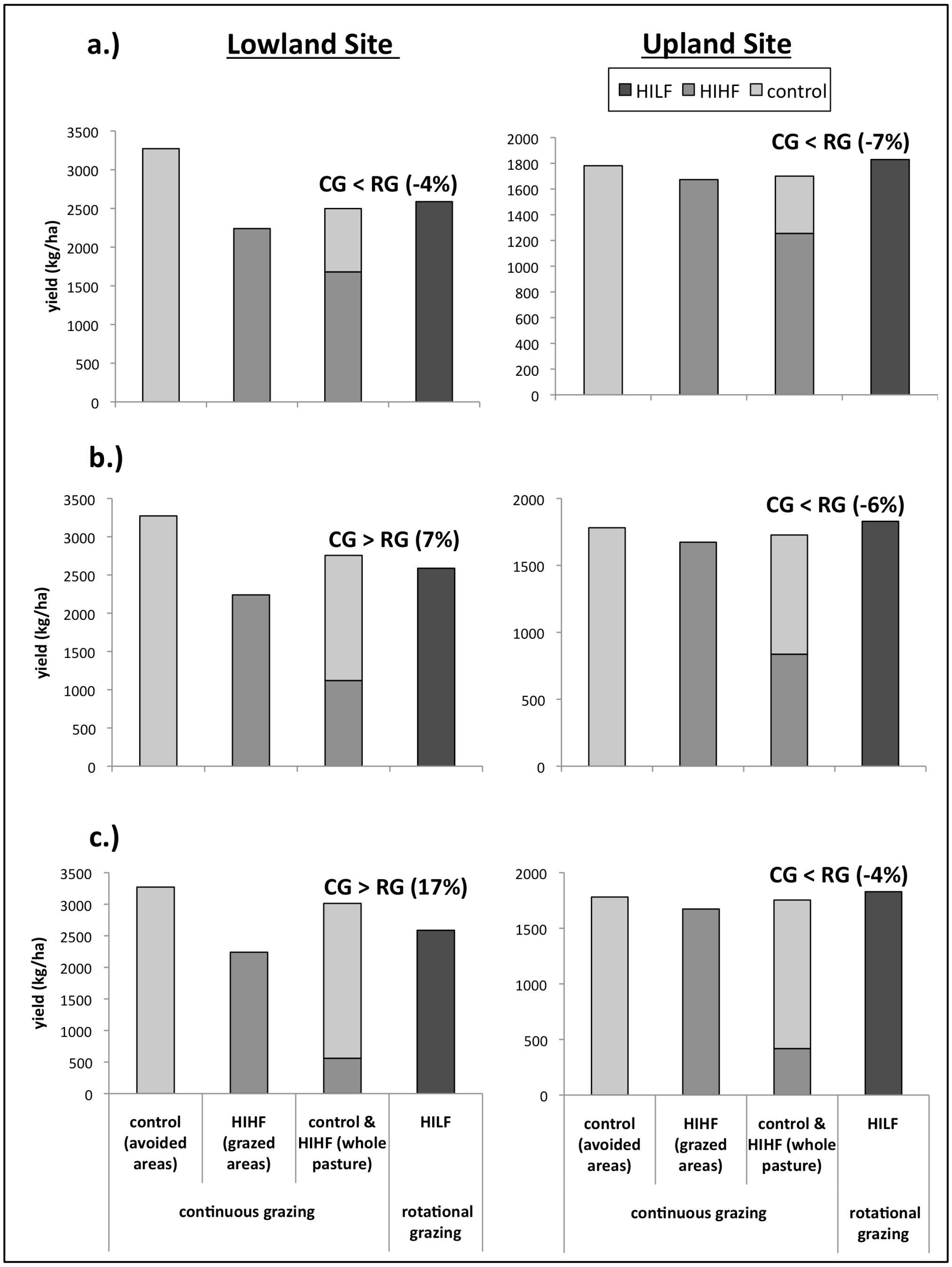

Figure 4-1. Conceptual model predicting plant community productivity under continuous and rotational grazing in lowland and upland sites of the Mixedgrass Prairie, assuming (1) that pasture yield consists of different proportions of both avoided areas (yielding similar to control defoliation) and recurrently grazed patches (yielding similar to high intensity high frequency defoliation [HIHF]) under continuous grazing [a.) 25% control and 75% HIHF, b.) 50% of both, c.) 75% control and 25% HIHF], and (2), rotationally grazed pastures are uniformly defoliated at high intensity and low frequency.

Photograph 4-1. Lowland site.

Photograph 4-2. Upland site.

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Chapter 5. Plant diversity and community composition responses to defoliation, moisture, and edaphic conditions in the Mixedgrass Prairie

5.1. Abstract

This study examined plant community compositional and diversity responses to various defoliation intensities and frequencies under contrasting watering treatments in the Dry Mixedgrass Prairie natural subregion of Alberta, Canada, from 2010 through 2012. Questions addressed included: (1) what is the relative influence of defoliation and moisture on plant species composition, (2) do defoliation frequency and intensity differ in their effect on composition, and (3) how does plant diversity respond to different defoliation and moisture regimes? Environmental parameters, including photosynthetically active radiation (PAR), soil temperature, and soil moisture, were also monitored to explain compositional and diversity responses. Treatments were applied in a fully randomized factorial design (defoliation x moisture) to 48 plots (n=6 replicates) within each of two sites, including a drier upland site and a mesic lowland site. Non-metric multidimensional scaling (NMS) ordination, multiple response permutation procedures (MRPP), and permutation-based MANOVA (perMANOVA) analyses indicated that plant compositional responses were largely determined by defoliation, particularly on the lowland site. Impacts of changing moisture on community composition were more apparent in the upland site. Plant diversity

increased under a greater frequency of defoliation in the lowland site, but decreased with more frequent defoliation in the upland site. Defoliation did not influence soil moisture, but increased PAR and soil temperature, whereas moisture addition predictably increased soil moisture, while reducing PAR and soil temperature. Results indicated that defoliation strongly alters plant composition by reducing canopy dominant, grazing susceptible grasses, and this can either increase or decrease diversity in mixedgrass communities, depending on edaphic conditions and the relative dominance of mid-grasses. Moreover, high moisture does not ameliorate defoliation effects, and defoliation frequency, rather than intensity, may play a greater role in altering plant community composition by reducing canopy dominant grasses and releasing shorter statured grasses.

5.2. Introduction

Grazing intensity (*i.e.*, stocking rate) and growing season precipitation are key determinants of plant species composition within grasslands. Clementsian theory predicts that species composition responds to these factors along a linear pathway (Clements 1936), implying that both have similar relative influence. However, both defoliation and moisture effects may have different relative influence and manifest at different temporal scales. For example, annual precipitation may have an overarching, long-term influence on community composition, within which grazing effects may manifest at shorter time scales (Biondini *et al.* 1998; Biondini and Manske 1996; Buitenwerf *et al.* 2011), although the opposite has also been found (Fuhlendorf *et al.* 2001).

Grazing effects may also interact with precipitation, such that favourable growing conditions may ameliorate, and environmental or resource stress may exacerbate, adverse effects of grazing on plants (Milchunas *et al.* 1989). Although plant communities can respond in ways that are nonlinear and stochastic in nature (Westoby *et al.* 1989), Clementsian theory applies well in grasslands where plants are either canopy dominant and relatively intolerant of defoliation (mid- and tall-grasses) or more decumbent and grazing tolerant (shortgrasses) (Milchunas *et al.* 1988), with the former and latter termed decreasers and increasers, respectively (Weaver 1954). Dominant grasses of the Dry Mixedgrass Prairie indeed include taller statured decreaser species and more decumbent increasers (Coupland 1961), suggesting that Clementsian theory may adequately predict the relative effects of defoliation (grazing intensity) and moisture (precipitation) on mixedgrass composition.

As plant species composition influences community productivity in mixedgrass prairies (Smoliak 1965; Willms and Jefferson 1993), the maintenance of favourable composition is an important objective of grazing management in the region (Adams *et al*. 2005). General management recommendations are to stock conservatively in order to minimize defoliation intensity on desirable plants and in turn maximize both range health and the abundance of tall-statured, decreaser grasses, under the premise that this will also maximize ecological function and plant community productivity (Adams *et al*. 2005).

Another management practice thought to conserve grassland composition is rotational grazing. By altering control over the distribution and timing of exposure to livestock, rotational grazing can allow better control over defoliation timing and frequency compared to continuous grazing (Derner *et al*. 1994). As a result, rotational grazing systems are perceived as superior to continuous grazing with respect to maintaining range health (seral condition) and community productivity, despite recent evidence to the contrary (Briske *et al*. 2008; Briske *et al*. 2011). With impetus among livestock managers to implement rotational grazing on semiarid rangelands, and the need to evaluate the merit of rotational grazing in mixedgrass prairies, it is important to understand how various defoliation intensities and frequencies, in conjunction with different moisture conditions, affect plant community composition.

Plant diversity may also respond to changes in species composition. Diversity can be defined based on the number of species (*i.e.*, richness), relative abundance of species (*i.e.*, evenness), and/or an index that considers both of these measures (*e.g.*, Shannon's index; Shannon 1948). Plant diversity is important in promoting community productivity and stability (Tilman *et al.* 2001; Tilman *et al.* 2006), and also has intrinsic conservation value (Symstad and Jonas 2011). Within grasslands of the Great Plains, grazing intensity can have varying influences on plant diversity, depending on whether tall- or short-grasses are dominant: diversity peaks under moderate grazing in tallgrass prairie, and little or no grazing in shortgrass prairie (Milchunas *et al.* 1988). However, diversity responses for mixedgrass plant communities remain unclear given that both shorter and taller species are co-dominant in these grasslands (Symstad and Jonas 2011). Grazing intensity effects on diversity in mixedgrass prairies may be indeterminate and site specific (Willms *et al.* 2002, Bai *et al.* 2001), but few studies have examined this directly using controlled defoliation regimes.

Finally, defoliation and moisture influences on grassland composition can be both direct and indirect. For example, moisture can directly promote individual plant growth, but also indirectly alter growth through interspecific competition arising from changes in the vigour of neighbouring species. Likewise, defoliation can alter light, moisture, and temperature regimes, and these factors in turn influence plant competition dynamics. For example, compensatory effects of defoliation may result from increased soil moisture arising from reduced leaf material and evapotranspiration, and increased water-use efficiency in plants

(McNaughton 1979), which may ameliorate adverse defoliation effects by improving conditions for plant regrowth.

This study assessed defoliation and moisture effects on plant community composition and diversity in the Dry Mixedgrass Prairie natural subregion of Alberta, Canada. Specific questions addressed include: (1) What are the relative effects of defoliation and moisture on community composition; (2) how do different defoliation intensities and frequencies, under different moisture regimes, influence community composition; and (3) how does diversity respond to gradients of increasing defoliation intensity and frequency and contrasting moisture conditions? This study also examined changes in environmental conditions in response to treatments in order to better understand the mechanisms responsible for plant community change. Specifically, defoliation's effect on soil moisture was of interest given that this may be one compensatory mechanism for plant recovery.

5.3. Methods

5.3.1. Site Description

Treatments were conducted at a relatively mesic lowland site and drier upland site, both located in the Brooks Plain of the Dry Mixedgrass Prairie natural subregion in Alberta, Canada (Adams *et al.* 2005). Mean annual precipitation and daily temperature are 354 mm and 4.2°C (Environment Canada 2013), and the growing season is approximately 185 days (>5˚C; Alberta Agriculture and Rural

Development 2013). Sites were chosen based on uniformity of topography and initial plant community composition. The lowland site (50° 53’ 40.2” N 111° 52’ 26.3” W) was subirrigated from adjacent uplands and had a Gleyed Eluviated Brown Chernozem soil (pH=6.3, EC=37µs/cm, organic matter content=2.5%). Soil texture of this site was relatively finer textured (Sandy Loam) compared to the upland site (Loamy Sand). The upland site (50° 52’ 23.8” N 111° 52’ 26.2” W) had a Rego Brown Chernozem soil (pH=6.7, EC=27µs/cm, organic matter content=1.3%). Initial range health scores based on the Alberta Range Health Assessment Guide for both sites were 80%, or healthy (Adams *et al*. 2003), and were both previously grazed for the long-term at a light-moderate stocking rate.

5.3.2. Experimental Design, Treatments and Response Parameters

Treatments of defoliation and moisture were combined in a fully randomized factorial design (4 x 2), with 6 replicates per site. Treatments were applied to 1 x 1 m plots, and separated by at least 0.5 m. Defoliation treatments were control, high intensity at low frequency (HILF), high intensity at high frequency (HIHF), and low intensity at high frequency (LIHF), conducted for 3 consecutive growing seasons from 2010 through 2012. Control plots were clipped to a 2 cm stubble height in late August, thereby simulating deferred defoliation. HILF and HIHF plots were clipped at 2 cm stubble heights every 3 and 6 weeks, respectively. In contrast, LIHF plots were clipped at a 5 cm stubble height every 3 weeks. In late May of 2010, plots were hand raked to remove litter (standing dead tillers and thatch). Low intensity clipping heights of 5 cm were used to prevent shorter statured species (e.g., *Bouteloua gracilis*) from escaping defoliation, thereby preventing confounding competitive interactions. High intensity clipping heights of 2 cm were used to ensure complete removal of leaf material. Moisture treatments included no watering (*i.e*., ambient moisture) and watering of plots to augment summer rainfall and maintain an equivalent of over 150 mm of monthly precipitation throughout the growing season; this is roughly double the average precipitation in June, the month of highest rainfall. The objective here was to remove moisture availability as a constraint for plant growth. Watering occurred at approximately 10 d intervals and all treatments commenced in early June and terminated in late August. Ambient precipitation (June-August) was greater than average in both 2010 and 2012 by 38 and 50%, respectively, in large part due to above normal precipitation in June, by 22-114% in all years of study.

In 2012 after 3 consecutive years of treatment, species composition was assessed with ocular estimates of vascular plant foliar cover at three times during the growing season: May 27, July 10, and August 20. To encompass all species (e.g. short-lived ephemerals) and account for the variable abundance of cool and warm season species during the growing season, cover values from all assessments (June-August) were averaged to create a composite measure. Soil moisture and temperature were measured every minute during the growing season (June-August) with a Decagon Devices© 5TM sensor and EM50 data logger; the logger was programmed to store a single mean value every 24 hr. This device uses signal filtering to minimize texture and salinity effects and has an accuracy of 3-

4% in fine-medium textured soils (Czarnomski *et al*. 2005). Light was measured 3 times during the growing season in 2012 with a Decagon Devices© AccuPar LP-80 light meter as the ratio of photosynthetically active radiation (PAR) (μmol m^{-2} s^{-1}) below and above the canopy. Clipped phytomass from plots was collected, dried at 60°C for 48 hrs and weighed.

5.3.3. Data Analysis

Shannon's diversity (H´) was estimated for each plot as $H' = \sum(Pi \times \ln Pi)$, where *Pi* is proportional foliar cover (relative to total cover) of each species. Evenness was measured by the formula of $H' \div \ln(s)$, where s is species richness and ln is the natural log. Shannon's diversity, evenness, and richness, as well as soil moisture, temperature, and PAR ratio measurements, were checked for normality and homogeneity of variance with Levene's and Shapiro-Wilk tests (SAS 9.2—SAS Institute, 1989), respectively, and subsequently analyzed with two-way analyses of variance (ANOVA). Sites were analyzed independently due to diversity response interactions with defoliation ($P<0.001$). Mean separation tests of significant fixed effects (defoliation and moisture) and their interactions were Tukey's adjusted. Significance was assessed at an alpha of $P \leq 0.05$.

Multivariate techniques (MJM Software Design, Gleneden Beach, OR) were used to summarize multi-dimensional plant community responses (using non-metric multidimensional scaling [NMS]), assess whether plant community composition responses were influenced by defoliation and moisture treatments (using a multiple-response permutation procedure [MRPP] and permutation based MANOVA [PerMANOVA]), and identify the specific plant species driving these community responses (using indicator species analysis [ISV]). Sorensen's distance measure was used in all analyses. MRPP was based on the probability of the delta statistic being smaller or equal to the expected delta based on 100 randomized trials. The perMANOVA assesses significance based on 4999 randomizations and the proportion of randomized trials with an indicator cover greater or equal to the observed cover value. Dufrêne and Legendres' indicator species analysis was run with 4999 randomizations of the Monte Carlo test. NMS procedures involved 100 runs with real data, a stability criterion of 0.000001, 10 iterations to evaluate stability, and a maximum of 500 iterations. The procedure was run 5 times to verify results. Using a vector scaling cut-off value of $r^2 > 0.2$, environmental factors (*e.g.*, PAR ratio, soil moisture, and soil temperature), significant indicator species cover, and other metrics (*e.g.*, accumulated aboveground phytomass, proportion of total phytomass comprised of forbs, and diversity metrics of Shannon's diversity and Simpson's dominance index, as well as species evenness and richness), were overlaid on resulting scatter plots (Figures 5-1 and 5-2).

5.4. Results

5.4.1. Plant Community Composition

According to the perMANOVA, plant community composition in the lowland site was influenced by defoliation ($P<0.001$) and moisture ($P=0.032$) (Table 5-2). Moreover, all defoliation treatments differed from one another ($P<0.05$) (data not shown) and did not interact with moisture ($P=0.30$). Defoliation effects were corroborated by the MRPP (A=0.252; $P<0.001$), but moisture effects were not given that moisture was not significant (A=0.009; $P=0.123$) (Table 5-2). Significant indicator species for defoliation treatments included *Hesperostipa comata* ($P<0.001$) and *Pascopyrum smithii* ($P<0.001$) with the control, *Tragopogon dubius* ($P=0.006$) with HILF, *Koeleria macrantha* ($P=0.029$) and *Gaura coccinea* ($P=0.041$) with LIHF, and *Bouteloua gracilis* ($P=0.026$), *Cirsium arvense* ($P=0.048$), and *Crepis tectorum* ($P<0.001$) with HIHF. For moisture treatments, only *B. gracilis* was associated with moisture addition ($P=0.017$).

Plant community composition in the upland site was influenced by both defoliation and moisture ($P<0.001$), as indicated by both the perMANOVA and MRPP, but with a smaller effect size for defoliation compared to the lowland site (A=0.138; Table 5-2). Indeed, only the control treatment differed from all others ($P<0.001$), while HILF, LIHF, and HIHF treatments remained similar ($P>0.10$) (data not shown). The defoliation by moisture interaction in the PerMANOVA ($P=0.022$; Table 5-2) indicated communities under HILF and both ambient moisture and moisture addition were similar (*P*=0.112), whereas all other defoliation treatments differed under contrasting moisture treatments (*P*<0.05; data not shown). Significant indicator species for defoliation included *H. comata* and *P. smithii* with the control (*P*<0.001), and *Carex spp*. was nearly significant for HIHF (*P*=0.055). For moisture treatments, *P. smithii* (*P*<0.001) and *B. gracilis* (*P*=0.046) were associated with moisture addition, whereas *Carex spp*. (*P*=0.010) and *Erysimum inconspicuum* (*P*<0.001) were associated with ambient moisture, and *T. dubius* was also nearly significant for this treatment as well (*P*=0.083; data not shown).

NMS ordination provided 2-dimensional solutions with final stress scores of 15.03 and 13.01 (*P*=0.0004) for the lowland and upland sites, respectively. Axes 1 and 2 represented 67.3 and 20.6% of the variation, respectively, for the lowland site, and 65.5 and 25.6% of variation, respectively, in the upland site (Table 5-3; Figures 5-1 and 5-2). Thus, the primary axis for both sites was axis 1 (the horizontal axis). For both sites, defoliation was positively associated with the primary axis (r=0.883 and 0.749, for the lowland and upland sites, respectively) (Table 5-3). In contrast, moisture was negatively and positively associated with the secondary (vertical) axis in the lowland (r=-0.389) and upland sites (r=0.668), respectively. Together this suggests that defoliation treatments largely explained species variation along the primary axis, while moisture treatments, to a lesser extent, explained results along the secondary axis. Overlay of environmental variables suggested defoliation promoted light (r > 0.76) and soil temperature (r > 0.29), as these were associated with the primary axis at both sites (Table 5-3).

Similarly, moisture addition was associated with the secondary axis in both sites (r > |0.30|). Particularly in the upland site, light (r=0.38) and soil temperatures (r=0.47), were associated with the secondary axis (Table 5-3), suggesting these parameters were reduced by moisture addition. These results were corroborated by the ANOVA (see Table 5-7).

Ordination also showed that diversity metrics corresponded differently with the primary axis, suggesting that defoliation had opposing effects on diversity at each of the two sites. For example, richness (r=0.48), Shannon's diversity (r=0.41), and evenness (r=0.40) were positively associated with the primary axis in the lowland site, although aboveground phytomass was negatively (r=-0.48) associated with the primary axis. However, at this same site, the proportion of biomass comprised of forbs (r=0.57) was positively associated with the primary axis (Table 5-3). In the upland site, Simpson's dominance index (r=0.65), Shannon's diversity (r=0.55), and evenness (r=0.72) were all negatively associated with the primary axis (Table 5-3). Indicator species responses, however, were relatively similar between sites, such that *H. comata* (r > |0.79|) and *P. smithii* (r > |0.63|) were negatively and *B. gracilis* (r>0.53) was positively associated with the primary axis (Table 5-3). Combined this suggests that defoliation promoted plant diversity in the lowland site by reducing canopy dominant, decreaser grasses (*H. comata* and *P. smithii*) and promoting the shortgrass species (*B. gracilis*), while at the same time reducing aboveground phytomass and promoting other forbs. In contrast, defoliation reduced diversity (albeit not richness) in the upland site by similarly changing the relative abundance of dominant graminoids. This suggests that canopy dominant grasses may have been less prevalent in controls of the upland site, which was indeed observed for *P. smithii* (Tables 5-4 and 5-5), and that defoliation did not promote the relative abundance of forbs at this location.

Ordination also showed that, despite some minor discrepancies, moisture addition generally had a similar influence on diversity and species responses in both sites. Specifically, both Simpson's dominance index (r>|0.41|) and Shannon's diversity (r>|0.45|) were consistently associated with the secondary axis at both sites. Evenness (r=0.49) and richness (r=-0.51) were associated with the secondary axis in the lowland and upland sites, respectively. In the upland site, phytomass (r=0.54) and the relative contribution of forbs to yield (r=-0.39) was positively and negatively, respectively, associated with the secondary axis. Among both sites, *B. gracilis* was consistently associated with the secondary axis (r>|0.45|), which was confirmed by the indicator species analyses. Collectively these results indicate that moisture addition reduced diversity at both sites (this was confirmed by the ANOVA for the upland site only) by promoting *B. gracilis* and reducing the relative abundance of various forbs.

5.4.2. Species Diversity, Evenness, and Richness

A total of 47 different species were encountered, with 33 and 29 at the lowland and upland sites, respectively. For the lowland site, only defoliation influenced (*P*<0.01) diversity (Shannon's index), richness, and evenness (Table 5-

6), whereas moisture influenced diversity and richness (*P*<0.01) and defoliation influenced diversity and evenness (*P*<0.02) in the upland site (Table 5-6). In the lowland site, all diversity metrics tended to peak under some specific combination of defoliation intensity and frequency: HILF and LIHF for diversity and evenness, and LIHF and HIHF for richness (Table 5-7). The opposite was observed in the upland site, where diversity and evenness peaked under deferred defoliation (controls), and reached the lowest levels under any form of high frequency defoliation. Species richness did not respond to defoliation (*P*=0.59). Finally, moisture addition reduced species richness and diversity in the upland site (*P*<0.01), but not species evenness (P=0.52). No diversity metrics were influenced by moisture in the lowland site (P>0.08) (Table 5-6).

5.4.3. Environmental Parameters

At each site, both defoliation and moisture treatments influenced light and soil temperature (*P*<0.002), whereas soil moisture was influenced by moisture treatments only (*P*<0.001). Additionally, there was a defoliation by moisture interaction for light in the upland (*P*<0.001), but not the lowland site (*P*=0.067; Table 5-8). Defoliation increased light levels relative to deferred (control) defoliation by at least 64 and 39% in the lowland and upland sites, respectively, with the greatest increases occurring under HIHF defoliation (Table 5-7). Moisture addition reduced PAR ratio levels by 13 and 9% in the lowland and upland sites, respectively. However, the defoliation by moisture interaction for the upland site (P<0.001) indicated that moisture addition reduced PAR ratio levels only in the control (*i.e.*, deferred) defoliation treatment at this location (Table 5-9); the nearly significant defoliation by moisture interaction (P=0.067) at the lowland site indicated that moisture addition reduced PAR ratio levels under both control and HILF defoliation treatments (data not shown). All defoliation treatments increased soil temperatures by at least 0.5°C, and plots were slightly warmer (≈0.6°C) under ambient moisture. Predictably, water addition increased soil moisture levels by 24 and 40% in the lowland and upland sites, respectively. However, in the lowland site, water addition increased soil moisture within the control and HILF defoliation treatments only, as indicated by the defoliation and moisture interaction at the lowland site (P=0.048) (Table 5-9).

5.5. Discussion

5.5.1. Composition Responses to Defoliation and Moisture

Studies have come to contrasting conclusions about whether grazing intensity or inter-annual variability in precipitation is the dominant driver of plant community compositional change on rangelands (precipitation: Biondini and Manske 1996, Biondini *et al*. 1998, Buitenwerf *et al*. 2011; grazing: Fuhlendorf *et al*. 2001). Plant community composition in this study was influenced predominantly by defoliation at both sites, but moisture effects remained apparent and were more important in the drier upland site. Defoliation effects were particularly strong at the mesic lowland site, within which plant assemblages (*i.e.*, communities) of unique composition formed under each defoliation treatment. Although edaphic conditions varied between sites, other characteristics also differed, the most notable being initial species composition. Late-seral, grazing sensitive grasses, such as *P. smithii* and *H. comata*, were more prevalent in the lowland site, where they were associated closely with control (deferred) defoliation. The lowland site also had a greater abundance of *K. macrantha* than the upland, which is a grazing tolerant midgrass (Coupland 1961), and associated here with LIHF defoliation. Having a greater variety of initial species in the lowland site with contrasting grazing responses may have allowed distinct communities to manifest under different defoliation regimes. Indeed, overall species richness was approximately 40% higher in the lowland, compared to the upland, site. Other studies support the notion that defoliation effects are greater under higher precipitation (Gillen and Sims 2006; Cheng *et al*. 2011). This may be because more productive areas tend to have greater species richness (Connell and Orias 1964), and consequently, competitive interactions among plants may play a greater role in determining community composition (Grime 2001).

As the relative influence of moisture addition on community composition differed between the sites examined here, moisture effects are likely to differ across areas of the Great Plains depending on edaphic conditions. This may account for why a generalized ecological theory regarding drivers of species composition on the Great Plains remains so elusive (see Symstad and Jonas 2011). Nevertheless, drought is commonly recognized as a significant driver of plant community change (Biondini and Manske 1996; Biondini *et al*. 1998). It is conceivable that the relative effect of either defoliation or moisture would depend on the relative magnitude of a given perturbation. By more than doubling growing season precipitation, moisture regimes were markedly altered in this experiment, but ambient rainfall remained relatively high in all three growing seasons (Table 5-1). As initial plant community composition of plots presumably equilibrated under the prevailing long-term moisture regime, lack of a moisture limitation perturbation, such as drought, within our control plots, may have constrained the relative effects of moisture.

Moreover, the timescale of this experiment was relatively short (3-years), and whereas the effect of defoliation may be relatively acute (Butler and Briske 1988), the effects of inter-annual variation in precipitation may manifest under longer time periods. Favourable moisture conditions may influence the composition of perennial graminoids by promoting tiller recruitment given that regeneration by seed can account for less than 1% of annual tiller recruitment (Benson and Hartnett 2006). Moreover, meristem limitations can occur in grasses of semiarid grasslands (Dalgleish and Hartnett 2006) and with parent tillers relying on annual tillering for regeneration (Langer 1956; Hendrickson and Briske 1997), the ability of any grass to increase in abundance may depend on its pre-existing tiller population, coupled with the ability of those tillers to recruit more than one tiller each growing season. Indeed, tiller recruitment following growing seasons of high precipitation may not occur until subsequent growing seasons (Hendrickson *et al.* 2000), and this could explain why, during wetter years, semiarid grasslands fail to realize the same relative production increases that occur in more humid grasslands (Knapp and Smith 2001; Reichmann *et al.* 2013). Consequently, changes in plant community composition under higher than average moisture availability may occur relatively gradually depending on the associated level of aridity vegetation is adapted to. Generally the northern Mixedgrass Prairie goes through decadal shifts in moisture regime (Sauchyn *et al.* 2003, Trouet *et al.* 2013). Perhaps plant communities, as regulated by demography processes, may respond at similar time scales, which highlights the need for longer-term experiments.

Two important species associated with moisture addition in this experiment include *B. gracilis* and *P. smithii*. The former is a decumbent, warm-season grass that increases with grazing, whereas the latter is a canopy dominant, cool-season species known to decline under increasing grazing pressure (Coupland 1961). This shared response is perplexing considering these grasses have such contrasting characteristics. However, one common characteristic of these grasses includes that both are rhizomatous (Moss 1994). Rhizomatous grasses in the Great Plains appear to be associated with more humid areas (Sims *et al.* 1978; Mack and Thompson 1982), suggesting that the adaptation of rhizomes favours grasses in more mesic environments. Rhizomes are underground shoots that are a source of meristems (basal buds), as well as stored carbohydrates and nutrients for growth (Reece *et al.* 2001). Rhizomes act as connective tissue for resource sharing between tillers (Cullen *et al.* 2005), and between tillers and roots of successive tiller generations (Jónsdóttir and Callaghan 1988). Consequently, rhizomes may assist tiller recruitment under high moisture conditions by ameliorating possible meristem limitations, directly providing stored resources for growth, and promoting water and nutrient uptake and sharing among tillers and roots.

5.5.2. Composition Responses to Defoliation Frequency and Intensity

Another objective of this study was to examine whether defoliation frequency or intensity differentially influence plant community composition in the Mixedgrass Prairie. Grazing systems are often used to control defoliation timing, frequency, and/or intensity. Indeed, the impetus for rotational grazing is often based on the perception that regulating the timing and frequency of grazing can maintain a desirable plant community (Briske *et al.* 2008). Results here suggest that neither frequency nor intensity of defoliation differ in their effect on grassland composition, although this could not be tested directly because the experimental design was not a full factorial with respect to defoliation frequency and intensity. Nevertheless, the more productive, taller-statured grasses (*H. comata* and *P. smithii*) favoured by control (deferred) defoliation are likely responsible for the differentiation among plant communities in response to defoliation, especially in the drier upland site. Moreover, although unique communities formed under each defoliation treatment in the lowland site, defoliation treatments were more similar to one another than to the control treatment (deferred defoliation). Of the three combinations of intensity and frequency of defoliation tested here, HILF produced a plant community most similar to the control, while HIHF defoliation was most dissimilar. This provides circumstantial evidence that defoliation frequency, rather than intensity, may play a greater role in regulating community composition by helping maintain late-seral, canopy dominant grasses, at least in more mesic mixedgrass communities.

5.5.3. Plant Diversity

Defoliation and moisture had divergent effects on plant diversity at the two sites. Indeed, both Willms *et al.* (2002) and Bai *et al.* (2001) found that mixedgrass prairie diversity responses to grazing were site dependent. Within the Great Plains, diversity is hypothesized to peak under moderate grazing in tallgrass and no grazing in shortgrass prairie (Milchunas *et al.* 1988). Notably, the more mesic lowland and xeric upland mixedgrass sites examined here had similar responses to those hypothesized for the tallgrass and shortgrass prairies, respectively. In the lowland site, diversity and evenness peaked under intermediate levels of defoliation (HILF, LIHF), but richness was similarly high under all defoliation regimes (HILF, LIHF, HIHF), whereas high frequency defoliation (HIHF, LIHF) reduced diversity and evenness, but not richness, in the upland site. These results indicate defoliation may promote diversity in the tallgrass prairie because it reduces the dominance of canopy dominant graminoids, thereby providing a niche for forbs and more decumbent, grazing tolerant grasses, whereas defoliation may reduce diversity in drier shortgrass communities because it increases the dominance of already dominant grazing tolerant shortgrasses (Milchunas *et al.* 1988). This suggests that the tallest grasses in this study, *H. comata* and *P. smithii*, are more dominant under deferred defoliation in the more mesic lowland site. Reducing canopy dominance of perennial grasses under defoliation seemed to promote forbs, including *Tragopogon dubius, Gaura coccinea*, and *Crepis tectorum*, as well as the invasive *Cirsium arvense*, but only within the lowland site. Indeed, although forbs make up a relatively small proportion of plant biomass compared to graminoids within grasslands, they contribute disproportionately more to diversity (Damhoureyeh and Hartnett 1997). Conversely, lack of a species richness response to increasing intensity and frequency of defoliation in the upland site may arise because defoliation merely altered the relative abundance of perennial grasses: increasing *B. gracilis* at the expense of *P. smithii* and *H. comata*. This actually increased species evenness, and consequently Shannon's index of diversity.

Moisture also influenced diversity, but only in the upland site. However, contrary to evidence that species richness tends to be greater in more mesic communities (Connell and Orias 1964), and in wetter years compared to drier years (Adler and Levine 2007; Wilson 2007), moisture addition reduced richness and diversity at the mesic site in the present study. This treatment also increased *P. smithii* and *B. gracilis*, suggesting these perennial grasses out-competed other species under high moisture.

5.5.4. Environmental Parameters

Finally, defoliation and moisture effects on plants, and thus plant communities, can be both intrinsic and extrinsic (McNaughton 1983). Intrinsic effects directly influence plant physiology or development, and extrinsic effects manifest indirectly, such as through altered environmental conditions. Extrinsic effects of defoliation may compensate for adverse effects of defoliation on plant physiology. For example, although defoliation may impede plant growth, it may also improve plant water status by reducing evapotranspiration and increasing soil moisture availability (McNaughton 1979), which is important given that soil moisture and fertility predominantly limit primary production in semiarid grasslands (Burke *et al.* 1998). Studies from other grasslands have found that defoliation and grazing can increase (Deutsch *et al.* 2010), decrease (Naeth *et al.* 1991; Zhao *et al.* 2011), or have no effect on soil moisture (Mapfumo *et al.* 2003), the latter of which was observed in this study. These mixed responses may arise because extrinsic effects of defoliation simultaneously increase and decrease soil moisture. For example, while defoliation can increase moisture by reducing plant transpiration, it can simultaneously decrease moisture by reducing infiltration and increasing evaporation. Indeed, in this study soil temperature and light intensity were greater under defoliation, suggesting evaporation would be higher. These conflicting effects may therefore nullify any beneficial effects of defoliation on soil moisture conservation. Moisture addition did markedly increase soil moisture, but also reduced soil temperature and light availability, indicating that enhanced vegetation growth was under greater competition for light.

5.6. Conclusion

The scope of this study was limited to two sites within the Mixedgrass Prairie over a relatively short period (3 growing seasons), but examined overall, a number of conclusions can be drawn. First, mixedgrass communities may be more sensitive to changes in defoliation regime, especially in wetter, more productive areas, than to changes in moisture, although the latter may play a greater role in drier, less productive areas of the landscape. Conversely, moisture does not appear to alter or ameliorate defoliation effects, and controlling defoliation frequency, as opposed to intensity, may better mitigate defoliation impacts on the abundance of late-seral, grazing susceptible perennial grasses. Second, the principle effect of defoliation on community composition appeared to be a reduction in canopy dominant, taller-statured grasses, which in turn, can either increase or decrease plant diversity. Where these grasses are dominant, increases in diversity may occur through the release of opportunistic forbs, which benefit from increased resources, including light availability. Where taller-statured grasses are less dominant, such as in drier areas, diversity may decrease given that shortgrasses may become more dominant and displace other species. Similarly, increasing moisture availability may reduce plant diversity in mixedgrass prairie communities by increasing perennial grasses, particularly rhizomatous species such as *B. gracilis* and *P. smithii*.

Overall, these results indicate that defoliation regimes (timing, intensity and frequency), as manipulated through grazing management, can strongly influence plant community composition and diversity. Moreover, although plant community responses may be similar under various moisture conditions, different areas of the Mixedgrass Prairie are likely to respond differently to similar types of management. Consequently, management strategies that consolidate areas of similar topography and edaphic conditions (*i.e.*, through fencing) may enhance management efficacy (Bailey and Brown 2011). Finally this study shows that where grazing is to take place during early to mid-summer, rotational grazing systems that utilize a HILF defoliation regime may have some merit in maintaining late-seral, grazing susceptible grasses as well as maximizing or maintaining plant diversity, at least over the short-term. Long-term studies are necessary to examine the extended community responses to these disturbance regimes.

Table 5-1. Ambient growing season precipitation (mm) and recent long-term averages for the Brooks area of Alberta, Canada.

	Year				Average[1]
	2009	2010	2011	2012	1971-2000
June	54	123	77	135	63
July	137	52	36	48	42
August	39	20	23	29	36
Total (June-Aug.)	230	195	135	212	141

[1] Environment Canada climate normals.

Table 5-2. Permutation based MANOVA *F* and *P* values and multiple response permutation procedure *A* and *P* values for tests of defoliation and moisture treatments within both a lowland and upland site in the Mixedgrass Prairie.

	PerMANOVA		MRPP	
	F value	*P* value	*A* value	*P* value
Lowland site				
Defoliation	14.1	**<0.001**	0.252	**<0.001**
Moisture	2.90	**<0.032**	0.009	0.12
Defol. x moist.	1.20	0.297		
Upland site				
Defoliation	9.29	**<0.001**	0.138	**<0.001**
Moisture	8.94	**<0.001**	0.049	**<0.001**
Defol. x moist.	2.18	**0.022**		

Table 5-3. Summary of Pearson correlation r-values among non-metric multi-dimensional scaling (NMS) ordination axes and environmental conditions, community metrics, and indicator species. Values in bold are correlations with r > |0.30|.

	Lowland site		Upland site	
	Axis 1	Axis 2	Axis 1	Axis 2
	----------------Plant species variance explained----------------			
	67.3%	20.6%	65.5%	25.6%
	------------------------------r values------------------------------			
Defoliation	**0.88**	0.11	**0.75**	-0.19
Defoliation frequency	**0.89**	0.10	**0.70**	-0.21
Defoliation intensity	**0.80**	0.02	**0.66**	-0.24
Moisture (treatment)	0.03	**-0.39**	-0.04	**0.67**
Photosynthetically active radiation (PAR)	**0.86**	-0.18	**0.77**	**-0.38**
Volumetric soil moisture	-0.08	**-0.31**	-0.17	**0.54**
Soil temperature (˚C)	**0.54**	0.20	**0.30**	**-0.47**
Shannon's diversity index	**0.41**	**0.45**	**-0.55**	**-0.50**
Simpson's dominance index	0.13	**0.62**	**-0.65**	**-0.42**
Species richness	**0.48**	-0.04	-0.04	**-0.51**
Species evenness	**0.40**	**0.49**	**-0.72**	-0.20
Aboveground accumulated phytomass	**-0.48**	-0.22	-0.16	**0.54**
Proportion of phytomass consisting of forbs	**0.57**	0.21	-0.23	**-0.39**
Hesperostipa comata	**-0.79**	**0.55**	**-0.86**	0.15
Pascopyrum smithii	**-0.90**	0.05	**-0.64**	**0.61**
Bouteloua gracilis	**0.54**	**-0.85**	**0.83**	**0.45**
Koeleria macrantha	-0.20	**0.52**	-	-
Carex spp.	-	-	0.25	**-0.59**
Cirsium arvense	0.18	-0.16	-	-
Crepis tectorum	**0.37**	**-0.31**	-	-
Erysimum inconspicuum	-	-	-0.04	-0.04
Gaura coccinea	0.26	-0.25	-	-
Tragopogon dubius	0.12	0.23	0.07	-0.08

Table 5-4. Mean percent foliar cover (± 95% confidence intervals) of species in the lowland site arising from 3 years of deferred (control), high intensity low frequency (HILF), low intensity high frequency (LIHF), and high intensity high frequency (HIHF) defoliation, as well as ambient moisture and moisture addition treatments.

Species	Defoliation				Moisture		Overall
	Control	HILF	LIHF	HIHF	Addition	Ambient	
Hesperostipa comata	17.4 ±3.9	8.1 ±2.7	3.0 ±2.0	1.9 ±1.0	8.9 ±3.6	6.3 ±2.3	7.6 ±2.2
Pascopyrum smithii	58.2 ±10.6	18.8 ±3.7	15.3 ±4.7	12.8 ±4.2	21.2 ±6.8	31.4 ±10.0	26.3 ±6.2
Bouteloua gracilis	8.9 ±3.2	30.6 ±8.5	29.9 ±9.7	38.1 ±10.3	20.8 ±6.1	32.9 ±7.5	26.9 ±5.1
Carex stenophylla, douglasii	6.5 ±1.6	12.1 ±4.2	13.3 ±2.8	14.1 ±2.2	11.3 ±2.6	11.7 ±2.1	11.5 ±1.6
Koeleria Macrantha	13.0 ±4.8	7.4 ±2.4	15.5 ±6.1	1.9 ±1.3	9.1 ±3.5	9.8 ±3.6	9.4 ±2.5
Calamovilfa longifolia	-	-	-	1.1 ±1.7	0.1 ±0.3	0.4 ±0.8	0.3 ±0.4
Agrostis scarbra	0.1 ±0.3	-	0.2 ±0.4	0.4 ±0.5	0.3 ±0.3	0.1 ±0.1	0.2 ±0.2
Poa sandbergii	0.4 ±0.8	-	-	-	-	0.2 ±0.4	0.1 ±0.2
Poa palustris	0.6 ±1.1	-	-	-	-	0.3 ±0.5	0.1 ±0.3
Achillea millifolium	-	0.9 ±1.8	0.4 ±0.4	0.9 ±1.6	0.6 ±0.8	0.5 ±0.9	0.5 ±0.6
Arabis dummondii	-	-	-	0.1 ±0.2	0.0 ±0.1	-	-
Artemisia frigida	2.9 ±1.9	3.5 ±1.2	4.7 ±1.2	3.6 ±2.8	4.2 ±1.6	3.1 ±1.1	3.7 ±0.9
Artemisia ludoviciana	-	-	0.8 ±1.6	-	-	0.4 ±0.8	0.2 ±0.4
Astragalus agrestis	1.1 ±1.2	0.7 ±0.6	1.3 ±0.9	0.3 ±0.4	1.0 ±0.7	0.7 ±0.4	0.8 ±0.4
Aster ericoides	0.8 ±0.9	-	0.9 ±0.7	0.2 ±0.2	0.4 ±0.5	0.5 ±0.4	0.5 ±0.3
Androsace occidentalis	-	0.2 ±0.3	-	-	0.1 ±0.1	-	0.0 ±0.1
Cirsium arvense	-	-	-	0.6 ±0.7	0.1 ±0.3	0.2 ±03	0.1 ±0.2
Crepis tectorum	-	-	0.0 ±0.1	0.4 ±0.3	0.1 ±0.1	0.2 ±0.1	0.1 ±0.1
Descuriania sophia	-	-	0.1 ±0.2	-	-	0.1 ±0.1	0.0 ±0.1
Gaura coccinea	0.2 ±0.2	0.5 ±0.8	1.1 ±0.6	0.4 ±0.4	0.3 ±0.2	0.9 ±0.5	0.6 ±0.3
Geum triflorum	0.1 ±0.2	-	0.1 ±0.2	0.1 ±0.1	0.0 ±0.1	0.1 ±0.1	0.1 ±0.1
Grindellia squarrosa	0.8 ±1.0	0.4 ±0.8	0.6 ±0.6	0.4 ±0.3	0.4 ±0.4	0.7 ±0.6	0.5 ±0.4
Haplopappus spinulosus	-	-	0.1 ±0.2	-	-	0.1 ±0.1	0.0 ±0.1
Heterotheca villosa	0.0 ±0.1	0.3 ±0.4	0.1 ±0.1	-	0.1 ±0.1	0.2 ±0.2	0.1 ±0.1
Phlox hoodii	-	-	-	0.1 ±0.1	-	0.0 ±0.1	-
Potentilla tridentata	0.1 ±0.3	-	0.1 ±0.2	-	-	0.1 ±0.2	0.1 ±0.1
Ratibida columnifera	-	0.4 ±0.7	-	0.3 ±0.3	0.1 ±0.1	0.3 ±0.4	0.2 ±0.2
Sonchus uliginosus	0.3 ±0.5	-	-	0.6 ±0.8	0.3 ±0.5	0.1 ±0.1	0.2 ±0.3
Tragopogon dubius	-	3.3 ±1.7	1.3 ±1.4	0.9 ±0.7	1.4 ±0.7	1.3 ±1.1	1.4 ±0.7
Taraxacum officinale	1.9 ±1.1	5.7 ±1.9	4.9 ±2.9	8.1 ±3.7	4.9 ±1.7	5.5 ±2.3	5.2 ±1.4
Vicia americana	-	0.9 ±1.5	0.3 ±0.7	-	0.6 ±0.8	0.1 ±0.1	0.3 ±0.4
Zizia aptera	-	-	-	0.2 ±0.4	-	0.1 ±0.2	0.1 ±0.1
Unknown forb	0.3 ±0.5	0.1 ±0.1	0.1 ±0.2	0.3 ±0.3	0.2 ±0.3	0.2 ±0.2	0.2 ±0.2
Total	113.7 ±8.9	93.7 ±10.5	94.3 ±7.7	87.6 ±8.8	86.5 ±5.7	108.2 ±6.2	97.3 ±5.2

Table 5-5. Mean percent foliar cover (± 95% confidence interval) of species in the upland site arising from 3 years of deferred (control), high intensity low frequency (HILF), low intensity high frequency (LIHF), and high intensity high frequency (HIHF) defoliation, as well as ambient moisture and moisture addition treatments.

Species	Defoliation				Moisture		Overall
	Control	HILF	LIHF	HIHF	Addition	Ambient	
Hesperostipa comata	27.8 ±6.9	11.3 ±3.3	9.2 ±3.7	4.8 ±2.6	14.1 ±5.4	12.5 ±3.4	13.3 ±3.2
Pascopyrum smithii	29.6 ±9.7	10.3 ±3.0	12.2 ±5.2	8.2 ±3.4	21.8 ±6.0	8.4 ±2.4	15.1 ±3.7
Bouteloua gracilis	19.5 ±4.4	44.0 ±9.1	45.6 ±11.3	41.2 ±12.2	43.2 ±9.0	32.0 ±5.8	37.6 ±5.5
Carex stenophylla, douglasii	11.7 ±2.9	15.1 ±2.0	18.3 ±2.8	19.4 ±3.7	14.0 ±1.8	18.2 ±2.5	16.1 ±1.6
Koeleria Macrantha	1.6 ±1.8	0.2 ±0.5	0.1 ±0.2	0.4 ±0.5	0.2 ±0.3	0.9 ±1.0	0.6 ±0.5
Poa sandbergii	-	0.1 ±0.1	-	0.1 ±0.2	-	0.1 ±0.1	0.0 ±0.1
Antennaria parvifolia	0.1 ±0.2	-	-	-	-	0.1 ±0.1	0.0 ±0.1
Artemisia frigida	1.4 ±1.2	0.9 ±0.9	0.5 ±0.5	1.2 ±0.8	0.9 ±0.6	1.1 ±0.7	1.0 ±0.4
Androsace occidentalis	-	0.0 ±0.1	-	-	-	-	-
Coryphantha vivipara	0.4 ±0.5	0.4 ±0.8	0.4 ±0.5	-	0.3 ±0.4	0.3 ±0.3	0.3 ±0.3
Crepis tectorum	-	0.0 ±0.1	-	0.1 ±0.2	-	0.1 ±0.1	0.0 ±0.1
Dalea Purpurea	1.7 ±3.3	-	-	-	-	0.8 ±1.6	0.4 ±0.8
Descuriania sophia	-	0.0 ±0.1	0.1 ±0.1	-	0.1 ±0.1	-	-
Erigeron glabellus	-	0.0 ±0.1	-	0.2 ±0.3	-	0.1 ±0.2	0.1 ±0.1
Erysimum inconspicuum	0.2 ±0.2	0.1 ±0.1	0.1 ±0.1	-	-	0.2 ±0.1	0.1 ±0.1
Gaura coccinea	0.7 ±1.4	0.1 ±0.2	-	0.6 ±1.3	0.7 ±0.9	0.1 ±0.1	0.4 ±0.5
Geum triflorum	-	-	-	0.1 ±0.2	-	0.0 ±0.1	-
Heterotheca villosa	-	-	0.2 ±0.3	0.2 ±0.4	0.0 ±0.1	0.2 ±0.2	0.1 ±0.1
Lithospermum incisum	-	0.1 ±0.2	0.0 ±0.1	-	-	0.1 ±0.1	0.0 ±0.1
Lygodesmia juncea	0.4 ±0.7	-	-	0.0 ±0.1	0.2 ±0.4	-	0.1 ±0.2
Oxytropis lagopus	-	0.2 ±0.5	-	-	-	0.1 ±0.2	0.1 ±0.1
Psoralia lanceolata	3.5 ±3.6	1.7 ±3.3	0.6 ±0.6	0.2 ±0.2	0.9 ±1.5	2.1 ±2.0	1.5 ±1.2
Sonchus uliginosus	-	-	-	0.1 ±0.1	-	0.0 ±0.1	-
Solidago spp.	0.1 ±0.1	-	-	-	-	0.0 ±0.1	-
Sphaeralcea coccinea	0.7 ±1.0	1.0 ±0.8	2.0 ±1.2	0.8 ±0.5	1.3 ±0.7	1.0 ±0.7	1.1 ±0.5
Tragopogon dubius	0.7 ±0.8	1.1 ±1.3	0.1 ±0.1	0.8 ±0.7	0.3 ±0.3	1.0 ±0.7	0.7 ±0.4
Taraxacum officinale	0.7 ±0.6	1.1 ±1.2	0.4 ±0.7	0.4 ±0.6	0.6 ±0.6	0.7 ±0.5	0.6 ±0.4
Vicia americana	0.9 ±0.9	1.3 ±1.9	-	1.3 ±1.7	11.1 ±1.0	0.7 ±0.9	0.9 ±0.7
Unknown Forb	-	0.1 ±0.2	0.1 ±0.1	0.3 ±0.3	0.0 ±0.1	0.3 ±0.2	0.1 ±0.1
Total	101.7 ±10.8	89.4 ±7.0	90.0 ±8.3	80.5 ±9.1	99.8 ±5.7	81.0 ±6.0	90.4 ±4.8

Table 5-6. ANOVA *F* and *P* values for tests of the effects of defoliation and moisture treatments on Shannon's diversity, and species richness and evenness within both a lowland and upland site in the Mixedgrass Prairie.

	Shannon's diversity		Species richness		Species evenness	
	F value	*P* value	*F* value	*P* value	*F* value	*P* value
Lowland site						
Defoliation	$6.67_{(3, 40)}$[1]	**<0.001**	$4.55_{(3, 40)}$	**0.008**	$6.53_{(3, 40)}$	**0.001**
Moisture	$2.15_{(1, 40)}$	0.15	$0.30_{(1, 40)}$	0.59	$3.16_{(1, 40)}$	0.083
Defol. x moist.	$0.72_{(3, 40)}$	0.55	$0.12_{(3, 40)}$	0.95	$1.12_{(3, 40)}$	0.35
Upland site						
Defoliation	$3.76_{(3, 48)}$	**0.017**	$0.64_{(3, 48)}$	0.59	$5.10_{(3, 48)}$	**0.004**
Moisture	$7.45_{(1, 48)}$	**0.009**	$8.40_{(1, 48)}$	**0.006**	$0.41_{(1, 48)}$	0.52
Defol. x moist.	$1.33_{(3, 48)}$	0.28	$1.05_{(3, 48)}$	0.38	$0.48_{(3, 48)}$	0.69

[1] Numerator and denominator degrees of freedom, respectively.

Table 5-7. Means and standard errors (in parentheses) for plant species diversity (Shannon's index), richness, and evenness, as well as photosynthetically active radiation (PAR) ratio (below and above the canopy), volumetric soil moisture, and soil temperature (˚C) under defoliation (deferred [control], high intensity low frequency [HILF], low intensity high frequency [LIHF], and high intensity high frequency [HIHF]) and moisture (ambient vs. addition) treatments. Post hoc mean comparisons are Tukey's adjusted.

	Defoliation					Moisture		
	Control	HILF	LIHF	HIHF		Addition	Ambient	
Lowland site								
Shannon's diversity	1.45^{B1}	1.81^{A}	1.78^{A}	1.63^{AB}	(0.06)	-	-	-
Species richness	7.92^{B}	9.42^{AB}	10.50^{A}	10.08^{A}	(0.53)	-	-	-
Species evenness	0.67^{B}	0.78^{A}	0.77^{A}	0.72^{AB}	(0.02)	-	-	-
PAR ratio	0.48^{C}	0.79^{B}	0.78^{B}	0.87^{A}	(0.02)	0.68^{b}	0.78^{a}	(0.01)
Soil moisture	-	-	-	-	-	0.31^{a}	0.25^{b}	(0.01)
Temperature	18.94^{B}	19.82^{A}	19.52^{A}	19.75^{A}	(0.12)	19.22^{b}	19.79^{a}	(0.08)
Upland site								
Shannon's diversity	1.54^{A}	1.38^{AB}	1.26^{B}	1.26^{B}	(0.07)	1.27^{b}	1.45^{a}	(0.05)
Species richness	-	-	-	-	-	6.14^{b}	7.43^{a}	(0.31)
Species evenness	0.81^{A}	0.74^{AB}	0.69^{B}	0.65^{B}	(0.03)	-	-	-
Light	0.64^{C}	0.89^{B}	0.88^{B}	0.94^{A}	(0.01)	0.80^{b}	0.88^{a}	(0.01)
Moisture	-	-	-	-	-	0.21^{a}	0.15^{b}	(0.004)
Temperature	20.99^{B}	21.58^{A}	21.51^{A}	21.53^{A}	(0.12)	21.05^{b}	21.75^{a}	(0.08)

[1] Within rows, means with different letters differ ($P < 0.05$).

Table 5-8. ANOVA *F* and *P* values testing the effects of defoliation and moisture treatments on photosynthetic active radiation (PAR) light ratio (below and above the canopy), volumetric soil moisture, and soil temperature in the Mixedgrass Prairie.

	PAR ratio		Soil moisture		Soil temperature	
	F value	*P* value	*F* value	*P* value	*F* value	*P* value
Lowland site						
Defoliation	$96.3_{(3, 40)}$[1]	**<0.001**	$0.01_{(3, 40)}$	1.00	$12.0_{(3, 40)}$	**<0.001**
Moisture	$28.8_{(1, 40)}$	**<0.001**	$44.4_{(1, 40)}$	**<0.001**	$24.3_{(1, 40)}$	**<0.001**
Defol. x moist.	$2.58_{(3, 40)}$	0.067	$2.87_{(3, 40)}$	**0.048**	$1.75_{(3, 40)}$	0.17
Upland site						
Defoliation	$118.8_{(3, 48)}$	**<0.001**	$0.65_{(3, 48)}$	0.59	$5.77_{(3, 48)}$	**0.002**
Moisture	$42.0_{(1, 48)}$	**<0.001**	$112.7_{(1, 48)}$	**<0.001**	$37.2_{(1, 48)}$	**<0.001**
Defol. x moist.	$10.6_{(3, 48)}$	**<0.001**	$0.54_{(3, 48)}$	0.66	$2.00_{(3, 48)}$	0.13

[1] Numerator and denominator degrees of freedom, respectively.

Table 5-9. Means and standard error values (in parentheses) for photosynthetically active radiation (PAR) ratio (below and above the canopy) in the upland site and volumetric soil moisture in the lowland site under defoliation (deferred [control], high intensity low frequency [HILF], low intensity high frequency [LIHF], and high intensity high frequency [HIHF]) and moisture (ambient vs. addition) treatments. Post hoc mean comparisons are Tukey's adjusted.

Moisture treatment	Defoliation				
	Control	HILF	LIHF	HIHF	
	------------------------PAR ratio----------------------				
Addition	^{B}[1] 0.55 ^{b}[2]	^{A}0.87^{a}	^{A}0.86^{a}	^{A}0.92^{a}	(0.02)
Ambient	^{B}0.74^{a}	^{A}0.91^{a}	^{A}0.91^{a}	^{A}0.95^{a}	
	---------------Volumetric soil moisture--------------				
Addition	^{A}0.32^{a}	^{A}0.32^{a}	^{A}0.29^{a}	^{A}0.30^{a}	(0.01)
Ambient	^{A}0.24^{b}	^{A}0.23^{b}	^{A}0.26^{a}	^{A}0.25^{a}	

[1] Means with different uppercase letters within the same row differ ($P < 0.05$).

[2] Means with different lowercase letters within the same column differ ($P < 0.05$).

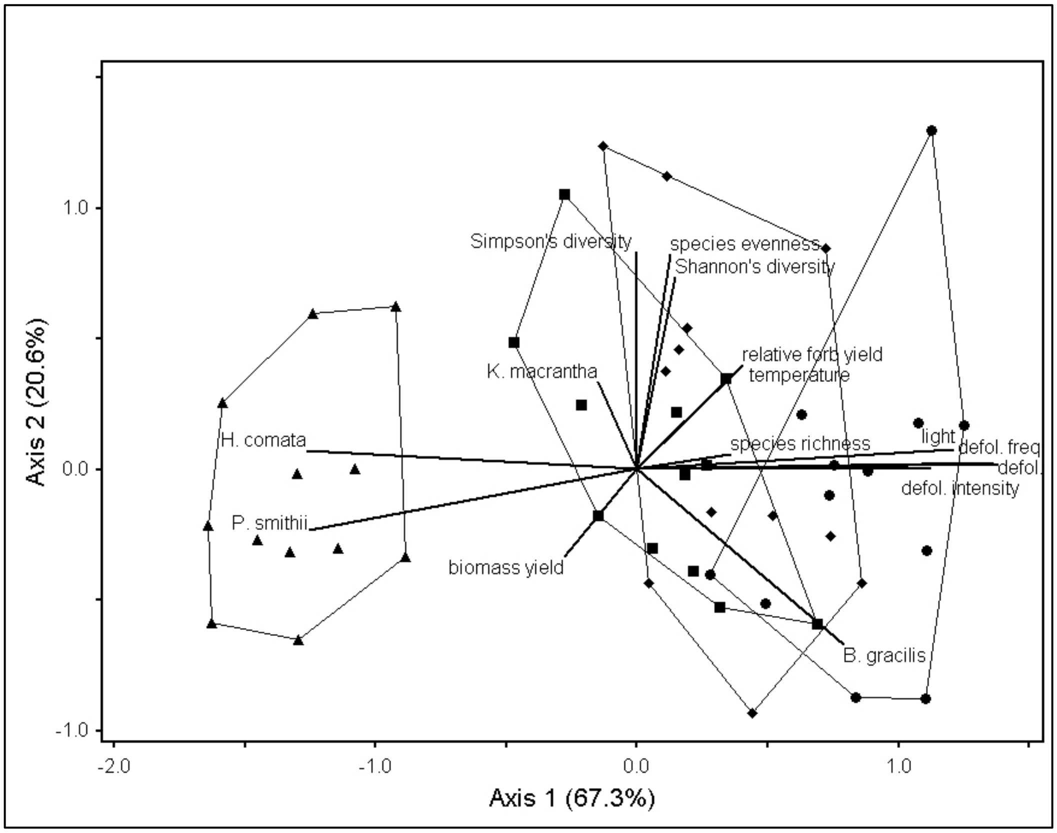

Figure 5-1. NMS ordination of a lowland Mixedgrass Prairie site overlaid (|r|>0.2) with treatments (moisture and defoliation, including frequency and intensity), environmental parameters (light [PAR], soil temperature, and soil moisture), diversity measures (Shannon's, Simpson's, evenness, and richness), significant ($P<0.05$) indicator species (*Pascopyrum smithii*, *Hesperostipa comata*, *Koeleria macrantha*, and *Bouteoua gracilis*), plot biomass yield, and relative forb yield (proportion of plot biomass consisting of forbs). Percent of variation associated with each axis is in parentheses and shapes represent plot defoliation treatment: control [▲], high intensity low frequency [■], low intensity high frequency [◆], and high intensity high frequency [●].

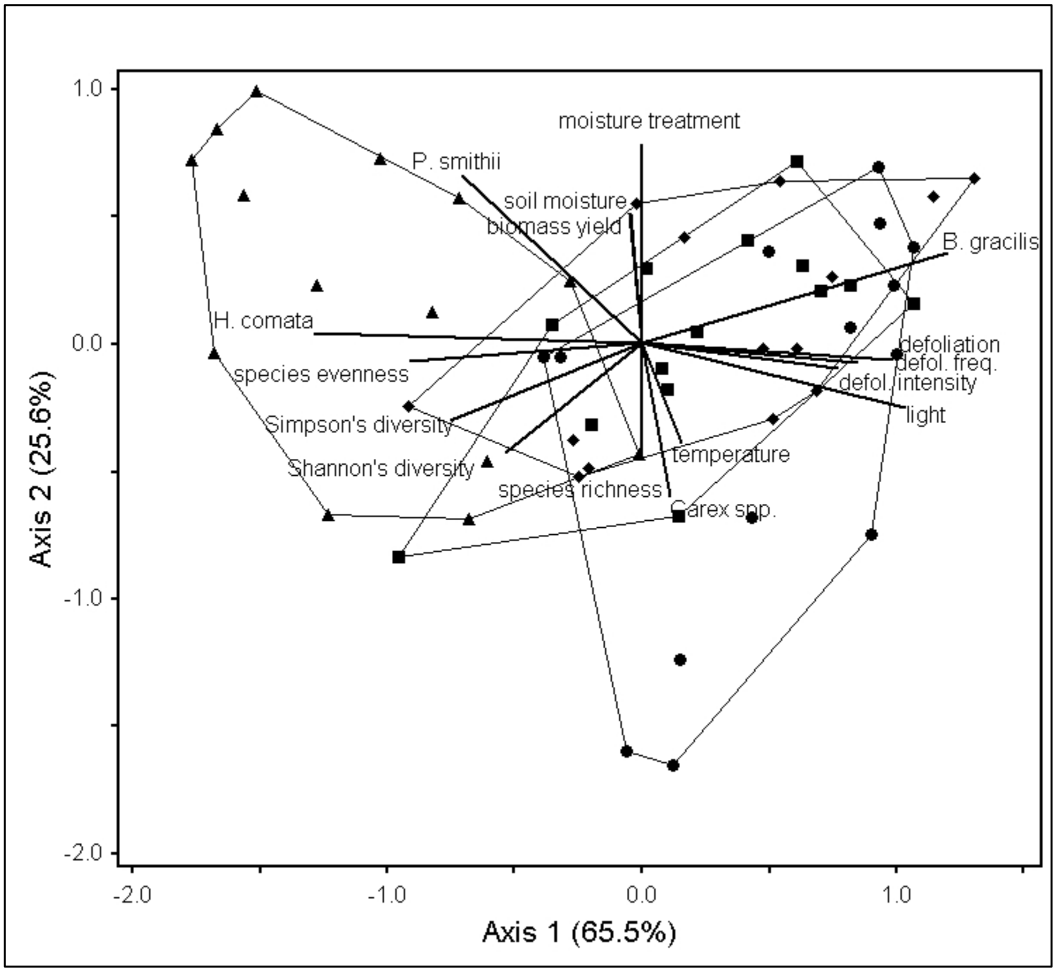

Figure 5-2. NMS ordination of an upland Mixedgrass Prairie site overlaid (|r|>0.2) with treatments (moisture and defoliation, including frequency and intensity), environmental parameters (light [PAR], soil temperature, and soil moisture), diversity measures (Shannon's, Simpson's, evenness, and richness), significant ($P<0.05$) indicator species (*Pascopyrum smithii*, *Hesperostipa comata*, *Koeleria macrantha*, and *Bouteoua gracilis*), plot biomass yield, and relative forb yield (proportion of plot biomass consisting of forbs). Percent of variation associated with each axis is in parentheses and shapes represent plot defoliation treatment: control [▲], high intensity low frequency [■], low intensity high frequency [◆], and high intensity high frequency [●].

5.7. Literature Cited

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Chapter 6. Leaf and tiller growth under clipping and watering in two grasses: a test of determinate growth

6.1. Abstract

Apical and axillary meristem growth was investigated in this experiment by examining leaf demography (age class) dynamics, tiller demography (reproductive vs. vegetative), and tiller survival and recruitment under different defoliation and moisture regimes in two canopy dominant midgrasses of the Mixedgrass Prairie that are of contrasting growth form: *Hesperostipa comata* (caespitose) and *Pascopyrum smithii* (rhizomatous). Defoliation treatments included deferred (control), high intensity at low frequency (HILF), low intensity at high frequency (LIHF), and high intensity at high frequency (HIHF). These were combined with moisture treatments of ambient moisture and moisture addition (4 x 2 factorial), and applied to 1 m^2 plots in both a relatively dry upland and more mesic lowland site (n = 6/site) in Alberta's Dry Mixedgrass Prairie natural subregion during the 2010 through 2012 growing seasons. *H. comata*, owing to its caespitose growth form, was hypothesized to have more determinate growth characteristics, such that defoliation would not promote continued phytomer production, moisture would not influence reproductive tiller allocation, and tiller survival would be favoured over recruitment. The opposite was hypothesized for *P. smithii*. Leaf growth patterns were more continuous in *P.*

smithii whereas *H. comata* attained peak leaf numbers earlier in the growing season and less readily replaced leaves that senesced later in the growing season, although defoliation increased leaf production and prevented senescence in both grasses. *H. comata* genets showed more consistent allocation to reproductive tillers, and both grasses increased reproductive tiller allocation under moisture addition, although this was more pronounced in *P. smithii*. Compared to *P. smithii*, *H. comata* tillers survived defoliation better, but tiller survival was lower under ambient moisture conditions, especially in the drier upland site. Tiller recruitment in *H. comata* was also relatively high, and compensated for defoliation and ambient moisture effects on tiller mortality. In contrast, defoliation markedly reduced tiller survival in *P. smithii*, and only under HILF defoliation did subsequent tiller recruitment compensate for this. *P. smithii* also recruited more tillers under moisture addition. These results suggest that morphological growth responses may indeed differ between these codominant caespitose and rhizomatous grass species from the Mixedgrass Prairie, with *H. comata* being more determinate in terms of leaf growth and reproductive tiller allocation. In contrast, *P. smithii* may be less determinate under favourable moisture conditions, as evidenced by both reproductive tiller allocation and tiller recruitment.

6.2. Introduction

Plant growth is termed 'determinate' when it is intrinsically constrained. However, in practical terms, deterministic growth describes multiple growth phenomena. For example, phytomer growth is said to be determinate given that phytomers can only elongate, whereas shoot growth is indeterminate because shoots can produce additional shoots, which can in turn, produce more shoots (Sosebee *et al.* 1977; Jackson *et al.* 1994). Similarly, determinate flowering refers to plants that flower once in the growing season compared to those that will flower multiple times if conditions allow (Taiz and Zeiger 2010). Deterministic growth is also used to describe how plants dominant in low resource/stressful environments generally have low growth rates regardless of ambient growing conditions (Brooker and Callaghan 1998). This pattern may occur because maintaining high photosynthetic capacity (*i.e.*, chlorophyll) has an associated metabolic cost that cannot be supported under low resource conditions. It may also arise because greater investment in herbivory defence (an avoidance mechanism) may be adaptive when the relative costs of regrowth (a tolerance mechanism) are higher, such as in low resource environments (Coley *et al.* 1985; Endara and Coley 2011). Production of defence compounds (tannins, alkaloids) and structures (lignin, trichomes) require photosynthate that could otherwise be allocated to growth, creating the so-called dilemma of plants to 'grow or defend' (Herms and Mattson 1992). Moreover, investing in characteristics that confer stress tolerance, such as a thick cuticle, osmotic regulation of cells, and a high root:shoot ratio, also may detract from growth.

Determinate growth has also been recognized in drier grasslands, such that aboveground net primary productivity of these ecosystems does not respond to inter- and intra-annual periods of higher resource availability to the same relative degree as more mesic grasslands (Paruelo *et al*. 1999; Knapp and Smith 2001; Reichmann *et al*. 2013). This response may be due to meristem limitations given that xeriphytic grasses generally have fewer basal buds available after the initial spring out-growth of the bud bank (Dalgleish and Hartnett 2006), meaning fewer tillers can emerge if conditions are favourable later in the growing season. Indeed, observed tiller dynamics (survival and production) largely explain sward productivity responses (Murphy and Briske 1992; Reichmann *et al*. 2013). However, phytomer production is another property of meristems that may influence determinate growth (Sharman 1945), and thus far has not been identified or tested as a mechanism limiting xeriphytic plant growth.

Esau (1977) described a determinate (vs. indeterminate) meristem as able to produce a fixed (vs. unlimited) number of phytomers. This has relevance for harvest management of basal meristem monocots. For example, rotational grazing allows managerial control over the timing and frequency of defoliation (Derner *et al*. 1994; Volesky 1994), and in turn may maximize sward productivity by delaying tiller senescence and promoting phytomer production throughout the growing season (Voisin 1961). Thus, provided ramet populations survive intermittent defoliation, phytomer growth dynamics may strongly influence sward production, and photosynthesis under recurrent defoliation (Parsons *et al*. 1988).

Tiller type can also influence growth. Plants can produce either reproductive or vegetative tillers, respectively. Reproductive tillers have determinate phytomer growth given that eventual production of an inflorescence eliminates additional phytomer growth. Reproductive shoots are also less tolerant of defoliation, presumably because floral induction is energetically expensive (meaning less photosynthate is available for regrowth) and the apical meristem becomes susceptible to removal by herbivores when phytomer internodes elongate (Branson 1953). Growing conditions can affect the proportion of tillers within genets that are reproductive (Olson and Richards 1989; Lafarge 2006; Tian *et al.* 2012). Consequently, although this in itself is an indeterminate growth response, it may also influence genet phytomer production potential and defoliation tolerance.

Finally, tiller longevity and fecundity may also influence phytomer growth. Tillers appear to have a finite lifespan of 2 years, with most surviving for only one growing season (Langer 1956; Briske and Butler 1989; Hendrickson and Briske 1997). Moreover, tiller recruitment from seed is seemingly rare (Benson and Hartnett 2006). This entails that annual replacement of tillers in perennial grasses largely must occur through activation of another axillary meristem (e.g., see Dalgleish and Hartnett 2006), and thus apical meristems are also renewed annually. However, it is not known how defoliation management may affect subsequent apical meristem longevity under recurrent defoliation. Defoliation can reduce tiller longevity and promote tiller recruitment (Zhang and Romo 1995; Hendon and Briske 1997). Although this may rejuvenate apical meristems, it may also deplete axillary meristem availability through the growing season as bud banks and carbohydrate reserves within parent tillers are depleted, which may in turn affect over-winter survival and plant vigour the following spring.

This experiment examined tiller demography and longevity as well as phytomer development, for two dominant grasses of the Dry Mixedgrass Prairie natural subregion: *Hesperostipa comata* and *Pascopyrum smithii*. These species are similar in that they are late-seral, canopy dominant midgrasses; however, they differ in that the former and latter are caespitose and rhizomatous, respectively. Rhizomes are underground tillers, but are also a source of meristems and act as storage organs of carbohydrate and nutrients for growth (Suzuki and Stuefer 1999). Rhizomes alone can be classified as indeterminate or determinate, such that some species have rhizomes that can produce multiple tillers, whereas the latter includes species with rhizomes that produce only a single tiller (Bedunah and Sosebee 1995). Nevertheless, indeterminate growth may be more characteristic of rhizomatous species given that rhizomes may ameliorate meristem limitations associated with plant adaptation to aridity. Indeed, rhizomatous graminoids, in general, may be better adapted to mesic environments (Mack and Thompson 1982; Derner and Briske 2001) and better tolerate herbivory (Benot *et al.* 2013). In contrast, some evidence suggests that caespitose grasses are better adapted to aridity (Sims *et al.* 1978; Mack and Thompson 1982) and have lower grazing tolerance (Milchunas and Lauenroth 1993). This suggests that rhizomatous and caespitose grasses may, in general, have more indeterminate and determinate growth characteristics, respectively.

The objectives of this experiment were to examine (1) whether recurrent growing season defoliation promotes phytomer growth, (2) whether increased moisture increases sexual reproductive effort as evidenced by an increase in tillers with an inflorescence, and (3) examine how defoliation and moisture influences the survival and fecundity of tillers. Hypotheses include that *P. smithii* would produce relatively more phytomers under recurrent defoliation, increase allocation to reproductive tillers under high moisture, and recruit more tillers under recurrent growing season defoliation, whereas *H. comata* may not increase allocation to reproductive tillers under high moisture conditions but may have greater tiller survival (as opposed to recruitment) under recurrent defoliation.

6.3. Methods

6.3.1. Site Description

Two study sites were located in the Brooks Plain within the Dry Mixedgrass Prairie natural subregion of Alberta, Canada. Mean annual precipitation and daily temperature in this area are 354 mm and 4.2°C, respectively (Adams *et al.* 2005). Sites were chosen based on uniformity of topography and plant community composition, with consistent presence of *P. smithii* and *H. comata*, and contrasting edaphic conditions (dry vs. wet). Site 1 (50° 53’ 40.2” N; 111° 52’ 26.3” W) was a relatively mesic, lowland range site with a Gleyed Eluviated Brown Chernozemic soil (Soil Classification Working Group [SCWG] 1998) of sandy loam texture (pH=6.3, EC=37µs/cm, organic matter content=2.5%). Vegetation composition consisted mostly of *P. smithii*, with *Koeleria macrantha* (Ledeb.) J.A. Schultes and *H. comata* as sub-dominants. Site 2 (50° 52’ 23.8” N; 111° 52’ 26.2” W) was a relatively xeric, upland range site with a Rego Brown Chernozemic soil (SCWG 1998) of loamy sand texture (pH=6.7, EC=27µs/cm, organic matter content=1.3%). Dominant vegetation at this site included *P. smithii*, *H. comata*, and *Bouteloua gracilis* (Willd. *ex* Kunth) Lag. *ex* Griffiths. Both sites had range health assessment scores of 80%, or healthy (Adams *et al.* 2003), and were previously grazed for the long-term at light-moderate stocking rates.

6.3.2. Treatments and Experimental Design

Treatments of defoliation and moisture were combined in a fully randomized factorial (4 x 2) design, with 6 replicates per site, and applied to 1 x 1 m plots, separated by at least 0.5 m. Plots were located by visual assessment for the presence of both *H. comata* and *P. smithii* tillers. Defoliation treatments were control, high intensity at low frequency (HILF), high intensity at high frequency (HIHF), and low intensity at high frequency (LIHF). Control plots were clipped to a 2 cm stubble height in late August. HILF and HIHF defoliation plots were clipped at 2 cm stubble heights every 3 and 6 weeks, respectively, while LIHF plots were clipped at a 5 cm stubble height every 3 weeks. Low intensity clipping heights of 5 cm were used to prevent shorter statured species (e.g., *Bouteloua gracilis*) from escaping defoliation, thereby preventing confounding competitive interactions. High intensity clipping heights of 2 cm were used to ensure complete removal of leaf material. Moisture treatments included not watering (*i.e.*, ambient moisture) and watering to augment rainfall and maintain an equivalent of over 150 mm of monthly precipitation throughout the growing season; this is double the average precipitation in June, the month of highest rainfall. The objective here was to remove moisture availability as a constraint for plant growth. Watering occurred at approximately 10 d intervals and all treatments commenced and terminated in early June and late August, respectively, in 2010 through 2012. Prior to initiating treatments, plots were hand-raked to remove litter. This was done to help separate previous years' standing dead tillers from the current year's growth.

6.3.3. Response Parameters and Data Analysis

In 2010, prior to each defoliation event, 10 tillers were randomly harvested from plot perimeters, measured to the tallest extended leaf (senescent tips were not measured), and assessed for leaf demography. Demography classes included emerging leaves (L1), fully formed mature leaves with ligules (L2), leaves showing signs of senescence (L3), and fully senesced leaves (s). Within the centre 0.5 x 0.5 m portion of plots, a focal *H. comata* bunchgrass was delineated using a wire ring for ongoing monitoring. Due to its rhizomatous habit, *P. smithii* tillers were assessed in each plot using a fixed area subplot of 0.2 x 0.2 m in the lowland and 0.25 x 0.25 m in the upland site. A larger subplot was used in the upland site because *P. smithii* was less abundant. Tiller numbers for focal *H. comata* genets ranged between 9-41 and 14-91 in the lowland and upland sites, respectively (means were 25 and 30, respectively). Basal areas of *H. comata* ranged between 3.1-41.3 and 6.6-62.9 cm^2 in the lowland and upland sites, respectively (means were 17.6 and 21.1 cm^2, respectively). Tiller numbers of *P. smithii* ramets within subplots ranged between 9-29 and 7-28 in the lowland and upland sites, respectively (means were 16 and 15, respectively). The number of vegetative and reproductive (*i.e.*, with a visible inflorescence) tillers was assessed within focal genets prior to each defoliation event. Moreover, tillers were marked with wire rings in early June 2010; this was done for all *P. smithii* and 6 *H. comata* tillers within focal genets. Marked tillers were again enumerated in late August 2010 and assessed. Fully senescent tillers were classified as dead and missing rings were noted.

For tiller demography, the objective was simply to assess defoliation effects on phytomer growth. However, because leaves were not marked, it was not possible to determine phytomer turnover (given that the number of leaves lost through abscission could not be determined) and thereby statistically test whether phytomer production differed among treatments. Instead, the number of leaves in each age class was summarized with Proc MEANS (SAS 9.2—SAS Institute, 1989), such that means and associated confidence intervals (95%) were stratified by defoliation, moisture, and defoliation x moisture combinations for each species and time period. Reproductive tillers were excluded from this analysis and moisture effects were ignored given that these were limited to *H. comata* and only manifested in late August. To summarize growth responses to defoliation, the number of leaves in each age class, together with tiller heights, were determined cumulatively for each high intensity defoliation treatment, as these resulted in complete removal of leaves and no senescent leaves were observed. This implies that phytomers were likely not missed due to leaf abscission. Responses in the high intensity defoliation treatments were compared to leaf demography dynamics under control defoliation; for which, although the number of leaves lost through abscission was unknown, this could be estimated by examining senescent leaf numbers at particular times of the growing season.

The number of reproductive and vegetative tillers was assessed for focal genets prior to each defoliation event. Early August best coincided with maximum tiller inflorescence production for both species. The proportion of tillers that were reproductive within genets were assessed for this period for the control defoliation treatment. Data were not normal and transformations were unsuccessful because a high proportion of genets produced no inflorescences; this was especially evident for *P. smithii*. Consequently, the effect of moisture conditions on the relative allocation to reproductive tillers was assessed using a non-parametric procedure, the Wilcoxon-Mann-Whitney test (SAS 9.2). This was used to compare reproductive tiller allocation among moisture treatments, both within each growing season and overall, using a two-tailed t-distribution and significance level of $P \leq 0.05$.

Tiller turnover was assessed in terms of both survival and recruitment. Survival (S) was defined as the proportion of tillers marked in early June that persisted until late August. To avoid under-estimating survival, rings missing at the end of the growing season were subtracted from the original pool of marked tillers. Recruitment (R) was an estimate of the proportion of tillers that produced at least one additional tiller during the growing season. This metric was derived by subtracting a tiller number change ratio over the growing season, which is the number of tillers within the entire genet remaining alive at the end of the growing season (f) relative to the beginning (i), from (S).

$$R = (f/i) - S$$

For example if a genet gained 50 percent more tillers by late August, its change ratio would be 1.5. Consequently, if survival of marked tillers was 100 percent, then as many as 50% of tillers (1.5 – 1 = 0.5) within the genet recruited another tiller during the growing season. This is a proxy estimate because it assumes tillers within the aforementioned 50% recruited only one additional tiller, whereas some may recruit more at the expense of others recruiting none. Survival and recruitment were checked for normality and homogeneity of variance using Shapiro-Wilk and Lavene's tests ($P \leq 0.05$), respectively (SAS 9.2). No transformations were necessary. A two-way ANOVA (SAS 9.2) was used to test defoliation and moisture effects on tiller survival and recruitment. Preliminary ANOVA indicated defoliation and moisture effects were consistent among sites, except for a three-way interaction among defoliation x moisture x site for tiller survival in *H. comata*, which indicated that tiller survival was relatively low (≈ 45%) among all defoliation regimes (even controls) within the drier upland site. Barring this, site was treated as a random factor in further analyses. *Post-hoc* mean comparisons among significant effects were Tukey's adjusted. Significance for main effects and interactions were assessed at $P \leq 0.05$ and 0.10, respectively. A more liberal probability level was used for interactions because the Tukey's procedure adjusts *P* values based on all possible comparisons among means, and only a subset of these comparisons were of interest for interpreting interaction terms.

6.4. Results

6.4.1. Leaf Demography

Under no growing season defoliation (control), leaf numbers in *H. comata* peaked in early June at 2.53 (95% C.I. = +/- 0.20) leaves per tiller, meaning that by this period each tiller had 2-3 leaves, with the majority of tillers having 1 emerging and fully mature leaf, and approximately half of tillers had a third leaf showing signs of senescence (Figure 6-1). Leaf numbers remained static until the middle of July, at which time a greater proportion of leaves showed signs of senescence and approximately 1 in 4 tillers had a fully senescent leaf. Subsequent declines in leaf number over the growing season corresponded with an increasing occurrence of senescent leaves. Indeed, by late August approximately 40% of tillers had fully senescent leaves and most tillers had approximately 2 leaves, one of which was fully mature with signs of senescing. Given that total leaf numbers corresponded with senescence rates, relatively little leaf turnover occurred in *H. comata*. However, despite decreases in leaf numbers since late June, tiller heights continued to increase from 14.5 (+/- 1.6) cm in early June to 27.3 (+/- 3.1) cm in early August (Figure 6-1). This suggests that continued tiller growth likely occurred from sheath elongation. By late August, tiller heights decreased to 22.1 (+/- 3.0) cm, likely due to leaf senescence.

In contrast, *P. smithii* under control defoliation continued to produce leaves throughout the growing season, with leaf numbers per tiller increasing from 2.71 (+/- 0.23) to 4.59 (+/- 0.37) over the period of early June to late August (Figure 6-1). And although leaves showed signs of senescence early in the experiment, with 75% of tillers having a senescing leaf, fully senescent leaves did not appear until the middle of July. By early August the majority of tillers had one fully senescent leaf; and by late August the mean number of senescent leaves was 1.23 (+/- 0.28) per tiller, meaning that some tillers had at least two senescent leaves at this time. Despite this, 79% of tillers were still producing an emerging leaf, as opposed to 53% in *H. comata*. Given that overall leaf numbers continued to increase in *P. smithii* despite ongoing leaf senescence, indicates that some leaf turnover occurred, and thus tillers produced more leaves than were present at the end of the growing season. Although it is unknown how many senescent leaves may have been lost through abscission, it is likely that most *P. smithii* tillers produced approximately 6 leaves over the growing season, as opposed to 2.5 in *H. comata*. Moreover, *P. smithii* tiller heights increased markedly until the middle of July, and then increased gradually to a peak height of 30.9 (+/- 2.2) cm (Figure 6-1). Thus, in contrast to *H. comata*, it appears that leaf senescence did not reduce *P. smithii* tiller heights later in the growing season.

Recurrent growing season defoliation markedly increased leaf production in both grass species (Figure 6-1). Defoliation to 2 cm removed all existing leaves, which necessitated regrowth from the emergence of new phytomers within clipped leaf sheaths. Phytomer regrowth increased the total number of leaves produced in *H. comata* to 6.8 and 9.9 under HILF and HIHF defoliation, respectively (Figure 6-1). This resulted in cumulative vertical tiller growth of 51.4 and 70.6 cm for each respective defoliation treatment. Similarly, *P. smithii* produced 9.4 and 12.5 leaves under HILF and HIHF defoliation, respectively, resulting in cumulative tiller height growth of 53.6 and 75.7 cm. Moreover, both defoliation treatments virtually eliminated the occurrence of senescent leaves in both grasses, indicating that no leaves were lost to abscission and leaf counts accurately reflect leaf production. Within six weeks of HILF defoliation, *H. comata* and *P. smithii* tillers typically produced an emerging leaf, as well as 1.2 and 2.4 mature leaves, respectively. And within 3 weeks of HIHF defoliation, *H. comata* and *P. smithii* tillers typically produced an emerging leaf, as well as 0.8 and 1.5 mature leaves, respectively. This suggests that the majority of leaf growth occurred within the first three weeks of defoliation (Figure 6-1).

6.4.2. Reproductive Tiller Allocation

Moisture addition increased allocation to reproductive tillers for both grasses under control defoliation (Figure 6-2), but more so in *P. smithii*. Overall, reproductive tiller allocation was greater under moisture addition for *H. comata*, although this was marginally significant (*P* = 0.055). Within years, however, it was significant for 2010 (*P* = 0.026), but not 2011 (*P* = 0.13) or 2012 (*P* = 0.48) (Table 6-2). In contrast, reproductive tiller allocation was significantly higher under moisture addition for *P. smithii* (*P* = 0.003), despite that 62, 24, and 53% of genets under this treatment did not produce reproductive tillers at all in 2010, 2011, and 2012, respectively—compared to 0, 31, and 38% for *H. comata* (data not shown). However, moisture effects on reproductive tiller allocation for *P. smithii* were more consistent. Reproductive tillers were relatively more abundant under moisture addition in 2012 (*P* = 0.040), but effects were less prominent in 2010 (*P* = 0.077) and 2011 (*P* = 0.074).

6.4.3. Tiller Demography

Overall, tiller survival for both grasses remained greater for controls relative to the other defoliation treatments. For *H. comata*, 75% of marked tillers under control defoliation survived the growing season, compared to 40-44% under all other defoliation regimes (Figure 6-3). However, moisture conditions further influenced *H. comata* tiller survival under control defoliation (*P* = 0.003) (Table 6-2), such that 58 and 92% of marked tillers survived the growing season under ambient and moisture addition, respectively. Moreover, tiller survival for controls was especially low under ambient moisture in the drier upland site compared to the lowland site (36 *vs*. 88%; data not shown), as indicated by a preliminary ANOVA that included site as a fixed factor (*P* = 0.022). In contrast, tiller survival was not influenced by moisture conditions for *P. smithii* ($P = 0.79$). Defoliation effects were also more pronounced in *P. smithii*, such that 95% of tillers survived under control defoliation compared to 27 and 5-6% under low and high intensity defoliation, respectively (Figure 6-3).

Defoliation and moisture effects on tiller recruitment differed between grasses. Regardless of defoliation ($P = 0.67$) and moisture ($P = 0.85$) treatments, at most 55% of *H. comata* tillers recruited another tiller during the growing season (Figure 6-3). The lone effect of moisture was to reduce recruitment under moisture addition within the control treatment ($P = 0.015$) to 28%, compared to 69% under ambient moisture. In contrast, recruitment peaked under HILF defoliation for *P. smithii*, such that 81% of tillers spawned another tiller during the growing season, compared to 37-56% of tillers under all other defoliation treatments ($P < 0.001$). Tiller recruitment was also higher under moisture addition (66%) compared to ambient moisture (47%) for *P. smithii* ($P < 0.001$).

6.5. Discussion

6.5.1. Leaf Demography

Previous research has shown that some grasses commonly produce a fixed number of leaves, and after which the continued emergence of phytomers only replaces leaves lost through senescence (Jones and Lazenby 1988). However, in low resource environments, it may be adaptive to invest more photosynthate in each leaf, thereby promoting longevity, stress tolerance, and herbivory deterrence, given that the relative cost of regrowth may be greater (Herms and Mattson 1992). In turn, this may constrain plant growth potential (Coley 1988), as plants may not have to produce as many phytomers to keep pace with senescence and maintain photosynthetic potential within the shoot. However, given that the relative cost of producing each phytomer would be greater than if fewer resources were allocated, this may limit the number of phytomers a meristem can produce. This notion is consistent with Grime's hypthesis that a trade-off may exist between stress tolerance and competitive dominance (Grime 1977), given that competitive plants commonly have rapid growth, and investment in stress tolerance strategies may constrain growth. Moreover, it is largely unknown how many phytomers an apical meristem can produce. It may be that graminoid meristems in themselves are determinate, and capable of producing only a fixed number of phytomers within a growing season.

P. smithii and *H. comata* are codominant in the semiarid mixedgrass prairie (Coupland 1961). However, synergies among tillers within caespitose genets may better equip this growth form to tolerate edaphically stressful environments. Caespitose grasses accumulate greater carbon and nitrogen resources beneath genets (Burke *et al*. 1998), and at the same time appear to limit intraspecific and asynchronistic competition among tillers for these resources (Olson and Richards 1989; de Kroon 1993). In contrast, *P. smithii* may persist in edaphically stressful environments by exploiting spatially adjacent microsites of higher fertility (Derner and Briske 2001). Due to *H. comata* being potentially better adapted to stressful environments, it was thus hypothesized that its leaf/phytomer growth would be more determinate, and as such defoliation would have little effect on the number of phytomers produced by tillers and leaves may not turnover as readily.

However, contrary to my hypothesis, defoliation markedly increased phytomer production over the growing season for both grasses, and this was especially true for the caespitose species *H. comata*. Indeed, it appears that in the absence of defoliation, *H. comata* had accumulated the maximum number leaves by early July, and few leaves were lost to senescence over the growing season. However, when leaves were removed by intermittent defoliation, regrowth occurred through the emergence of new phytomers enclosed within clipped leaf sheaths. Recurrent defoliation (HIHF) increased phytomer production by 4-fold in *H. comata*, compared to 2-fold in *P. smithii*. However, because clipping ceased in late August (near the end of the growing season), it is unknown how long this regrowth trend would have continued, but growing conditions were likely not sustained beyond the month of September. Future experiments addressing this question should mark individual leaves to better track leaf fate (*i.e.*, senescence and abscission), as well as grow plants under greenhouse conditions to extend the growing season length. Finally, it was unknown how much regrowth was due to tillering and subsequent rejuvenation of apical meristems. Although in most cases regrowth was visibly noticeable from within previously clipped leaf sheaths, some tiller turnover was evident under defoliation, especially in *P. smithii*. Consequently, future experiments should also mark and recurrently monitor the same individual tillers.

Contrary to defoliation effects, plant growth responses in the absence of growing season defoliation suggest that *H. comata* and *P. smithii* may have more determinate and indeterminate leaf growth, respectively. For example, control *H. comata* plants reached maximum leaf numbers by early June, after which they steadily declined as emergent leaves could not keep pace with leaf senescence. In contrast, leaf numbers for *P. smithii* steadily increased throughout the summer despite the fact that leaves were senescing at that time. These differing leaf growth patterns suggest that leaf turnover only occurred in *P. smithii*, indicating this grass likely produced more phytomers than were present on tillers at the end of the growing season. Further, these results suggest that *P. smithii* may extend leaf growth throughout the growing season, and thus have a more continuous growth pattern, whereas *H. comata* may concentrate leaf growth early in the growing season.

6.5.2. Reproductive Tiller Allocation

Field observations in this study indicate that tiller demography is determined early in the growing season. For example, when tillers where marked in early June, *H. comata* reproductive tillers were readily identifiable due to their larger size and apparent vigour, even though inflorescences were not yet visible. Indeed, reproductive tiller development often requires a short-day cool period, followed by vernalization and a long-day warm period (Heide 1994). This entails that reproductive shoot apices may form either in early spring or late winter, which indeed is the case for some species (Canode *et al.* 1972). Moreover, some evidence indicates that tiller recruitment may be determined by conditions the previous growing season (Hendrickson *et al.* 2000; Reichmann *et al.* 2013), perhaps because early spring growth depends on carbohydrate reserves from the previous year (Sanada *et al.* 2010). However, it is not entirely clear how growth processes manifest in perennial grasses. Tillers appear to have a finite lifespan (Langer 1956; White 1977; Hendrickson and Briske 1997), with most not living more than one growing season. This entails that annual tiller replacement must occur through tillering from basal buds and the provision of carbohydrate reserves from parent tillers, although connectivity to parent tillers requires that roots from the successive parent tillers support growth of daughter tillers for multiple generations (Jónsdóttir and Callaghan 1988).

Mechanisms controlling the demography of successive tiller generations are largely unknown. Inflorescence development may jeopardize tiller survival given the greater energetic demands of producing a seedhead (meaning less carbohydrates are available for growth the following spring) and culm elongation increases the likelihood of defoliation and loss of the apical meristem. This entails that it may be adaptive for only a subset of the ramet population to produce an inflorescence in order for the surrounding vegetative tillers ensure genet survival, which indeed appears to be the case (see Branson 1953). For a caespitose grass, reproductive tillers typically occur within the interior of the genet (personal observation), which also tends to be where the older tiller generations are located (Wan and Sosebee 2000). This could indicate that successive tiller generations remain vegetative and accumulate carbohydrate and extensive root systems until a threshold is reached, perhaps in terms of carbohydrate reserves or growing conditions, that then allows the subsequent tiller generation to become reproductive.

In this experiment, regardless of moisture conditions, not all genets produced reproductive tillers; and reproductive tillers were particularly sparse in *P. smithii*. Branson (1953) similarly found that *P. smithii* in Montana produced a low ratio (0.06) of reproductive relative to vegetative tillers. Nevertheless, moisture conditions appeared to increase the number of reproductive tillers for *P. smithii*. And although a greater proportion of *H. comata* genets produced reproductive tillers, moisture influences on reproductive tiller numbers were largely not significant in this species (except in 2012). This is consistent with my hypotheses that reproductive tiller allocation would be more and less determinate in *H. comata* and *P. smithii*, respectively. However, moisture conditions did not increase reproductive tiller numbers for *P. smithii* until the final year of the experiment, suggesting that extended periods of high resource availability are necessary. This makes sense if mechanisms controlling tiller demography respond to interannual resource availability. For example, favourable growing conditions in 2010 and 2011 may have increased carbohydrate reserves available for subsequent growing seasons, eventually promoting reproductive tiller allocation. In contrast, moisture conditions appeared to influence reproductive tiller allocation in *H. comata* only during 2010. Reasons for this are unknown, but 2010 was the only year that nearly all genets produced reproductive tillers; whereas in

2011 and 2012, nearly 60% of tillers under ambient moisture failed to produce any reproductive tillers, compared to approximately 35% under moisture addition. In general, *H. comata* was noticeably abundant in 2010; reproductive tillers were also very tall, with an average height of 63 cm (C.I. ± 12, n = 12) and some as tall as 99 cm. This perhaps suggests that growing conditions were particularly favourable in 2009. If this is the case, then exceptionally high allocation to reproductive tillers in 2010 may have adversely affected *H. comata* ability to recruit additional reproductive tillers in subsequent growing seasons. Moreover, deferred defoliation (in late August) for control genets may have inadvertently reduced reproductive tiller allocation in 2011 and 2012.

6.5.3. Tiller Demography

Genet population dynamics are the result of both tiller survival and recruitment. Tiller recruitment (*i.e.*, tillering) largely occurs in early spring (Benson and Hartnett 2006), but can also be an important regrowth process following defoliation (Caldwell *et al.* 1981). Mechanisms controlling this process are not fully understood, but evidence indicates tillering is influenced by light penetration (Deregibus *et al.* 1985; Casal *et al.* 1990) and resource availability (Olson and Richards 1989). However, plant moisture adaptation and meristem availability may also play a role, such that basal bud availability may be more limiting in xeriphytic grasses (Dalgleish and Hartnett 2006). This inherent constraint on growth may also limit tillering as a regrowth response following defoliation, perhaps because the relative costs of regrowth through this process may exceed that of regrowing from the existing apical meristem. Moreover, tillering within bunchgrasses may be constrained by ramet density within the genet, which limits recruitment to tussock peripheries (Briske and Butler 1989). Xeriphytic bunchgrasses, such as *H. comata*, may thus trade recruitment propensity for tiller survivability. In contrast, rhizomatous grasses such as *P. smithii* may have lower and higher tiller survival and recruitment, respectively, under recurrent defoliation.

Tiller survival results in this experiment largely corroborate the aforementioned hypotheses. For example, although growing season defoliation compromised tiller survival for both grasses, this was especially pronounced in *P. smithii*, suggesting *H. comata* may have greater defoliation tolerance. However, tiller survival of *H. comata* under deferred (*i.e.*, control) defoliation was similarly low compared to all other defoliation regimes. This was especially pronounced in the drier upland site. Reasons for this are unknown, and remain surprising given that ambient rainfall conditions were above average for all three growing seasons. Perhaps tiller mortality was due to greater resource competition among tillers within the genet under ambient moisture conditions.

In contrast to tiller survival, recruitment patterns for *H. comata* did not support my hypothesis that this species is determinate in growth response. *H. comata* readily recruited tillers, and this appeared to fully compensate for tiller mortality, even that associated with defoliation and ambient moisture conditions. Tiller recruitment was also prominent in *P. smithii*, but in contrast to expectations, this did not keep pace with defoliation induced tiller mortality, except perhaps under HILF defoliation. This finding corroborates other evidence that *P. smithii* decreases under defoliation (Lauenroth *et al.* 1985). Nevertheless, tiller recruitment remained the dominant growth response through which *P. smithii* coped with defoliation. Moreover, high moisture conditions also promoted tillering in *P. smithii*. This result parallels other evidence that *P. smithii*, and perhaps other rhizomatous grasses (such as *Bouteloua gracilis*), increase when moisture conditions are favourable (Chapter 5). Together these responses are consistent with the more indeterminate growth patterns hypothesized for this rhizomatous grass.

6.6. Conclusion

H. comata and *P. smithii* constitute the majority of biomass production in the Dry Mixedgrass Prairie natural subregion within the northern portion of the Great Plains of North America (Coupland 1961). Consequently, meristem growth processes of these grasses may strongly influence productivity dynamics under different climatic conditions and grazing regimes. This experiment specifically explored whether meristem growth is more determinate and indeterminate in *H. comata* and *P. smithii*, respectively, in response to defoliation and moisture treatments. However, contrary to this prediction, defoliation influenced phytomer production as well as tiller survival and reproduction in both grasses, suggesting neither has determinate meristem growth in response to varied defoliation.

Perhaps meristems themselves, being regions of active cell generation, allow growth plasticity by mediating plant growth in response to herbivory.

Results here also showed differences in meristem growth dynamics between grasses. For example, *P. smithii* recruited phytomers continuously throughout the growing season even while older phytomers senesced, whereas leaf turnover was less evident in *H. comata*. *P. smithii* also showed greater flexibility in photosynthate allocation to reproductive tillers; whereas reproductive tiller allocation was more consistent within *H. comata* genets. Finally, although both *H. comata* and *P. smithii* recruited new tillers in response to growing season defoliation, recruitment did not keep pace with tiller mortality in *P. smithii*, and only *P. smithii* recruited more tillers under moisture addition. Consequently, due to more determinate leaf growth, consistent allocation to reproductive tillers, and greater tiller survival and recruitment capacity, *H. comata* may have more stability within the plant community under variable growing conditions and ongoing herbivory. *P. smithii*, in contrast, might respond more opportunistically, especially in wetter years, by producing leaves throughout the growing season (extending growth), increasing reproductive tiller allocation (and perhaps seed production), and recruiting new tillers. These contrasting growth strategies, perhaps reflective of their growth forms, may facilitate co-existence of these grasses within their shared niche as canopy dominant midgrasses.

Table 6-1. Ambient growing season precipitation (mm) and recent long-term averages for the Brooks area of Alberta, Canada.

	Year				Average[1]
	2009	2010	2011	2012	1971-2000
June	54	123	77	135	63
July	137	52	36	48	42
August	39	20	23	29	36
Total (June-Aug.)	230	195	135	212	141

[1] Environment Canada climate normals.

Table 6-2.Tiller survival and recruitment ANOVA *F*-ratio and *P*-values for *Hesperostipa comata* and *Pascopyrum smithii* under defoliation and moisture treatments.

	Survival		Recruitment	
	F-ratio	*P*-value	*F*-ratio	*P*-value
H. comata				
Defoliation	11.5 $_{(3, 94)}$[1]	**< 0.001**	0.52 $_{(3, 94)}$	0.67
Moisture	1.1 $_{(1, 94)}$	0.30	0.04 $_{(1, 94)}$	0.85
Defol. x moist.	4.9 $_{(3, 94)}$	**0.003**	3.7 $_{(3, 94)}$	**0.015**
P. smithii				
Defoliation	216.0 $_{(3, 95)}$	**< 0.001**	11.3 $_{(3, 95)}$	**< 0.001**
Moisture	0.0 $_{(1, 95)}$	0.96	12.8 $_{(1, 95)}$	**< 0.001**
Defol. x moist.	0.35 $_{(3, 95)}$	0.79	2.5 $_{(3, 95)}$	0.064

[1] Numerator and denominator degrees of freedom, respectively.

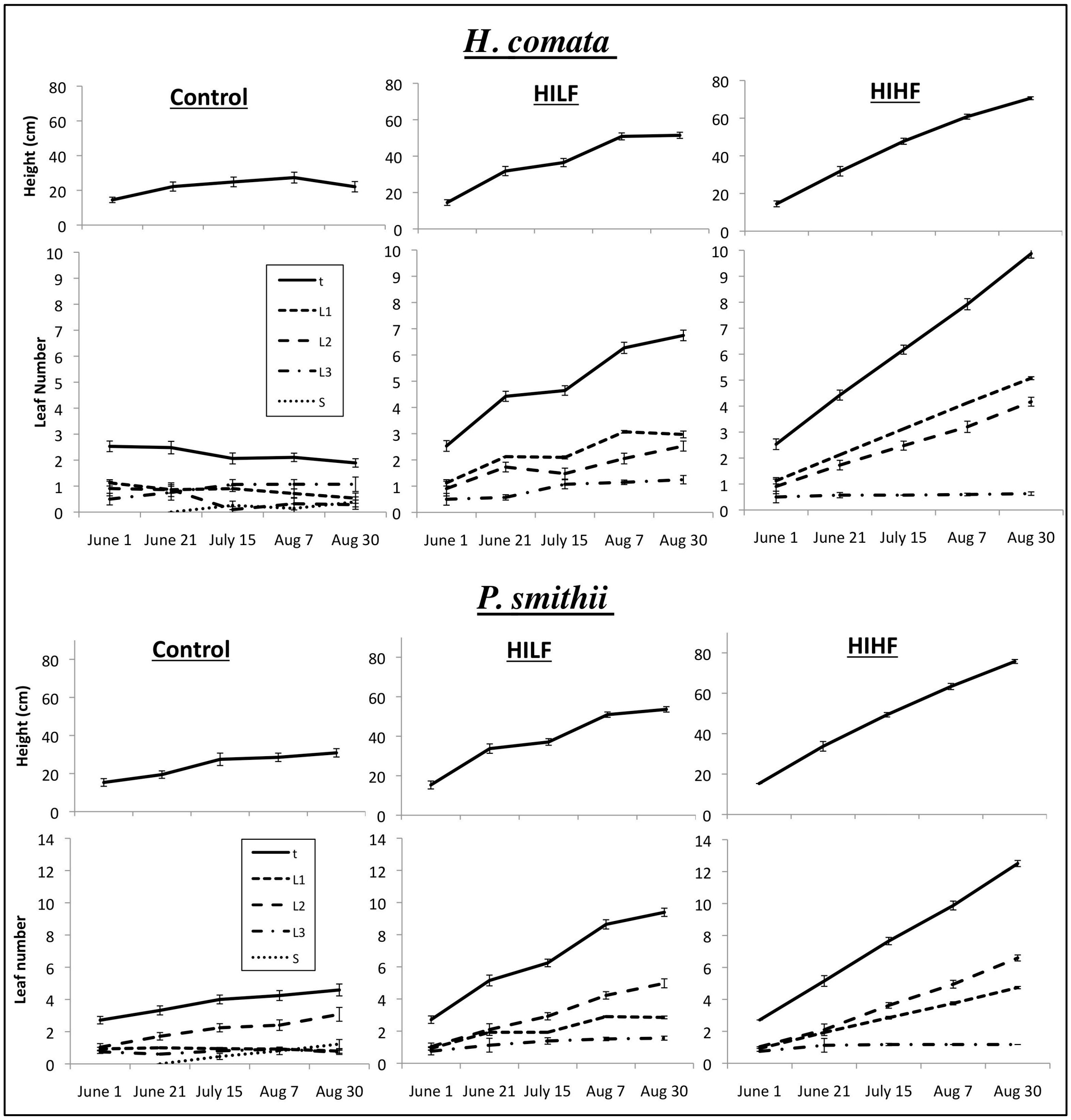

Figure 6-1. *Hesperostipa comata* and *Pascopyrum smithii* maximum plant height, seasonal leaf number (t), and leaf demography dynamics for vegetative tillers under the defoliation treatments of deferred (control), high intensity at low frequency (HILF), and high intensity at high frequency (HIHF). Leaf demography classes include newly emerging leaves (L1), fully mature leaves (L2), leaves showing signs of senescence (L3), and fully senescent leaves (s). Leaf numbers and heights for HILF and HIHF defoliation are cumulative.

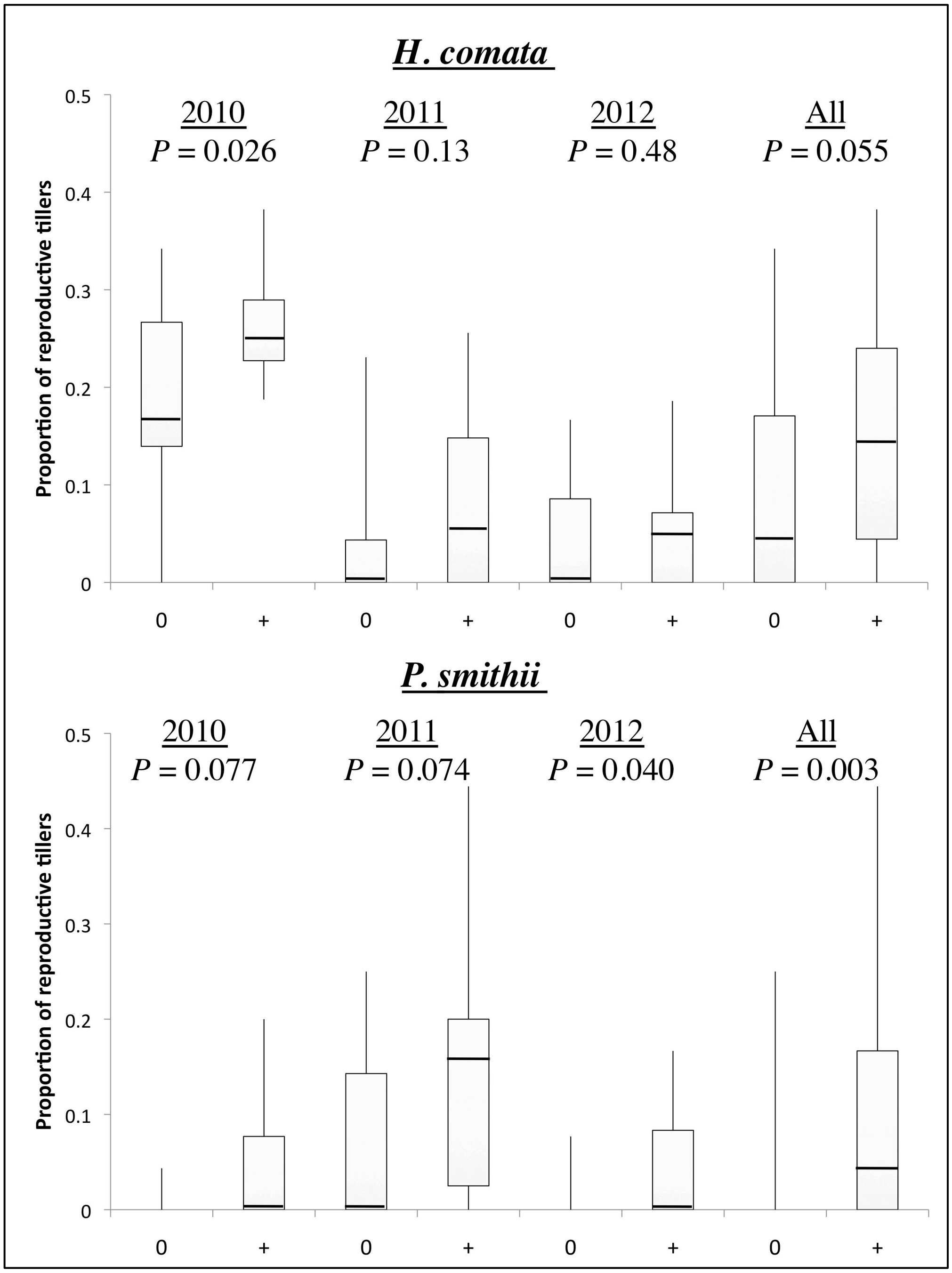

Figure 6-2. Proportion of genet tillers producing an inflorescence in *Hesperostipa comata* and *Pascopyrum smithii* under ambient moisture conditions (0) and moisture addition (+). Bars show upper and lower 25% of observations on either side of the median, whereas lines show the remaining distribution of observations. *P* values represent probability of similarity between moisture treatments during the growing seasons of 2010-2012, as well as all growing seasons combined.

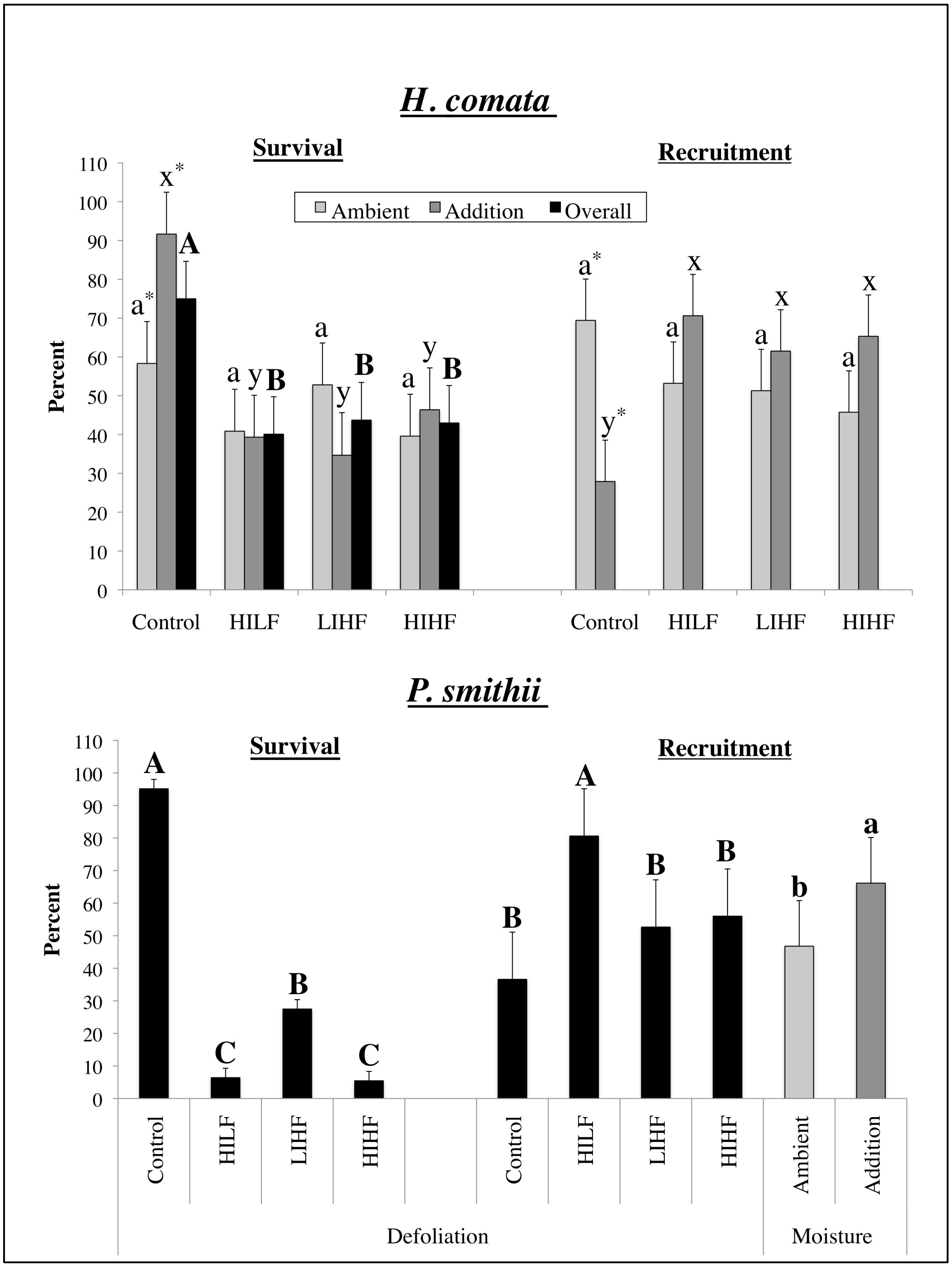

Figure 6-3. Mean percentage of marked tillers surviving the growing season (2010) and the estimated percentage of tillers that recruited at least one additional tiller for *Hesperostipa comata* and *Pascopyrum smithii* under defoliation treatments of deferred (control), high intensity at low frequency (HILF), low intensity at high frequency (LIHF), and high intensity at high frequency (HIHF) and moisture treatments of ambient moisture and moisture addition. Mean comparisons are Tukey's adjusted and means with the same letter are not significantly different ($P \leq 0.05$ for main effects, and $P \leq 0.10$ for interactions of defoliation by moisture). Asterisks denote mean separation among moisture treatments within the same defoliation treatment.

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Chapter 7. Synthesis

7.1. Compensatory Growth, Determinate Growth, and Rotational Grazing

Rangelands commonly consist of semiarid grasslands that have remained uncultivated because climatic and edaphic conditions are not conducive to 'more conventional' crop agriculture (Burke *et al*. 1994). Rangelands also encompass multiple-use areas (*i.e*., forest management and conservation lands) for which livestock grazing is a compatible land use. The dilemma commonly faced for North America rangelands is that, although these areas either evolved under large ungulate herbivory (*e.g*., bison) or have some capacity to sustain grazing, conventional grazing practices cannot emulate historical grazing regimes (McNaughton 1993). Factors such as water development, winter-feeding, fencing, and predator control all entail that current ranching practices differ greatly from the transhumance type grazing regimes of roving, gregarious herbivores. The subsequent dilemma for the range science profession is to understand the production limitations and potential of semiarid grasslands to sustain livestock production and provide other ecosystem services.

There is growing impetus among the ranching community to shift attention from livestock production to plant community composition and health. Within this more holistic framework, rotational grazing is commonly recognized as a means to maximize plant community productivity and range health (Savory

1999). Defoliation regimes commonly associated with rotational grazing (*i.e.*, high intensity defoliation at low frequency, or HILF) have clear plant community production benefits in relatively mesic grasslands, including pasture lands within the Aspen Parkland (De Bruijn and Bork 2010; De Bruijn *et al.* 2003; Donkor *et al.* 2003; Donkor *et al.* 2002), Tallgrass Prairie (Turner *et al.* 1993), and saltmarsh grasslands (Hik *et al.* 1991), presumably because herbage within these communities can sustain repeated heavy use and regrow vigorously. Indeed, a meta-analysis has shown that compensatory plant responses in graminoids are more common in high resource environments (Hawks and Sullivan 2001). Included among the differences between these areas and more arid rangelands is that pasturelands and more mesic rangelands consist predominantly of rhizomatous plants with high grazing tolerance and regrowth potential (Sims *et al.* 1978; Mack and Thompson 1982), although rhizomatous grasses also occur within semiarid grasslands where microsites of higher fertility exist (Derner and Briske 2001).

This thesis addressed the question of whether production potential of semiarid rangelands is constrained by plant morphophysiology. My hypothesis was that determinate growth characteristics in caespitose grasses would limit compensatory regrowth responses to defoliation, regardless of growing (moisture) conditions. This was tested by comparing growth responses of co-occuring and phylogenetically similar caespitose and rhizomatous grasses under varied clipping and watering treatments. However, a conundrum associated with this method was that results (growth responses) would invariably depend on the species, and even genotypes within species (Peterson 1962), selected for comparison. Moreover, grazing tolerance, which is largely determined by regrowth potential (Caldwell *et al*. 1981) and plant height (Peterson 1962, Detling and Painter 1983), is not solely a characteristic of plant growth form. A meta-analysis did find that, in general, bunchgrasses are less grazing tolerant (Milchunas and Lauenroth 1993). However, there are some very grazing tolerant bunchgrasses, albeit these are usually agronomic (*e.g*., *Bromus riparius, Agropyron cristatum*) or short-statured species (*e.g*., *Koeleria macrantha*). Likewise, not all rhizomatous grasses are grazing tolerant (e.g., *Pascopyrum. smithii*, see Chapter 3).

The definition of determinate growth used in this experiment represents growth that is decoupled from resource availability. Evidence suggests that xeriphytic plants do not have the same propensity to capitalize on fortuitous growing conditions by increasing growth (Knapp and Smith 2001), but mechanisms for this are not entirely clear. Growth involves cell division, differentiation, and enlargement. Cell division occurs only in meristematic regions, meaning that growth is largely controlled by meristem activity. Graminoids also grow by reproducing vegetatively and spawning another plant through the process of tillering. Growth in this experiment was largely quantified based on yield (biomass), but some other growth mechanisms were also assessed, including tiller population dynamics and individual tiller phytomer production. Determinate growth was hypothesized to constrain compensatory yielding for caespitose grasses.

Chapters 2 and 3 compared tiller population and yield dynamics among grasses of contrasting growth form and similar niches. Across these experiments, no consistent evidence for determinate growth in caespitose grasses was evident. In the greenhouse, the two agronomic grasses of contrasting growth form (*B. inermis* and *B. riparius*) and the two rhizomatous wheat grasses (*E. lanceolatus* and *P. smithii*) had compensatory yielding under HILF defoliation, such that yields under this defoliation treatment were largely similar to controls, or at least more favourable compared to HIHF defoliation, such as in the case of *P. smithii* (Chapter 2). However, this same growth response did not extend to *P. smithii* in the field (Chapter 3). Conversely, while the caespitose *H. comata* did not have compensatory growth responses to HILF defoliation in the greenhouse, it did so in the field (Chapter 2 vs. Chapter 3). Some authors contend that plants may display more innate growth characteristics in the greenhouse (Grime 2001), but these conflicting results further complicate identification of growth characteristics associated with plant growth form.

The only consistent evidence of determinate growth for a caespitose grass occurred in the field experiment where moisture addition failed to influence *H. comata* growth. More than doubling growing season moisture did not promote tillering, phytomer production, or plant yield in the caespitose *H. comata*, but did so in the rhizomatous *P. smithii* (Table 7-1, Figure 7-1 and 7-2; Chapter 3). Moreover, moisture addition also increased the cover of two dominant rhizomatous grasses, *P. smithii* and *Bouteloua gracilis*, within the plant community (Chapter 5).

Conversely, defoliation effects on growth responses were difficult to classify as determinate or indeterminate. For example, defoliation promoted individual tiller growth rates (Chapter 3) and seemingly promoted phytomer production (Chapter 5) for both *H. comata* and *P. smithii* in the field (Figure 7-1 and 7-2), which is a clear indeterminate compensatory growth response for both growth forms (Table 7-1). However, defoliation also reduced tiller numbers and, subsequently, plant yield, which is neither a clear determinate or indeterminate response (Table 7-1). This was especially pronounced in *P. smithii*, whereas *H. comata* showed compensatory yielding under HILF defoliation (Chapter 3), but this was likely due to tiller population persistence under this defoliation regime rather than any form of compensatory growth *per se* (Figure 7-1 and 7-2).

Consequently, rather than determinate growth constraining compensatory responses, compensatory regrowth appeared to be more a function of plant grazing tolerance. This was especially evident in the field experiment where yield dynamics largely reflected defoliation and moisture effects on tiller populations (Chapter 3). Consequently, the largest constraint on productivity in the field experiment was likely defoliation sensitivity in productive, canopy dominant midgrasses, such as *H. comata* and *P. smithii*, but especially the latter (Chapter 4 and 5). The second overarching constraint on compensatory responses appeared to be the limited growing season length. Both *P. smithii* and *H. comata* are cool season grasses that concentrate growth early in the growing season (Chapter 4). This entails that although recurrent growing season defoliation stimulated phytomer production in the latter portion of the summer, growth rates were so low that this contributed very little to overall yield and was further nullified by declining tiller populations (Chapter 3; Table 7-1).

These constraints impose two fundamental dilemmas for conventional grazing management. Rotational grazing strategies that use high animal densities to attain homogenous utilization likewise depend on plant regrowth for regrazing opportunities. However, limited compensatory regrowth, especially in grazing sensitive canopy dominant grasses and later in the growing season, entail that recovery periods necessary to maintain plant community productivity may exceed the growing season length (Bailey and Brown 2011). This nullifies any benefit of adopting rotational grazing for the purpose of promoting plant community productivity, and further validates the conventional management recommendation of conservative stocking and utilization (Holechek *et al*. 2004), at least within the Mixedgrass Prairie.

7.2. Plant Growth Under Defoliation: A Model

This study contributed to our understanding of how defoliation mediates plant growth, and the role meristems play in regulating growth. The conceptual model in Figure 7-3 illustrates the trade-offs in growth thought to be associated with defoliation, provided apical meristems remain intact. All growth originates from photosynthates (PHO) produced by the plant. The source of PHO for growth can come directly from photosynthesis or from stored resources in the crown of the plant. PHO can be used for storage, respiration, or growth. Growth can be allocated to roots, leaves (phytomers), or reproduction. Reproduction can occur through tillering or by producing an inflorescence. Given that defoliation eliminates photosynthesis if leaf material is lost, regrowth must occur from stored PHO. Given that respiration demand is lower (because of lost tissue), the majority of PHO is likely allocated to growth after respiration demands are met. Results from Chapter 2 suggest that defoliation compromises root growth, especially in *P. smithii* and *E. lanceolatus*. Moreover, reproductive tillers are vulnerable to defoliation given that apical meristems can be lost during floral induction. Consequently, PHO can be allocated to either phytomer production or tillering. However, mechanisms mediating whether regrowth occurs through tillering or phytomer production are not fully understood (Murphy and Briske 1992; Tomlinson and O'Connor 2004). Tillering is an inherently slower process than phytomers regrowing from an existing apical meristem. However, little is known about whether apical meristems in graminoids are determinate in the number of phytomers they produce. If so, this would necessitate plant regrowth from tillering. Moreover, reproductive tillers likely depend on tillering for regrowth given apical meristems are often lost to grazing and production of an inflorescence ends phytomer growth potential. Both phytomer production and tillering were important regrowth processes for both *H. comata* and *P. smithii* in this study (Chapter 3 and 6).

This conceptual model also illustrates the limitation of plants to persist under recurrent defoliation given that this compromises other important uses of photosynthate, such storage, root growth, and sexual reproduction. Consequently, defoliation may promote compensatory responses (at least in terms of shoot growth) in the short-term by altering resource allocation, but plant fitness may decline under sustained defoliation pressure. This would account for the general decrease in plant productivity under defoliation over time observed in this study, suggesting that defoliation has an accumulative effect. This could also account for the merit of rotational grazing systems that allow for periodic deferment of use on given pastures for an entire growing season, as this period may allow plant recovery and seed set.

7.3. An Alternative Paradigm

This study used controlled treatments to investigate plant and plant community responses to specific defoliation and moisture regimes. The benefit of this procedure is that specific mechanisms and hypotheses regarding plant responses could be investigated. However, interpreting results in the context of grazing management is tenuous at best given that emergent properties invariably play a role at larger spatial and temporal scales, especially given that rotational grazing may promote better overall spatial utilization, but at a potential cost to individual animal gains (Norton 1998). Future experiments should seek to better understand how grazing system imposed defoliation regimes affect long-term plant community and livestock productivity. Moreover, the role heterogeneous landscapes and livestock selectivity may play in maximizing livestock productivity and ecosystem services (*i.e.*, biodiversity) also warrants further research (Fuhlendorf and Engle 2001).

This study showed that compensatory regrowth potential is indeed greater in drier range sites dominated by more grazing tolerant (but less productive) forages. The dominant increaser grass promoted by defoliation in the Mixedgrass Prairie is *Bouteloua gracilis* (Chapter 5), which also happens to be a warm-season species. The presence of warm-season graminoids distinguishes Great Plains grasslands from those in the Great Basin, where bison were notably scarce (Mack and Thompson 1982). Warm-season graminoids are further hypothesized to be an important forage resource for bison later in the growing season when cool-season grasses lose quality. This indicates that compensatory responses and plant-animal synergies may be possible, but perhaps under overall lower plant community productivity within the Mixedgrass Prairie. Grazing lawns also appear to play an important role in plant-herbivore interactions (McNaughton 1984), although this phenomenon is generally undesirable with regards to range management. Graminoids that occupy these areas show unique adaptations to cope with herbivory (Detling and Painter 1983), and herbivores also benefit from having spatially concentrated, high quality forage produced later in the growing season. Consequently, it warrants consideration that perhaps maximizing plant community productivity and utilization (*i.e.*, homogeneity of grazing pressure) may not be the ultimate measures of grazing system efficacy. Future research should seek to better understanding evolutionary synergies between plants and grazing animals, and how grazing systems can capitalize on such synergies.

Table 7-1. Growth responses (increase [+], decrease [-], or no effect [0]) for *Pascopyrum smithii* and *Hesperostipa comata*, classified as determinate (D), indeterminate (I), or neither (?), under treatments of repeated growing season defoliation and moisture addition. Based on results from Chapter 3.

Growth Parameter	*P. smithii*				*H. comata*			
	Defoliation		Moisture		Defoliation		Moisture	
	Effect	Response	Effect	Response	Effect	Response	Effect	Response
Tiller Growth Rate	0 / (+)	D / I	(+)	I	(+)	I	0	D
Tiller Number	(-)	?	0 / (+)	D / I	0/(-)	?	0	D
Plant Yield	(-)	?	(+)	I	(+)/0/(-)	?	0	D

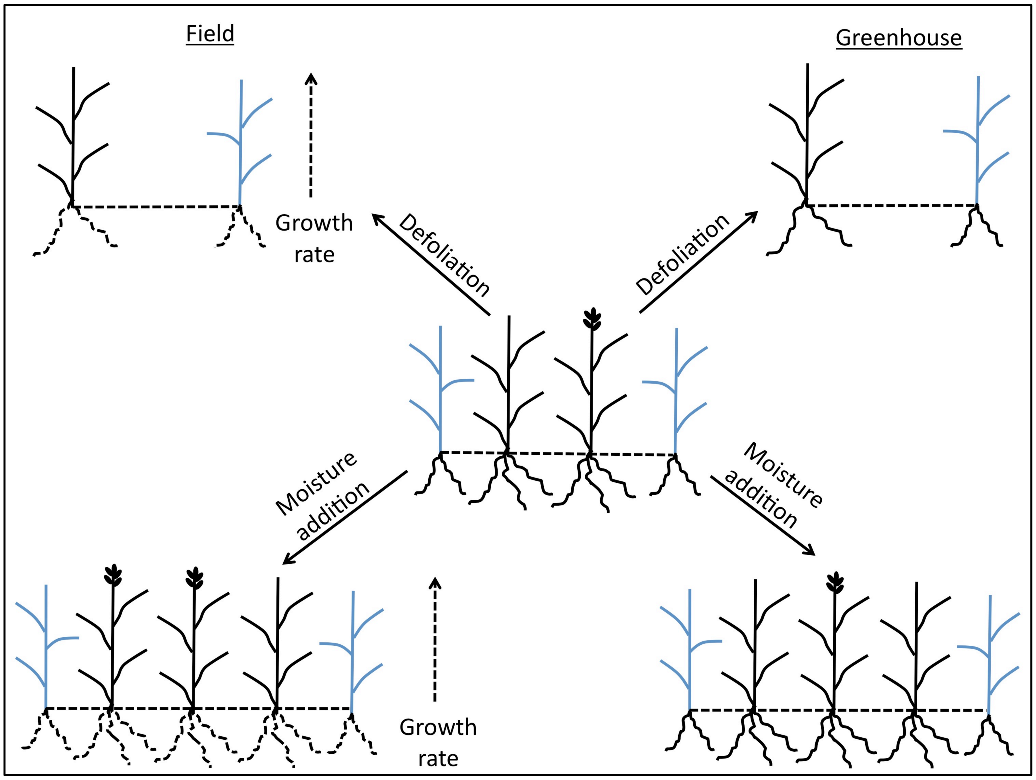

Figure 7-1. Defoliation (HILF) and moisture addition effects on *Pascopyrum smithii* genets in the field and greenhouse experiments. Roots were not measured in the field experiment.

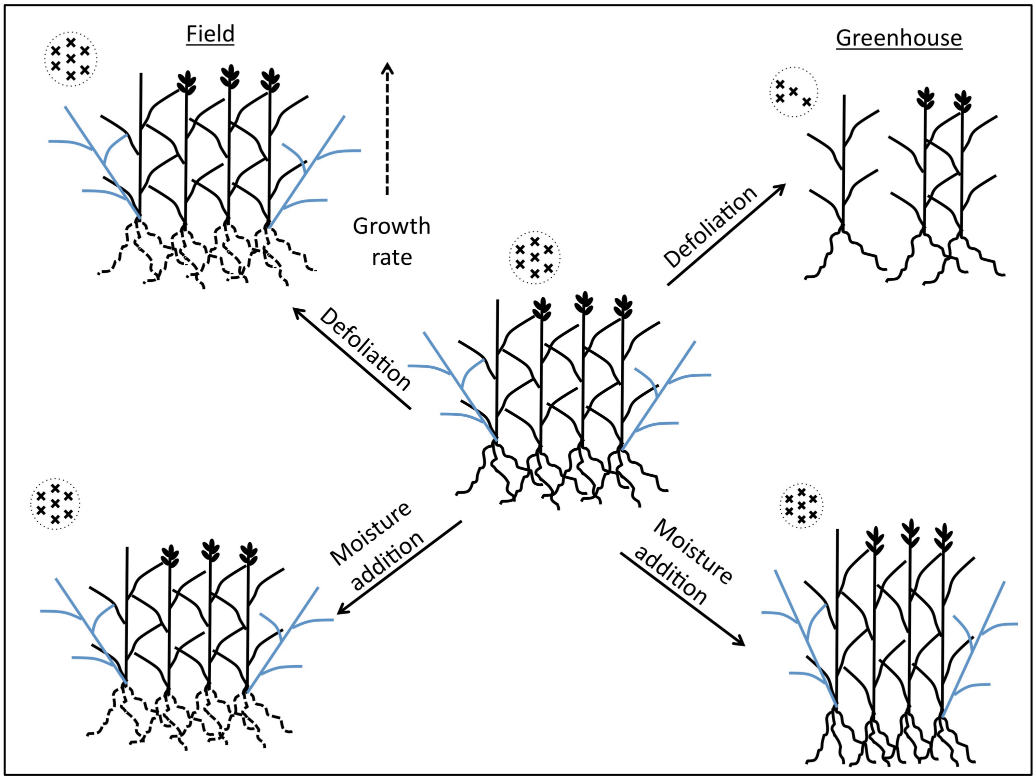

Figure 7-2. Defoliation (HILF) and moisture effects on *Hesperostipa comata* genets in the field and greenhouse experiments. Roots were not measured in the field experiment.

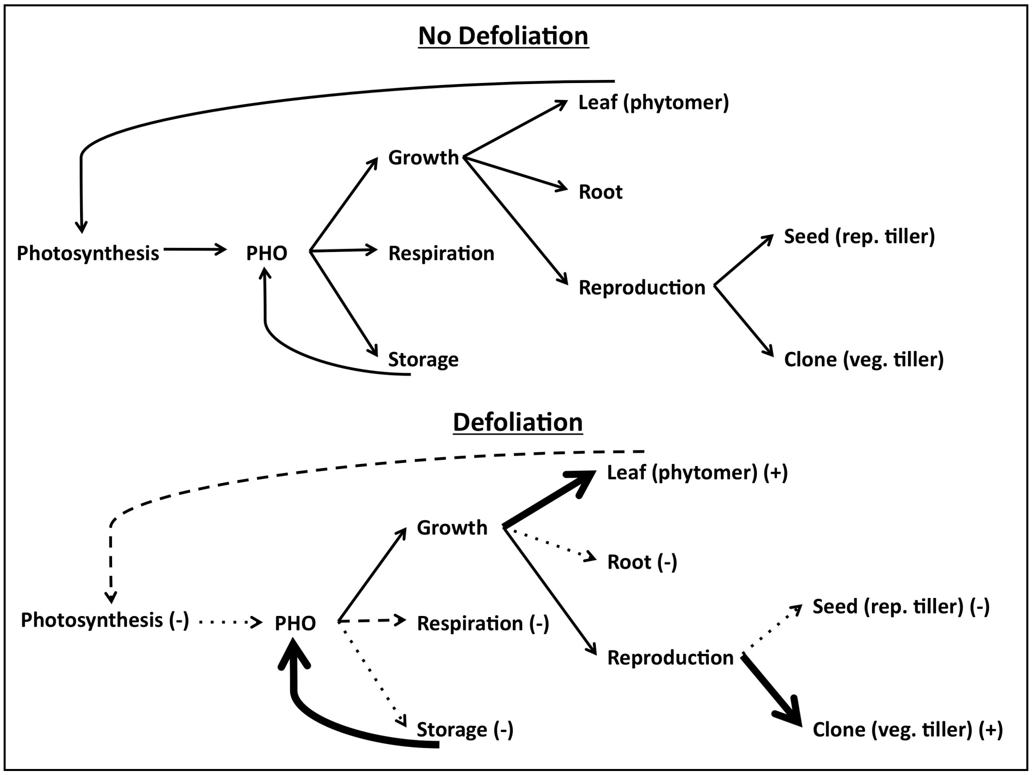

Figure 7-3. Conceptual model depicting theoretical effects of defoliation on photosynthate (PHO) allocation and growth priorities in graminoids. Thicker arrow lines denote an increase, dotted lines show a temporary cessation, and dashed lines show a temporary reduction followed by a resumption in allocation.

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