



Tiller dynamics of blue grama and western wheatgrass subjected to drought and grazing
by Erik Jason Eneboe

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in
Range Science

Montana State University

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Abstract:

The impacts of drought and grazing on tiller growth rates, axillary tiller emergence, tiller density, annual tiller replacement and aboveground net primary production were investigated on field-grown plants of western wheatgrass [*Pascopyrum smithii* Rydb. (Love)], and blue grama [*Bouteloua gracilis* (H.B.K.) Lag. ex Griffiths]. Response was determined by weekly measurements of 270 blue grama tillers and 329 western wheatgrass tillers in 1994 and 320 blue grama tillers and 341 western wheatgrass tillers in 1995. A growing season drought (from 19 May to 25 October 1994) was imposed on six 5 X 10 meter plots by a single automated rainout shelter while six adjacent plots received natural precipitation. Grazing treatments were grazed during and after drought, grazed during drought and ungrazed after drought, and ungrazed during and after drought. Plots were moderately grazed (45-55% utilization) in late May and late June in 1994 and 1995. Control plots received 28% below average precipitation in 1994 while drought plots received 70% below average precipitation. Yearly precipitation was 19% below average on all plots in 1995, but spring (March, April and May) precipitation was 20% above average. Tiller growth rates were analyzed using repeated measures ANOVA. Tiller replacement, axillary tiller emergence, and net primary production were analyzed using ANOVA. Tiller density was analyzed by ANOVA using initial tiller density as a covariate. Drought had minimal impacts on tiller relative and absolute growth rates of both species due in part to dry conditions on control plots. Drought did not affect ($p > .05$) tiller growth rates the year following drought. Moderate defoliation early in the growing season (28 May) increased ($p < .05$) tiller relative growth rates compared to ungrazed tillers for both species in both years of the study. Absolute and relative growth rates later in the growing season were not different ($p < .05$) from zero for both species in both years. Grazing increased ($p < .01$) axillary tiller emergence of both species compared to ungrazed tillers. However, axillary tiller emergence was 79% and 91% less ($p < .001$) under drought conditions for blue, grama and western wheatgrass, respectively. Axillary tiller emergence of western wheatgrass was similar ($p > .10$) between drought and grazing treatment the year following drought. Ungazed blue grama tillers exhibited lower ($p < .05$) axillary tiller emergence the year following drought compared to tillers that were grazed both years and only grazed during drought. Drought and grazing had no effect ($p > .05$) on tiller density or tiller replacement of both species. Net primary production of blue grama was not affected ($p > .30$) by drought or grazing in both years. However, net primary production of western wheatgrass was lower ($p < .05$) under drought conditions in both years of the study. It appears that moderate grazing in the Northern Great Plains during and after drought do not adversely affect tiller processes under the conditions of this study. These results also indicate that shortterm tiller dynamics may be regulated by factors other than drought or grazing.

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SUBJECTED TO DROUGHT AND GRAZING

by

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This thesis has been read by each member of the thesis committee and has been found to be satisfactory regarding content, English usage, format, citations, bibliographic style, and consistency, and is ready for submission to the College of Graduate Studies.

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Date

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ABSTRACT

The impacts of drought and grazing on tiller growth rates, axillary tiller emergence, tiller density, annual tiller replacement and aboveground net primary production were investigated on field-grown plants of western wheatgrass [*Pascopyrum smithii* Rydb. (Love)] and blue grama [*Bouteloua gracilis* (H.B.K.) Lag. ex Griffiths]. Response was determined by weekly measurements of 270 blue grama tillers and 329 western wheatgrass tillers in 1994 and 320 blue grama tillers and 341 western wheatgrass tillers in 1995. A growing season drought (from 19 May to 25 October 1994) was imposed on six 5 X 10 meter plots by a single automated rainout shelter while six adjacent plots received natural precipitation. Grazing treatments were grazed during and after drought, grazed during drought and ungrazed after drought, and ungrazed during and after drought. Plots were moderately grazed (45-55% utilization) in late May and late June in 1994 and 1995. Control plots received 28% below average precipitation in 1994 while drought plots received 70% below average precipitation. Yearly precipitation was 19% below average on all plots in 1995, but spring (March, April and May) precipitation was 20% above average. Tiller growth rates were analyzed using repeated measures ANOVA. Tiller replacement, axillary tiller emergence, and net primary production were analyzed using ANOVA. Tiller density was analyzed by ANOVA using initial tiller density as a covariate. Drought had minimal impacts on tiller relative and absolute growth rates of both species due in part to dry conditions on control plots. Drought did not affect ($p > .05$) tiller growth rates the year following drought. Moderate defoliation early in the growing season (28 May) increased ($p < .05$) tiller relative growth rates compared to ungrazed tillers for both species in both years of the study. Absolute and relative growth rates later in the growing season were not different ($p < .05$) from zero for both species in both years. Grazing increased ($p < .01$) axillary tiller emergence of both species compared to ungrazed tillers. However, axillary tiller emergence was 79% and 91% less ($p < .001$) under drought conditions for blue grama and western wheatgrass, respectively. Axillary tiller emergence of western wheatgrass was similar ($p > .10$) between drought and grazing treatment the year following drought. Ungrazed blue grama tillers exhibited lower ($p < .05$) axillary tiller emergence the year following drought compared to tillers that were grazed both years and only grazed during drought. Drought and grazing had no effect ($p > .05$) on tiller density or tiller replacement of both species. Net primary production of blue grama was not affected ($p > .30$) by drought or grazing in both years. However, net primary production of western wheatgrass was lower ($p < .05$) under drought conditions in both years of the study. It appears that moderate grazing in the Northern Great Plains during and after drought do not adversely affect tiller processes under the conditions of this study. These results also indicate that short-term tiller dynamics may be regulated by factors other than drought or grazing.

CHAPTER 1

INTRODUCTION

Grasslands of the Northern Great Plains encompass approximately 96 million hectares in the United States and Canada (Singh et al. 1983). This area extends from central Wyoming to southern Saskatchewan, bounded on the west by the Rocky Mountains and on the east by a line near the 97th meridian (Singh et al. 1983). A large portion of the plant communities within the Northern Great Plains are dominated by western wheatgrass and blue grama (Willms and Jefferson 1993, Lauenroth et al. 1994). Western wheatgrass (*Pascopyrum smithii*, Rydb.) is a cool season (C₃) grass and blue grama (*Bouteloua gracilis*, [H.B.K.] Lag. ex Griffiths) is a warm season (C₄) grass. In western North Dakota and eastern Montana these two grasses comprise approximately 40% and 60% of the aboveground biomass, respectively (Lauenroth and Whitman 1977, Karl et al. 1993). Lewis (1970) determined botanical composition of three different Northern Great Plains sites and found they consisted of 15% western wheatgrass and 17% blue grama. Therefore, these two grasses play major roles in the vegetational ecology of the Northern Great Plains.

North American bison (*Bison bison*) numbers may have exceeded 40 million (equal to 7.2 million animal units AU), on the Great Plains before European settlement (England and Devos 1969, Mack and Thompson 1982). Presently the Northern Great Plains livestock industry is heavily dependent on the native vegetation of the region supporting about 6.5 million AU (USDA Agri. Stat. 1993) and 450,000 AU (Willms and Jefferson 1993) in the United States and Canada, respectively. Therefore, herbivores have been involved in the ecology of the Northern Great Plains region in the past and will most likely be involved in the future.

As in most rangeland environments, periodic droughts are common in the Northern Great Plains region. In eastern Montana, Campbell (1936) predicted two or three years out of 10 would be drought years. Hurtt (1951) estimated droughts in Montana occur on average once every five years. Precipitation records for the 40 years period from 1944 to 1984, support Hurtt's (1951) estimate with droughts occurring in 21% of the years (Holechek et al. 1989).

Vegetation of the Northern Great Plains has evolved under periodic grazing and droughts. Both drought and grazing affect plant productivity, which increase with intensity of stress, such that plant sustainability may be impaired (Ludlow 1986). When defoliation occurs under drought conditions, which is a common case for rangeland grasses (Ludlow 1986), knowledge of how individual plants and plant communities persist becomes important.

One problem in designing research to quantify drought and grazing effects is the inability to include non-drought control plots in field drought studies. Past research that attempted to quantify drought and grazing impacts has primarily focused in two areas. First, research has involved vegetation responses of rangelands that have been grazed before, during, and after natural droughts (Ellison and Woolfolk 1937, Whitman et al. 1943, Hurtt 1951, Coupland 1958, Reed and Peterson 1961). In these studies grazing occurred before, during, and after droughts therefore interactions between water stress and defoliation are unclear due to the confounded treatments (i.e. drought and grazing occurred at the same time). Secondly, researchers have studied the combined effects of clipping and water stress on individual plants within greenhouses (Sosebee and Wiebe 1971, Mohammad et al. 1982). Greenhouses provide very controlled environments, but do not mimic plant responses *in situ*. Recently, controlled studies in naturally competing environments have been used to separate water stress and

defoliation effects at the individual plant level (Busso et al. 1989, 1990, Busso and Richards 1993, 1995).

Individual grass plants consist of an assemblage of tillers initiated from a single axillary bud of ontogenetically older tillers (Hyder 1972, Briske 1986, 1989, 1991). Following establishment, long term survival of perennial grass plants and plant populations in communities ultimately depend on growth, survival, recruitment and replacement of individual tillers (Richards et al. 1987, Olson and Richards 1988a, 1988b, 1988c, Bullock et al. 1994, Zhang and Romo 1995). However, quantitative studies on the impacts of grazing during and after drought on tiller population dynamics are lacking. In addition, the affect of rest (no grazing) following drought is not well documented.

The objectives of this study were to determine effects of grazing during and after a growing season drought on tiller growth rates (relative and absolute), axillary tiller emergence, tiller density, annual tiller replacement and net primary production of western wheatgrass and blue grama. These grass species were used in this study because of their economical and ecological importance in the Northern Great Plains.

CHAPTER 2

LITERATURE REVIEW

Introduction

This literature review will begin with an overview of the hierarchical levels of grasslands and then discuss some structural and functional attributes important to the Northern Great Plains to orient the reader to the ecosystem in which the study occurs. The review will then focus on three areas: 1) effects of drought on plants, 2) effects of grazing on plants and 3) combined effects of drought and grazing on plants. Emphasis will be on the rangelands of the Northern Great Plains and western wheatgrass and blue grama where information is available.

Hierarchical Levels of Grassland Vegetation

Grassland vegetation is organized as a series of hierarchical levels of atomic particles, molecules, cells, organs, tillers, individual plants, plant populations and plant communities that collectively effect the production and sustainability of grassland systems (Briske 1989). This is because organizational levels may respond to certain stresses in very dissimilar manners (Briske 1989). For example, grazing may increase plant density on the community level while reducing basal area on the individual plant level (Butler and Briske 1988). Thus, it is important to reorganize differences between these hierarchical levels to accurately evaluate vegetation dynamics.

Individual grass plants consist of an assemblage of tillers initiated from a single axillary bud of ontogenetically older tillers (Briske 1986, 1989, 1991, Hyder 1972). A tiller is defined as an

accumulation of successive phytomers differentiated from a single apical meristem (Briske 1986, 1989, 1991). Individual phytomers, which consist of a blade, sheath, node, internode, and axillary bud, form the basic unit of grass growth (Briske 1986, 1989, 1991, Hyder 1972). Tillers are generally annual plant structures, but can be produced during regrowth following grazing. For example, Olson and Richards (1988b) found that grazing of crested wheatgrass [*Agropyron desertorum* (Fisch. ex Link) Schult.] during internode elongation increased the growth of axillary tillers.

The processes involved in tiller initiation are unclear. Hypotheses vary as to whether the plant hormone auxin (IAA) directly or indirectly inhibit axillary tiller development (Murphy and Briske 1992). With direct inhibition hypotheses, it is believed the auxin produced in the apical meristem and young leaves directly inhibits bud outgrowth. On the other hand, the indirect hypotheses subscribes to the evidence suggesting that auxins produced in the apical meristem block the synthesis or utilization of cytokinin within axillary buds thereby inhibiting their growth. However, apical bud removal does not always promote tiller initiation in grasses (Murphy and Briske 1992, Richards et al. 1987). Murphy and Briske (1992) stated that environmental variables such as resource availability, radiation quality and competition may play primary roles in tiller initiation.

Longterm sustainability of individual plants and plant populations in communities ultimately depend on growth, survival, recruitment and replacement of individual tillers (Olson and Richards 1988a, 1988b, 1988c, Richards et al. 1987, Bullock et al. 1994). In the extreme case, if tiller recruitment is suspended for an interval equivalent to the longevity of

the most recently developed tillers, the plant would lose all meristematic potential and die (Briske 1991). In addition, Richards et al. (1987) found that the maintenance of crested wheatgrass was dependent upon the winter survival of fall produced tillers.

A plant grows by the gain and loss of parts. There have been many methods that try to quantify this relationship. Primary techniques in quantifying this relationship involves measuring changes in plant dry weight or biomass (Harper 1980). The major problem involved with this methods is that it is destructive and measurements on the same plot or plant cannot be made through time. Analysis of individual plants and plant parts (buds, leaves, tillers ect.) is non-destructive, so individual plants and plant parts can be followed over time (Harper 1980). The advantage of following individuals over time is that one knows the preexisting condition of that individual and can follow the fate of that individual over time. Responses to treatments such as drought and grazing can be judged on a variety of parameters such as tiller birth and death rate, leaf number, or tiller growth rates. Community analysis may indicate no differences in biomass due to a grazing treatment, but individual tillers within the pasture may have quite different tiller birth or growth rates. Studying the effect of drought and grazing at the tiller level will indicate mechanisms of how plants respond to these stresses.

Historical Perspective

Vegetation of the Northern Great Plains has evolved under interactions between grazing and periodic droughts. Prior to European settlement the Northern Great Plains was the home of nomadic Indian tribes and large numbers of bison, prairie dogs, elk, pronghorn, bighorn

sheep, and deer (Lauenroth et al. 1994). North American bison (*Bison bison*) numbers may have exceeded 40 million (72,000,000 animal units AU), of which most occupied the central Great Plains region (Mack and Thompson 1982, England and Devos 1969). In the 1800s settlers began reducing bison herds across the Great Plains, replacing them with domestic livestock (Lauenroth et al. 1994). In the 17 western states grazing livestock numbers peaked in the mid-1930s at 27 million AU (Chapline 1936). By 1943 following implementation of the Taylor Grazing Act, the rangelands of North and South Dakota, Nebraska, Wyoming and Montana supported about 5.9 million AU (Stoddard and Smith 1943). Presently the Northern Great Plains livestock industry is heavily dependent on the native vegetation of the region supporting about 6.5 million AU (USDA Agri. Stat. 1993) and 450,000 AU (Willms and Jefferson 1993) in the United States and Canada.

As in most rangeland environments, periodic droughts are common in the Northern Great Plains. A drought year is defined as 75% or less than the longterm average annual precipitation (Valentine 1990, Society for Range Management 1974). Reynolds (1954) estimates droughts occur at intervals of two to five years in southwestern Arizona. In eastern Montana, Campbell (1936) predicted two or three years out of 10 would be drought years. Hurtt (1951) estimated droughts in Montana occur on average once every five years. Precipitation records for the 40 years period from 1944 to 1984 support Hurtt's (1951) estimate with droughts occurring in 21% of the years (Holechek et al. 1989). Both drought and grazing affect plant productivity, which increase with intensity of stress, such that plant sustainability may be impaired (Ludlow 1986). Although other environmental factors are

important to plant productivity, this review will largely focus on how drought and grazing effect rangeland vegetation.

Northern Great Plains Structure and Function

Physiography and Soils

Grasslands of the Northern Great Plains encompass approximately 96 million hectares in the United States and Canada (Singh et al. 1983). Geographically this area extends from central Wyoming to southern Saskatchewan, bounded on the west by the Rocky Mountains and on the east by a line near the 97th meridian (Singh et al. 1983). This region includes western North and South Dakota, eastern Montana, northeastern Wyoming, northwestern Nebraska, southeastern Alberta and southern Saskatchewan (Holechek et al. 1989, Goetz 1987, Singh et al. 1983).

The principle soils associated with the Northern Great Plains are of the order Mollisol (Holechek et al. 1989, Goetz 1987, Singh et al. 1983). Mollisols are well-developed soils with thick, dark surface horizons high in organic matter and bases. Soils of the drier western portions of this region are Aridisols which are lower in organic matter but still show pedogenic horizons (Goetz 1987, Singh et al. 1983). Soil orders of Entisols and Alfisols also occur on limited areas of this region.

Climate

The climate of the Northern Great Plains is semiarid with a distinct north to south temperature gradient and west to east precipitation gradients. Southern regions of the Northern Great Plains have higher average annual temperatures (ave. 8-12°C) than the

northern regions (ave. 0°C) (Lauenroth et al. 1994, Singh et al. 1983). As a result of this temperature gradient, average frost-free period increases from approximately 100 days in the north to 140 days in the south (Holechek et al. 1989). Average annual precipitation on the Northern Great Plains increases from about 300mm in the west to 600-900mm in the east (Lauenroth et al. 1994, Goetz 1987). Seventy to eighty percent of the annual precipitation is received during the April through September growing season (Holechek et al. 1989, Goetz 1987, Singh et al. 1983, Lauenroth and Whitman 1977).

Primary Production

Lauenroth et al. (1994), Singh et al. (1983), Lauenroth and Whitman (1977) estimated annual aboveground net primary production (ANPP) on the Northern Great Plains to be about 3,000 kg/ha with peak standing crop occurring anywhere from late June to late July. However, vegetational production of the Northern Great Plains is highly variable from year to year. For example, in eastern Montana estimated ANPP varied from 1780 kg/ha in 1927 to 250 kg/ha in 1934 due to different amounts of precipitation (Campbell 1936). Sims and Singh (1978) reported below ground net primary production (BNPP) from three Northern Great Plains sites averaged 8,470 kg/ha while Lauenroth and Whitman (1977) estimate ranged from 9,310-12,210 kg/ha. Sims and Singh (1978) reported total net primary production (NPP) varied from 2,250-14,250 kg/ha within the Northern Great Plains region.

Differences in NPP between years and sites can be attributed to many factors, but precipitation is generally the most important factor. Reynolds (1954) in southwestern Arizona reported magnitude of rangeland forage production was primarily a function of precipitation. In this research between 1924 and 1950, annual precipitation ranged from 127-584mm and

ANPP ranged from 39-763 kg/ha. Similarly, Reed and Peterson (1961) reported that ANPP varied from 602 kg/ha in 1938 with 147mm of annual precipitation to 1690 kg/ha in 1944 with 370mm of annual precipitation. Likewise, Clarke et al. (1947) reported pre-drought (1932) ANPP averaged 410 kg/ha whereas after 2 drought years (1936) ANPP only averaged 183 kg/ha in southern Alberta and Saskatchewan. Sims et al. (1978) reported precipitation and evapotranspiration accounted for 50-70% of the variability of ANPP in the Great Plains while solar radiation and annual temperature accounted for 80-90% of the variability of BNPP. Sims and Singh (1978) found there was a linear relationship between increasing ANPP with increasing precipitation in ten western grasslands. On the other hand, there was a inverse relationship with increasing BNPP with decreasing mean annual temperature. Sims and Singh (1978) attributed 48% of the NPP variability to precipitation. Water is essential for plant life and is often the most limiting factor influencing plant productivity in arid and semiarid rangelands.

Rangeland plants are also affected by environmental factors such as temperature, light, atmosphere, nutrients, and fire during all phases of growth and development (Haferkamp 1987). Many of these factors can act either singly or in combination to affect plant productivity (Haferkamp 1987). Interactions between air temperature, soil temperature, the evaporative power of the atmosphere (Lauenroth and Whitman 1977), soil nutrients, temporal distribution of precipitation, water use efficiency (Willms and Jefferson 1993) and litter (Willms et al. 1993) have been reported to influence NPP, but to a lesser degree than annual precipitation.

Plants maintain life through an energy storing process called photosynthesis. In the presence of sunlight glucose is formed when water and carbon dioxide (CO₂) are fixed in the chlorophyll (Olson and Lacey 1988). Factors affecting this process are extremely important. Sunlight and CO₂ in the atmosphere are not influenced by management and are seldom limiting for rangeland plants (Holechek et al. 1989). However light may become limiting if shading occurs causing a decline in photosynthetic rates (Harper 1977). Water is essential for photosynthesis and is often the most limiting factor.

Vallentine (1989) reported that soil nutrient deficiencies (primarily nitrogen) reduce forage production. For example, fertilization rates of 45 and 88 kg/ha of nitrogen increased above ground biomass of blue grama 64 and 103% above controls, respectively (Reed and Dwyer 1971). Although forage production on semiarid rangelands can often be increased 50-100% by the application of fertilizer, it still may not be an economically viable practice (Vallentine 1989). Greatest benefits from rangeland fertilization can be expected in areas receiving greater than 635mm of annual precipitation (Vallentine 1989).

Ambient air temperature is also important to plant growth. Optimum growth (dry matter increase of relative growth rate) temperatures for C₃ and C₄ grasses are approximately 20-25° and 30-35°C, respectively (Haferkamp 1987). Bokhari and Singh (1974) found a decline in the growth rate of western wheatgrass (C₃) at temperatures of 30°C compared to temperatures of 13° and 24°C. Stubbendieck and Burzlaff (1969) reported that higher soil temperature (>10°C) resulted in four week earlier tiller development of blue grama compared to cooler soil temperatures (<10°C). Total biomass of western wheatgrass was two times greater when grown at cooler temperatures, 20°C compared to 35°C and total biomass of

blue grama was 3 times greater when grown at warmer temperatures, 35°C compared to 20°C (Kemp and Williams 1980). In addition, Frank and Ries (1990) stated that morphological development was primarily controlled by temperature whereas forage production was a function of available soil water and nitrogen.

Fire is also a natural factor on rangelands and probably no range site has developed without being influenced by burning (Vallentine 1989). Fire can effect plants directly through heat damage or indirectly by reducing competition and releasing resources such as water, nutrients and light (Haferkamp 1987). Plant response following fire varies among species and depends on plant morphology and phenological stage of development when burned (Higgins et al. 1989, Vallentine 1989). Recovery following fire will ultimately be influenced by growing point location and amount of meristematic tissue lost during fire. Busso et al. (1993) found that burning *Stipa tenuis* Phil. decreased total axillary bud numbers 82%, but burned plants had similar tiller numbers and biomass compared to unburned plants after the growing season.

The botanical composition of the Northern Great Plains is best described as mixed grass prairie because it contains short, mid, and tall grasses as well as both cool and warm season grasses (Lauenroth et al. 1994, Holechek et al. 1989). Short and midgrasses predominate this region, with the tall grasses being limited to more mesic sites (Lauenroth et al. 1994). The majority of the mid-height grasses are cool season (C₃ photosynthetic pathway) grasses which initiate growth early in the spring, while the shortgrasses are typically warm season (C₄ photosynthetic pathway) species which initiate growth in late spring to early summer (Lauenroth et al. 1994, Singh et al. 1983).

A large portion of the Northern Great Plains vegetation are dominated by western wheatgrass and blue grama (Lauenroth et al. 1994, Wilms and Jefferson 1993). Western wheatgrass is a cool season (C_3) midgrass and blue grama is a warm season (C_4) shortgrass. In western North Dakota and eastern Montana these two grasses comprise 40% and 60% of the aboveground biomass, respectively (Lauenroth and Whitman 1977, Karl et al. 1993). Lewis (1970) determined botanical composition of three different Northern Great Plains sites and found they consisted of 15% western wheatgrass and 17% blue grama. Therefore, these two grasses play major roles in the ecology of the Northern Great Plains.

Western wheatgrass and blue grama maintain themselves in the community primarily by vegetative reproduction (Gould and Shaw 1983, Stubbendieck et al. 1992) and rarely through seedling establishment (Karl et al 1993). Karl et al. (1993) found that 95% of all seedlings found on a eastern Montana mixed grass prairie site were annual plants and perennial grass seedlings were few (<5%). Seedling establishment and survival of grass species have been shown to be reduced by adult neighbors (Aguilera and Lauenroth 1993, Samuel and Hart 1992). Samuel and Hart (1992) found that after transplanting four-week-old blue grama seedlings into bare soil openings with diameters of 0,4,8, and 16 cm seedling survival was 42,79,88 and 92% following the first growing season. Greater seedling survival of blue grama under optimum soil water conditions was found only when bare soil openings were 30cm in diameter compared to smaller openings (Aguilera and Lauenroth 1993). Samuel and Hart (1992) concluded for successful seedling establishment of blue grama in existing swards, large artificial or natural openings must be created. Prolonged drought conditions may create such large openings bare soil openings. Therefore, seedlings may play important roles in the

recovery of grass plants following droughts provided conditions are optimum (Weaver and Albertson 1944).

Impacts of Drought

Each plant species has different strategies for coping with drought. Ludlow (1986) defined three coping strategies. Annual plants exhibit an "escape" strategy in which they germinate early in the growing season, grow rapidly, flower, seed, and die before soil moisture is depleted. Some perennial plants exhibit an "avoidance" strategy where deep roots or early dormancy help plants endure dry periods. However a majority of plants possess a "tolerance" strategy which includes osmotic and stomate adjustments, reduced leaf area and continued root growth during drought. In this section effects of drought on physiological processes, individual plants and plant communities will be discussed.

Physiological and Individual Plant Responses.

Water is essential for plant life and consists of 80-95% of the mass of growing plant tissue (Taiz and Zeiger 1991, Hsiao et al. 1985). Root systems extract water from the soil and transport it to the leaves through the xylem where it is then used for photosynthesis. The mechanism for water transport within plants include bulk flow, diffusion and osmosis. Bulk flow moves water from a high pressure area to a low pressure area. Diffusion moves water from regions of high water concentration (low solute concentration) to low water concentration (high solute concentration). Osmosis is the process by which water moves between plant cells, across membranes via concentration gradients. These gradients depend on the chemical potential of water, or water potential (Taiz and Zeiger 1991).

Water potential is directly related to osmotic pressure (cell solute concentration) and cell turgor pressure (cell pressure) (Taiz and Zeiger 1991). This relationship may be written as:

$$\text{water potential} = \text{cell turgor pressure} - \text{osmotic pressure.}$$

Water in plant moves from regions of high water potentials to regions of low water potentials (Taiz and Zeiger 1991). Water movement and water balance within plants is maintained by changing water potential.

Adjustments in osmotic pressure is one way that plants change water potential to cope with water stress. Solute accumulation in leaf tissue of water stressed plants has been reported for *Eustachys paspaloides*, an east African C₄ grass and sorghum (*Sorghum bicolor* [L.] Moench) (Toft et al. 1987, Jones and Turner 1978). Solute accumulation by cells results in a decreased water potential and a greater attraction for water, while maintaining cell turgor pressure. Maintenance of turgor pressure enables the continuation of cell elongation at lower water potentials. However, osmotic adjustments may only be a short-term drought strategy. Toft et al. (1987) found water stressed plants delayed permanent wilting for 24 hours through osmotic adjustment compared to non-stressed plants. Therefore, osmotic adjustment was not a mechanism for reducing the effects of long-term drought.

Leaf extension rates are very sensitive to water deficits (Busso and Richards 1993, Hsiao et al. 1985, Ong et al. 1985, Boyer 1970). Busso and Richards (1993) found leaf extension rates of crested wheatgrass were 70% lower in drought stressed plants compared to non-stressed plants. Drying of soils from -3.0 to -4.0 bars reduced elongation 10% and elongation completely stopped when leaf water potential reached -6.5 bars (Hsiao et al. 1970). Reduced leaf growth under water stress has been attributed primarily to a reduction in cell turgor

pressure associated with a reduced leaf water potential (Boyer 1968). Boyer (1970) found it was not possible to obtain leaf tissue growth with a water potential of zero. Leaf growth of sunflower (*Helianthus annuus* L.) occurred only when leaf water potentials were above -3.5 bars and therefore require a minimum turgor of -6.5 bars for enlargement (Boyer 1968).

Lower growth rates under water stress will ultimately affect plant morphological characteristics (Busso 1988). For example, leaf number (Reed and Peterson 1961), leaf size (Nesmith and Richie 1992, Hogenboom et al. 1987), plant height (Chung and Trlica 1980, Reed and Peterson 1961, Coupland 1958, Ellison and Woolfolk 1937), flowering stalks, (Coupland 1958) and tiller numbers (Haferkamp et al. 1992) are all reduced by water deficits. Tiller numbers of northern wheatgrass [*Agropyron dasystachyum* (Hook.) Scribn.] were found to be positively correlated with soil water ($r=.77$) (Zhang and Romo 1995). After three consecutive years of imposed drought, axillary bud numbers of crested wheatgrass and bluebunch wheatgrass (*Agropyron spicatum* (Pursh) Scribn & Smith) plants were lowest under the drought treatments compared to higher moisture levels (Busso et al. 1989). This reduces the bud pool for future tiller generations which reduces competitive abilities and ultimately lowers the plant's longterm success in the community (Zhang and Romo 1995, Busso 1988, Busso et al. 1989). Low water supply may cause a carbohydrate build up in plant tissues (Busso et al. 1990) because water stress restricts growth relatively more than photosynthesis (Boyer 1970). For example, Chung and Trlica (1980) found greater ^{14}C translocation to roots in water stressed blue grama. Busso et al. (1990) found that after two years of imposed drought, crested wheatgrass and bluebunch wheatgrass had seven times higher total nonstructural carbohydrate (TNC) pools in the roots and crowns compared to

non-stressed plants. These results indicate that regrowth of these species would not be limited by carbohydrate availability and may exhibit rapid spring growth following elevation from drought (Busso 1988). Wisiol (1979) found that water stressed blue grama had concentrations of proline 90 times higher than controls. Proline has also been reported to increase 67 and 43% in crested and western wheatgrass, respectively, in response to water stress compared to controls (Frank 1994). Proline is a protein that is closely related to new growth through its role as a precursor of hydroxyproline, essential for cell wall protein (Wisiol 1979). Increased concentrations in proline may also serve as a readily available pool of nitrogen for recovering plants following drought.

Net photosynthesis (P_n) has been shown to recover from leaf water potentials as low as -92 bars in *Panicum maximum* var. *trichoglume* (Ludlow and Ng. 1976). However, time needed to regain pre-stress levels of photosynthesis increased with increasing water stress. Wolf and Parish (1982) reported tillers of tall fescue (*Festuca arundinacea* Schreb.) exposed to short-term (<28 hours), severe water stress (wilted) displayed rapid leaf elongation immediately after watering. With longer periods of water stress (>28 hours) elongation was suspended for at least two hours (Wolf and Parish 1982). Hogenboom et al. (1987) reported water stressed soybean [*Glycine max* (L.) Merr. 'braxton'] shoot growth was greater than plants grown without water stress (.025 vs. .020 m/day) after rewatering drought stressed plants. Thus, no longterm differences were observed between drought and nondrought stressed plants. Sala and Lauenroth (1982) reported 5mm or less rainfall events increased leaf water potentials and stomatal conductance of field grown blue grama within 12 hours and this activity lasted for two days. They concluded that small rainfall events are ecologically

important for the survival of this plant. But despite increased physiological activity and leaf elongation after rewatering drought stressed plants, final biomass was still less than that for unstressed plants (Chung and Trlica 1980).

Population and Community Level Responses.

The earliest response of vegetation during drought is reduced forage production (Weaver and Albertson 1944) although other changes in the vegetation characteristics have been documented. Gibbens and Beck (1988) reported that after 40 years of data collection, drought appears to have tremendous influences upon perennial grass basal area and vulnerability and recovery of grass species depend on plants ability the tolerate drought.

Between 1934 and 1935 the Northern Great Plains region recieved about 25% of the average annual precipitation thereby causing extensive changes in the vegetation (Reed and Peterson 1961). Drought reduced total basal area from 28% in 1933 to 2% in 1937 in south eastern Montana (Reed and Peterson 1961) and from 30% in 1933 to 13% in 1936 in western North Dakota (Whitman et al. 1943) in response to drought. Sanberg bluegrass (*Poa secunda* Presl) was the only perennial grass species in southeastern Montana that increased in basal area during the drought, increasing from 75% (Hurtt 1951) to 400% (Reed and Peterson 1961) depending upon study site. Sandbergs bluegrass uses the "avoidance" drought strategy by early spring completion of the growth cycle, before extreme soil moisture depletion (Olson 1982). Between 1933 and 1937 western wheatgrass and blue grama basal area declined 90 and 95%, respectively (Hurtt 1951). In addition, density of western wheatgrass and blue grama declined 74 and 75% in southeast Montana (Ellison and Woolfolk 1937) and 67 and 64% in western North Dakota (Whitman et al. 1943), respectively.

Vegetation of the Northern Great Plains are continually changing with climatic variables. During extended dry periods species composition shifts towards shortgrass (blue grama) by eliminating the midgrass component. For example, cover of midgrasses were decreased to near zero, however shortgrasses were more drought tolerant and tended to dominated during the 1930s drought (Newbauer et al. 1980, White et al. 1978, Coupland 1958). In contrast, species composition shifts toward midgrass domination with less shortgrass cover when rainfall is above average (Newbauer et al. 1980, White et al. 1978, Coupland 1958). For example, above average precipitation caused total plant basal area to increase 23% in southern Canada between 1940-1950 (Coupland 1958) and 61% during 1963-1976 in southeastern Montana (Newbauer et al. 1980). Newbauer et al. (1980) found that species composition on silty, sandy and thin hilly range sites, shifted from 16% midgrass [western wheatgrass, needleandthread (*Stipa comata* Trin. & Rupr.)], prairie junegrass (*Koeleria pyramidata* Lam. Beauv.), 71% shortgrass [blue grama and threadleaf sedge (*Carex filifolia* Nutt.)] in 1936 to 30% midgrass/53% shortgrass in 1976 in response to 13 years of above average rainfall. Western wheatgrass composition has been documented to increase with increasing precipitation (Coupland 1958, Newbauer et al. 1980).

Shifts in species composition can be attributed to the difference in drought tolerance between C₃ and C₄ grasses. Warm season (C₄) grasses (i.e. blue grama) have evolved under arid environments and are more efficient in photosynthesizing during drought than C₃ grasses (Gould and Shaw 1993). Warm season grasses can store CO₂ in the bundle sheath cells at night. This allows the plant to photosynthesize during the day at the high levels of CO₂ while keeping the stomates closed. Stomate closure during the day minimizes water loss through

transpiration. This is a fundamental reason why C₄ shortgrasses may dominate during drought periods and the C₃ midgrasses decrease. Therefore, continual changes in vegetation of the Northern Great Plains can be expected in plant communities as the precipitation changes (Olson et al. 1985).

Most plant species suffer during drought. One year of favorable precipitation is generally not enough to restore the vegetation to predrought conditions (Ellison and Woolfolk 1937). Reed and Peterson (1961) reported that recovery of western wheatgrass and blue grama to predrought conditions following the 1930s drought was not complete within eight years. On the other hand, Whitman et al. (1943) reported blue grama recovered to predrought conditions in 2-3 years whereas western wheatgrass completely recovered in 6 years after the severe drought conditions of the 1930s. Recovery rate following drought depends upon: predrought conditions of vegetation (vigor), degree of depletion of vegetation during drought; plant species remaining, dust burial damage, grazing intensity before, during and after drought, and the amount and distribution of precipitation following drought (Coupland 1958).

Impacts of Herbivory

Physiological and Individual Plant Response

Defoliation results in the loss of photosynthetic tissue which alters a plant's ability to produce photosynthate. Available evidence indicates that when an individual leaf blade is removed, net photosynthetic rates (P_n) per unit of intact area of the damaged leaf is decreased. Detling et al. (1979a) reported simulated grasshopper grazing (25% leaf removal)

of western wheatgrass decreased P_n 66%. However, undamaged leaves on defoliated plants showed increased P_n . When 50-75% of western wheatgrass tillers were removed by clipping, P_n of remaining undamaged leaves averaged 25-35% greater than leaves of the same age in undamaged control plant (Painter and Detling 1981, Detling and Painter 1983). Caldwell et al. (1981) observed leaf blades on regrowing tillers of defoliated plants had greater photosynthetic capacities than leaf blades growing on undefoliated plants. In spite of apparent compensatory photosynthesis, enhanced plant performance following grazing is questionable (Detling 1987). Nowak and Caldwell (1984) reported that compensatory photosynthesis was greatest in the two oldest leaves at the time of defoliation. These leaves contributed only a small portion of the photosynthetic area, therefore contribution to total carbon assimilation was rather small.

To understand defoliation effects on primary production, it is important to consider P_n of whole growing plants (Detling 1987). Detling et al. (1979b) measured the P_n of the entire shoot systems of defoliated and undefoliated blue gamma plants. They found mean P_n per unit of leaf area of defoliated plants was reduced by 60% immediately following defoliation. However, three days after defoliation, mean P_n rates on regrowing defoliated plants had exceeded that of non-defoliated plants by 21% and remained higher for at least 10 days. Detling (1987) stated initial declines in P_n following defoliation were probably due to reductions in individual leaf P_n rates and increased proportion of less efficient photosynthetic structures (i.e. high stem:leaf) while increased P_n rates 3-4 days following defoliation are probably due to increased photosynthesis of remaining undamaged tissue and a increase in leaf to stem ratio.

Reece et al. (1988) found that under short duration grazing, tiller number per plant increased 65% for blue grama and needleandthread. Zhang and Romo (1995) reported defoliation of northern wheatgrass enhanced tillering 71% and survival compared to controls. In contrast however, most of the recent literature indicates that defoliation generally decreases tillering in perennial grasses (Murphy and Briske 1992). Olson and Richards (1988c) reported that tiller replacement was inversely related to grazing intensity. Stroud et al. (1985) reported that clipping western wheatgrass to 2-5cm heights 4 times during the growing season, decreased tiller density 57%, while controls increased 28%. Tiller numbers have also been reported to decrease under heavy defoliation for little bluestem (Bulter and Briske 1988). Biweekly defoliations of pinegrass (*Calamagrostis rubescens* Buckl.) to 5, 10, and 15cm stubble heights decreased tiller density 95, 55, and 25% compared to controls, respectively (Stout et al. 1980).

Grazing tolerant plants may have the ability to rapidly produce more tillers in response to defoliation. For example, when crested and bluebunch wheatgrass plants were clipped to 5-7 cm heights, grazing tolerant crested wheatgrass produced 18 times more tillers than the grazing sensitive bluebunch wheatgrass (Mueller and Richards 1986). Although species produced more tillers when grazed, tiller replacement on heavily grazed crested wheatgrass was inadequate for plant maintenance, particularly those grazed during or after internode elongation (Olson and Richards 1988a).

Tillers are frequently produced within 2-3 weeks after defoliation (Olson and Richards 1988b, Richards et al. 1988) and the rate of tillering depends on many variables. For example, Olson and Richards (1989a) showed heavy grazing of crested wheatgrass before internode

elongation seldom affected tiller replacement, while grazing during or after internode elongation increased over winter mortality of fall produced tillers and reduced the number and height of replacement tillers. Two and six week intervals of defoliation of northern wheatgrass in south-central Saskatchewan had little influence of tiller survival, but initiating defoliation near the time of tiller emergence reduced survival whereas delaying defoliation until August increased tiller survival (Zhang and Romo 1995). Enriched red light at the base of undefoliated dallisgrass (*Paspalum dilatatum* Poir.) increased tiller numbers three times compared to those with no supplemental red light (Deregibus et al. 1985). In contrast, defoliation reduced tiller recruitment 88% with or without enriched red light at the base of little bluestem plants (Murphy and Briske 1994). Tiller recruitment appears to be regulated in a density dependent manner minimizing the overproduction of tillers within clones (Murphy and Briske 1994). The complexity of mechanisms regulating axillary bud growth and the large number of potential intervening factors (e.g. environmental variables, species-specific responses, stage of development, frequency and intensity of defoliation) minimize the likelihood of consistent tillering responses to defoliation between species (Briske and Richards 1994).

Defoliation may be more appropriately viewed as a means of altering the timing or season of tiller recruitment (Murphy and Briske 1992). For example, Bullock et al. (1994) found heavy summer grazing of *Agrostis stolonifera* and *Lolium peretene* did not affect tiller density but increased tiller turnover by higher tiller birth and death rates. This "flush" of tillers following grazing may reduce maximum tiller recruitment in defoliated plants relative to periods of maximum recruitment in undefoliated plants (Bulter and Briske 1992). In addition,

increased tiller recruitment following spring grazing of crested wheatgrass did not contribute to tiller recruitment the following season due to greater tiller mortality in grazed plants than in ungrazed plants (Olson and Richards 1988a). Therefore, in spite of a brief period of increased recruitment immediately following defoliation, grazed plants may not produce greater number of tillers than undefoliated plants when evaluated over one or more growing seasons (Briske and Richards 1994).

Changing tiller populations affect photosynthate production in grazed plants which influences above and belowground biomass production. Plant response to defoliation may depend on the timing, frequency, and amount removed during a grazing event. Grazing has been shown to increase plant production compared to ungrazed plants. Shoot weights were 66% and 29% greater than controls for heavy and moderate clipping, respectively at the end of an 80 day growing period (Bokhari and Singh 1974). This study was conducted in a green house under ideal growing conditions.

End of season blue grama tiller weights under short duration grazing (3.8 AU/ha) were shown to decrease 26% compared to ungrazed tillers (Reece et al. 1988). Stout et al. (1980) found that light, moderate and heavy clipping of pinegrass within three British Columbia Douglas fir (*Pseudotsuga menziesii*) zones on average decreased final biomass 55% compared to controls because tiller height were 16% shorter than controls. In comparing continuous grazing to uniform clipping, Stroud et al. (1985) reported that two years of continuous grazing treatment did not affect herbage production of western wheatgrass, but under uniform extreme clipping decreased 67% compared to controls.

Root production also generally decreases with increasing grazing intensity. Richards (1984) found that root growth length of grazing tolerant crested wheatgrass was 50% that of intact plants. Belowground biomass of western wheatgrass decreased as herbage removal increased after two years of simulated grazing (Stroud et al. 1985). Ingham and Detling (1984) found that western wheatgrass and little bluestem [*Schizachyrium scoparium* (Michx.) Nash] BNPP was 50-60% lower on more heavily grazed sites. Increased intensity of defoliation resulted in reduced root biomass of both western wheatgrass and blue grama (Santos and Trlica 1978). Ingham and Detling (1984) concluded that reduced root production following grazing was due to less aboveground photosynthetic area and less proportion of photosynthate going to the roots. However, root production has been reported to be unaffected or increased in response to grazing; Buwai and Trlica (1977) reported that undefoliated blue grama and western wheatgrass had the same root weights as did plants heavily defoliated.

Recovery

Following defoliation, plants must rapidly reestablish above ground tissue to maintain themselves in the community. Traditional views of plant regrowth were that carbohydrates stored in the roots were the primary sources of carbon following regrowth, however this hypothesis has been discounted. Richards and Caldwell (1985) quantified the amount of carbon supplied to regrowth from storage organs compared to current photosynthesis of crested and bluebunch wheatgrass. They found that crested wheatgrass produced more regrowth than bluebunch wheatgrass but the differences in regrowth were not correlated with non-structural carbohydrate concentration, total pools or the amount of carbohydrates.

utilized during regrowth. Current photosynthesis supplied 89-99% of the carbon used for regrowth and utilization of carbon reserves exceeded utilization of photosynthesis only for 2-5 days. Bokhari (1977) found that carbohydrates stored in roots of western wheatgrass were utilized for regrowth following clipping until aboveground tissue was reestablished in about 10 days. Even when regrowth potential was reduced by loss of apical meristems, utilization of current photosynthesis during regrowth immediately exceeded utilization of stored carbon sources (Richards and Caldwell 1985). Carbohydrate reserves rarely limit regrowth and should be thought of as a short-term buffer to "jump start" regrowth (Richards and Caldwell 1985). Richards and Caldwell (1985) concluded that meristematic limitations were the dominant control in shoot regrowth in crested and bluebunch wheatgrass.

Allocation of photosynthetic products within grasses is altered by defoliation (Briske 1991, Briske and Richards 1994). Generally, grazing tolerant plants have flexible carbon allocation and utilize more of their current photosynthesis products for the synthesis of new shoots following defoliation (Briske and Richards 1994, Briske 1991, Ingham and Detling 1984, Richards 1984). Detling et al. (1980) reported that 40% of the new growth of undefoliated blue gama plants were in the roots and crowns, while only 20% of the new growth of defoliated plants were in the roots and crowns. Relatively more resource allocation to shoot systems and curtailed root growth in crested wheatgrass resulted in three to five times the photosynthetic surfaces compared to bluebunch wheatgrass, which continued root growth (Caldwell et al. 1981).

Inter-tiller resource allocation following defoliation is a potential mechanism of herbivory tolerance by facilitating tiller survival and rapid reestablishment of photosynthetic surfaces

(Briske and Richards 1994). Resource import rates from attached undefoliated tillers were increased following partial tiller defoliation (Welker et al. 1987). Resource import may not represent an absolute increase because defoliation reduces the total resource requirement by decreasing shoot mass and total carbohydrate sink size. Modifications in resource allocation were controlled by the relative size of sinks (Briske and Richards 1994). For example, apical meristems and young leaves exhibit large sinks compared to roots, sheath and stems (Briske and Richards 1994). Consequently, if defoliation removes the predominant shoot sinks (apical and intercalary meristems), resources are allocated to smaller sinks (roots, sheaths and stems).

Replacement of photosynthetic surfaces following grazing is largely a function of the number, source and location of meristems following defoliation (Briske 1991). The basal position of the apical meristem, as exhibited by culmless grasses (e.g. blue grama), limit the removal of growing points by grazing animals (Hyder 1972). On the other hand, culmed grasses (e.g. western wheatgrass) elevate growing points above the soil surface and therefore can be easily removed by grazing animals (Hyder 1972). Culmed grasses growth is similar to culmless grasses at first in that a number of leaves reach maturity before internode elongation (Hyder 1972). Leaves can be removed without stopping leaf regrowth before internode elongation begins, at the time of floral induction. When apical meristems are elevated they become susceptible to removal by grazing during internode elongation. Leaf replacement and additional growth after apical meristem removal originates from axillary buds which produce new shoots (Hyder 1972). This may explain why Santos and Trlica (1978) found that

increased frequency of clipping decreased aboveground production of western wheatgrass, but had little effect on blue grama in a greenhouse experiment.

Growth will occur most rapidly from intercalary meristems, followed by newly formed leaf primordia and least rapidly from newly initiated axillary buds (Hyder 1972, Briske 1986). When existing meristems are removed by grazing, leaf replacement must originate from axillary buds of grazed tillers (Briske 1992). Tillering ensures perennation of rangeland plants by providing a meristematic source for the production of subsequent tillers in the spring or when existing meristems are removed by grazing (Briske 1993).

Phenological stage at the time of defoliation plays an important role in the recovery of plants. Olson and Richards (1988b) reported that relative tiller growth rates of crested wheatgrass tussocks grazed before internode elongation were greater than ungrazed tussocks. However, tussocks grazed during and after internode elongation decreased tiller relative growth rates compared to ungrazed tussocks (Olson and Richards 1988b). Miller et al. (1990) reported that during five growing seasons the amount of regrowth of crested wheatgrass produced by summer dormancy was 64% less for plants clipped during apical meristem elevation compared to plants clipped in the vegetative stage. On the other hand, defoliation has been reported to increase plant performance above that of undefoliated plants. Bokhari and Singh (1974) reported that clipped western wheatgrass shoots continued to grow throughout the 80 day experiment while unclipped shoots stopped growth after 50 days in a greenhouse study. Growth rates were greatest with moderate clipping (10cm height) and slowest with no clipping (Bokhari and Singh 1974).

Overcompensation of plant processes (i.e. such as P_n or biomass production) following grazing has been documented. However, insufficient data are available to support the conclusion that it is widely occurring in grassland ecosystems (Briske and Richards 1994). Belsky (1986) reviewed 48 studies referencing aboveground production in response to grazing and found that 34 documented a decrease in production, 5 reported no change and 9 reported increase production. It is possible that plants partially compensate for lost tissue. Partial compensation implies that plant productivity is not suppressed in direct proportion to frequency and intensity of defoliation (McNaughton 1983), but only infrequently increase total growth beyond that of undefoliated plants (Briske and Richards 1994). In fact, Idaho fescue (*Festuca idahoensis* Elmer) plants exposed to full competition with extreme clipping treatments, even under complete protection from or defoliation for five years, still produced less the two-thirds than biomass of controls (Mueggler 1975).

Population and Community Level Responses

The effects of grazing on NPP of ten western United States grasslands were unaffected (Sims et al. 1978) and increased an average of 10% (Sims and Singh 1978). In addition, Smoliak et al. (1972) reported that belowground plant biomass was 21,086 and 29,465 kg/ha on ungrazed and grazed pasture in southern Alberta, respectively. Root response to defoliation can be very different between species and does not always decrease root growth. For example, Richards (1984) found that root growth of bluebunch wheatgrass was not affected by grazing during a 9 day regrowth period. Root response following defoliation may very well be a function of resource allocation within a particular plant.

Vogel and Van Dyne (1966) found neither moderate grazing (35% removal) nor complete protection from grazing caused any changes in basal cover of grasses, sedges, forbs, litter and bare soil during a four year study in the Northern Great Plains. Living plant cover on protected areas changed from 13.1% in 1953 to 12.5% in 1957 and on grazed areas from 12.1% to 12.4%. Hofman and Ries (1989) reported no changes in live plant basal area classes between 1982 and 1988 (30% in grazed and 32.5% in ungrazed areas).

On a Northern Great Plains site in Wyoming, botanical composition did not differ between light and heavy grazing after six years (Hart et al. 1988). Changes in species composition with grazing in the Northern Great Plains are generally of a greater magnitude than on the shortgrass steppe, although change may be slower than in the more productive tallgrass types (Lauenroth et al. 1994). The shortgrass component usually increases with grazing and decreases without grazing (Lauenroth et al. 1994). Thurow et al. (1988) reported that after 6 years of continuously, heavy stocked (4.6 ha/AU) pastures in the Edwards Plateau region of Texas, midgrass cover was eliminated whereas midgrasses basal area increased in continuously, moderately stocked (8.1 ha/AU) pastures. In a four year enclosure in western North Dakota, Smoliak et al. (1972) reported that basal area of blue grama increased with increased grazing intensity (.3% ungrazed, 3.6% heavy) whereas basal area of western wheatgrass and needleandthread decreased (1.3% ungrazed, .7% heavy and 2.2% ungrazed, .5% heavy) with increasing grazing pressure. Brand and Goetz (1986) reported the major differences between grazing enclosures protected for 40 years and adjacent grazed areas (40-50% utilization) was species composition. The production of blue

grama was lower on ungrazed pastures, but mid and tallgrasses were more dominant in only one of the four exclosures.

Changes in ANPP of the Northern Great Plains in response to grazing are generally negative or not significant (Lauenroth et al. 1994). After four years of grazing, Hofman and Ries (1988) observed 31% and Vogel and Van Dyne (1966) observed 12% greater production on protected areas. Six to eight years of heavy grazing at 65% removal reduced production 37% in South Dakota and nine years of heavy grazing (65%) reduced forage production 13% in North Dakota, compared to ungrazed sites (Sims and Singh 1978). Brand and Goetz (1986) reported greater production in protected areas in southwestern North Dakota in only one of four different sites after 40 years of 45% utilization of the above ground primary production. Lacey and Van Poolen (1981) reviewed 12 field studies of moderately grazed (40 to 60% removal of current years growth) and ungrazed rangelands in the western United States and found 68% higher standing crop on sites protected from livestock grazing.

Plants grow in communities where they compete with neighboring plants for resources. Neighbor plant removal 60 cm around Idaho fescue plants increased herbage production three-fold and flowering stocks four-fold (Mueggler 1970). Olson and Richards (1989) found that elimination of competing vegetation one meter in diameter around crested wheatgrass increased the size of individual tillers and stimulated spring tiller production two fold. Competition with neighboring plants will determine the degree individual plants are able to recover from external factors like drought, grazing and fire (Caldwell 1984) Meuggler (1972) demonstrated this very clearly for the grazing intolerant species bluebunch wheatgrass.

The effects of extreme defoliation at a time when this species is sensitive to grazing could be more than offset by eliminating competing vegetation. Unclipped plants subjected to competing vegetation produced less herbage and had reduced flowering stocks compared to plants subjected to extreme clipping in the absence of competing vegetation. Mueggler (1972) stated that it may be competition, not removal of plant parts that limits plant recovery following grazing.

Changing environmental conditions may provide enhanced growing conditions for one plant over another in grazed systems (Haferkamp 1987). For example, soils beneath crested wheatgrass plants defoliated in the boot stage were consistently wetter than soils under undefoliated plants (Miller et al. 1990). The reduction in soil water depletion resulting from clipping was attributed to reduced leaf area removal and growth (Caldwell et al. 1981, Richards 1984). Delayed soil moisture depletion may increase the period of availability of active plant growth, but generally at the end of the growing season soil water is similar between grazed and ungrazed pastures (Miller et al. 1990, Wraith et al. 1987).

Competitive ability may constrain growth to an equal or greater extent than the direct effects of defoliation (Briske and Richards 1994). For example, if grazing increases the availability of soil water, a competitive advantage would be gained by ungrazed plants. These studies indicate the importance of plant-plant competition and thus greatly influences recovery rates following disturbances. Misleading information can arise when extrapolation of defoliation research is conducted in the absence of natural competitive environments.

Interaction Effects of Drought and Grazing

Available data indicates that precipitation overrides grazing influences. Dwyer et al. 1984, Reed and Peterson (1961), Hurtt (1951), Coupland (1958), Clarke et al. (1947), Whitman et al. (1943), Ellison and Woolfolk (1937) stated that major trends in the vegetation characteristics of the Northern Great Plains are determined by major changes in precipitation and that changes in these major trends are influenced by grazing intensity. Hurtt (1951) found six of the Northern Great Plains most dominant range species declined 90% in abundance due to drought regardless of the stocking rates. In addition, drought has been shown to reduce cover 57% (Whitman et al. 1943), density 75% (Ellison and Woolfolk 1937), and basal area 93% (Reed and Peterson 1961) of dominant Northern Great Plains plants.

Many studies have documented plant community changes in response to drought and grazing (Weaver and Albertson 1936, Ellison and Woolfolk 1937, Whitman et al. 1943, Hurtt 1951, Albertson et al. 1957, Coupland 1958, Reed and Peterson 1961, Newbauer et al. 1980, Olson 1982, Olson et al. 1985). They primarily focused on reductions of basal area, forage production or other aggregate measures of plant responses. These studies did not address individual plant recovery from these stresses. Mohammad et al. (1982) examined the effects of water stress and defoliation on individual crested wheatgrass and russian wildrye (*Elymus junceus* Fisch) plants and found heavy defoliation (80%) and high water stress (1.8% soil moisture) resulted in a 100% death and no regrowth of either species in a greenhouse experiment. Although, greenhouse experiments using individual plants were very controlled

and limited external variables, plants were not in natural competing environments and thus interpretation of results to *in situ* situations are limited.

A central problem in natural systems is that the effects of drought and grazing are usually confounded. For example, many times overgrazing accompanies drought because of the reduced forage production (Ludlow 1986). Busso and Richards (1993) found leaf extension rates of crested and bluebunch wheatgrass were lowest under the combined effects of water stress and clipping compared to higher water levels and that plants defoliated under water stress did not regrow. Busso et al. (1989) also found that the number of axillary buds on tillers of the above species to decrease one year in the water stressed and defoliated plants compared to water stressed undefoliated plants.

Interactions between drought and grazing after drought periods is largely unknown. Whitman et al. (1943) reported Northern Great Plains vegetation recovered to predrought conditions in about 8 years. However, it is unclear if the above recovery period was due to drought alone or the reduced stocking rate following drought. Ganskopp and Bedell (1981) found that a severe one-year drought (49% of average) in eastern Oregon, reduced growth and available forage of Idaho fescue, bluebunch wheatgrass, crested wheatgrass and Thurber needlegrass (*Stipa thurberiana* Piper), but did not have as much effect on these grasses as previous levels of grazing. However, in this study (Ganskopp and Bedell 1981) effects of drought on these grasses were not possible to assess since no predrought measurements were made for comparison.

After drought, individual plant recovery may be limited by decrease tiller emergence (Zhang andromo 1995), decreased axillary bud banks for future tiller production (Busso et

al. 1989), reduced growth rates (Busso and Richards 1989), or enhanced by increased total nonstructural carbohydrates concentrations in drought stressed plants (Busso et al. 1990). Quantitative studies on the effects of grazing during and after drought recovery rates in controlled studies set in natural systems are lacking.

There is no question that defoliation before, during, and after drought conditions has pronounced effects on vegetation. However, it is less clear if vegetational responses are due to grazing during, after, or both during and after. It may be possible that grazing during drought has less effects on rangeland vegetation compared to grazing both during and after drought. Therefore, questions regarding how grazing during and following drought affect recovery and sustainability of the Northern Great Plains vegetation, merits further investigation. Furthermore, the immediate effects of drought and grazing and how these stresses interact to effect recovery of western wheatgrass and blue grama tillers on the Northern Great Plains region is unknown.

CHAPTER 3

METHODS

Study Area

Research was conducted on the Fort Keogh Livestock and Range Research Laboratory near Miles City, Montana (46°19'45"N 105°49'45"W). The area is representative of the semi-arid mixed grass prairie of the Northern Great Plains. Native vegetation on the 22,500-ha research station is a grama-needlegrass-wheatgrass (*Bouteloua-Stipa-Agropyron*) mix (Kuchler 1964). Long-term annual precipitation averages 356 mm with about 60-70% received during the mid-April through mid-September growing season (NOAA 1994). Temperatures may exceed 38°C during summer and decrease to -40°C during winter. The average frost-free period is 150 days.

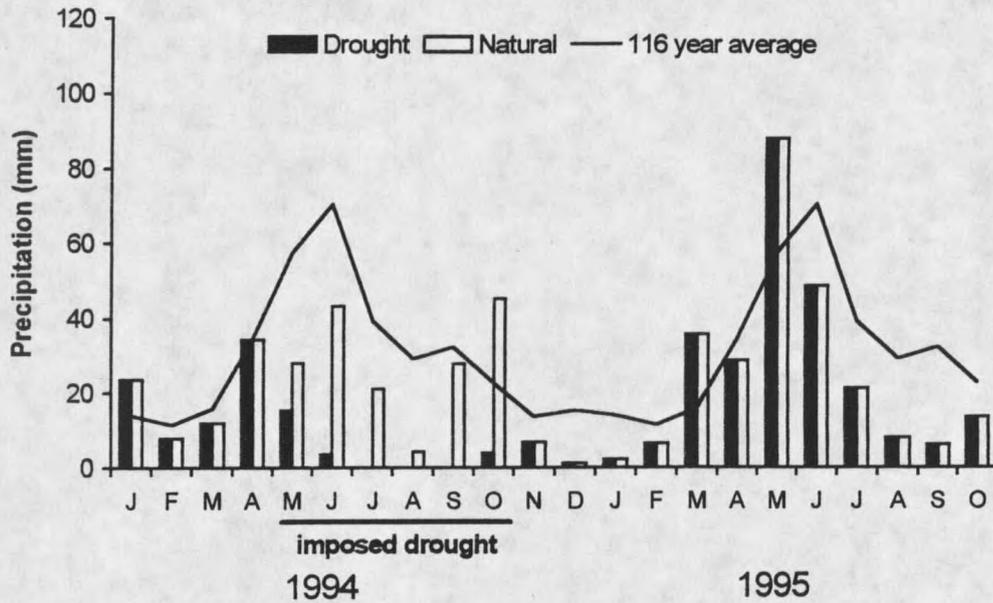
The experiment was conducted during the 1994 and 1995 growing seasons on native rangeland that had not been grazed two years prior to the study. Precipitation in the area was 30% (530 mm) above average the year before the study. The study site was located on a toe slope position, silty range site and in fair range condition (SCS). The soils are very deep, well-drained, fine, montmorillonitic, frigid Aridic Ustochrepts. Vegetation at the site was dominated by blue grama (40-45% by weight) and western wheatgrass (30-35% by weight).

Design and Treatments

A completely randomized split-plot design was used in which precipitation regime was whole-plot and grazing was the sub-plot. Drought and natural precipitation treatments were imposed on twelve 5 X 10 m plots (6 for each precipitation treatment). A rainout-shelter (ROS) was constructed over six plots to impose a one-year severe growing season drought. The ROS automatically covered the drought plots whenever a sensor was moistened by precipitation from 19 May to 25 October (1994). Monthly precipitation and distribution of rainfall events during the study are reported in Figures 1 and 2. Control plots (natural precipitation) received 260 mm of precipitation in 1994 which was 28% below average for the area. Drought treatments received 110 mm of precipitation in 1994 which was 70% below average. Yearly precipitation in 1995 was 290 mm (19% below average). Although precipitation in 1995 was below average, rainfall in March, April, and May was 20% above average.

One of three grazing treatments, replicated once per whole-plot, were randomly applied to each plot. Grazing treatments were: 1) grazed during drought (1994) and grazed after drought (1995, GG), 2) grazed during drought (1994) and ungrazed after drought (1995, GU) and, 3) ungrazed during drought (1995) and ungrazed after drought (1995, UU). Plots were moderately grazed (45-55% utilization) on 30 May in 1994 and 1995 and 28 June in 1994 and 3 July in 1995 (Fig. 3.). Plots were defoliated by six ewes (*Ovis aries*) with twin lambs at side.

a.



b.

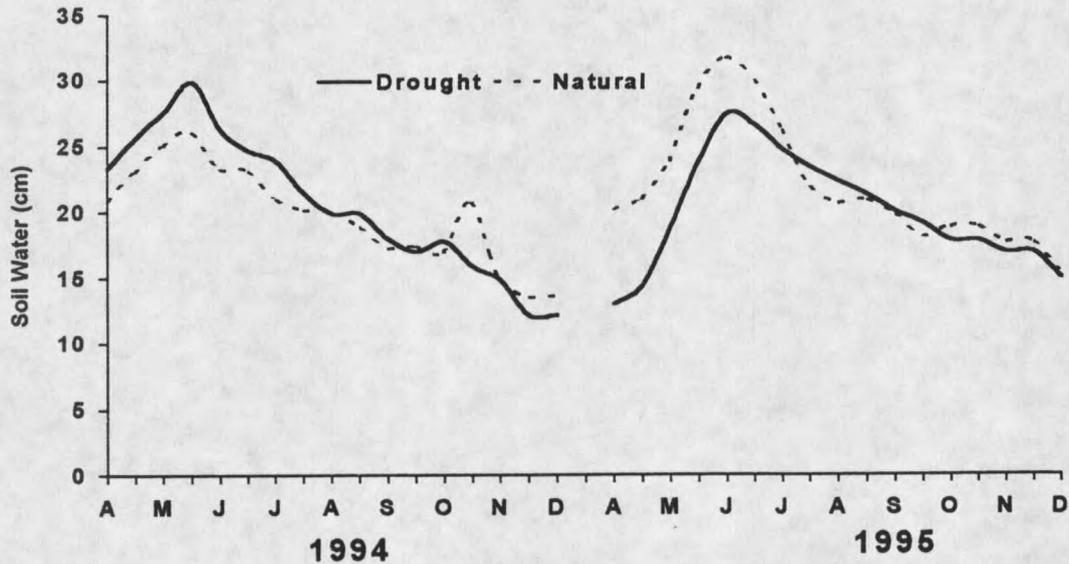
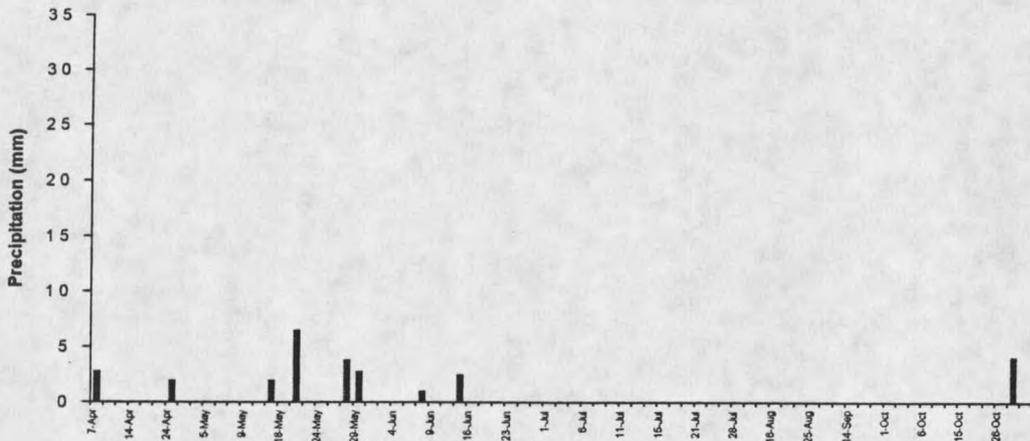
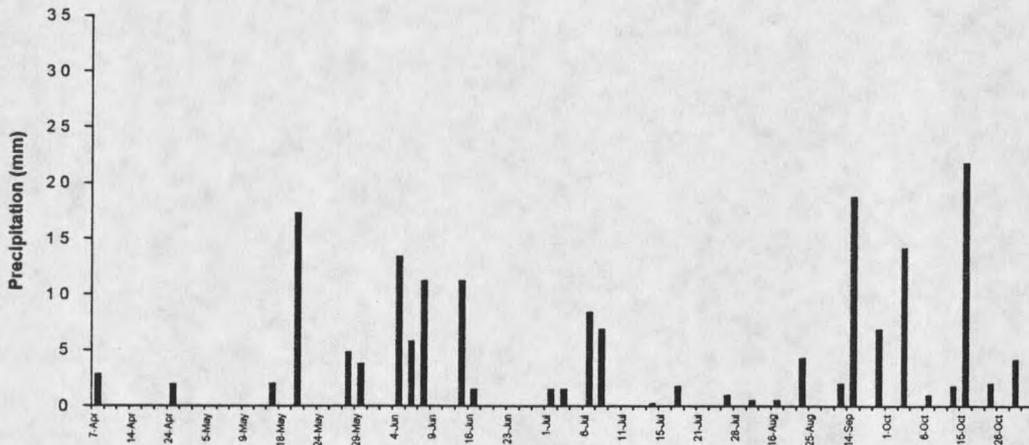


Figure 1. Monthly precipitation from January 1994 to October 1995 on drought imposed plots, natural precipitation plots, and 116 year average in Miles City, Mt. Drought was imposed from 19 May to 7 October 1994 (a). Centimeters of soil water for drought and natural precipitation treatments from April to December in 1994 and 1995 (b).

a.



b.



c.

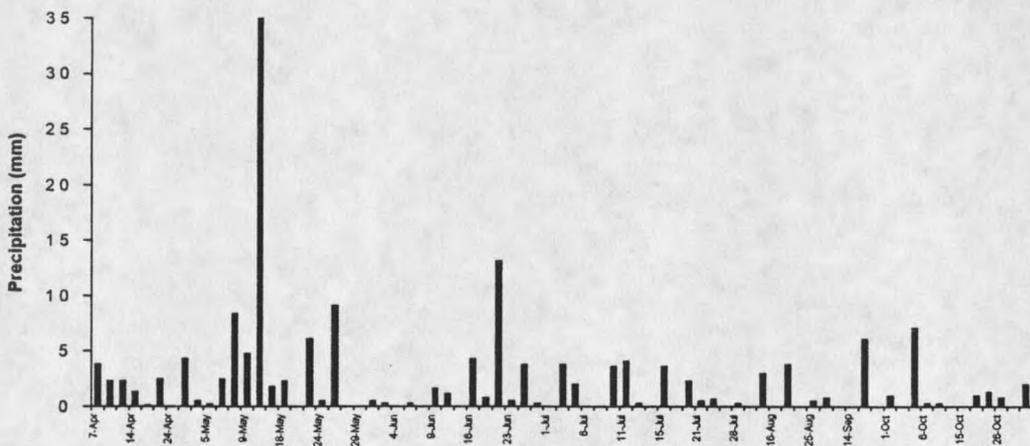


Figure 2. Growing season distribution of precipitation events on drought imposed plots in 1994 (a), natural precipitation plots in 1994 (b), and all plots the year following drought in 1995 (c).

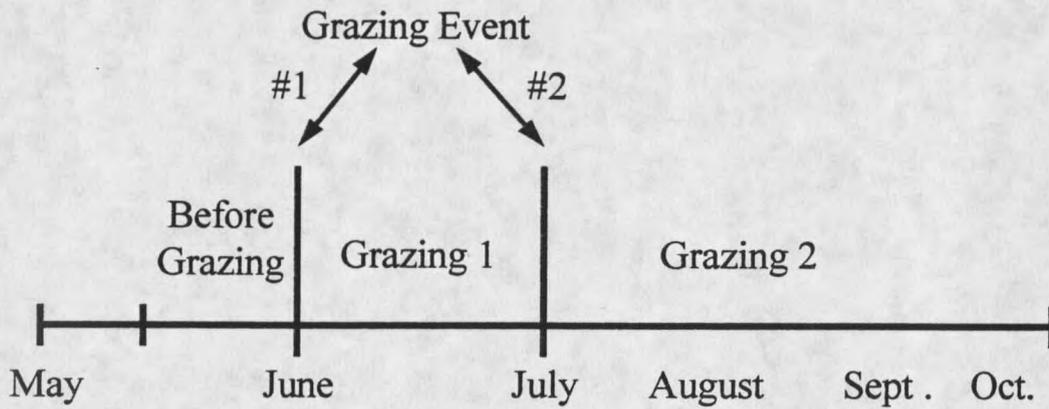


Figure 3. Time line of grazing event during the 1994 and 1995 growing seasons. Grazing events occurred on 30 May and 28 June in 1994. Grazing events occurred on 30 May and 3 July in 1995. Before grazing was the last two weeks in May. Grazing 1 was the month of June. Grazing 2 was the months of July, August, September and October.

Tiller Marking

Six permanent 14 X 18 cm quadrats per plot were randomly established within mixed blue grama and western wheatgrass communities. Random locations were determined by throwing a ring over the shoulder. Quadrats had to be in areas not previously sampled before, at least 50 cm away from the plot edge, and at least 5 tillers of blue grama and of western wheatgrass had to be present. Quadrats were permanently marked by driving two 15 cm spikes into the ground, one in the lower left and one upper right corner when facing north. The lower left nail head was painted white to establish 00,00 for marked tiller location. If a marked tiller, at anytime during the growing season, produced axillary tillers, they were marked with black colored wire rings and evaluated the same as a primary tiller. The same quadrats were used for the duration of the research.

Within each quadrat five representative western wheatgrass and blue grama tillers exhibiting green growth were selected for tiller measurements. Tillers selected were interspersed throughout the quadrat as much as possible. Colored wire rings were used to permanently mark tillers by placed them around the base of each tiller at the soil surface. For each species within a quadrat, one ring color was used to reduce the possibility of tiller misidentification. A new set of tillers were remarked, in the same manner described above, in 1995.

Tiller Measurements

Weekly measurments (17 weeks 1994, 14 weeks 1995) were taken on 270 blue grama tillers and 329 western wheatgrass tillers in 1994 and 320 blue grama tillers and 341 western

wheatgrass tillers in 1995. Tiller measurements started in mid-May and continued weekly through August with additional fall readings taken to incorporate any autumn growth. Information gathered on an individual tiller during each visit included: height, phenology, number of leaves, axillary tillering and tiller senescence.

Measuring tillers nondestructively prevented direct estimates of cumulative biomass through time. Height measurements were converted to biomass by developing height-weight relationships of tillers adjacent to the plots. Tusler (1993) described the method used. For each species, tillers were measured, clipped at the soil surface and bundled together with other tillers of the same height (± 1 cm). Five bundles per species representing the range of heights for those tillers found in the experimental plots were collected before each grazing event. Individual bundles containing 5 western wheatgrass and 10 blue grama tillers were placed in plastic bags, transported to the laboratory and immediately cut into segments. Tiller bundles were cut into segments of 1 and 3cm in length, from the base upward, for blue grama and western wheatgrass, respectively. Each segment was placed into a numbered bag beginning with #1, which was closest to the soil surface. All segments were then dried at 60°C for 48 hours. Individual segments were removed from the dryer and immediately weighed to the nearest .0001 g. Height and weight were then regressed to develop equations (Table 1).

Tiller relative growth rates ($\text{g g}^{-1} \text{d}^{-1}$) were calculated according to Radford (1967) as:

$$\text{RGR} = (\log_e W_{t+1} - \log_e W_t) * I^{-1}$$

where W was tiller weight (g), t was initial time (d), and I was the time increment (d). Tiller absolute growth rates (g d^{-1}) were calculated according to Radford (1967) as:

$$\text{AGR} = (W_{t+1} - W_t) * I^{-1}$$

	1994		1995	
	<u>equation</u>	<u>r²</u>	<u>equation</u>	<u>r²</u>
Blue Grama	$y = -.019 + .0047x$.84	$y = -.021 + .0045x$.85
Western Wheatgrass	$y = -.031 + .0084x$.80	$y = -.077 + .0100x$.88

Table 1. Regression equations used to convert tiller height measurements (x) to tiller weight (y) for blue grama and western wheatgrass.

were W was tiller weight (g), t was initial time (d), and I was the time increment (d).

Axillary tillering was defined as any marked tiller that produced additional (secondary) tillers within the growing season. Axillary tillering represents the proportion of marked tillers that produced at least one secondary tiller.

Density of western wheatgrass was determined by counting the number of live tillers within each quadrat. Because of the "mat-like" growth form of blue grama, density was determined by counting the number of tiller within a 5.75 cm² circular plot. Circular plots were randomly located within a quarter of the quadrat. Density was measured 24 May in 1994 and 1995.

Tiller replacement was defined as the ability of tillers to replace themselves from one spring to the next. Replacement represents the proportion of marked tillers that replaced themselves following one year of treatments. Only one year of data on density and tiller replacement were collected.

Standing crop inside 10 randomly located 250 cm² quadrats per plot was harvested monthly by species. Samples were oven dried at 60°C, separated into live and dead components and then weighed. Aboveground net primary production (ANPP) was calculated for blue grama and western wheatgrass by summing all positive increments in standing crop from April to November (Singh et al. 1975).

Data Analysis

Relative and absolute tiller growth rates were analyzed using a univariate repeated measures analysis of variance (ANOVA). Growth rates were analyzed using average growth

rates within three distinct periods (see Fig. 1). These periods included: 1) before grazing (1994, 1995 n=2 weeks); 2) after grazing event one (1994 n=4 weeks, 1995 n=5 weeks); and 3) after grazing event two (1994 n=8 weeks, 1995 n=4 weeks). Generally, before grazing was the last two weeks in May, after grazing event #1 was the month of June and, after grazing event #2 was July, August, September and October. Two-way ANOVA was used to determine the effects of drought and grazing on percent axillary tillering and percent tiller replacement. Tiller growth rates, axillary tiller emergence, and tiller replacement are reported for tillers that were grazed during both grazing events (e.g. grazed twice). Because initial tiller density varied between plots before treatments were imposed, ANOVA using initial tiller density as a covariate was used to determine changes in tiller densities between drought and grazing treatments. Means were separated by a priori linear contrasts and were considered to be significantly different when $p < .05$. Individual plots were the experimental units for all analyses.

The experimental design has logistical limitations for the drought treatments. In the case of the rainout shelter, cost precluded classical treatment replication. Hurlbert stated (1984, p.199):

...when the cost of replication is very great, experiments involving unreplicated treatments may also be the only or best option.

The drought treatment was not replicated therefore, any tests on the effects of drought using ANOVA could be considered invalid. However, the use of a single rainout shelter to test the effects of drought is common throughout the literature (Busso 1988, Busso et al. 1989, Busso et al. 1990, Frank and Ries 1990, Nesmith and Richie 1992, Busso and Richards 1993, Busso

and Richards 1995) even though true replication was lacking. Statistical tests used in this thesis were conservative in that the experimental units were not quadrats, individual plants, or individual tillers. I will place emphasis on the results when differences in plant response under the different treatments are large and statistical veracity of the data is obvious.

CHAPTER 4

RESULTS

Blue Grama

Approximately 98% (265 out of 270 marked tillers) and 97% (309 out of 320 marked tillers) of marked blue grama tillers remained in a vegetative phenological stage for the 1994 and 1995 growing seasons, respectively. Utilization levels by drought and grazing treatments are listed in Table 2. On average, utilization was $39\% \pm \text{SE } 7\%$ and $47\% \pm \text{SE } 8\%$ on blue grama tillers for the first and second grazing event in 1994. Utilization was $23\% \pm \text{SE } 5\%$ and $45\% \pm \text{SE } 3.5\%$ for the first and second grazing event in 1995. Analysis of drought and grazing effects on blue grama tillers are listed in Table 3 (1994) and Table 4 (1995).

Grazing During Drought (1994).

Relative growth rates of blue grama tillers in 1994 are listed in Figure 4a. Relative growth rates of blue grama tillers were 29% lower ($p=.01$) under drought conditions compared with natural precipitation before grazing. Tiller relative growth rates were similar between drought and natural conditions following the first ($p=.83$) and the second grazing events ($p=.30$). However, the analysis indicated the grazing period by drought interaction was not significant ($p=.21$). Relative growth rates of blue grama tillers varied between grazing period and grazing treatment (grazing period*grazing treatment $p=.01$). Grazed blue grama tillers exhibited 107% greater ($p=.02$) relative growth rates compared to ungrazed tiller after the first grazing event, but were similar ($p=.08$) following the second grazing event.

a. 1994

	Grazing event # 1		Grazing event # 2	
	<u>Drought</u>	<u>Natural</u>	<u>Drought</u>	<u>Natural</u>
GG	32 ± 4	47 ± 3	36 ± 2	53 ± 14
GU	39 ± 3	40 ± 14	50 ± 4.5	48 ± 3
UU	0	0	0	0

b. 1995

	Grazing event # 1		Grazing event # 2	
	<u>Drought</u>	<u>Natural</u>	<u>Drought</u>	<u>Natural</u>
GG	17 ± 1.3	28 ± 3.3	49 ± 2.3	41 ± .2
GU	0	0	0	0
UU	0	0	0	0

c. 1994

	Grazing event # 1		Grazing event # 2	
	<u>Drought</u>	<u>Natural</u>	<u>Drought</u>	<u>Natural</u>
GG	47 ± 12	44 ± 16	69 ± 2	50 ± .8
GU	57 ± 4.6	48 ± 10	64 ± 1	45 ± 5.6
UU	0	0	0	0

d. 1995

	Grazing event # 1		Grazing event # 2	
	<u>Drought</u>	<u>Natural</u>	<u>Drought</u>	<u>Natural</u>
GG	46 ± .5	62 ± 2.8	51 ± 1.2	42 ± 3.5
GU	0	0	0	0
UU	0	0	0	0

Table 2. Percent utilization (on a dry weight basis) of grazed tillers under drought and natural precipitation for blue grama (a and b) and western wheatgrass (c and d). Each mean ± standard error represents the average utilization of grazed tillers averaged across two plots. Utilization was similar ($p > .05$) between grazing treatments in 1994 and 1995.

a.

	<u>Between</u> Subjects		<u>Within</u> Subjects				
	Drought (D)	Grazing Treat. (G)	D*G	Grazing Period (P)	P*D	P*G	P*D*G
<u>B.G.</u>							
Relative	.1332	.0683	.5412	.0001	.2134	.0106	.4926
Absolute	.0173	.1073	.1441	.0001	.0781	.1379	.6771
<u>W.WG.</u>							
Relative	.6091	.0022	.5395	.0001	.2293	.0008	.4273
Absolute	.1292	.0211	.5370	.0001	.2970	.3050	.6048

b.

	Model	Drought (D)	Grazing Treat. (G)	D*G
<u>B.G.</u>				
Axillary Tillering	.0008	.0001	.0047	.0768
Tiller Density	.0698	.3191	.0666	.6462
Tiller Replacement	.7286	.1896	.7487	.9943
Primary Production	.3970	.9474	.7565	.1360
<u>W.WG.</u>				
Axillary Tillering	.0001	.0001	.0419	.0780
Tiller Density	.0075	.0829	.0855	.0690
Tiller Replacement	.2012	.0942	.4886	.1726
Primary Production	.0504	.0048	.6618	.4247

Table 3. Statistical analysis of grazing during drought (1994). Repeated measures ANOVA table and p-values for growth rates of blue grama (B.G.) and western wheatgrass (W.WG.) tillers in 1994 (a). ANOVA table and p-values for axillary tiller emergence, tiller density, tiller replacement, and aboveground net primary production of blue grama (B.G.) and western wheatgrass (W.WG.) in 1994 (b).

a.

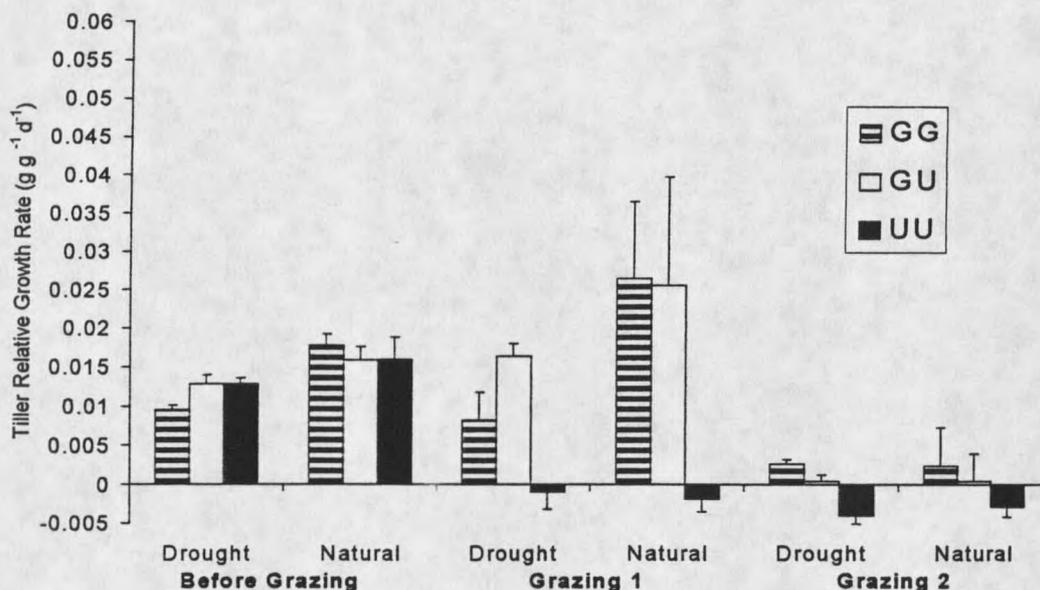
	<u>Between Subjects</u>		<u>Within Subjects</u>				
	Drought (D)	Grazing Treat. (G)	D*G	Grazing Period (P)	P*D	P*G	P*D*G
<u>B.G.</u>							
Relative	.0039	.0002	.0156	.0001	.0202	.0035	.0960
Absolute	.6691	.0045	.7429	.0001	.3133	.0003	.5097
<u>W.WG.</u>							
Relative	.6922	.0020	.8390	.0001	.8487	.0001	.4781
Absolute	.3371	.3103	.8638	.0001	.9117	.0266	.6123

b.

	Model	Drought (D)	Grazing Treat. (G)	D*G
<u>B.G.</u>				
Axillary Tillering	.0410	.1581	.0125	.5013
Primary Production	.8437	.3870	.8444	.7176
<u>W.WG.</u>				
Axillary Tillering	.2568	.1755	.1233	.8461
Primary Production	.0806	.0297	.1303	.2516

Table 4. Statistical analysis of grazing after drought (1995). Repeated measures ANOVA table and p-values for growth rates of blue grama (B.G.) and western wheatgrass (W.WG.) tillers in 1995 (a). ANOVA table and p-values for axillary tiller emergence and aboveground net primary production of blue grama (B.G.) and western wheatgrass (W.WG.) in 1995 (b).

a. 1994



b. 1995

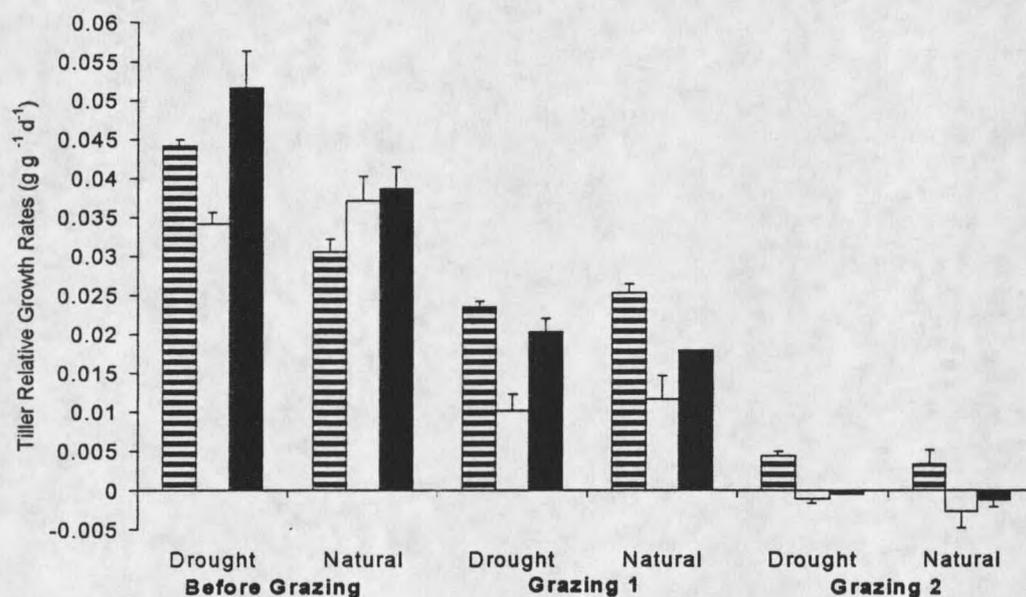


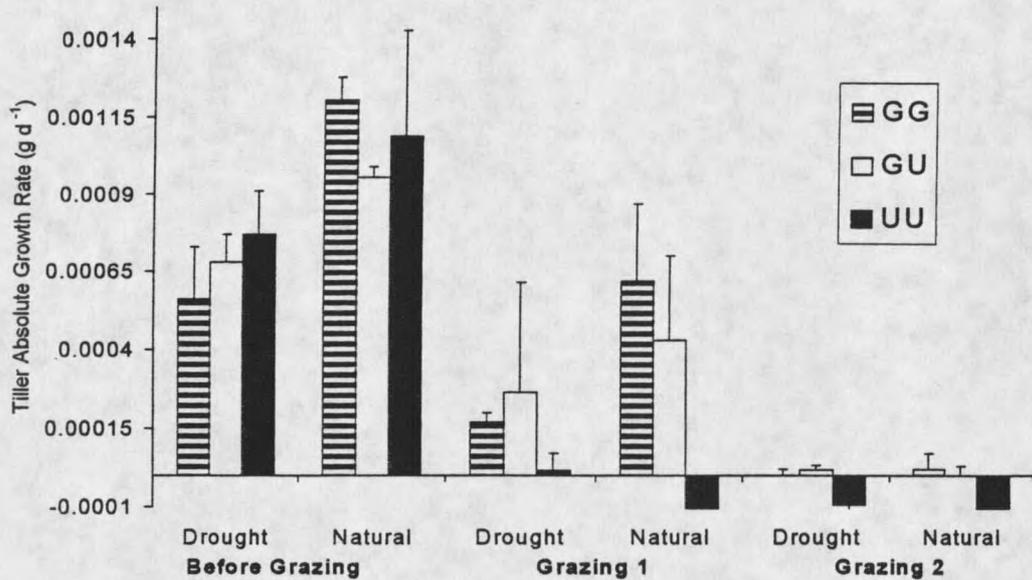
Figure 4. Relative growth rates ($\text{g g}^{-1} \text{d}^{-1}$) for blue grama tillers in response to grazing during drought (a) and grazing after drought (b). Grazing treatments are grazed during and after drought (GG), grazed during drought and ungrazed after drought (GU), and ungrazed during and after drought (UU). Each bar represents the mean growth rate before grazing (1994 and 1995 $n=2$ weeks), after the first grazing event (grazing 1, 1994 $n=4$ weeks, 1995 $n=5$ weeks), and following the second grazing event (grazing 2, 1994 $n=8$ weeks, 1995 $n=4$ weeks). Vertical bars are standard errors ($n=2$).

Relative growth rates of all treatment combinations were not different ($p > .05$) than zero after the second grazing event.

Absolute growth rates of blue grama tillers in 1994 are listed in Figure 5a. Repeated measures ANOVA indicated insignificant grazing period by drought ($p = .08$) and grazing period by grazing treatment ($p = .14$) interactions. Absolute tiller growth rates were 38% lower ($p = .03$) under drought conditions compared with natural precipitation before grazing. Absolute tiller growth rates were similar between drought and natural conditions following both the first grazing event ($p = .30$) and the second grazing event ($p = .88$). Grazed blue grama tillers exhibited 116% greater ($p = .02$) absolute growth rates compared to ungrazed tillers after the first grazing. Grazed blue grama tillers exhibited 645% greater ($p = .007$) absolute growth rates compared to ungrazed tillers following the second grazing event. After the first and second grazing event grazed tillers had positive absolute growth rates while ungrazed tillers had negative absolute growth rates. Absolute growth rates of all treatment combinations were not different ($p > .05$) than zero after the second grazing event.

Axillary tiller emergence varied in magnitude between precipitation and grazing treatments (drought*grazing $p = .08$). Drought reduced ($p = .0001$) total axillary tiller emergence of blue grama 79% (Fig. 6a.). Grazing increased ($p = .0016$) axillary tiller emergence 67% compared to ungrazed treatments (Fig. 6a.). Sixty percent of blue grama daughter tillers were produced after the first grazing event (Fig. 7a.). Of the blue grama tillers that produced axillary tillers under drought conditions, none produced more than one. In contrast, of the blue grama tillers that produced axillary tillers in normal precipitation, 18% produced two secondary tillers.

a. 1994



b. 1995

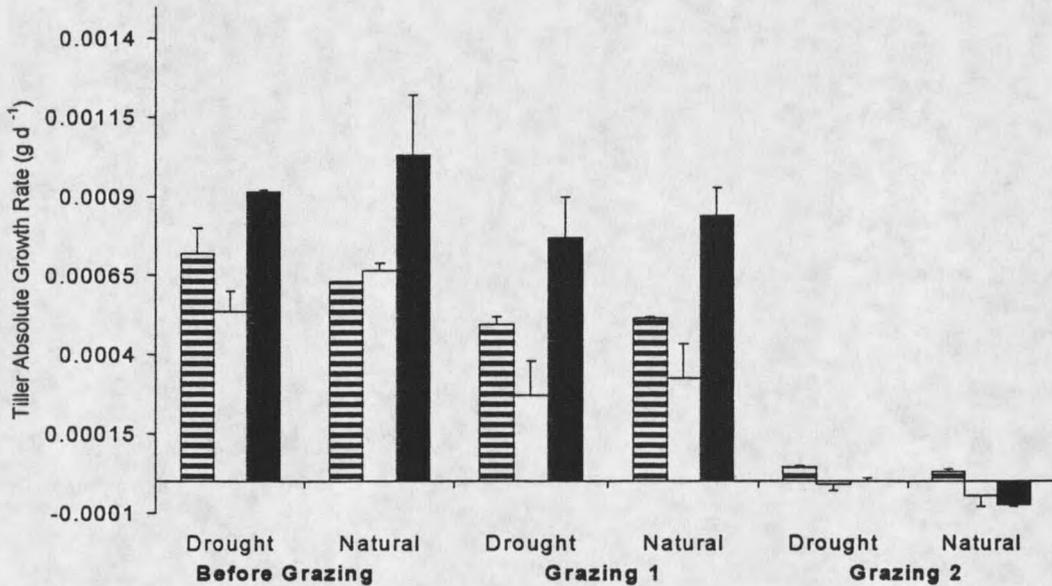
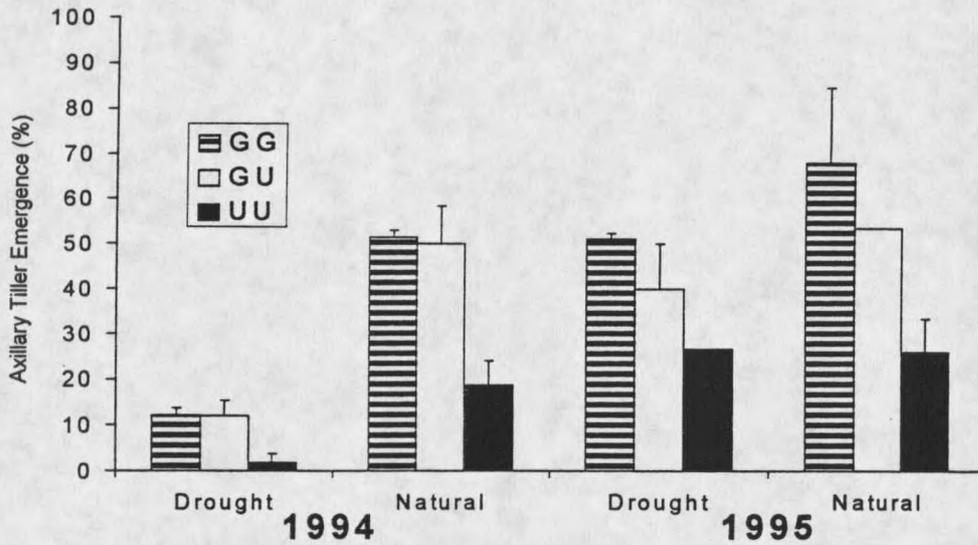


Figure 5. Absolute growth rates (g d^{-1}) for blue grama tillers in response to grazing during drought (a) and grazing after drought (b). Grazing treatments are grazed during and after drought (GG), grazed during drought and ungrazed after drought (GU), and ungrazed during and after drought (UU). Each bar represents the mean growth rate before grazing (1994 and 1995 $n=2$ weeks), after the first grazing event (grazing 1, 1994 $n=4$ weeks, 1995 $n=5$ weeks), and following the second grazing event (grazing 2, 1994 $n=8$ weeks, 1995 $n=4$ weeks). Vertical bars are standard errors ($n=2$).

a. blue grama



b. western wheatgrass

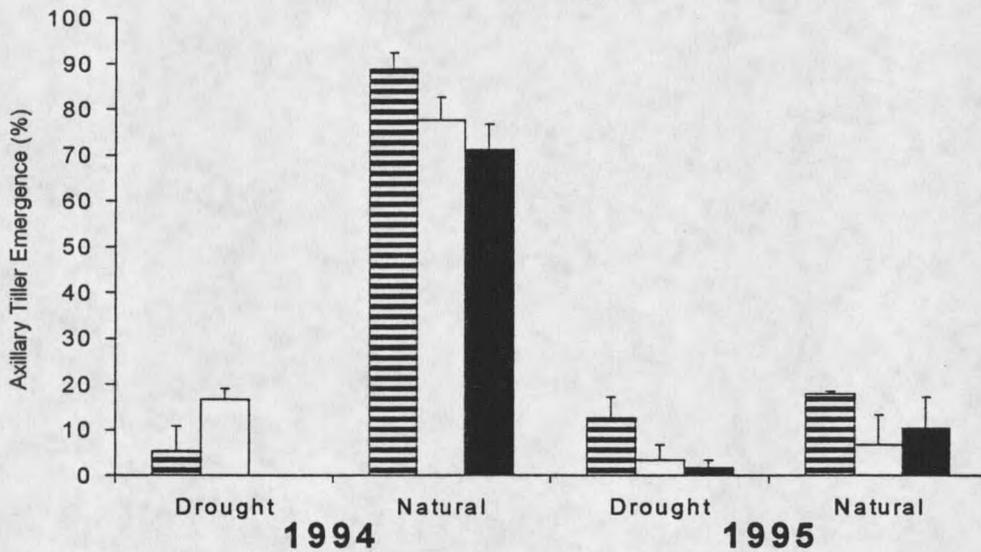
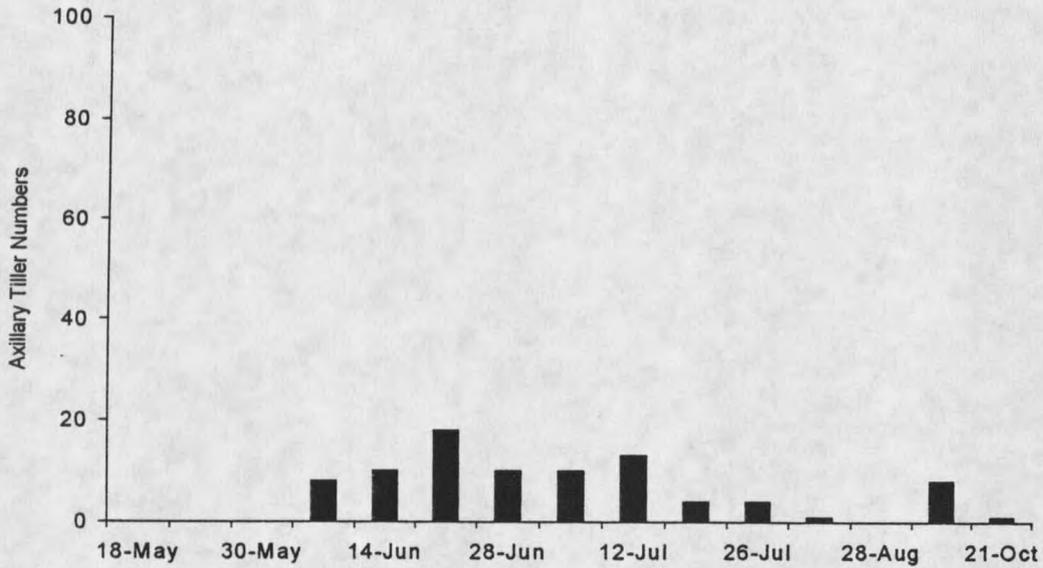


Figure 6. Total axillary tiller emergence on blue grama (a) and western wheatgrass (b) in response to grazing during drought (1994) and grazing after drought (1995). Grazing treatment are grazed during and after drought (GG), grazed during drought and ungrazed after drought (GU), and ungrazed during and after drought (UU). Each bar represents the mean percent axillary tiller production of marked tillers that produced at least one secondary tiller per growing season. Vertical bars are standard errors (n=2).

a. 1994



b. 1995

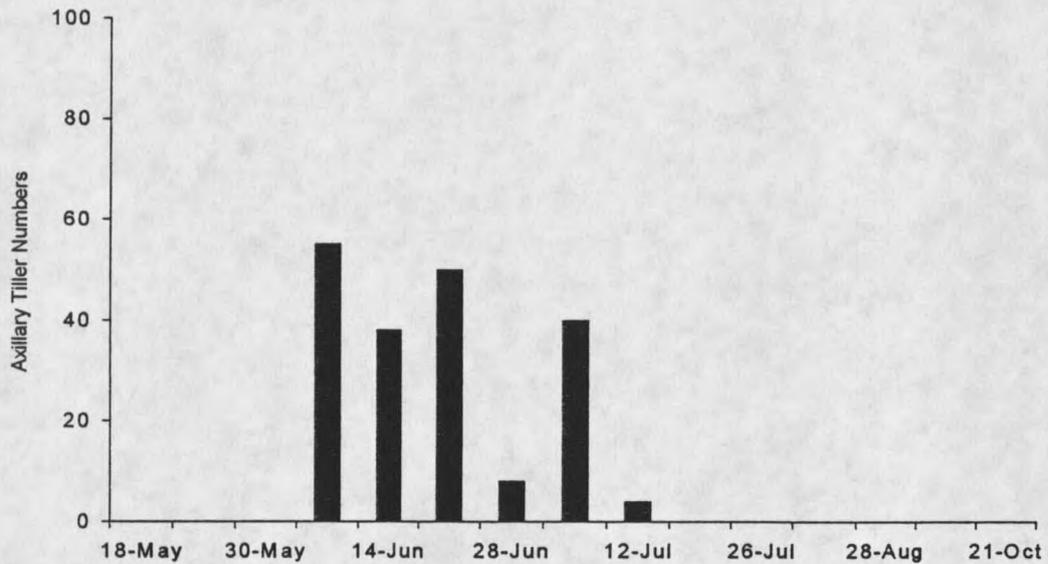


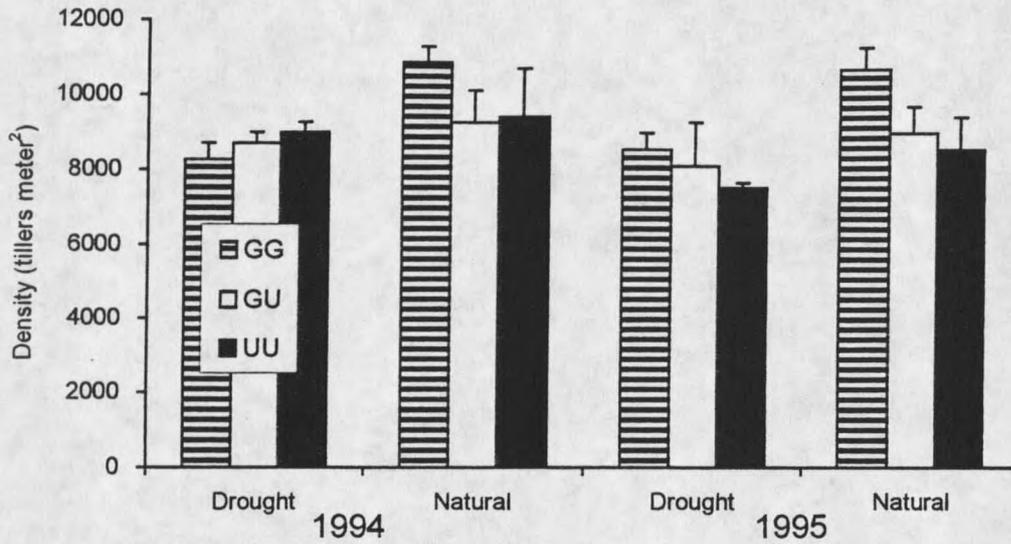
Figure 7. Distribution of axillary tillers produced by blue grama in 1994 (a) and 1995 (b). Each bar represents the total number (sum across all treatments) of axillary tillers that developed on a particular date. The first grazing event occurred on 30 May in 1994 and 1995. The second grazing event occurred on 28 June in 1994 and 3 July in 1995.

Tiller density of blue grama was not affected by one year of drought ($p=.32$ Fig. 8a.). Tiller density changes were variable across grazing treatments, but not different ($p=.07$). The ability of marked blue grama tillers to replace themselves annually was not affected by drought ($p=.19$) or grazing treatment ($p=.75$ Fig. 9a). In addition, aboveground net primary production of blue grama was not affected by drought ($p=.95$) or grazing ($p=.76$ Fig. 10a.).

Grazing After Drought (1995).

Relative growth rates of blue grama tillers in 1995 are listed in Figure 4b. The analysis revealed significant grazing period by drought ($p=.02$) and grazing period by grazing treatment ($p=.004$) interactions. Tillers exposed to the drought in 1994 had 18% greater ($p=.01$) relative growth rates compared to tillers under natural conditions prior to grazing. Tiller relative growth rates were similar between drought and natural conditions following the first ($p=.83$) and the second ($p=.30$) grazing events. Ungrazed tillers exhibited 19% greater ($p=.02$) relative growth rates compared to tillers that were grazed the previous year (GG, GU) before defoliation treatments in 1995. Blue grama tillers that were grazed both years had 22% greater ($p=.02$) relative growth rates compared to ungrazed tillers and 55% greater ($p=.0003$) relative growth rates compared to tillers grazed the previous year (GU) following the first grazing event. After the second grazing event, relative growth rates of tillers grazed both years were 121% greater ($p=.009$) than ungrazed tillers ($p=.009$) and 147% greater ($p=.004$) than tillers grazed the previous year. Relative growth rates of all treatment combinations were not different ($p>.05$) than zero after the second grazing event.

a. blue grama



b. western wheatgrass

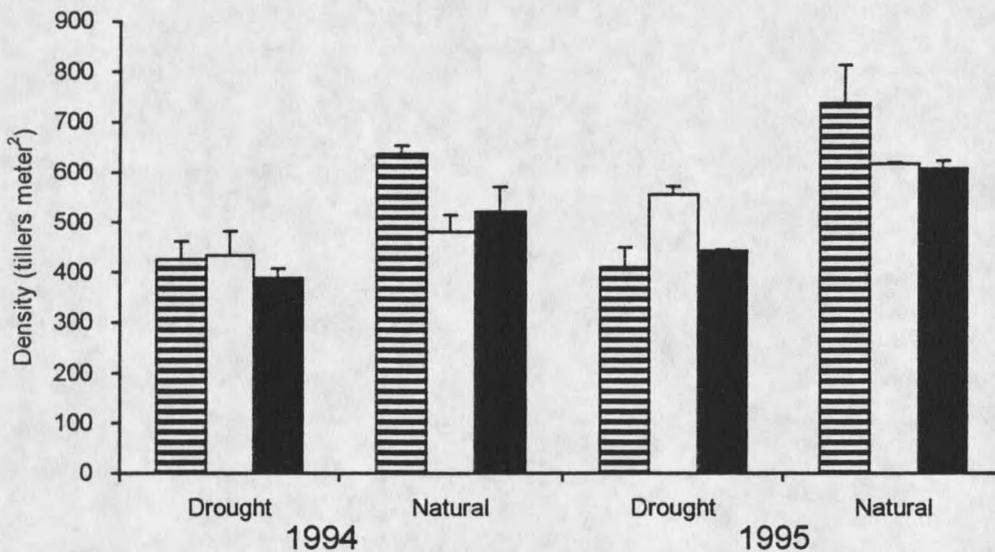
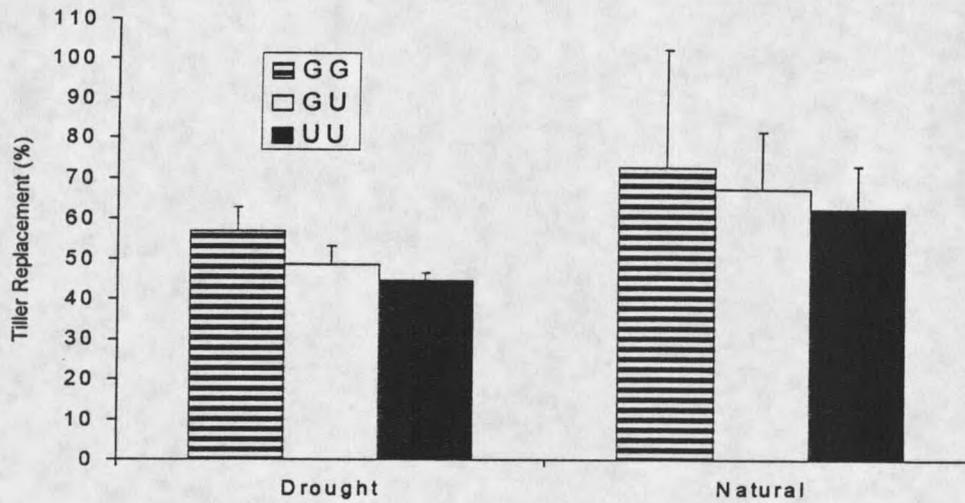


Figure 8. Tiller density (tillers meter⁻²) on blue grama (a) and western wheatgrass (b) in response to drought and grazing. Grazing treatments are grazed during and after drought (GG), grazed during drought and ungrazed after drought (GU), and ungrazed during and after drought (UU). Note the different y-axis scales. Vertical bars are standard errors (n=2).

a. blue grama



b. western wheatgrass

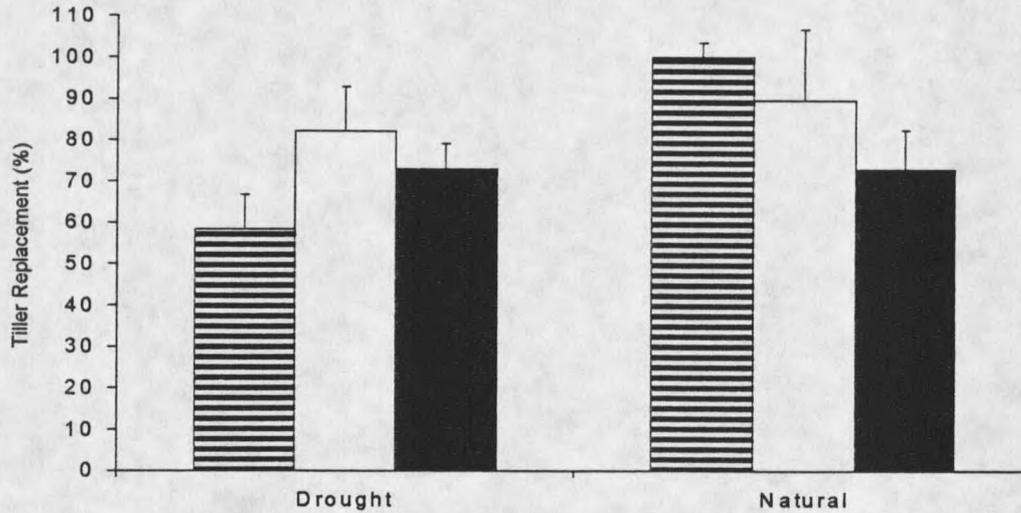


Figure 9. Tiller replacement in the spring of 1995 on blue grama (a) and western wheatgrass (b) in response to drought and grazing treatments. Grazing treatments are grazed during and after drought (GG), grazed during drought and ungrazed after drought (GU), and ungrazed during and after drought (UU). Each bar represents the mean percent of marked tiller that replaced themselves. Vertical bars are standard errors (n=2).

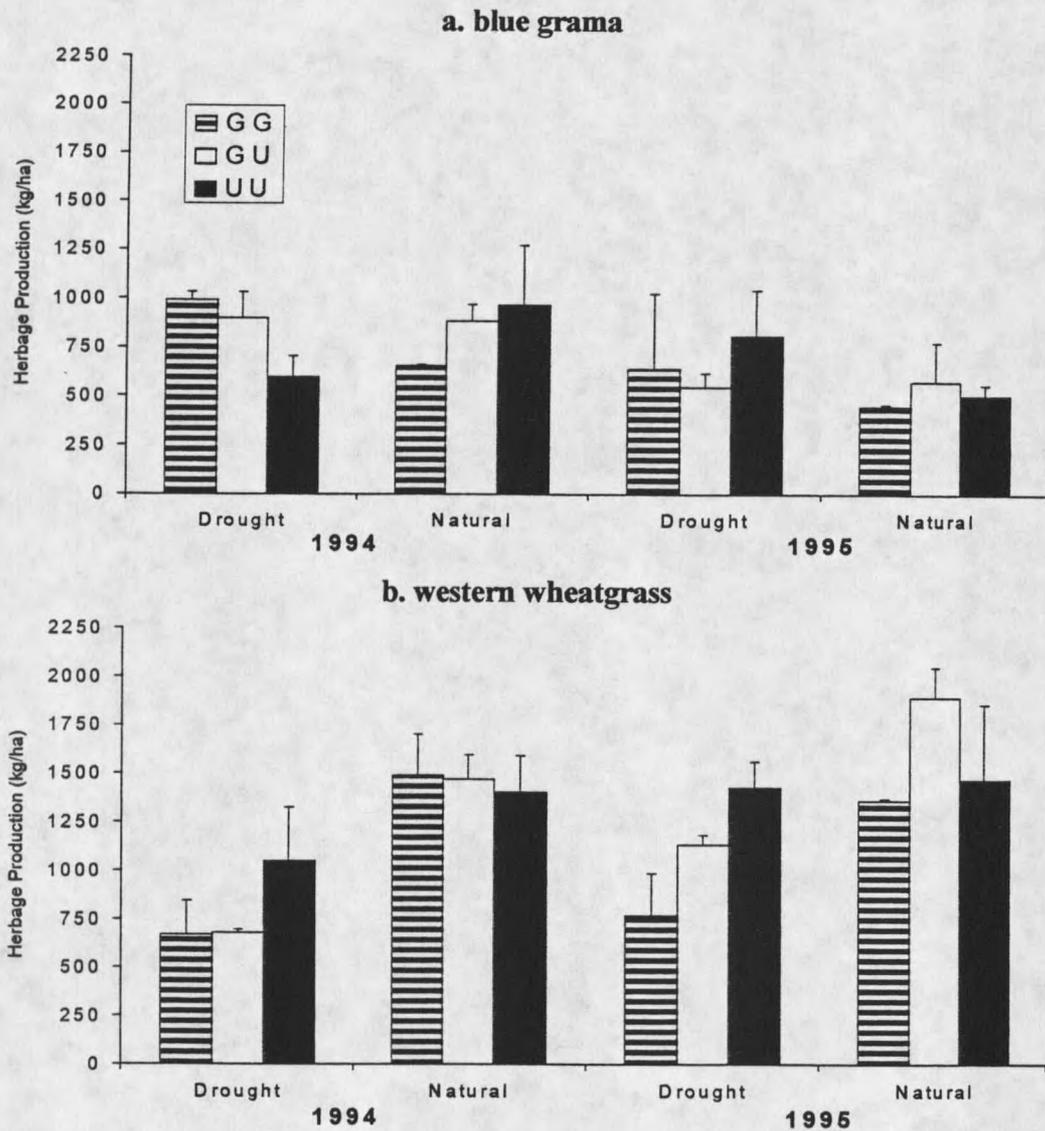


Figure 10. Estimated aboveground net primary production in response to grazing during drought (1994) and grazing after drought (1995) for blue grama (a) and western wheatgrass (b). Grazing treatments are grazed during and after drought (GG), grazed during drought and ungrazed after drought (GU), and ungrazed during and after drought (UU). Vertical bars are standard errors ($n=2$).

Absolute growth rates of blue grama tillers in 1995 are reported in Figure 5b. Absolute tiller growth rates were similar between drought and natural conditions before grazing ($p=.50$) and after the first grazing event ($p=.50$). Tillers exposed to drought the year before exhibited greater ($p=.03$) absolute growth rates compared to natural conditions following the second grazing event. However, the grazing period by drought interaction was not significant ($p=.31$). Although absolute growth rates were different ($p=.03$) between drought and natural precipitation in 1995 after the second grazing event, growth rates were less than $.00001 \text{ g d}^{-1}$ and not different ($p>.05$) than zero. Absolute growth rates of blue grama tillers varied between grazing period and grazing treatment (grazing period*grazing treatment $p=.0003$). Absolute growth rates of ungrazed tillers were 34% greater ($p=.01$) than tillers that were grazed the previous year (GG, GU) prior to defoliation treatments in 1995. Following the first grazing event, ungrazed tillers had 38% greater ($p=.01$) absolute growth rates than tillers grazed both years and had 63% greater ($p=.0008$) absolute growth rates than tillers which were grazed only the previous year. Tillers which were grazed two years exhibited 186% greater ($p=.01$) absolute growth rates compared to ungrazed tillers and tillers grazed the previous year following the second grazing event. However, absolute growth rate for blue grama tillers grazed both years was only $.00003 \text{ g d}^{-1}$. At this rate it would take 33,333 days to accumulate one gram of material per tiller. In addition, following the second grazing event absolute growth rates of all treatment combinations were not different ($p>.05$) than zero.

Axillary tiller emergence in 1995 was similar ($p=.20$) between drought and natural conditions (Fig. 6a.). Axillary tiller emergence for ungrazed tillers was 57% lower ($p=.005$) than tillers that were grazed both years (GG) and 22% lower ($p=.04$) than tillers that were

grazed the previous year (GU). Axillary tiller emergence in 1995 was similar ($p=.14$) between tillers grazed both years (GG) and tillers that were only grazed the first year (GU) of the study (Fig. 6a.). Ninety-eight percent of the axillary tiller emergence occurred after the first grazing event (Fig. 7.b.). On average $30\% \pm SE 5\%$ of the blue grama tillers that produced axillary tillers produced two secondary tillers. Aboveground net primary production of blue grama in 1995 was not affected by drought ($p=.39$) or grazing ($p=.84$).

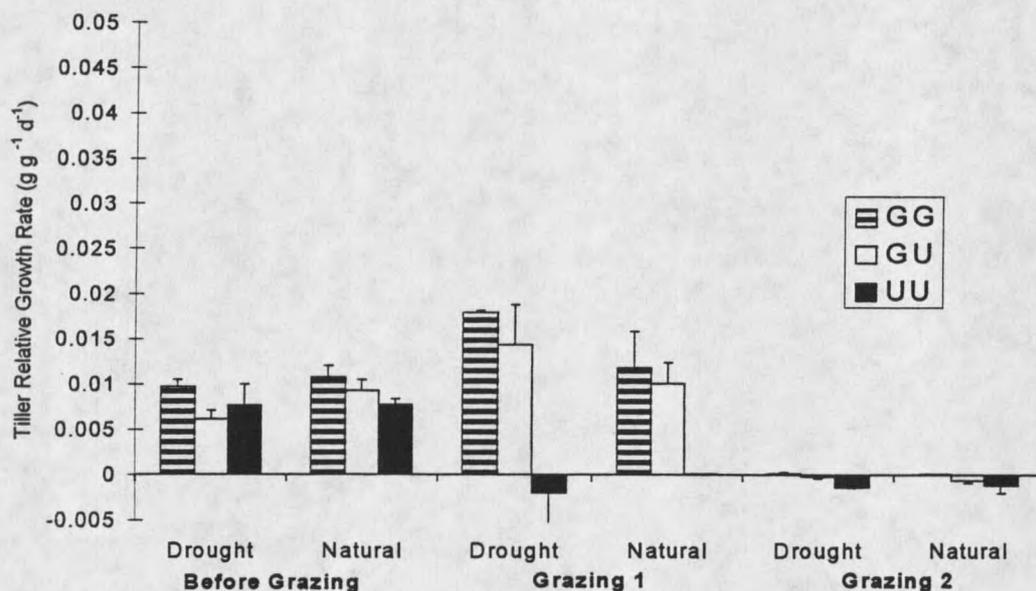
Western Wheatgrass

Approximately 98% (323 out of 329 marked tillers) and 94% (322 out of 341 marked tillers) of marked western wheatgrass tillers remained in a vegetative phenological stage for the 1994 and 1995 growing seasons, respectively. Utilization levels by drought and grazing treatments are listed in Table 2. On average, utilization was $49\% \pm SE 9\%$ and $51\% \pm SE 8\%$ on western wheatgrass tillers for the first and second grazing event in 1994, respectively. Utilization of western wheatgrass was $53\% \pm SE 7\%$ and $46\% \pm SE 4.5\%$ for the first and second grazing event in 1995, respectively. Analysis of drought and grazing effects on western wheatgrass tillers are listed in Table 3 (1994) and Table 4 (1995).

Grazing During Drought.

Relative growth rates of western wheatgrass tillers in 1994 are listed in Figure 11a. Repeated measures ANOVA indicated a insignificant grazing period by drought interaction ($p=.23$). Relative growth rates of western wheatgrass tillers were similar between drought and natural conditions before grazing ($p=.24$), after the first grazing event ($p=.32$), and after the

a. 1994



b. 1995

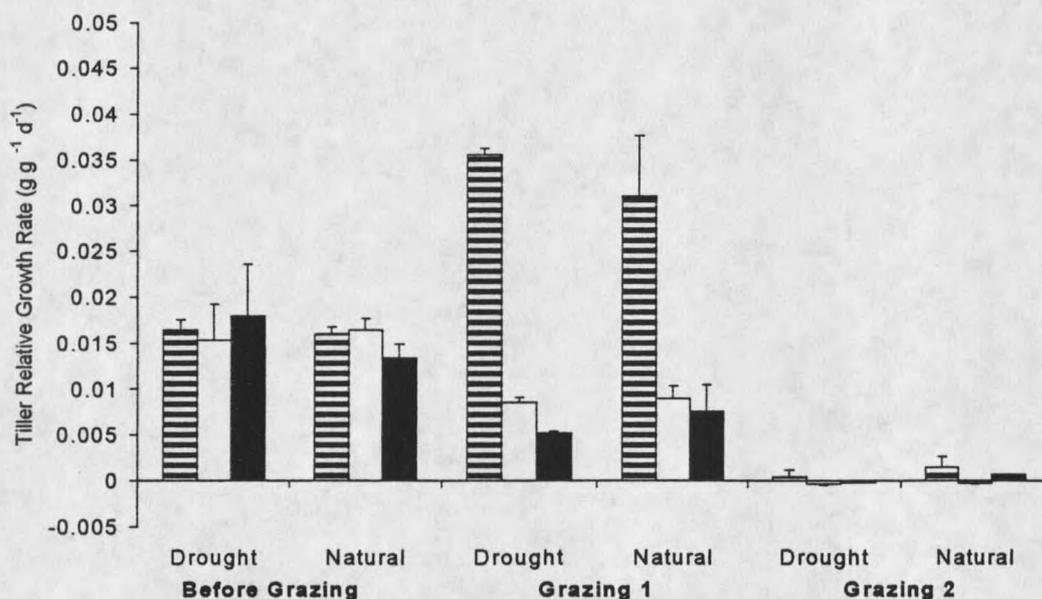


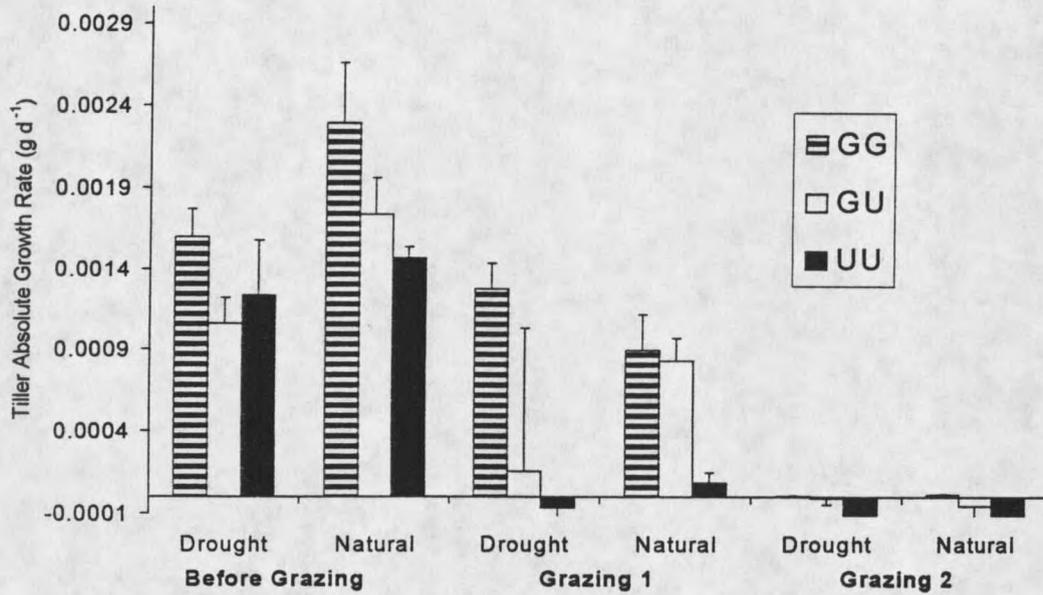
Figure 11. Relative growth rates ($\text{g g}^{-1} \text{d}^{-1}$) for western wheatgrass tillers in response to grazing during drought (a) and grazing after drought (b). Grazing treatments are grazed during and after drought (GG), grazed during drought and ungrazed after drought (GU), and ungrazed during and after drought (UU). Each bar represents the mean growth rate before grazing (1994 and 1995 $n=2$ weeks), after the first grazing event (grazing 1, 1994 $n=4$ weeks, 1995 $n=5$ weeks), and following the second grazing event (grazing 2, 1994 $n=8$ weeks, 1995 $n=4$ weeks). Vertical bars are standard errors ($n=2$).

second grazing event ($p=.81$). Relative growth rates of western wheatgrass tillers varied between grazing period and grazing treatment (grazing period*grazing treatment $p=.0008$). Grazed western wheatgrass tillers had 107 and 800% greater relative growth rates compared to ungrazed tillers following the first ($p=.002$) and the second grazing event ($p=.02$), respectively. Although a large difference in relative growth rates existed following the second grazing event, the highest growth was $.0001 \text{ g g}^{-1} \text{ d}^{-1}$. Also, after the second grazing, grazed tillers exhibited positive growth rates while ungrazed tillers exhibited negative growth rates. However, relative growth rates of all treatment combinations were not different ($p>.05$) than zero after the second grazing event.

Absolute growth rates of western wheatgrass tillers in 1994 are listed in Figure 12a. Repeated measures ANOVA revealed insignificant grazing period by drought ($p=.30$) and grazing period by grazing treatment ($p=.31$) interactions. Absolute tiller growth rates was 27% less ($p=.04$) under drought compared to natural precipitation before grazing, but were similar after the first grazing event ($p=.69$) and after the second grazing event ($p=.76$). Absolute tiller growth rates were similar between grazing treatments before grazing ($p=.10$) and after the first grazing event ($p=.12$). Following the second grazing event absolute growth varied between grazing treatments ($p=.02$). Absolute growth rate after the second grazing were not different ($p>.05$) than zero between all treatments.

Axillary tiller production varied in magnitude between precipitation and grazing treatments (drought*grazing $p=.08$). Drought reduced ($p=.0001$) total axillary tiller emergence of western wheatgrass 91% (Fig. 6b.). Grazed western wheatgrass tillers exhibited greater ($p=.01$) axillary tiller emergence compared with ungrazed tillers (Fig. 6b.). More than

a. 1994



b. 1995

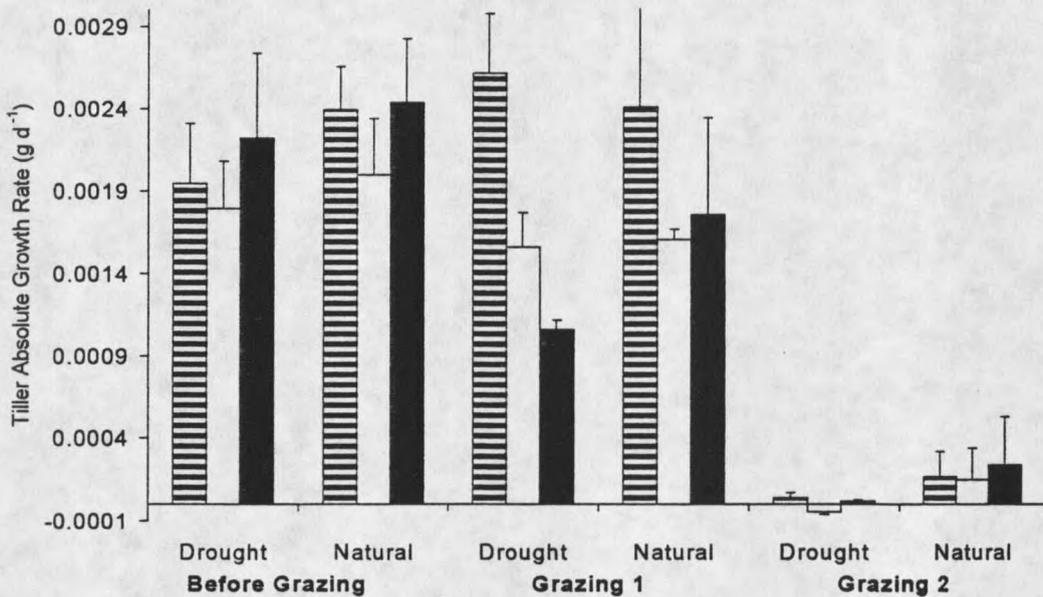
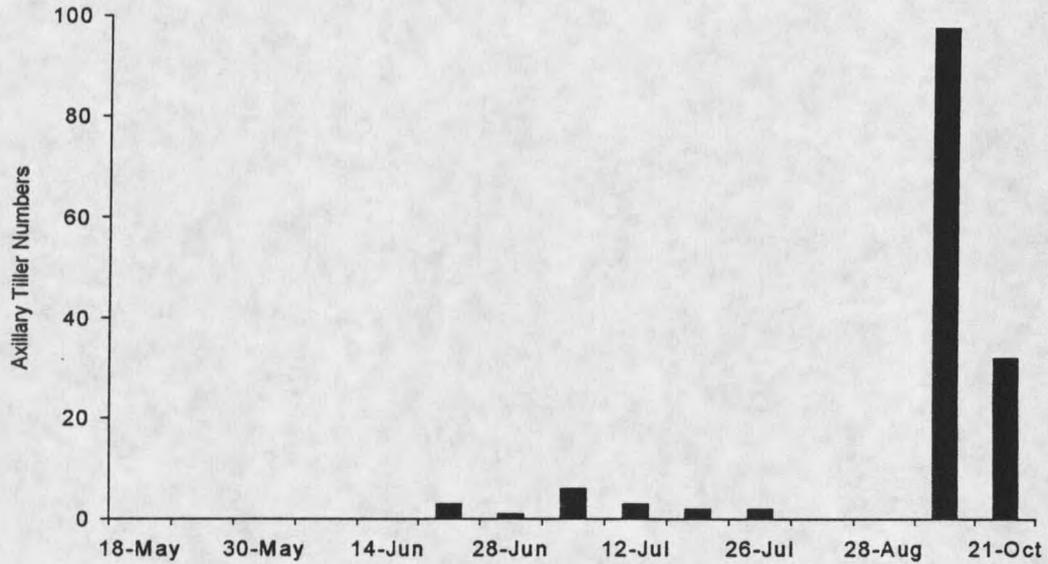


Figure 12. Absolute growth rates (g d⁻¹) for western wheatgrass tillers in response to grazing during drought (a) and grazing after drought (b). Grazing treatments are grazed during and after drought (GG), grazed during drought and ungrazed after drought (GU), and ungrazed during and after drought (UU). Each bar represents the mean growth rate before grazing (1994 and 1995 n=2 weeks), after the first grazing event (grazing 1, 1994 n=4 weeks, 1995 n=5 weeks), and following the second grazing event (grazing 2, 1994 n=8 weeks, 1995 n=4 weeks). Vertical bars are standard errors (n=2).

a. 1994



b. 1995

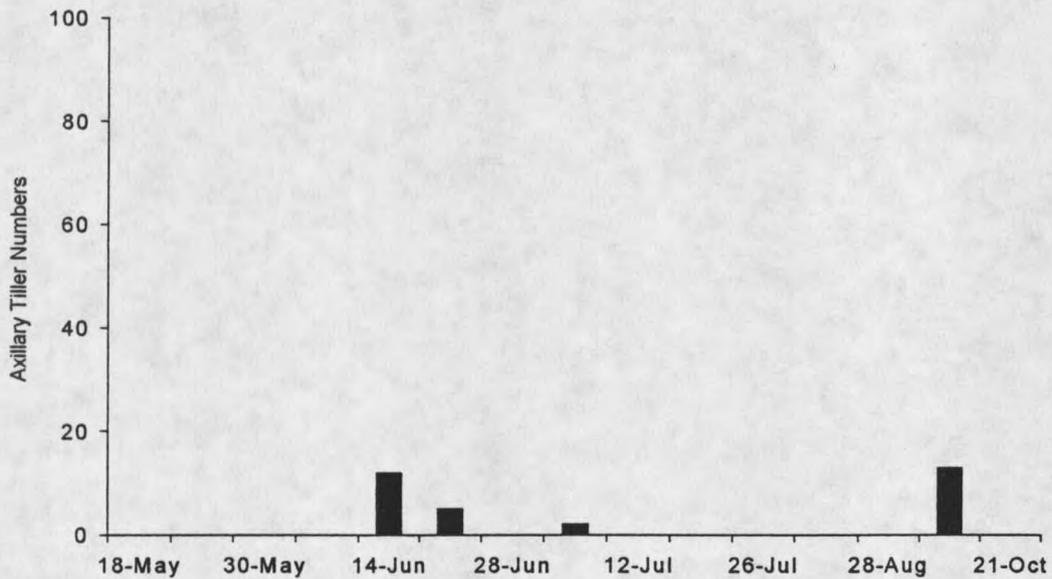


Figure 13. Distribution of axillary tillers produced by western wheatgrass in 1994 (a) and 1995 (b). Each bar represents the total number (sum across all treatments) of axillary tillers that developed on a particular date. The first grazing event occurred on 30 May in 1994 and 1995. The second grazing event occurred on 28 June in 1994 and 3 July in 1995.

95% of the western wheatgrass axillary tillers were produced in the fall (September and October) of 1994 (Fig. 13a.). In addition, of the western wheatgrass tillers that exhibited axillary tillering under drought conditions, none produced more than one. In contrast, of the western wheatgrass tillers that produced secondary tillers, 11% produced two daughter tillers. Changes in tiller densities varied in magnitude between drought and grazing treatments (drought*grazing $p=.07$). Tiller density of western wheatgrass was not affected by drought ($p=.09$) or grazing ($p=.09$, Fig. 7b.). However, tiller density tended to be higher in 1995 than in 1994 for all treatments. For example, tiller density tended to increase ($p=.09$) 18 and 20% for drought and natural conditions following one year of treatments. Tiller density tended to increase ($p=.09$) 15, 30 and 12% for grazing treatments UU, GU and GG, respectively, following one year of treatments. Tiller replacement averaged $71\% \pm \text{SE } 6\%$ under drought conditions and $87\% \pm \text{SE } 7\%$ under natural precipitation (Fig 8b.). Although annual replacement proportions of marked blue grama tillers was 20% less under drought conditions compared to natural precipitation, they were not different ($p=.09$). Grazing did not affect tiller replacement ($p=.49$, Fig. 9b.). Aboveground net primary production of western wheatgrass was 45% lower ($p=.005$) under drought compared to natural precipitation (Fig. 10b.). However, aboveground net primary production was similar ($p=.66$) between grazing treatments (Fig. 10b.).

Grazing After Drought (1995).

Relative growth rates of western wheatgrass tillers in 1995 are listed in Figure 11b. The analysis indicated a insignificant grazing period by drought interaction ($p=.85$). Tiller relative

growth rates were similar between drought and natural condition treatments before grazing ($p=.60$), after the first grazing ($p=.82$), and after the second grazing ($p=.68$). Relative growth rates of western wheatgrass tillers varied between grazing period and grazing treatment (grazing period*grazing treatment $p=.0001$) Western wheatgrass tillers that were grazed both years exhibited 81% and 73% greater relative growth rates compared to ungrazed tillers ($p=.0001$) and tillers that were grazed the previous year ($p=.0002$) following the first grazing event, respectively. Tillers grazed both years had similar relative growth rates compared to ungrazed tillers ($p=.06$) and tillers grazed the previous year ($p=.07$) following the second grazing. Relative growth rates of all treatment combinations were not different ($p>.05$) than zero after the second grazing event.

Absolute growth rates of western wheatgrass tillers in 1995 are reported in Figure 12b. Repeated measures ANOVA indicated a insignificant grazing period by drought interaction ($p=.91$). Tiller absolute growth rates were similar between drought and natural condition treatments before grazing ($p=.37$), after the first grazing ($p=.61$), and after the second grazing ($p=.20$). Absolute growth rates of western wheatgrass tillers varied between grazing period and grazing treatment (grazing period*grazing treatment $p=.03$). Absolute growth rates were similar ($p=.07$) between grazing treatments after the first grazing event. Tillers grazed both years had a absolute growth rate of $.0025 \text{ g d}^{-1}$ while tillers ungrazed in 1995 (GU, UU) had absolute growth rates of $.0016$ and $.0014 \text{ g d}^{-1}$ following the first grazing. Absolute tiller growth rates following the second grazing event were similar ($p=.88$) between all grazing treatments. In addition, absolute growth rates of all treatment combinations were not different ($p>.05$) than zero after the second grazing event.

Axillary tiller emergence was similar between drought ($p=.19$) and grazing treatments ($p=.12$) in 1995 (Fig. 6b.). Only 26% of the western wheatgrass axillary tillers were produced in the fall (September and October) of 1995 (Fig. 13b.). No western wheatgrass tillers that exhibited secondary tillering in 1995 produced more than one daughter tiller. Aboveground net primary production of western wheatgrass at the end of the growing season in 1995 was 30% lower ($p=.03$) under drought conditions compared to natural precipitation (Fig. 10b.). Aboveground net primary production of western wheatgrass was not affected by grazing treatment ($p=.13$).

Summary

A summary of drought and grazing treatment effects on blue grama and western wheatgrass in 1994 and 1995 are listed in Table 5. Drought did not negatively impact tiller absolute and relative growth rates of both species in both years. Axillary tiller emergence was reduced under drought for both species in 1994. Axillary tiller emergence was not affected by the previous years drought at the end of the growing season in 1995. Grazing increased axillary tiller emergence of both species in both 1994 and 1995. In the spring of 1995, following one year of drought and grazing treatments, tiller replacement or tiller density of both species were similar between all treatments. Aboveground net primary production of blue grama was not affected by drought or grazing in both years. Aboveground net primary production of western wheatgrass was not affected by grazing in both years, but was lower under drought in both 1994 and 1995.

a. 1994

	<u>B.G.</u>		<u>W.WG.</u>	
	Drought	Grazing	Drought	Grazing
AGR	0	0	0	0
RGR	0	+	0	+
ATE	-	+	-	+
DEN	0	0	0	0
REP	0	0	0	0
PROD	0	0	-	0

b. 1995

	<u>B.G.</u>		<u>W.WG.</u>	
	Drought	Grazing	Drought	Grazing
AGR	+	+	0	+
RGR	0	+	0	+
ATE	0	+	0	0
PROD	0	0	-	0

Table 5. Summary of drought and grazing effects ($p < .05$) on tiller absolute growth rates (AGR), tiller relative growth rates (RGR), axillary tiller emergence (ATE), tiller density (DEN), tiller replacement (REP), and aboveground net primary production (PROD) for blue grama (B.G.) and western wheatgrass (W.WG.) in 1994 and 1995. Zero (0) indicates no effect, plus (+) indicates a positive effect, and minus (-) indicates a negative effect.

CHAPTER 5**DISCUSSION****Drought Responses**

Past research has indicated that plant growth is very sensitive to water deficits (Busso and Richards 1993, Hsiao et al. 1985). Surprisingly, in our study the overall impacts of drought on tiller growth rates were minimal and when differences existed they were usually early in the growing season. For example, relative growth rates of water stressed western wheatgrass tillers were similar to non-stressed tillers at all times during the study and drought only reduced absolute growth rates before grazing in 1994. Although drought reduced absolute growth of western wheatgrass before grazing in 1994 this effect did not appear to be carried over the following growing season (i.e. growth similar rates in 1995). In contrast, blue grama under drought conditions, exhibited lower relative and absolute growth rates before grazing in 1994. Blue grama tillers that were water stressed the year before tended to have higher relative growth rates the year following drought compared to tillers that received natural precipitation.

Overall, drought did not affect growth rates of both species late in the growing season of 1994 and 1995. Following the second grazing event for both years growth rates of both species were not different than zero. Drought decreased relative growth rates of blue grama and western wheatgrass only before grazing in 1994 and decreased absolute growth rates of blue grama before grazing in 1994. Limited growth rate differences of tillers between drought and natural precipitation in 1994 and 1995 may be attributed to precipitation dynamics during

these years. For example, below average summer precipitation received on control plots in 1994 may have precluded large growth rate differences. In addition, although small summer rainfall events (<5mm) have been reported to increase physiological activity of blue grama (Sala and Lauenroth 1982) our results suggest that this increased activity may not translate to increased growth. Our results also suggest that there were no carry over effects of a one year drought on growth rates for either western wheatgrass or blue grama. Limited carry over effects may be a result of above average precipitation in March, April and May of 1995. Reduced leaf growth may occur under more prolonged drought (Busso and Richards 1993).

Axillary tiller emergence of blue grama and western wheatgrass in 1994 was severely reduced under drought conditions (Fig. 5). These results agree with Zhang and Romo (1995) who reported that the number of northern wheatgrass tillers emerging was positively correlated with soil water. Bullock et al. (1994) reported in that 45% below average precipitation resulted in decreased axillary tiller emergence. Drought conditions imposed in 1994 did not affect total axillary tiller emergence at the end of the growing season in 1995 of either blue grama or western wheatgrass. Similarly, a one year drought did not limit tiller numbers the following spring for crested and bluebunch wheatgrass (Busso and Richards 1995). Lower axillary tiller production of western wheatgrass tillers in 1995 was probably a result of the dry fall. (Fig. 1,2.). Reduced fall tillering in dry autumns have been reported for crested wheatgrass and bluebunch wheatgrass (Busso et al. 1989).

Tiller density and replacement of both species were similar between drought and natural conditions the spring of 1995. Crested and bluebunch wheatgrass had similar numbers of active axillary buds following one year of drought conditions (Busso et al. 1989). Therefore,

one year of drought did not limit the number of axillary buds, which would prevent future tillers from being produced. Only after three consecutive years of drought conditions did Busso et al. (1989) note reduced numbers of metabolically active axillary buds. Blue grama and western wheatgrass tillers may have the ability to become dormant during short term droughts until conditions become favorable to grow without adverse affects. Plots received above average precipitation in the spring following drought, which may explain why tiller replacement and density were not impacted by the previous years drought. The number of western wheatgrass tillers in each quadrat were relatively easy to count because of its rhizomatous growth habit. However, counting tillers of blue grama was difficult because of its mat-forming growth habit. Blue grama tillers were counted in a area the size of a quarter and estimated tiller numbers were highly dependent on quadrat location.

It has been reported that during extended dry periods on the Northern Great Plains species composition shifts towards shortgrasses and a corresponding reduction of the midgrass component (Newbauer et al. 1980, White et al. 1978, Coupland 1958). Our results agree with these studies. Primary production of western wheatgrass exposed to drought condition was significantly lower in 1994 and 1995 compared to plants which received naturally occurring precipitation. Reduced absolute growth exhibited by western wheatgrass prior to grazing in 1994 and reduced fall tillering under drought in 1994 probably caused lower net primary production of western wheatgrass during drought. Lower primary production in 1995 may have been due to lack of fall tillering. Although not significant, tiller replacement of western wheatgrass tended to be lower ($p=.09$) under drought conditions compared to natural conditions and may have contributed to the lower aboveground net primary production

observed in 1995. Aboveground primary production of blue grama was not affected by drought both years even though absolute and relative growth rates were lower in 1994 under drought before grazing and relative growth rates were higher in 1995 for tillers previously exposed to drought.

Less mass of western wheatgrass was present during and after drought compared to the total herbaceous mass. Shifts in species composition may be attributed to the difference in drought tolerance between C_3 and C_4 grasses. Warm season (C_4) grasses (i.e. blue grama) have evolved under arid environments and are more efficient in photosynthesizing during drought than C_3 grasses (Gould and Shaw 1993).

Tiller level processes of western wheatgrass seemed to explain individual plant production responses to drought and grazing. However, the connection between tillers and individual plant response for blue grama was less clear. Hierarchical levels may respond uniformly to influence total vegetation dynamics, but frequently additional complexity is encountered by the occurrences of opposing responses between or among levels (Briske 1989).

Grazing responses

When plants were grazed, rate of regrowth from existing meristematic tissue depended on the time of the grazing event. Grazing usually increased relative and absolute growth rates compared to ungrazed tillers following the first grazing event (30 May 1994 and 1995). Relative and absolute growth rates following the second grazing event (28 June 1994, 3 July 1995) were generally close to zero or negative. Relative tiller growth rates of crested wheatgrass plants grazed before internode elongation tended to be greater than ungrazed

plants (Olson and Richards 1988b). In contrast, Olson and Richards (1988b) reported that crested wheatgrass grazed during and after internode elongation had lower tiller relative growth rates compared to ungrazed plants. In our study 97% of the 1260 individual tillers that were marked and followed over two years were in a vegetative stage. Therefore, time of grazing within a growing season (i.e. May or August) may ultimately influence the rate of tiller regrowth, rather than phenological stage. However, phenological stage of grasses are most certainly correlated with soil drying (Fig. 1b.).

Increased tiller growth may be explained by increased photosynthetic rates of the remaining foliage (Detling and Painter 1983, Nowak and Caldwell 1984), by using more resources for shoot development at the expense of root growth (Richards 1984) or by greater soil water availability under grazed areas compared to ungrazed areas (Wraith 1987). However, low growth rates following the second grazing event may simply be limited by available water late in the growing season and therefore may be independent of phenological stage.

The emergence of axillary tillers in blue grama and western wheatgrass in 1994 was stimulated by grazing. Tillering following defoliation has been reported to increase in blue grama (Reece et al. 1988), northern wheatgrass (Zhang and Romo 1995) and crested wheatgrass (Olson and Richard 1988b). Tillering after defoliation may be attributed to the removal of apical meristems (Hyder 1972). However, removal of tiller apices of crested wheatgrass alone did not stimulate tillering (Richards et al. 1988). In this experiment heavy clipping, which removed both apical meristems and leaves, resulted in increased tillering (Richards et al. 1988).

Grazing did not stimulate western wheatgrass tillering in the growing season following drought. However, blue grama plants grazed both years and plants grazed the first year and not the second year had greater axillary tillering than plants that were ungrazed both year. Increased tillering the year following grazing may have been enhanced by the opening of the canopy, increasing the amount of red light at the base of the plant (Deregibus et al. 1985, Casal et al. 1985). However, defoliation has been reported to have greater influence on tillering than enhanced red light at the base of tillers (Murphy and Briske 1994). In addition, because the plants in the study area were of low stature and plant canopies were open, light was probably not limited at the base of tillers.

Blue grama seemed to produce more axillary tillers in response to grazing (Fig. 7.) compare to western wheatgrass which produced a majority of tillers in the fall (Fig. 13.). Grazing tolerant plants may have the ability to rapidly produce more tillers in response to defoliation. For example, when crested and bluebunch wheatgrass plants were clipped to 5-7 cm heights, grazing tolerant crested wheatgrass produced 18 times more tillers than the grazing sensitive bluebunch wheatgrass (Mueller and Richards 1986).

Defoliation may be more appropriately viewed as a means of altering the timing or season of tiller recruitment (Murphy and Briske 1992). For example, following one year of treatments in our study, tiller number of both species were not affected following one year of treatments. Similarly, Bullock et al. (1994) found that summer grazing of *Agrostis stolonifera* and *Lolium peretene* did not affect tiller density but increased tiller turnover by higher tiller birth and death rates. This "flush" of tillers following grazing may reduce maximum tiller recruitment in defoliated plants relative to periods of maximum recruitment in undefoliated plants (Bulter and

Briske 1992). Therefore, in spite of a brief period of increased tillering immediately following defoliation, grazed plants may not produce more tillers than undefoliated plants when evaluated over one or more growing seasons (Briske and Richards 1994).

Grazing did not affect tiller densities and replacement for both western wheatgrass and blue grama. Heavy grazing of crested wheatgrass before internode elongation seldom affected tiller replacement (Olson and Richard 1988a). In addition, Olson and Richards (1988c) reported that tiller replacement was inversely related to grazing intensity. Negligible impacts of grazing on tiller replacement and density probably occurred because grazed plants were only moderately utilized (50%) and precipitation in the spring of 1995 was above average.

Elevated tillering and growth rates by blue grama and western wheatgrass may represent an attempt to overcompensate in response to defoliation (McNaughton 1983). However, end of season biomass accumulation did not differ between grazing treatment in 1994 and 1995 for either blue grama or western wheatgrass.

CHAPTER 6**IMPLICATIONS**

Regrowth following grazing during drought is limited primarily by reduced axillary tiller production and secondarily by regrowth of existing meristematic tissue. Moderate grazing during drought did not appear to reduce annual maintenance of these grasses. However, care should be taken in interpreting results for blue grama tiller density because of possible measurement error and western wheatgrass tiller replacement because drought may have an affect ($p=.09$). Grazing both during and after drought did not influence tiller growth or axillary tiller emergence. In addition, drought and grazing impacts evaluated over two years did not affect total net primary production of this site (Heitschmidt, unpublished data).

These results demonstrate a one year growing season drought and moderate grazing (both before and after drought) did not appear to adversely affect specific tiller processes. Furthermore, different tiller parameters measured (i.e. tiller growth rates, axillary tiller emergence, tiller density or replacement) and different hierarchical levels (i.e. individual tiller, plant biomass, site productivity) resulted in different interpretations of effects to the same treatments. Consequently, it is important to consider several levels when evaluating grassland dynamics in response to disturbances in order to avoid misleading conclusions.

Rest from grazing following drought under our study conditions was not necessary and did not prove to be beneficial to either western wheatgrass or blue grama. Tiller response are probably influenced by several other factors including: utilization during and after drought, degree of drought, length of drought, time of defoliation, and precipitation after drought. It

should be noted that above average precipitation before drought and above average spring precipitation the spring following drought probably influenced our results. In addition, the study site was not grazed two years prior to this research and may have also influenced the results.

Tiller processes may be regulated in a density dependent manner and independent of short-lived external stresses. Precipitation was 30% percent above average the year before this study and therefore tiller populations at this time may represent tiller numbers approaching carrying capacity at this site. Possibly that tiller population size before our study began may have controlled tiller processes (tiller growth, tillering, replacement and tiller density) to a greater extent than the drought and grazing treatments. Future research should address cumulative effects of grazing during and after drought on tiller dynamics. In addition, greater care should be taken when interpreting yearly precipitation compared to long-term average precipitation. Yearly average precipitation may have little meaning when determining impacts of drought. Precipitation amount within a specific time (i.e. spring) of the year may be a better measure of drought. For example, in 1995 average precipitation was 20% below normal, but plants seemed to have recovered from the previous years drought. In the spring of 1995 rainfall was above average and it is possible that this allowed plants adequate resources at the right time to recover.

Spring precipitation in the Northern Great Plains may be the driving factor in plant dynamics, however, further research on the effects of drought time are needed. Our results indicate that elimination of livestock during or after a one year severe growing season drought is not necessary to maintain plant populations on the tiller level. Pastures stocked moderately

during and after drought did not adversely affect sustainability of dominate native grasses on the Northern Great Plains under the conditions of this study.

Scientific judgments on treatments effects are determined by comparing p-values to a alpha value which is subjectively set by a researcher. Setting the critical alpha value to $p < .10$ may be more conservative in quantifying impacts compared to a critical alpha value of $p < .05$ because it allows for a greater chance of detecting a significant treatment effect. However, significant drought and grazing effects in this study were established when p-values of interactions and main effects were less than .05. Different interpretations of drought and grazing effects could be reach if the critical alpha value is changed form $p < .05$ to $p < .10$. In fact, several interactions and main effects become significant at $p < .10$ that were not significant at the $p < .05$ level (see Tables 3 and 4).

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