# EFFECTS OF ENVIRONMENTAL FACTORS

# Range Plant Growth and Development Are Affected by Climatic Factors

Llewellyn L. Manske PhD
Report DREC 11-3019c Range Scientist
North Dakota State University
Dickinson Research Extension Center

Range plant growth and development are regulated by climatic conditions. The long-term climatic conditions determine the type of vegetation in that region. The most ecologically important climatic factors affecting rangeland plant growth are light, temperature, water (precipitation), and water deficiency. These factors require consideration during the development of long-term rangeland management strategies (Manske 2011).

**Temperature**

Temperature, an approximate measurement of the heat energy available from solar radiation, is an important factor because most plant biological activity and growth occur within only a narrow range of temperatures, between 32°F (0°C) and 122°F (50°C) (Barbour et al. 1987). High temperatures limit biological reactions because the complex structures of proteins are disrupted or denatured. Although respiration and photosynthesis can continue slowly at temperatures well below 32°F if plants are physiologically "hardened", low temperatures limit biological reactions because water becomes unavailable when it is frozen and because available energy is inadequate.

Low temperatures define the length of the active growing season. The growing season for annually seeded plants corresponds approximately to the frost-free period, the number of days between the last day with minimum temperatures below 32°F (0°C) in the spring and the first day with minimum temperatures below 32°F (0°C) in the fall (Ramirez 1972). Perennial plants maintain physiological processes throughout the year. Winter dormancy in perennial plants is not total inactivity but reduced activity (Leopold and Kriedemann 1975). Perennial grassland plants can grow actively beyond the frost-free period if temperatures are above the level that freezes water in plant tissue and soil. Perennial plants begin active growth more than 30 days before the last frost in spring and continue growth after the first frost in fall; the growing season for perennial plants is considered to be between the first 5 consecutive days in spring and the last 5 consecutive days in fall with a mean daily temperature at or above 32°F (0°C), generally from mid April through mid October. Low air temperature during the early and late portions of the growing season and high temperatures after mid summer greatly limit plant growth (Jensen 1972).

Different plant species have different optimum temperature ranges. Cool-season plants, which are $C_3$ photosynthetic pathway plants, have an optimum temperature range of 50° to 77°F (10° to 25°C). Warm-season plants, which are $C_4$ photosynthetic pathway plants, have an optimum temperature range of 86° to 105°F (30° to 40°C) (Coyne et al. 1995).

Large fluctuations in seasonal and daily air temperature occur in the Northern Plains. The large diurnal change in temperature during the growing season, which has warm days and cool nights, is beneficial for plant growth because warm days increase the photosynthetic rate and cool nights reduce the respiration rate (Leopold and Kriedemann 1975).

**Water (Precipitation)**

Water, an integral part of living systems, is ecologically important because it is a major force in shaping climatic patterns and biochemically important because it is a necessary component in physiological processes (Brown 1995). Water is the principal constituent of plant cells, usually composing over 80% of the fresh weight of herbaceous plants. Water is the primary solvent in physiological processes by which gases, minerals, and other materials enter plant cells and by which these materials are translocated to various parts of the plant. Water is the substance in which processes such as photosynthesis and other biochemical reactions occur and a structural component of proteins and nucleic acids. Water is also essential for the maintenance of the rigidity of plant tissue and for cell enlargement and growth in plants (Brown 1977, Brown 1995).

**Water Deficiency**

The climatic conditions in the Northern Plains cause frequent periods when plants experience water stress. Rain deficiency periods in which 75% or less of the long-term mean precipitation is received are classified as droughts. Periods of drought conditions can last for a full year or a complete growing season, but water deficiency periods of one month are long enough to limit herbage production greatly. Water deficiency conditions during May, June, and July are not frequent. These months constitute the primary period of production for range plant communities. August, September, and October experience water deficiency conditions more than half the time and are not dependable for positive water relations. The water relations during this latter portion of the growing season limit range plant growth and herbage biomass accumulation (Manske 2011). Frequent late-season water deficiency limits shrub and tree growth more than grass growth.

**Water Stress**

Temperature and precipitation act together to affect the physiological and ecological status of range plants. The balance between rainfall and potential evapotranspiration determines a plant's biological water potential status. Precipitation-evapotranspiration levels interact and influence the rates of the carbon and nitrogen cycles. Evaporation rates are dependent on temperature: as average temperature decreases, evaporation rate decreases; as temperature increases, evaporation rate increases. The mixed grass and short grass prairie regions have greater evapotranspiration demand than precipitation. The tall grass prairie region has greater precipitation than evapotranspiration demand.

The native vegetation in the Northern Plains comprises a mixture of cool-season and warm-season species. The relationship between temperature and evaporation levels affects the ratio of cool-season to warm-season grasses in the plant species composition. The northern portion of the region has lower average temperature and lower evaporation rate; these conditions result in a higher percentage of cool-season species. The southern portion of the region has higher average temperature and greater evaporation rate; these conditions result in a higher percentage of warm-season species. A mixture of cool- and warm-season species is highly desirable because the herbage biomass production remains more stable over wide variations in seasonal temperature, precipitation, and evaporation levels.

During periods when rainfall is lower than evapotranspiration demand, a water deficiency exists. Under water deficiency conditions, the rate of water loss from transpiration exceeds the rate of water absorption by the roots, and plants undergo water stress. Water stress can vary from a small decrease in water potential (as in midday wilting on warm clear days) to the lethal limit of dessication. Although range plants have mechanisms that help reduce damage from water stress, water deficiency conditions lasting a month cause plants to experience water stress severe enough to reduce herbage production (Brown 1977, Brown 1995). The annual variation in temperature, precipitation, and evaporation affects the severity and duration of water deficiency, which in turn affect the levels of water stress.

**Plant Water Stress**

Plants experiencing water stress conditions respond at different inhibitory levels in relationship to the severity of the water deficiency. Early stages of water stress slow shoot and leaf growth. Leaves show signs of wilting, folding, and discoloration. Tillering and new shoot development are reduced, but root production may be increased. Senescence of older leaves is accelerated. Cell wall formation, cell division, and protein synthesis are reduced. As water stress increases, enzyme activity declines and the formation of necessary compounds slows or ceases. The stomata begin to close, and rates of transpiration and photosynthesis decrease. Respiration and translocation are substantially reduced as water stress increases. When water stress becomes severe, most functions nearly or completely cease and severe damage occurs. Leaf and root mortality induced by water stress progresses from the tips to the crown, its rate increasing with increasing stress. If water stress is prolonged or becomes more severe, the condition can be lethal. Plant death occurs when the meristems become dehydrated beyond the limits required to maintain cell turgidity and biochemical activity (Brown 1995).

Plants in water stress have limited growth and reduced photosynthetic activity. Plant vigor is decreased, carbohydrate storage is reduced, and root biomass is reduced. Plant height and herbage biomass accumulation are reduced. Leaf senescence increases and, as a result, nutritional quality of forage decreases. The rate of sexual reproduction is diminished as a result of a decrease in seed stalk numbers and height and a reduction in numbers of seeds in the seed heads. Rate of vegetative reproduction is reduced because the number of axillary buds and the number of secondary tillers decrease.

Basal cover is reduced because of mortality of entire plants or portions of plants, and open spaces in the plant community increase because of a decrease in plant numbers. The species composition shifts to an increase in species with advanced water-stress resistance mechanisms and a decrease in drought-susceptible species. Occurrence of some forbs and weedy species increases because of their ability to exploit the open spaces. Quantity and quality of wildlife habitat diminish. Livestock performance decreases because of the reductions in the quantity and quality of available forage, which in turn cause a reduction in milk production and a corresponding reduction in calf rate of gain and weaning weight. During extended periods of water stress, stocking rates generally need to be reduced.

**Light**

Light is the ultimate source of energy and the most important ecological factor affecting plant growth. Variations in quality, intensity, and duration of light affect plant growth. Light is necessary for photosynthesis, the process that converts light energy into chemical energy. The rate of photosynthesis varies with different wavelengths, but the quality (wavelength) of sunlight does not vary enough in a given region to have an important differential effect on the rate of photosynthesis. The intensity of sunlight (measurable energy) and duration of sunlight (length of day or photoperiod), however, do vary sufficiently to affect plant growth. Light intensity varies greatly with season and time of day because of changes in the angle of incidence of the sun's rays and the distance light travels through the atmosphere. Light intensity also varies with the amount of humidity and cloud cover because atmospheric moisture absorbs and scatters light rays. However, the greatest variation in intensity of light received by range plants results from the various degrees of shading from other plants. Because most range plants require full sunlight or very high levels of sunlight for best growth, shading can reduce or limit growth of range plants. Duration of sunlight (day-length period or photoperiod) is one of the most dependable cues by which plants time their activities in temperate zones. The buds or leaves of a plant contain sensory receptors, specially pigmented areas that detect day length and night length and can activate one or more hormone and enzyme systems that bring about physiological responses. The phenological development of rangeland plants is triggered primarily by changes in the length of daylight, although other environmental factors produce secondary effects and may cause slight variations in the pattern of phenological development. The tilt of the earth's axis in conjunction with the earth's annual revolution around the sun produces the seasons and changes the length of daylight, which increases from the beginning of the growing season until mid June then decreases to the end of the growing season. Photoperiod (day-length period) for a given date and locality remains the same from year to year (Odum 1971, Daubenmire 1974, Barbour et al. 1987).

Changes in day length (photoperiod) function as the timer and trigger that activates or stops physiological processes initiating growth and flowering and activates the process of hardening for resistance to low temperatures in the fall and winter. Vegetative growth is triggered by photoperiod and temperature (Langer 1972, Dahl 1995), and reproductive initiation is triggered primarily by photoperiod (Roberts 1939, Leopold and Kriedemann 1975, Dahl 1995) but can be slightly modified by temperature and precipitation (McMillian 1957, Leopold and Kriedemann 1975, Dahl and Hyder 1977, Dahl 1995). Cool- and warm-season plants respond to changes in photoperiod differently. Generally, most cool-season plants are long-day plants, and most warm-season plants are short-day plants. Long-day plants reach the flowering stage after exposure to a critical photoperiod and during the period of increasing daylight between the beginning of active growth and mid June, usually flowering before 21 June. Short-day plants are induced into flowering by day lengths that are shorter than a critical length and that occur during the period of decreasing day length after mid June, usually flowering after 21 June. Short-day plants are technically responding to the increase in the length of the night period rather than to the decrease in the day length (Weier et al. 1974, Leopold and Kriedemann 1975).

**Management Implications**

The combined influences of light, temperature, and precipitation affect the quantity and quality of plant growth in the Northern Plains and can limit livestock production if not considered during the planning of long-term grazing management strategies. Strategies based on phenological growth stages of the major grasses can be planned by calendar date after the relationships between growth stage of the grasses and date have been determined. Implementation of such strategies has the potential to maintain the stability of the grassland ecosystem, enhance quantity and quality of herbage, and sustain livestock production.

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## Literature Cited


**Barbour, M.G., J.H. Burk, and W.D. Pitts. 1987.** Terrestrial plant ecology. The Benjamin/Cummings Publishing Co., Menlo Park, CA. 634p.

**Brown, R.W. 1977.** Water relations of range plants. p. 97-140. *in* R.E. Sosebee (ed.). Rangeland plant physiology. Range Science Series No. 4. Society for Range Management. Denver, CO.

**Brown, R.W. 1995.** The water relations of range plants: adaptations of water deficits. p. 291-413. *in* D.J. Bedunah and R.E. Sosebee (eds.). Wildland plants: physiological ecology and developmental morphology. Society for Range Management. Denver, CO.

**Coyne, P.I., M.J. Trlica, and C.E. Owensby. 1995.** Carbon and nitrogen dynamics in range plants. p. 59-167. *in* D.J. Bedunah and R.E. Sosebee (eds.). Wildland plants: physiological ecology and developmental morphology. Society for Range Management. Denver, CO.

**Dahl, B.E., and D.N. Hyder. 1977.** Developmental morphology and management implications. p. 257-290. *in* R.E. Sosebee (ed.). Rangeland plant physiology. Range Science Series No. 4. Society for Range Management. Denver, CO.

**Dahl, B.E. 1995.** Developmental morphology of plants. p. 22-58. *in* D.J. Bedunah and R.E. Sosebee (eds.). Wildland plants: physiological ecology and developmental morphology. Society for Range Management. Denver, CO.

**Daubenmire, R.F. 1974.** Plants and Environment. John Wiley and Sons, New York, NY. 422p.

**Jensen, R.E. 1972.** Climate of North Dakota. National Weather Service, North Dakota State University, Fargo, ND. 48p.

**Langer, R.H.M. 1972.** How grasses grow. Edward Arnold, London, Great Britain. 60p.

**Leopold, A.C., and P.E. Kriedemann. 1975.** Plant growth and development. McGraw-Hill Book Co., New York, NY. 545p.

**Manske, L.L. 2011.** Environmental factors to consider during planning of management for range plants in the Dickinson, North Dakota, region, 1892-2010. NDSU Dickinson Research Extension Center. Range Research Report DREC 11-1018n. Dickinson, ND. 40p.

**McMillan, C. 1957.** Nature of the plant community. III. Flowering behavior within two grassland communities under reciprocal transplanting. American Journal of Botany 44(2):144-153.

**Odum, E.P. 1971.** Fundamentals of ecology. W.B. Saunders Company. Philadelphia, PA. 574p.

**Ramirez, J.M. 1972.** The agroclimatology of North Dakota, Part 1. Air temperature and growing degree days. Extension Bulletin No. 15. North Dakota State University, Fargo, ND. 44p.

**Roberts, R.M. 1939.** Further studies of the effects of temperature and other environmental factors upon the photoperiodic response of plants. Journal of Agricultural Research 59(9):699-709.

**Weier, T.E., C.R. Stocking, and M.G. Barbour. 1974.** Botany: an introduction to plant biology. John Wiley and Sons, New York, NY. 693p.

# Plant Water Stress Frequency and Periodicity in Western North Dakota

Llewellyn L. Manske PhD, Sheri Schneider, John A. Urban, and Jeffery J. Kubik
Report DREC 10-1077 Range Research Program Staff
North Dakota State University
Dickinson Research Extension Center

Water stress develops in plants when the rate of water loss from transpiration exceeds the rate of water absorption by the roots. The excessive loss of plant water causes cells to lose turgor and, consequently, wilting of plant structures. Water stress reduces plant growth and development during growing season months with water deficiency which results when precipitation amounts are lower than the evapotranspiration rates. Conditions that create water deficiencies are variable with monthly changes in temperature and precipitation. Soil water losses increase with increases in evapotranspiration demand. Evaporation rates increase as temperature increases. For each increase of 1° C in mean monthly temperature, an increase of 2 mm of monthly precipitation are required to prevent water deficiency and plant water stress. Plants in water stress have limited growth and herbage biomass accumulation. Water stress can vary in degree from a small decrease in water potential, as in midday wilting on warm, clear days, to the lethal limit of desiccation. Early stages of water stress slow shoot and leaf growth. Leaves show signs of wilting, folding, and discoloration. Tillering and new shoot development decrease. Root production may increase. Senescence of older leaves accelerates. Rates of cell wall formation, cell division, and protein synthesis decrease. As water stress increases, enzyme activity declines and the formation of necessary compounds slows or ceases. The stomata begin to close; this reaction results in decreased rates of transpiration and photosynthesis. Rates of respiration and translocation decrease substantially with increases in water stress. When water stress becomes severe, most functions nearly or completely cease and serious damage occurs. Leaf and root mortality induced by water stress progresses from the tips to the crown. The rate of leaf and root mortality increases with increasing stress. Water stress can increase to a point that is lethal, resulting in damage from which the plant cannot recover. Plant death occurs when meristems become so dehydrated that cells cannot maintain cell turgidity and biochemical activity (Brown 1995).

A research project was conducted to determine the frequency and periodicity of water stress in perennial rangeland plants of western North Dakota. Plant water stress develops in plant tissue during growing season months with water deficiency conditions. The frequency, or rate of occurrence, of water stress conditions affects the percentage of total potential quantity and quality of herbage biomass produced by plants and the periodicity, or rate of reoccurrence, of water stress conditions affects the percentage of time that plant production is limited during growing season months.

**Procedures**

Monthly periods with water deficiency can be identified by the ombrothermic diagram technique reported by Emberger et al. (1963). This method graphs mean monthly temperature (°C) and monthly precipitation (mm) on the same axis, with the scale of the precipitation data at twice that of the temperature data. The resulting ombrothermic diagram shows monthly periods in which precipitation is greater than the evapotranspiration rate set by the mean monthly temperature and identifies monthly periods with water deficiency conditions, unfavorable periods during which perennial plants experience water stress. Water deficiency exists during months when the precipitation data bar drops below the temperature data curve. Ombrothermic diagrams were developed from historical climatological data of temperature and precipitation collected during the 118 year period from 1892 through 2009 at the Dickinson Research Extension Center, latitude 46° 53' N, longitude 102° 49' W, elevation 2,500 feet, Dickinson, North Dakota, USA.

**Results and Discussion**

The long-term (118 year) mean annual temperature was 40.9º F. January was the coldest month, with a mean temperature of 11.5º F. July and August were the warmest months, with mean temperatures of 68.8º F and 67.0º F, respectively (table 1). Perennial grassland plants are capable of active growth for periods longer than the frost-free period. The growing season for perennial plants was considered to be between the first 5 consecutive days in spring and the last 5 consecutive days in fall with the mean daily temperature at or above 32º F. In western North Dakota, the growing season for perennial plants was considered to be generally from mid April through mid October (6.0 months). The long-term mean annual precipitation was 16.0 inches (table 1). The growing season precipitation (April to October) was 13.5 inches, 84.5% of the annual precipitation. The early portion of the growing season (April to July) received 9.5 inches, 59.5% of the annual precipitation and the latter portion of the growing season (August to October) received 4.0 inches, 25.0% of the annual precipitation. Total precipitation received during the nongrowing season (November through March) was only 2.5 inches, 15.6% of the annual precipitation (table 2).

The long-term (118 year) ombrothermic diagram (figure 1) showed near water deficiency conditions during August, September, and October, a finding indicating that rangeland plants generally had difficulty growing and accumulating biomass during these 3 months. Favorable water relations occurred during April, May, June, and July, a period during which rangeland plants were capable of growing and accumulating herbage biomass.

The monthly ombrothermic diagrams for 118 years, 1892 to 2009, were reported in Manske (2010). Simplified representations of the ombrothermic water deficiency data were placed in table 3a, b, c. The first score of years, 1890 to 1909, with 18 years of data, had 43.0 growing season months with water deficiency conditions, 39.8%, for a mean of 2.4 months with water deficiency per growing season (table 3a). The second score of years, 1910 to 1929, had 34.0 growing season months with water deficiency conditions, 28.3%, for a mean of 1.7 months with water deficiency per growing season (table 3a). The third score of years, 1930 to 1949, had 43.5 growing season months with water deficiency conditions, 36.3%, for a mean of 2.2 months with water deficiency per growing season (table 3b). The fourth score of years, 1950 to 1969, had 37.0 growing season months with water deficiency conditions, 30.8%, for a mean of 1.9 months with water deficiency per growing season (table 3b). The fifth score of years, 1970 to 1989, had 37.5 growing season months with water deficiency conditions, 31.3%, for a mean of 1.9 months with water deficiency per growing season (table 3c). The sixth score of years, 1990 to 2009, had 36.5 growing season months with water deficiency conditions, 30.4%, for a mean of 1.8 months with water deficiency per growing season (table 3c). The 118 year period, 1892 to 2009, had 231.5 growing season months with water deficiency conditions, 32.7%, for a long-term mean of 2.0 months with water deficiency per growing season (table 3a, b, c).

Growing seasons that had no months with water deficiency conditions occurred seven times, 1912, 1920, 1941, 1951, 1982, 1985, and 1998, 5.9%, for a long-term mean of about 1 growing season without water deficiency in 16.9 years (table 3a, b, c).

Precipitation levels during an entire growing season compared to the long-term mean for 118 years separated growing seasons into dry, wet, or normal categories. Dry growing seasons received less than 75% of the long-term mean precipitation. Growing seasons with precipitation amounts at less than 75% and greater than 50% of the long-term mean were considered to have moderate drought conditions. Growing seasons with precipitation amounts at less than 50% of the long-term mean were considered to have severe drought conditions. Wet growing seasons received greater than 125% of the long-term mean precipitation. Growing seasons with precipitation amounts at greater than 125% and less than 150% of the long-term mean were considered to have moderate wet conditions. Growing seasons with precipitation amounts at greater than 150% of the long-term mean were considered to have extreme wet conditions. Normal growing seasons received greater than 75% and less than 125% of the long-term mean precipitation.

The first score of years, 1890 to 1909, with 18 years of data, had 5 dry growing seasons, 27.8%, for a mean of 1 dry growing season in 3.6 years. All 5 dry growing seasons had moderate drought conditions (table 3a). The second score of years, 1910 to 1929, had 3 dry growing seasons, 15.0%, for a mean of 1 dry growing season in 6.7 years. Two dry growing seasons had moderate drought conditions and one dry growing season, 1919, had severe drought conditions (table 3a). The third score of years, 1930 to 1949, had 5 dry growing seasons, 25.0%, for a mean of 1 dry growing season in 4.0 years. Three dry growing seasons had moderate drought conditions and two dry growing seasons, 1934 and 1936, had severe drought conditions (table 3b). The fourth score of years, 1950 to 1969, had 3 dry growing seasons, 15.0%, for a mean of 1 dry growing season in 6.7 years. All three dry growing seasons had moderate drought conditions (table 3b). The fifth score of years, 1970 to 1989, had 1 dry growing season, 5.0%, for a mean of 1 dry growing season in 20.0 years. The one dry growing season, 1988, had severe drought conditions (table 3c). The sixth score of years, 1990 to 2009, had 1 dry growing season, 5.0%, for a mean of 1 dry growing season in 20.0 years. The one dry growing season had moderate drought conditions (table 3c). The 118 year period, 1892 to 2009, had 18 dry growing seasons, 15.3%, for a mean of 1 dry growing season in 6.6 years. Fourteen dry growing seasons had moderate drought conditions, 11.9%, for a mean of 1 growing season with moderate drought conditions in 8.4 years, and four dry growing seasons, 1919, 1934, 1936, and 1988, had severe drought conditions, 3.4%, for a mean of 1 growing season with severe drought conditions in 29.5 years.

The first score of years, 1890 to 1909, with 18 years of data, had 1 wet growing season, 5.6%, for a mean of 1 wet growing season in 18.0 years. The one wet growing season had moderate wet conditions (table 3a). The second score of years, 1910 to 1929, had 4 wet growing seasons, 20.0%, for a mean of 1 wet growing season in 5.0 years. Three wet growing seasons had moderate wet conditions and one wet growing season, 1914, had extreme wet conditions (table 3a). The third score of years, 1930 to 1949, had 3 wet growing seasons, 15.0%, for a mean of 1 wet growing season in 6.7 years. Two wet growing seasons had moderate wet conditions and one wet growing season, 1941, had extreme wet conditions (table 3b). The fourth score of years, 1950 to 1969, had 4 wet growing seasons, 20.0%, for a mean of 1 wet growing season in 5.0 years. All four wet growing seasons had moderate wet conditions (table 3b). The fifth score of years, 1970 to 1989, had 6 wet growing seasons, 30.0%, for a mean of 1 wet growing season in 3.3 years. Five wet growing seasons had moderate wet conditions and one wet growing season, 1982, had extreme wet conditions (table 3c). The sixth score of years, 1990 to 2009, had 3 wet growing seasons, 15.0%, for a mean of 1 wet growing season in 6.7 years. Two wet growing seasons had moderate wet conditions and one wet growing season, 1998, had extreme wet conditions (table 3c). The 118 year period, 1892 to 2009, had 21 wet growing seasons, 17.8%, for a mean of 1 wet growing season in 5.6 years. Seventeen wet growing seasons had moderate wet conditions, 14.4%, for a mean of 1 growing season with moderate wet conditions in 6.9 years, and four wet growing seasons, 1914, 1941, 1982, and 1998, had extreme wet conditions, 3.4%, for a mean of 1 growing season with extreme wet conditions in 29.5 years.

The first score of years, 1890 to 1909, with 18 years of data, had 12 normal growing seasons, 66.7%, for a mean of 1 normal growing season in 1.5 years (table 3a). The second score of years, 1910 to 1929, had 13 normal growing seasons, 65.0%, for a mean of 1 normal growing season in 1.5 years (table 3a). The third score of years, 1930 to 1949, had 12 normal growing seasons, 60.0%, for a mean of 1 normal growing season in 1.7 years (table 3b). The fourth score of years, 1950 to 1969, had 13 normal growing seasons, 65.0%, for a mean of 1 normal growing season in 1.5 years (table 3b). The fifth score of years, 1970 to 1989, had 13 normal growing season, 65.0%, for a mean of 1 normal growing season in 1.5 years (table 3c). The sixth score of years, 1990 to 2009, had 16 normal growing seasons, 80.0%, for a mean of 1 normal growing season in 1.3 years (table 3c). The 118 year period, 1892 to 2009, had 79 normal growing seasons, 66.9%, for a mean of 1 normal growing season in 1.5 years.

The 118 year period, 1892 to 2009, had 231.5 growing season months with water deficiency conditions, 32.7%, for a mean of 2.0 months with water deficiency per growing season; this long-term period had 7.0 growing seasons with no water deficiency conditions, 5.9%, for a mean of 1 growing season without water deficiency months in 16.9 years; this long-term period had 18 growing seasons with dry conditions, 15.3%, for a mean of 1 dry growing season in 6.6 years; this long-term period had 21 growing seasons with wet conditions, 17.8%, for a mean of 1 wet growing season in 5.6 years; and this long-term period had 79 growing seasons with normal conditions, 66.9%, for a mean of 1 normal growing season in 1.5 years (table 4).

The periodicity, or rate of reoccurrence, of water deficiency conditions was not distributed evenly among the growing season months. April, May, June, and July received 59.5% of the annual precipitation and had 35.9% of the water deficiency months. August, September, and October received 25.0% of the annual precipitation and had 64.1% of the water deficiency months. Water deficiency months occurred in April, May, June, and July during 20 years (16.9%), 16 years (13.6%), 12 years (10.2%), and 45 years (38.1%) between 1892 and 2009, respectively (table 5). Water deficiency conditions occurred in August, September, and October during 62 years (52.5%), 59 years (50.0%), and 55 years (46.6%) during the 118 year period, respectively (table 5). August, September, and/or October had water deficiency conditions during 106 years, 89.8% of the past 118 years. Rangeland perennial plants produced most of their growth in leaf and flower stalk height (Goetz 1963) and in herbage biomass weight (Manske 1994) during May, June, and July because of the generally advantageous water conditions. The high periodicity of water deficiency conditions during August, September, and October limited rangeland plant growth and herbage biomass accumulation.

## Conclusion

The average 6 month perennial plant growing season, mid April to mid October, had water deficiency conditions during 2 months, 32.7%. These periods with precipitation shortages were the normal weather conditions for western North Dakota. Growing seasons without water deficiency conditions were actually the abnormal phenomenon and occurred during only 5.9% of the growing seasons. Growing seasons with dry conditions occurred during 15.3% of the years; growing seasons with moderate drought conditions occurred during 11.9% of the years; and growing seasons with severe drought conditions occurred during 3.4% of the years. Growing seasons with wet conditions occurred during 17.8% of the years; growing seasons with moderate wet conditions occurred during 14.4% of the years; and growing seasons with extreme wet conditions occurred during 3.4% of the years. Growing seasons with normal conditions occurred during 66.9% of the years during the 118 year period from 1892 to 2009. May, June, and July had water deficiency conditions 13.6%, 10.2%, and 38.1% of the time, respectively. August, September, and October had water deficiency conditions 52.5%, 50.0%, and 46.6% of the time, respectively. Water deficiency conditions reoccurred at a mean rate of 19.7% during the early portion of the growing season (April-July) and reoccurred at a mean rate of 49.7% during the latter portions of the growing season (August-October). Water deficiency conditions during growing season months caused water stress in perennial rangeland plants that limited herbage biomass growth in quantity and quality that, subsequently, resulted in reduced livestock weight production. Implementation of the twice-over rotation system which is a biologically effective grazing management strategy that activates compensatory physiological processes, activates vegetative reproduction of secondary tillers from axillary buds, and stimulates soil organism activity in the rhizosphere reduces the negative impacts caused from plant water stress by increasing plant density, reducing soil temperature, reducing evaporation of soil water, improving soil structure and water infiltration, improving soil water holding capacity, and increasing available soil mineral nitrogen to levels greater than one hundred pounds per acre.

| Table 1. Long-term mean temperature and precipitation. | | | | |
|---|---|---|---|---|
| | | Mean Monthly Temperature | | Monthly Precipitation |
| | | °F | | inches |
| | Jan | 11.47 | | 0.41 |
| | Feb | 15.28 | | 0.41 |
| | Mar | 26.18 | | 0.74 |
| | Apr | 41.54 | | 1.41 |
| | May | 52.79 | | 2.33 |
| | Jun | 61.96 | | 3.55 |
| | Jul | 68.75 | | 2.23 |
| | Aug | 67.00 | | 1.72 |
| | Sep | 56.11 | | 1.32 |
| | Oct | 43.70 | | 0.96 |
| | Nov | 28.45 | | 0.53 |
| | Dec | 16.94 | | 0.41 |
| | Mean | 40.85 °F | Total | 16.00 inches |

| Table 2. Seasonal precipitation distribution. | | | |
|---|---|---|---|
| | | Inches | Percent |
| | Average Annual Precipitation | 16.00 | |
| | Growing Season (Apr-Oct) | 13.52 | (84.50%) |
| | Apr, May, Jun, Jul | 9.52 | (59.50%) |
| | Aug, Sep, Oct | 4.00 | (25.00%) |
| | Nongrowing Season (Nov-Mar) | 2.50 | (15.63%) |

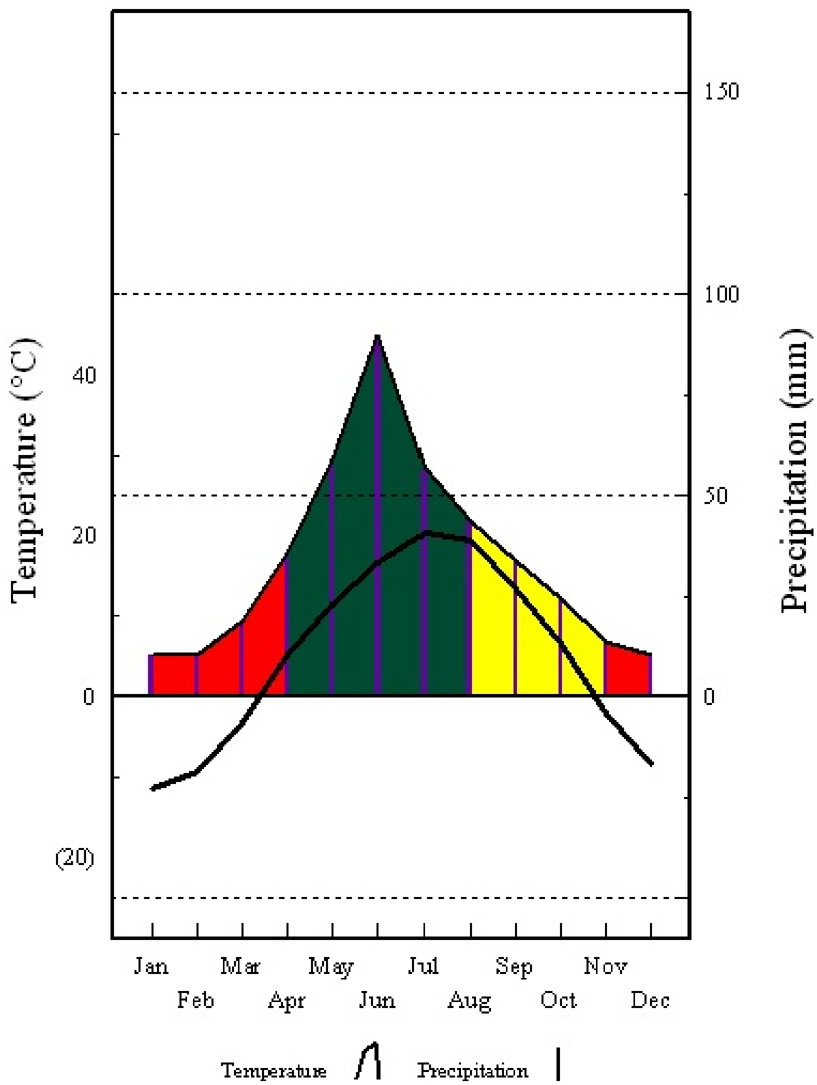
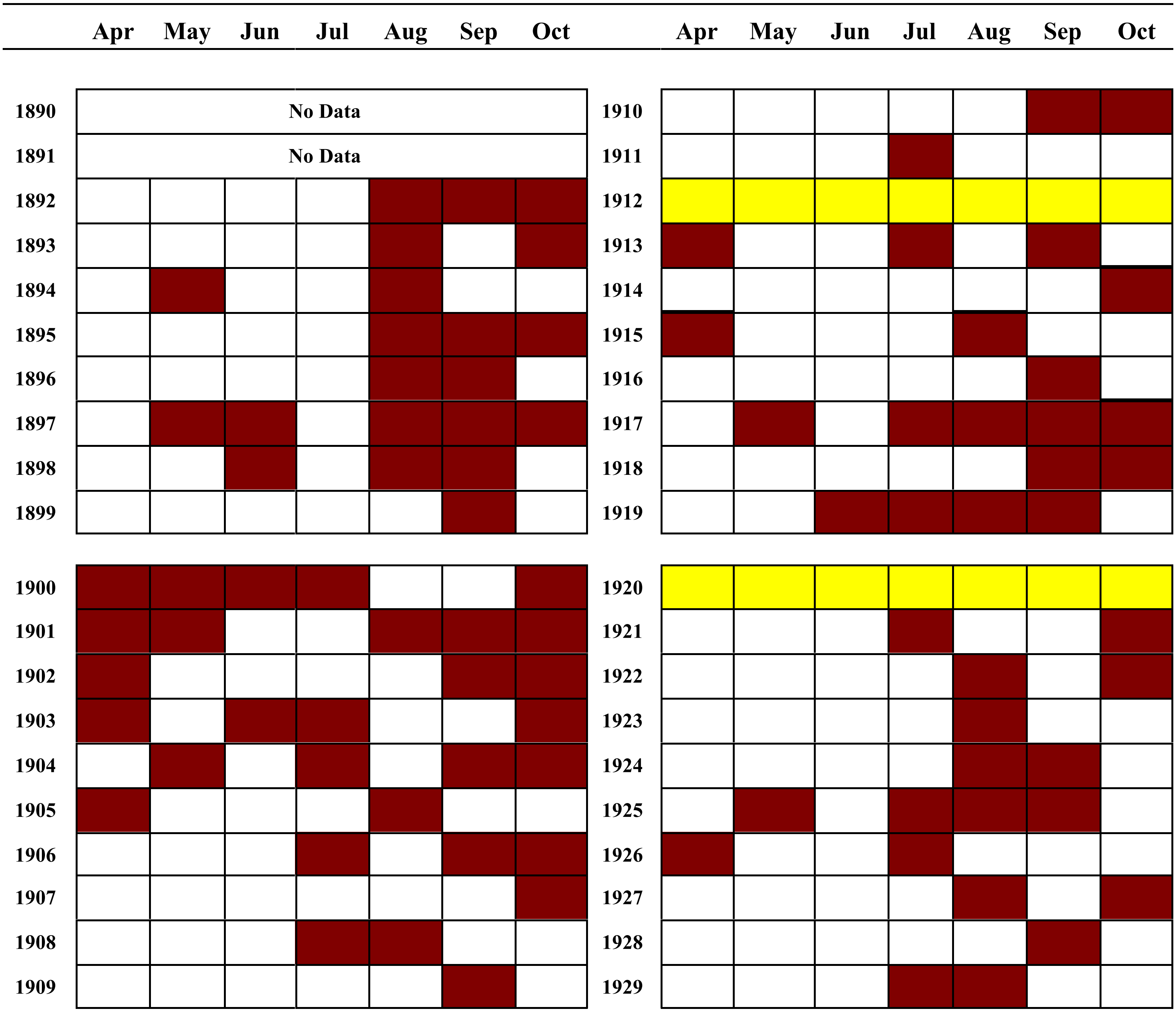



**Fig. 1. Ombrothermic diagram of long-term (1892-2009) mean monthly temperature and monthly precipitation at Dickinson, North Dakota.**

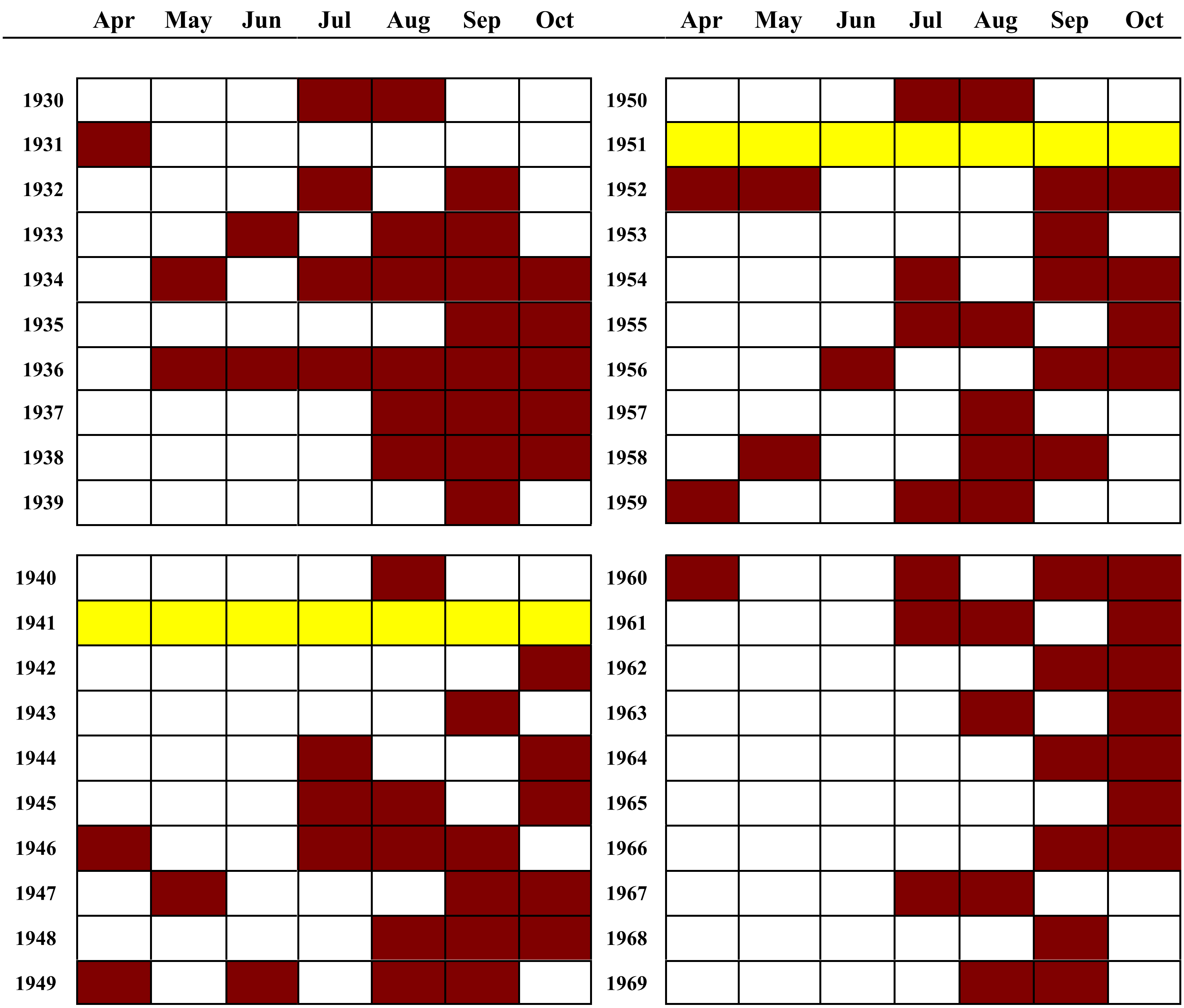
Table 3a. Growing season months with water deficiency conditions that caused water stress in perennial plants.




| 1892-1909 18 Years | | |
|---|---|---|
| Months with water deficiency (dark red) | 39.8% | 2.4 months/yr |
| Years with no water deficiency (yellow) | 0.0% | 0 yr in 18 yrs |
| Dry growing seasons | 27.8% | 1 yr in 3.6 yrs |
| Wet growing seasons | 5.6% | 1 yr in 18 yrs |
| Normal growing seasons | 66.7% | 1 yr in 1.5 yrs |

| 1910-1929 20 Years | | |
|---|---|---|
| Months with water deficiency (dark red) | 28.3% | 1.7 months/yr |
| Years with no water deficiency (yellow) | 10.0% | 1 yr in 10 yrs |
| Dry growing seasons | 15.0% | 1 yr in 6.7 yrs |
| Wet growing seasons | 20.0% | 1 yr in 5 yrs |
| Normal growing seasons | 65.0% | 1 yr in 1.5 yrs |

Table 3b. Growing season months with water deficiency conditions that caused water stress in perennial plants.



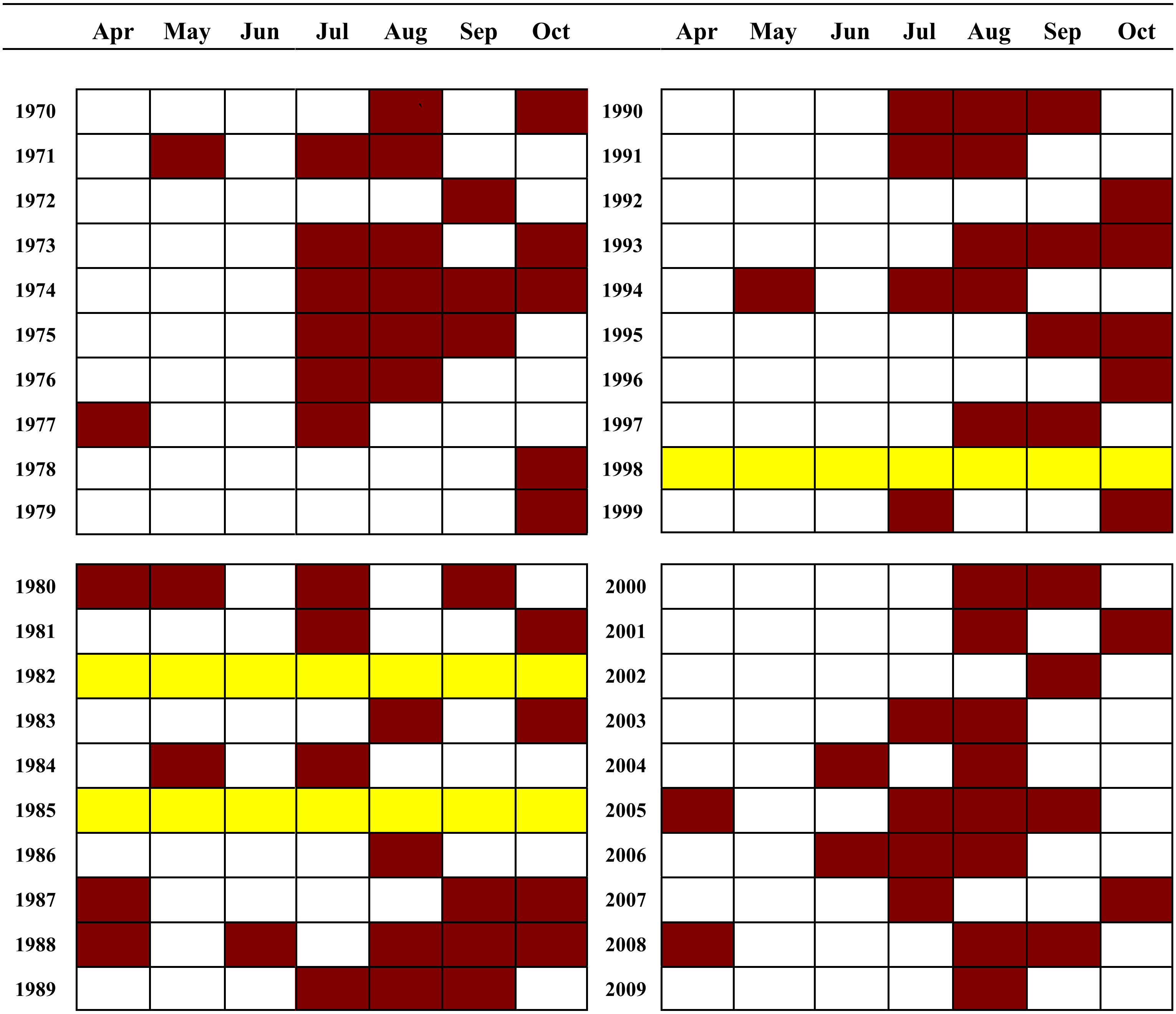

**1930-1949 20 Years**

| | | |
|---|---|---|
| Months with water deficiency | 36.3% | 2.2 months/yr |
| Years with no water deficiency | 5.0% | 1 yr in 20 yrs |
| Dry growing seasons | 25.0% | 1 yr in 4 yrs |
| Wet growing seasons | 15.0% | 1 yr in 6.7 yrs |
| Normal growing seasons | 60.0% | 1 yr in 1.7 yrs |

**1950-1969 20 Years**

| | | |
|---|---|---|
| Months with water deficiency | 30.8% | 1.9 months/yr |
| Years with no water deficiency | 5.0% | 1 yr in 20 yrs |
| Dry growing seasons | 15.0% | 1 yr in 6.7 yrs |
| Wet growing seasons | 20.0% | 1 yr in 5 yrs |
| Normal growing seasons | 65.0% | 1 yr in 1.5 yrs |

Table 3c.  Growing season months with water deficiency conditions that caused water stress in perennial plants.




**1970-1989   20 Years**

| | | |
|---|---|---|
| Months with water deficiency | 31.3% | 1.9 months/yr |
| Years with no water deficiency | 10.0% | 1 yr in 10 yrs |
| Dry growing seasons | 5.0% | 1 yr in 20 yrs |
| Wet growing seasons | 30.0% | 1 yr in 3.3 yrs |
| Normal growing seasons | 65.0% | 1 yr in 1.5 yrs |

**1990-2009   20 Years**

| | | |
|---|---|---|
| Months with water deficiency | 30.4% | 1.8 months/yr |
| Years with no water deficiency | 5.0% | 1 yr in 20 yrs |
| Dry growing seasons | 5.0% | 1 yr in 20 yrs |
| Wet growing seasons | 15.0% | 1 yr in 6.7 yrs |
| Normal growing seasons | 80.0% | 1 yr in 1.3 yrs |

| Table 4. Summary of water stress conditions. | | |
|---|---|---|
| 1892 to 2009 118 years | | |
| Months with Water Deficiency | 32.7% | 2.0 months/year |
| Growing Seasons with no Water Deficiency | 5.9% | 1 yr in 16.9 years |
| Dry Growing Seasons | 15.3% | 1 yr in 6.6 years |
| Wet Growing Seasons | 17.8% | 1 yr in 5.6 years |
| Normal Growing Seasons | 66.9% | 1 yr in 1.5 years |

Table 5. Periodicity of percent frequency of water deficiency occurring during growing season months.

| April | May | June | July | August | September | October |
|---|---|---|---|---|---|---|
| 16.9% | 13.6% | 10.2% | 38.1% | 52.5% | 50.0% | 46.6% |

## Literature Cited

**Brown, R.W. 1995.** The water relations of range plants: adaptations to water deficits. Pages 291-413. *in* D.J. Bedunah and R.E. Sosebee (eds.). Wildland plants: physiological ecology and developmental morphology. Society for Range Management. Denver, CO.

**Dickinson Research Center. 1892-2009.** Temperature and precipitation weather data.

**Emberger, C., H. Gaussen, M. Kassas, and A. dePhilippis. 1963.** Bioclimatic map of the Mediterranean Zone, explanatory notes. UNESCO-FAO. Paris. 58p.

**Goetz, H. 1963.** Growth and development of native range plants in the mixed grass prairie of western North Dakota. M.S. Thesis, North Dakota State University, Fargo, ND. 165p.

**Manske, L.L. 1994.** Problems to consider when implementing grazing management practices in the Northern Great Plains. NDSU Dickinson Research Extesion Center. Range Management Report DREC 94-1005, Dickinson, ND. 11p.

**Manske, L.L. 2010.** Environmental factors to consider during planning of management for range plants in the Dickinson, North Dakota, region, 1892-2009. NDSU Dickinson Research Extension Center. Range Research Report DREC 10-1018m. Dickinson, North Dakota. 37 p.

# Grazing Starting Dates

Llewellyn L. Manske PhD
Report DREC 08-3017c
Ran ge Scientist
North Dakota State University
Dickinson Research Extension Center

Grassland herbage production can be sustained at relatively high levels only when grass plants retain adequate leaf area. Heavy grazing of native rangeland pastures that repeatedly removes a great proportion of the leaf area has long been known to cause reductions in grassland herbage production. Grazing during early spring prior to range readiness also deprives grass plants of needed leaf area and results in reductions in grass growth, herbage production, and economic returns. The reductions in herbage production and in economic returns vary with grazing starting date and grazing strategies. These reductions in herbage production and economic returns are quantified in this report.

**Methods**

Data reported by Campbell (1952) from a four-year grazing study conducted at Swift Current, Saskatchewan, and data reported by Rogler et al. (1962) and Lorenz (per. com.) from a four-year clipping study conducted at Mandan, North Dakota, were summarized, and the amounts of herbage produced on treatments with defoliation starting at various dates were compared to the potential aboveground herbage biomass. Data collected during grazing studies conducted from 1982 to 1987 at Dickinson, North Dakota, were used to compare herbage production, animal performance, and economic net returns (gross minus pasture and forage costs) for three grazing strategies: 1) a seasonlong treatment with grazing starting 15 May, 2) a seasonlong treatment with grazing starting 15 June, and 3) a three-pasture twice-over rotation grazing system with grazing starting 1 June.

**Results**

Percent reductions from the potential herbage biomass that are caused by defoliation treatments with different starting dates are shown in table 1 and figure 1. The percentages of the reductions in herbage biomass at Swift Current, Mandan, and Dickinson are quite similar for the various defoliation starting dates. These reductions in herbage biomass show that when grazing on native rangeland is started in early May, more than 75% of potential herbage biomass will not be produced. When grazing is started in mid May, 45% to 60% of the potential herbage biomass will not be produced and will not be available for grazing livestock. When the starting date of grazing is between early June and early July, the reductions from potential herbage biomass are not great. When the starting date of grazing is delayed until early July, nearly all of the potential herbage biomass will grow and be available to grazing livestock, but the nutritional quality of the herbage will be at or below crude protein levels required for lactating cows (Whitman et al. 1951, Manske 1999b). When the starting date is deferred until mid July, after plants have produced seed, less than potential herbage biomass will be available to grazing livestock because of senescence and the translocation of cell material to belowground plant structures. The nutritional quality of the herbage on deferred grazing strategies will be below the crude protein requirements for lactating cows (Whitman et al. 1951, Manske 1999b), individual cow and calf performance will be reduced (Manske 1994), and net return per cow-calf pair will be 15% lower than net return per cow-calf pair on the seasonlong treatment with grazing starting 15 June, after the third-leaf stage (Manske 1996). The major long-term problem with a deferred management strategy that starts grazing after grass seed development is the reduction in native-grass basal cover (Sarvis 1941, Manske et al. 1988). Data from these native rangeland defoliation studies indicate that starting grazing between early June and early July causes the least reduction in herbage production, herbage nutritional quality, and grass plant density.

The phenological growth stage of grass plants can be used as an indicator of when grazing can be started without detriment to plant health and herbage production. Grass plants are physiologically capable of tolerating grazing pressure after they have reached the 3.0 or 3.5 new leaf stage (Manske 1999a). Grazing grass plants that have not reached the third new leaf stage negatively affects grass growth. Grazing grass plants after they have reached the third new leaf stage and before they have reached the flowering stage stimulates vegetative tiller production from axillary buds and subsequently increases herbage biomass production (Manske 1994). Most native cool-season grasses reach the third new leaf stage around early June, and most native warm-season grasses reach the third new leaf stage around mid June (Manske 1999a). Seasonlong grazing management strategies on native rangeland should delay grazing until mid June, but rotation grazing systems that are based on grass biological requirements and that stimulate tiller growth from axillary buds could start grazing in early June.

Comparisons between seasonlong grazing that starts before the third new leaf stage and seasonlong grazing that starts after the third new leaf stage show that starting grazing 15 May, before the third new leaf stage, causes a 45% reduction in herbage biomass production (table 1), a 29% reduction in stocking rate, a 14% reduction in calf average daily gain (ADG), and a 40% reduction in calf gain per acre (table 2) compared to starting grazing 15 June, after the third new leaf stage. The reduction of animal performance on seasonlong grazing that starts before the third new leaf stage causes an 80% reduction in net return after pasture costs per cow-calf pair and a reduction of 89% per acre compared to seasonlong grazing that starts after the third new leaf stage (table 2). The seasonlong treatment with grazing starting after the third new leaf stage causes less physiological damage to grass plants resulting in greater herbage biomass production, greater animal performance, and higher economic returns after pasture costs than does the seasonlong treatment with grazing starting before the third new leaf stage (table 2).

Comparisons between seasonlong grazing and twice-over rotation grazing that start after the third new leaf stage show that seasonlong grazing causes a 29% reduction in stocking rate, a 6% reduction in calf average daily gain (ADG), a 33% reduction in calf gain per acre, a 33% reduction in returns after pasture costs per cow-calf pair, and a 53% reduction in returns after pasture costs per acre (table 2) compared to twice-over rotation grazing. The twice-over rotation system with grazing starting after the third new leaf stage also has grazing periods designed to coordinate with grass phenological development and to meet the biological requirements of grass plants (Manske 1999a) and grazing animals (Manske 1994).

The biologically effective twice-over rotation system results in a 98% and 40% increase in stocking rate, a 23% and 6% increase in calf average daily gain (ADG), a 148% and 49% increase in calf gain per acre, a 630% and 49% increase in returns after pasture costs per cow-calf pair, and a 1872% and 111% increase in returns after pasture costs per acre (table 2) compared to seasonlong treatments with grazing starting before the third new leaf stage and grazing starting after the third new leaf stage, respectively. Grazing systems with rotation dates designed to match grass plant growth and phenological development and to meet the biological requirements of the plants produce greater herbage biomass and improve animal performance. Seasonlong grazing and grazing systems with rotation dates set in an arbitrary sequence not coordinated with grass growth and phenological development are antagonistic to plant physiological processes and to ecosystem biogeochemical processes resulting in reductions in plant and animal production.

Table 1. Percent reduction from potential aboveground herbage biomass on defoliation treatments with different starting dates.

| Starting dates of defoliation | Swift Current[a] grazing data | Mandan[b] clipping data | Dickinson grazing data |
|---|---|---|---|
| 1 May | -78% | -76% | - |
| 15 May | -46% | -57% | -45% |
| 1-5 Jun | -13% | -43% | - |
| 15-20 Jun | -7% | -33% | -21% |
| 1-5 Jul | 0% | -8% | - |
| 15-20 Jul | -18% | 0% | 0% |
| 1 Aug | - | -13% | - |

[a]Campbell 1952
[b]Rogler et al. 1962
[b]Lorenz (per. com.)

Table 2. Comparisons of costs, production, and net returns on native rangeland managed by seasonlong and twice-over rotation grazing systems with grazing starting before and after the 3rd leaf stage.

| | | Seasonlong starting before 3rd leaf | Seasonlong starting after 3rd leaf | Twice-over Rotation starting after 3rd leaf |
|---|---|---|---|---|
| Stocking rate (acres/AUM) | (ac) | 4.04 | 2.86 | 2.04 |
| Calf ADG | (lb) | 1.80 | 2.09 | 2.21 |
| Calf gain/acre | (lb) | 13.59 | 22.55 | 33.64 |
| Pasture cost/cow/calf pr | | | | |
| @$8.76/ac | ($) | 212.34 | 111.25 | 78.84 |
| Cost/lb calf gain | ($) | 0.64 | 0.39 | 0.26 |
| Net return/cow/calf pr | | | | |
| @$0.70/lb | ($) | 18.24 | 89.18 | 133.10 |
| Net return/acre@$0.70/lb | ($) | 0.75 | 7.02 | 14.79 |

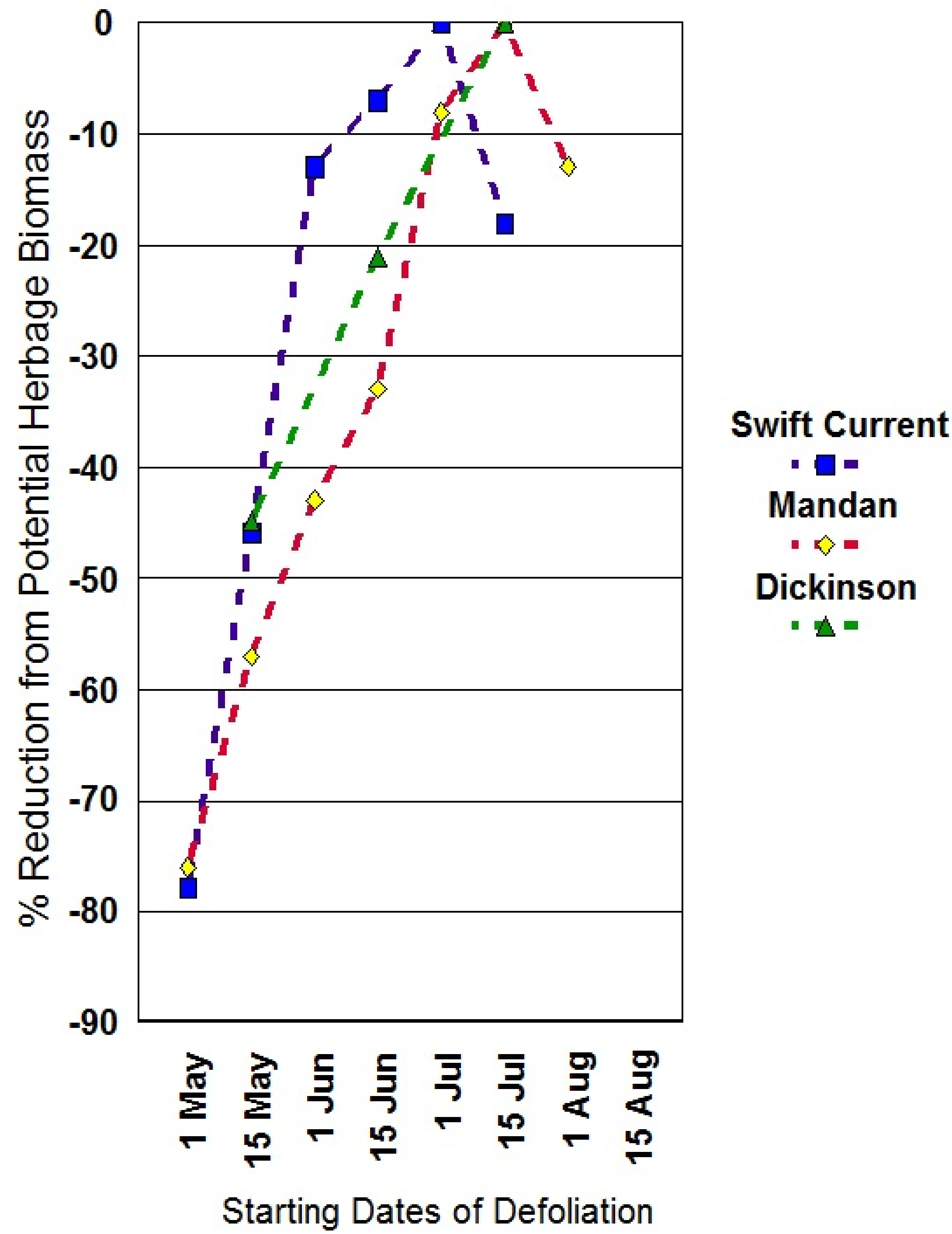



**Fig. 1. Percent reduction from potential aboveground herbage biomass on defoliation treatments with different starting dates.**

**Discussion**

The amount of herbage biomass produced on grasslands decreases when plants are defoliated before the third new leaf stage. The earlier defoliation is started, the greater the decrease in herbage production. Early spring growth depends both on carbohydrate reserves and on photosynthetic products from the active leaf area of the tiller. Before the third new leaf stage, the plant has little leaf area and low carbohydrate levels. Defoliation of the plant at this time results in reduced rates of herbage production (Coyne et al. 1995) because the plant produces little photosynthetic product and must depend upon stored carbohydrates, which are usually not adequate for complete recovery of growth. This early spring damage causes a reduction in herbage biomass production for the entire growing season. The reduction in herbage biomass reduces stocking rate and animal performance and results in lower economic returns after pasture costs per cow-calf pair and per acre.

Sustaining high levels of herbage production on grasslands requires that grazing not begin before the plants have reached the 3.0 or 3.5 new leaf stage. Delaying grazing on native rangeland until 1 June, when cool-season grasses reach the third new leaf stage, requires that another type of pasture forage be available for grazing earlier. Some domesticated perennial cool-season grasses reach the third new leaf stage three to five weeks earlier than native cool-season grasses and can be grazed as complementary spring pastures before native rangeland reaches grazing readiness. Domesticated cool-season grass pastures like crested wheatgrass or smooth bromegrass can be grazed from early May, after they have reached the third new leaf stage, to early June, when native cool-season grasses reach the third new leaf stage. Like native rangeland, complementary spring domesticated grass pastures should be grazed only after plants have reached the third new leaf stage. The start of the grazing season on domesticated grass pastures is restricted to very late April or early May, because no perennial grasses in the Northern Plains reach the third new leaf stage before late April.

**Summary**

Grazing native rangeland before the grass plants reach the third new leaf stage causes reductions in herbage biomass production and subsequent reductions in stocking rate and animal performance. These reductions result in lower economic returns after pasture costs for a livestock operation. Herbage biomass production can be increased, along with stocking rate, animal performance, and net returns after pasture costs, when grazing is started after the third new leaf stage. Herbage production can be further increased when grazing started after the third new leaf stage is coordinated with grass phenological growth to meet the biological requirements of the grass plants. With such management, stocking rate, calf average daily gain, calf gain per acre, net returns after pasture costs per cow-calf pair, and net returns after pasture costs per acre will also increase.

Acknowledgment

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## Literature Cited


**Campbell, J.B. 1952.** Farming range pastures. Journal of Range Management 5:252-258.

**Coyne, P.I., M.J. Trlica, and C.E. Owensby. 1995.** Carbon and nitrogen dynamics in range plants. p. 59-167. *in* D.J. Bedunah and R.E. Sosebee (eds.). Wildland plants: physiological ecology and developmental morphology. Society for Range Management, Denver, CO.

**Manske, L.L., W.T. Barker, and M.E. Biondini. 1988.** Effects of grazing management treatments on grassland plant communities and prairie grouse habitat. USDA. Forest Service. General Technical Report RM-159. p. 58-72.

**Manske, L.L. 1994.** Ecological management of grasslands defoliation. p. 130-136. *in* F.K. Taha, Z. Abouguendia, and P.R. Horton (eds.). Managing Canadian rangelands for sustainability and profitability. Grazing and Pasture Technology Program. Regina, Saskatchewan.

**Manske, L.L. 1996.** Economic returns as affected by grazing strategies. p. 43-55. *in* Z. Abouguendia (ed.). Total Ranch Management in the Northern Great Plains. Grazing and Pasture Technology Program, Saskatchewan Agriculture and Food. Regina, Saskatchewan.

**Manske, L.L. 1999a.** Can native prairie be sustained under livestock grazing? p. 99-108. *in* J. Thorpe, T.A. Steeves, and M. Gollop (eds.). Proceedings of the Fifth Prairie Conservation and Endangered Species Conference. Provincial Museum of Alberta. Natural History Occasional Paper No. 24. Edmonton, Alberta.

**Manske, L.L. 1999b.** Annual nutritional quality curves for graminoids in the Northern Great Plains. NDSU Dickinson Research Extension Center. Summary Range Management Report DREC 99-3014. Dickinson, ND. 14p.

**Rogler, G.A., R.J. Lorenz, and H.M. Schaaf. 1962.** Progress with grass. North Dakota Agricultural Experiment Station. Bulletin 439. Fargo, ND. 15p.

**Sarvis, J.T. 1941.** Grazing investigations on the Northern Great Plains. North Dakota Agricultural Experiment Station. Bulletin 308. Fargo, ND. 110p.

**Whitman, W.C., D.W. Bolin, E.W. Klosterman, H.J. Klostermann, K.D. Ford, L. Moomaw, D.G. Hoag, and M.L. Buchanan. 1951.** Carotene, protein, and phosphorus in range and tame grasses of western North Dakota. North Dakota Agricultural Experiment Station. Bulletin 370. Fargo, ND. 55p.

# Grass Growth in Height

Report DREC 00-3020

Llewellyn L. Manske, Ph.D.
Range Scientist
North Dakota State University
Dickinson Research Extension Center

The mixed grass prairie consists of an assemblage of mid grasses, short grasses, and sedges. Each species exhibits a characteristic growth pattern during its seasonal development from active vegetative growth in spring through the stages of flower stalk growth.

An understanding of the growth patterns of grassland plants is essential for development of proper management practices for grassland ecosystems. At the Dickinson Experiment Station, Dr. Warren C. Whitman and Dr. Harold Goetz conducted an 8-year study designed to collect quantitative data on the seasonal progress in height growth of leaves and flower stalks of major species in the mixed grass prairie of western North Dakota. A summary of some of their data is included in this report.

**Procedures**

From 1955 through 1962, Whitman and Goetz collected leaf and stalk height measurements for major graminoids. Plant heights were determined by measuring leaves and flower stalks of an average of 10 ungrazed lead tillers of each species to the nearest 1 cm. Measurements were collected at approximately 7- to 10-day intervals from early April to mid September. Leaf heights were measured from the ground to the tips of extended leaves. Flower stalk heights were measured from the ground to the tips of the inflorescences.

**Grass Height Growth**

Goetz (1963) reported the average percentage of growth completed at sequential intervals. These percentages were based on the average maximum leaf and flower stalk heights. A summary of these data is shown in tables 1 and 2 and figure 1. Upland sedges complete 100% of their growth in leaf and flower stalk height by 30 June. Cool-season grasses complete 100% of their growth in leaf and flower stalk height by 30 July. Warm-season grasses complete 100% of their growth in leaf height and 91% of their growth in flower stalk height by 30 July. In warm-season grasses, a small amount of flower stalk elongation occurs after 30 July.

**Herbage Biomass**

Peak aboveground herbage biomass is usually reached during the last 10 days of July. Herbage weight of ungrazed plants increases during May, June, and July. After the end of July, herbage weight decreases because the rate of senescence of the grass leaves exceeds the rate of growth. During senescence, cell material from the aboveground structures is translocated to the belowground structures; this movement results in a reduction in weight of aboveground structures.

**Precipitation Pattern**

The seasonal distribution of northern mixed grass prairie precipitation occurs in the Plains Precipitation Pattern (Humphrey 1962), with most of it occurring during the growing season (85%) and the greatest amounts occurring in spring and early summer. The precipitation received during May, June, and July accounts for 51% of the annual precipitation (Manske 2000).

**Conclusion**

The primary period of growth in graminoid leaf and flower stalk height and of accumulation in aboveground herbage weight occurs during the remarkably short period of May, June, and July, which coincides with the period of greatest precipitation.

Acknowledgment

I am grateful to Amy M. Kraus for assistance in preparation of this manuscript. I am grateful to Sheri Schneider and Lisa Vance for assistance in production of this manuscript.

Table 1. Mean percent growth in leaf height completed by sample date for ungrazed plants of major graminoid species from western North Dakota mixed grass prairie.

| | 15 May | 30 May | 30 Jun | 30 Jul | 30 Aug | 30 Sep |
|---|---|---|---|---|---|---|
| **UPLAND SEDGES** | **75** | **93** | **100** | **-** | **-** | **-** |
| Western Wheatgrass | 54 | 69 | 92 | 100 | - | - |
| Needleandthread | 40 | 62 | 97 | 100 | - | - |
| Prairie Junegrass | 72 | 84 | 93 | 100 | - | - |
| Plains Reedgrass | 68 | 78 | 95 | 100 | - | - |
| **COOL SEASON GRASSES** | **59** | **73** | **94** | **100** | **-** | **-** |
| Blue Grama | 34 | 48 | 82 | 100 | - | - |
| Prairie Sandreed | 16 | 39 | 88 | 100 | - | - |
| **WARM SEASON GRASSES** | **25** | **44** | **85** | **100** | **-** | **-** |

Goetz. 1963. MS Thesis. NDSU

Table 2. Mean percent growth in flower stalk height completed by sample date for ungrazed plants of major graminoid species from western North Dakota mixed grass prairie.

| | 15 May | 30 May | 30 Jun | 30 Jul | 30 Aug | 30 Sep |
|---|---|---|---|---|---|---|
| **UPLAND SEDGES** | **66** | **82** | **100** | **-** | **-** | **-** |
| Western Wheatgrass | 0 | 0 | 91 | 100 | - | - |
| Needleandthread | 0 | 39 | 85 | 100 | - | - |
| Prairie Junegrass | 0 | 42 | 100 | - | - | - |
| Plains Reedgrass | 0 | 0 | 100 | - | - | - |
| **COOL SEASON GRASSES** | **0** | **20** | **94** | **100** | **-** | **-** |
| Blue Grama | 0 | 0 | 68 | 94 | 100 | - |
| Prairie Sandreed | 0 | 0 | 0 | 88 | 100 | - |
| **WARM SEASON GRASSES** | **0** | **0** | **34** | **91** | **100** | **-** |

Goetz. 1963. MS Thesis. NDSU

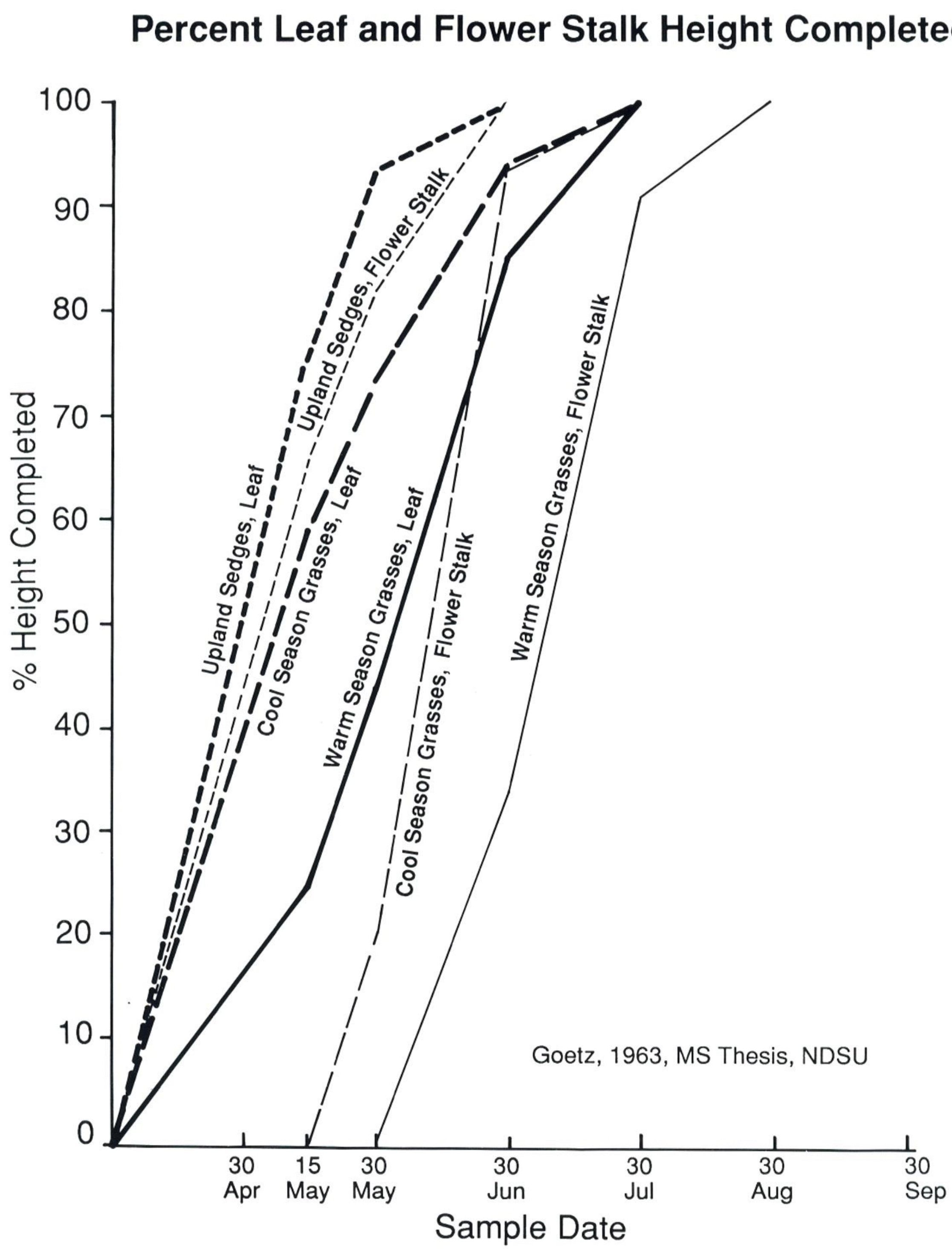


**Fig 1.** Mean percent growth in leaf and flower stalk height completed by sample date from ungrazed plants of three categories of graminoids from western North Dakota mixed grass prairie.

## Literature Cited

**Goetz, H. 1963.** Growth and development of native range plants in the mixed prairie of western North Dakota. M. S. Thesis, North Dakota State University, Fargo, ND. 165p.

**Humphrey, R. R. 1962.** Range ecology. The Ronald Press Company, New York, NY. 234p.

**Manske, L. L. 2000.** Environmental factors to consider during planning of management for range plants in the Dickinson, North Dakota, region, 1892-1999. NDSU Dickinson Research Extension Center. Range Research Report DREC 00-1018c. Dickinson, ND. 36p.

# Effects of Fall Grazing on Grass-Leaf Height

Report DREC 03-1031b

Llewellyn L. Manske PhD
Ran ge Scientist
North Dakota State University
Dickinson Research Extension Center

## Introduction

Grazing beef cattle on native rangeland during the fall season is an optional management practice that has been followed in the Northern Plains. Fall occurs between the autumnal equinox (22 September) and the winter solstice (21 December) and includes October, November, and December. The practice of grazing during these months, frequently incorrectly referred to as “winter grazing”, persists in part because of the common belief that grazing after frost in the fall does not harm perennial plants. A search of the pertinent scientific literature does not produce data to support the belief that native grasses are unaffected by late-season grazing. In fact, results of a study conducted from 1958 to 1962 at the Dickinson Research Extension Center indicates that fall grazing is detrimental to perennial grasses, greatly reducing leaf height of graminoid plants the following growing season.

## Methods

Following World War II, the beef herd at the Dickinson Experiment Station was managed with a contemporary repeated spring, summer, and fall seasonal pasture grazing schedule. During the growing season, the 40-acre fall pasture was used as a native-grass study area on which basic plant growth data were collected for numerous range-related investigations. An exclosure (A) was constructed on the fall pasture during the spring of 1958, and a second exclosure (B) was constructed during late summer of 1961. From 1958 to 1962, Dr. Warren C. Whitman and Dr. Harold Goetz conducted a study designed to evaluate the effects fall grazing had on the height of grass leaves during the following growing season. Data from that study were reported by Goetz (1963).

Plant heights were determined by measuring leaves of an average of ten ungrazed lead tillers of each species to the nearest 1 cm during the growing seasons following fall treatments. Measurements were collected at approximately 7- to 10-day intervals from early April to mid September. Leaf heights were measured from the ground to the tips of extended leaves. Leaf-height measurements for needleleaf sedge (*Carex eleocharis*), needle and thread (*Stipa comata*), western wheatgrass (*Agropyron smithii*), and blue grama (*Bouteloua gracilis*) were collected in the fall-grazed pasture and in exclosures A and B, which were not grazed in the fall. A summary of these data and their interpretation is the primary subject of this report.

Growing-season conditions affect range plant growth (Manske 1998) and are a factor to be considered in the assessment of grass and sedge growth. The average monthly temperature and monthly precipitation data for 1958 to 1962 from the Dickinson Research Extension Center (Manske 2000) were used to characterize growing-season conditions as normal, drought, and wet.

## Results

Goetz (1963) reported maximum leaf heights (table 1) of ungrazed lead tillers of needleleaf sedge, needle and thread, western wheatgrass, and blue grama measured from 1958 though 1962. Goetz (1963) stated that the data show that leaf heights for the four species of grasses and sedge were greater inside the exclosures than outside on the fall-grazed rangeland, irrespective of moisture conditions. Goetz (1963) concluded that the results of the study indicate a great reduction in maximum leaf height because of decreased vigor of the plants on rangeland subjected to fall grazing.

Maximum leaf heights of major graminoids on rangeland grazed during the fall were reduced 23.0%, 17.3%, 30.4%, and 43.0% for needleleaf sedge, needle and thread, western wheatgrass, and blue grama, respectively, compared to maximum leaf heights on treatments not fall grazed (table 2). Fall grazing reduced maximum leaf height of major graminoids 28.4% during the succeeding growing season.

Maximum leaf heights of the major graminoid species were affected by growing-season weather conditions in addition to the fall grazing treatments. The weather conditions of the growing seasons from 1958 to 1962 are summarized in table 3. The growing-season conditions of 1959 and 1961 were normal, the growing seasons of 1958 and 1960 had drought conditions with average precipitation levels 8.8% below normal, and the growing-season conditions of 1962 were wet, with precipitation levels 21% above the long-term mean.

Maximum leaf heights were shorter under drought growing-season conditions than under normal growing-season conditions for major graminoids on the treatments not fall grazed (table 4). During growing seasons with drought conditions, maximum leaf heights decreased 25.8%, 14.0%, and 11.8% for needleleaf sedge, needle and thread, and blue grama, respectively, from maximum leaf heights during growing seasons with normal conditions. During the study conducted by Whitman and Goetz, maximum leaf height of western wheatgrass was 8.0% greater during growing seasons with drought conditions than during growing seasons with normal conditions (table 4). This inconsistency can be explained by the precipitation patterns of the drought and normal growing seasons of 1958 to 1961 (table 3). Western wheatgrass completes most of its growth during May and June. Precipitation levels for June were greater than three inches in each of the two years with drought-condition growing seasons, 1958 and 1960. During the two years in which growing-season conditions were normal, 1959 and 1961, precipitation levels were greater than three inches during June only in 1959. These differences between the precipitation patterns of the drought and normal growing seasons can cause the observed differences in leaf heights of western wheatgrass. Precipitation occurring during important growth periods can greatly benefit single grass species even during growing seasons with generally stressful conditions. Maximum leaf height of major graminoids was reduced 11% in growing seasons with drought conditions.

Maximum leaf heights were greater under wet growing-season conditions than under normal growing-season conditions for major graminoids on the treatments not fall grazed (table 4). During the growing season with wet conditions, maximum leaf heights were 22.5%, 46.6%, 69.7%, and 65.4% greater for needleleaf sedge, needle and thread, western wheatgrass, and blue grama, respectively, than maximum leaf heights attained during growing seasons with normal conditions. Maximum leaf height of major graminoids increased 51% in the growing season with wet conditions.

In 1959 and 1961, when the growing season conditions were normal, leaf heights (table 5) of the major species on the treatments not fall grazed were greater than leaf heights of the plants on the treatments grazed the previous fall. Fall grazing reduced maximum leaf height of major graminoids 20.8% during the growing seasons with normal conditions.

In 1958 and 1960, when the growing seasons had drought conditions, leaf heights (table 5) of the major species on the treatments not fall grazed were not much greater than leaf heights of the plants on the treatments grazed the previous fall. Leaf heights of needleleaf sedge and needle and thread on treatments not grazed in the fall did not differ from leaf heights on the fall-grazed treatments (table 5). Fall grazing reduced maximum leaf height of major graminoids 9.4% during the growing seasons with drought conditions.

In 1962, when the growing season conditions were wet, leaf heights (table 5) of all the major species on the treatments not fall grazed were considerably greater than leaf heights of the plants on the treatments grazed the previous fall. Leaf height of blue grama on exclosure A was more than twice the leaf height of the fall-grazed plants (table 5). Fall grazing reduced maximum leaf height of major graminoids 31.2% during the growing season with wet conditions.

Upland sedges attained an average maximum leaf height of 12.0 cm (4.7 in) in early to mid June during growing seasons with normal conditions. Leaf height of upland sedges was reduced 26% under drought conditions and increased 23% under wet conditions. Fall grazing reduced maximum leaf height of upland sedges 23%.

Needle and thread attained an average maximum leaf height of 19.3 cm (7.6 in) in late June to early July during growing seasons with normal conditions. Drought conditions reduced leaf height 14% from leaf height during normal conditions, and wet conditions increased leaf height 47% over leaf height during normal conditions. Fall grazing reduced maximum leaf height of needle and thread 17%.

Western wheatgrass attained an average maximum leaf height of 23.8 cm (9.4 in) by mid July during growing seasons with normal conditions. Wet conditions increased leaf height 70%. In growing seasons with drought conditions but with greater than three inches of precipitation in June, leaf height for western wheatgrass was not reduced. Drought conditions with below-normal precipitation in June would cause a reduction in maximum leaf height for western wheatgrass. Fall grazing reduced maximum leaf height of western wheatgrass 30%.

Blue grama attained an average maximum leaf height of 12.7 cm (5.0 in) in early to mid July during growing seasons with normal conditions. Under drought conditions, leaf height decreased 12%, and under wet conditions leaf height increased 65%. Fall grazing reduced maximum leaf height of blue grama 43%.

Growth in height of the major graminoid species of the mixed prairie in the Northern Plains was affected by grazing during the fall as well as by precipitation patterns and moisture conditions during the growing season. Fall grazing damaged perennial grasses and reduced grass growth in leaf height during normal, drought, and wet growing-season conditions.

**Discussion**

Data collected by Whitman and Goetz during their study clearly show that fall grazing on native rangeland damages range plants and reduces leaf height by diminishing the vigor of the plants. The range condition of pastures that have a history of being grazed during the fall season can be improved if the fall grazing location is changed from the native range pasture to pastures of an alternative forage type like a variety of perennial wildrye (Altai, Russian, basin) or to a spring-seeded winter cereal pasture. The data from Goetz (1963) can be used to help predict the levels of improvement in the major species after the fall grazing practice has been changed. The average maximum leaf height of the major native range graminoids could be expected to increase 17.2% during the first year if the growing season had normal conditions and 33.3% if the first growing season had wet conditions. An increase of 42.5% in leaf height could be expected within four years of a change from grazing native rangelands in the fall.

**Conclusion**

The scientific results from the five-year research project Dr. Whitman and Dr. Goetz conducted at the Dickinson Research Extension Center provide evidence that fall grazing of native rangeland causes biological damage to the major rangeland species. Leaf heights of the major graminoids of the mixed grass prairie are affected by the grazing management practices used during the previous fall season and by the precipitation pattern and moisture conditions of the growing season. Not the benign practice it is commonly believed to be, fall grazing of rangeland causes a decrease in plant vigor and a great reduction in leaf height (28%) of the major graminoids during the succeeding growing season, regardless of the growing-season moisture conditions.

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Table 1. Maximum leaf height [centimeters (cm) and inches (in)] of ungrazed lead tillers measured during growing seasons following treatments fall grazed or not fall grazed (1958-1962), data from Goetz (1963).

| Year | Upland sedge | | Needle and thread | | Western wheatgrass | | Blue grama | |
|---|---|---|---|---|---|---|---|---|
| Treatment | (cm) | (in) | (cm) | (in) | (cm) | (in) | (cm) | (in) |
| 1958 | | | | | | | | |
| Initial | 9.0 | 3.5 | 16.7 | 6.6 | 23.0 | 9.1 | 9.7 | 3.8 |
| 1959 | | | | | | | | |
| Exclosure A (1 yr) | 10.7 | 4.2 | 20.0 | 7.9 | 22.3 | 8.8 | 12.0 | 4.7 |
| Fall Grazed | 9.0 | 3.5 | 19.0 | 7.5 | 20.0 | 7.9 | 9.0 | 3.5 |
| 1960 | | | | | | | | |
| Exclosure A (2 yr) | 8.7 | 3.4 | 16.5 | 6.5 | 28.3 | 11.1 | 12.7 | 5.0 |
| Fall Grazed | 9.0 | 3.5 | 17.0 | 6.7 | 19.0 | 7.5 | 8.0 | 3.1 |
| 1961 | | | | | | | | |
| Exclosure A (3 yr) | 13.3 | 5.2 | 18.6 | 7.3 | 25.3 | 10.0 | 13.3 | 5.2 |
| Fall Grazed | 9.0 | 3.5 | 16.0 | 6.3 | 22.0 | 8.7 | 7.0 | 2.8 |
| 1962 | | | | | | | | |
| Exclosure A (4 yr) | 16.3 | 6.4 | 29.5 | 11.6 | 41.7 | 16.4 | 25.0 | 9.8 |
| Exclosure B (1 yr) | 13.0 | 5.1 | 27.0 | 10.6 | 39.0 | 15.4 | 17.0 | 6.7 |
| Fall Grazed | 11.0 | 4.3 | 23.0 | 9.1 | 26.0 | 10.2 | 11.5 | 4.5 |

Table 2. Average maximum leaf height [centimeters (cm) and inches (in)] of ungrazed lead tillers measured during growing seasons following treatments fall grazed or not fall grazed (mean of 1958-1962), summary of data from Goetz (1963).

| Treatments | | Exclosure | Fall grazed | Percent difference from treatments not fall grazed (%) |
|---|---|---|---|---|
| Upland sedge | (cm) | 12.6 | 9.7 | -23.0 |
| | (in) | 5.0 | 3.8 | |
| Needle and thread | (cm) | 23.1 | 19.1 | -17.3 |
| | (in) | 9.1 | 7.5 | |
| Western wheatgrass | (cm) | 32.6 | 22.7 | -30.4 |
| | (in) | 12.8 | 8.9 | |
| Blue grama | (cm) | 16.5 | 9.4 | -43.0 |
| | (in) | 6.5 | 3.7 | |

Table 3. Summary of weather conditions during study of fall grazing effects on leaf height (1958-1962).

| Year | | 1958 | 1959 | 1960 | 1961 | 1962 |
|---|---|---|---|---|---|---|
| Growing-season precipitation | (in) | 9.42 | 11.56 | 8.54 | 12.65 | 16.41 |
| Percent of long-term mean precipitation | (%) | 69.44 | 85.21 | 62.95 | 93.25 | 120.96 |
| Months with water stress | | May, Aug, Sep | Apr, Jul, Aug | Apr, Jul, Sep, Oct | Jul, Aug, Oct | Sep, Oct |
| Percent growing-season months with water stress | (%) | 50 | 42 | 50 | 42 | 25 |
| Months with > 3" precip. | | Jun, Jul | Jun, Sep | Jun | Sep | May, Jul |
| Spring conditions | | Dry | Dry | Dry | Normal | Wet |
| Fall conditions | | Dry | Wet | Dry | Normal | Dry |
| Growing-season conditions | | Drought | Normal | Drought | Normal | Wet |

Data from Manske 2000

Table 4. Average maximum leaf height [centimeters (cm) and inches (in)] of ungrazed lead tillers measured during three growing-season conditions on treatments not fall grazed (1958-1962), summary of data from Goetz (1963).

| Growing-season conditions | | Normal | Drought | | Wet | |
|---|---|---|---|---|---|---|
| Treatments | | Exclosure | Exclosure | % Difference from Normal (%) | Exclosure | % Difference from Normal (%) |
| Upland sedge | (cm) | 12.0 | 8.9 | -25.8 | 14.7 | +22.5 |
| | (in) | 4.7 | 3.5 | | 5.8 | |
| Needle and thread | (cm) | 19.3 | 16.6 | -14.0 | 28.3 | +46.6 |
| | (in) | 7.6 | 6.5 | | 11.1 | |
| Western wheatgrass | (cm) | 23.8 | 25.7 | +8.0 | 40.4 | +69.7 |
| | (in) | 9.4 | 10.1 | | 15.9 | |
| Blue grama | (cm) | 12.7 | 11.2 | -11.8 | 21.0 | +65.4 |
| | (in) | 5.0 | 4.4 | | 8.3 | |

Table 5. Maximum leaf height [centimeters (cm) and inches (in)] of ungrazed lead tillers measured during three growing-season conditions following treatments fall grazed or not fall grazed (1958-1962), summary of data from Goetz (1963).

| Growing-season conditions | | Normal | | Drought | | Wet | | |
|---|---|---|---|---|---|---|---|---|
| Years | | 1959 & 1961 | | 1958 & 1960 | | 1962 | | |
| Treatments | | Exclosure A | Fall grazed | Exclosure A | Fall grazed | Exclosure A | Exclosure B | Fall Grazed |
| Upland sedge | (cm) | 12.0 | 9.0 | 8.9 | 9.0 | 16.3 | 13.0 | 11.0 |
| | (in) | 4.7 | 3.5 | 3.5 | 3.5 | 6.4 | 5.1 | 4.3 |
| Needle and thread | (cm) | 19.3 | 17.5 | 16.6 | 16.8 | 29.5 | 27.0 | 23.0 |
| | (in) | 7.6 | 6.9 | 6.5 | 6.6 | 11.6 | 10.6 | 9.1 |
| Western wheatgrass | (cm) | 23.8 | 21.0 | 25.7 | 21.0 | 41.7 | 39.0 | 26.0 |
| | (in) | 9.4 | 8.3 | 10.1 | 8.3 | 16.4 | 15.4 | 10.2 |
| Blue grama | (cm) | 12.7 | 8.0 | 11.2 | 8.8 | 25.0 | 17.0 | 11.5 |
| | (in) | 5.0 | 3.1 | 4.4 | 3.5 | 9.8 | 6.7 | 4.5 |

## Literature Cited

**Goetz, H. 1963.** Growth and development of native range plants in the mixed prairie of western North Dakota. M.S. Thesis, North Dakota State University, Fargo, ND. 165p.

**Manske, L.L. 1998.** Environmental factors' effect on range plants. NDSU Dickinson Research Extension Center. Summary Range Research Report DREC 98-3006. Dickinson, ND. 3p.

**Manske, L.L. 2000.** Environmental factors to consider during planning of management for range plants in the Dickinson, North Dakota, region, 1892-1999. NDSU Dickinson Research Extension Center. Range Research Report DREC 00-1018c. Dickinson, ND. 36p.

# Proactive Management of Pestiferous Grasshopper Habitat

Llewellyn L. Manske PhD
Research Professor of Range Science
North Dakota State University
Dickinson Research Extension Center
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Large scale grasshopper outbreaks extending throughout the western portion of North America occurred during the 1930's and 1980's and smaller scale regional outbreaks have occurred almost every year someplace in the Northern Plains. It is realistic to predict that grasshopper outbreaks will occur in the near future someplace in the Northern Plains.

Grasshoppers are a natural component of native rangelands and domesticated grasslands of the Northern Plains. Grasshopper population densities ordinarily remain at levels that can be supported by the resources of the ecosystem. All of the pestiferous rangeland grasshopper species of the Northern Plains remain year after year on the land where they hatch. At low densities, grasshoppers are not a problem. However, when favorable conditions decrease mortality rates, increase available food plants, and/or increase access to direct sunlight, pestiferous rangeland grasshopper populations can increase to problem densities.

Pestiferous rangeland grasshopper population densities are regulated by the mortality rates caused by natural enemies, by the availability of nutritious food plants, and by the level of access to direct sunlight throughout the day. Grasshoppers living on rangelands of the Northern Plains have adequate nutritious food plants available even during dry growing seasons but are limited by restricted access to direct sunlight except during growing seasons with high water deficiencies or drought conditions or on heavily grazed, poorly managed, or double used grazinglands with considerable bareground areas and reduced grass plant stature. Beef producers that use the old traditional range management concepts to manage the aboveground perennial grass resources for a single primary use as forage for livestock cause spiraling degradation of the ecosystem that results in reduced grass plant density, increased size and number of bareground areas, and decreased grass herbage biomass production creating habitat favorable for pestiferous grasshoppers. Land managers create their own grasshopper problems with poor land management practices.

On traditionally managed grazinglands in the Northern Plains, grasshopper populations tend to reach high outbreak densities when plant canopy height and ground cover are reduced and herbage production is low. These conditions occur as a result of grazing-management-caused problems or during years with hot temperatures and low precipitation (Onsager 1996, 2000). The grasshopper population outbreaks can occur as the outward expansion of a "hot spot" or as an escalation of low to high numbers across an area (Lockwood, Brewer, and Schell 1996).

Grazing management strategies that repeatedly remove most of the vegetation on grasslands reduce plant density and herbage biomass production. Areas with open vegetation canopy and spots of bare ground are favorable grasshopper habitat. With reduced vegetation canopy cover and enlarged areas of bare ground, the amount of solar radiation that reaches the soil surface increases, as does the airflow over the ground. The reduced vegetation structure results in higher air and soil temperatures and lower humidity in grasshopper habitat.

Grassland habitat with open vegetation canopy and areas of bare ground provides ideal basking sites, where grasshoppers warm themselves in the early morning sun to speed metabolic rates and increase growth rates (Belovsky et al. 2000). Patches of bare ground also are favored egg-laying sites. Higher soil and air temperatures accelerate grasshopper egg development, growth and maturation of young insects, and egg production of adult females. In addition, habitat with intense sunlight and low humidity near the soil discourages the growth of important pathogens that cause grasshopper diseases. As a result, mortality rates of immature grasshoppers decline and greater numbers of the insects survive into adulthood.

Many traditional management practices produce habitat favorable for grasshopper population outbreaks. Common practices that help grasshopper populations increase to problem levels include beginning grazing before plants have reached the third-leaf stage; grazing spring and summer pastures or haylands during the fall; and management treatments such as seasonlong, deferred, and repeat seasonal grazing that leave little residual vegetation following defoliation periods.

Proactive management of grasshopper habitat must reduce the grasshoppers strengths and exploit the grasshoppers weaknesses. Grasshoppers have a major survival strength that relegates proactive management of grasshopper habitat to a neverending annual challenge. Grasshoppers have high fecundity potential, each adult female can produce 100 to 200 viable eggs. Because of this remarkable inherent ability, grasshoppers can increase the population density multifold from one growing season to the next. A one year lapse in land management diligence can lead to a major grasshopper outbreak.

Fortunately, grasshoppers have two major weaknesses that render grasshopper population numbers vulnerable to proactive management of the residuum vegetation structure of their habitat. The first weakness is that grasshoppers are cold blooded and are unable to regulate their body temperature metabolically. Grasshoppers need to bask on open bareground areas to collect direct incident solar radiation to raise their body temperatures to the preferred optimal high levels above 95° F (35° C). When grasshoppers can not achieve the optimal body temperature during most of the day, their growth and development rates slow, the length of time nymphs are at each instar stage increases, nymph mortality increases, the number of nymphs reaching the adult stage decreases, maturation time after adults fledge increases, the quantity of viable eggs produced by each adult female greatly decreases, and the resident grasshopper population remains low.

The second vulnerable weakness is that grasshopper eggs require a total of 500 to 600 DD day-degrees of heat from direct incident solar radiation for complete development of the embryo; this includes about 400 DD of heat during the first summer and an additional 150 DD of heat during the following spring to complete embryonic development and hatching. All except one of the pestiferous rangeland grasshoppers deposit their egg pods below the soil surface in bareground patches. Bareground egg pod sites accumulate heat units rapidly and increase the rates of embryonic development. Shading of the soil surface at the egg laying sites from grass canopy cover reduces the quantity of incident solar radiation that decreases the accumulation of heat units, reduces the rate of embryo development delaying egg hatch, and reduces the number of hatchlings produced.

A joint research project was conducted in western North Dakota by Dr. Lee Manske, NDSU, Dickinson Research Extension Center, Dickinson, ND, and Dr. Jerry Onsager, retired research entomologist, USDA-Agricultural Research Service, Sidney, MT, to evaluate and compare the grassland habitat conditions and grasshopper population numbers on a seasonlong grazing treatment and a twice-over rotation treatment (Manske and Onsager 1996, Stelljes 1996).

The twice-over rotation grazing treatment had denser basal cover, less bare ground, and greater herbage biomass than the seasonlong treatment. The grass basal cover on the twice-over rotation treatment was 25.2% greater than that on the seasonlong treatment (Manske 1995, 1996). The average percent of ground not covered by vegetation was lowest on the twice-over rotation treatment, followed by the seasonlong treatment, and greatest on the nongrazed treatment. The twice-over rotation treatment had 31% less open area in the vegetation canopy than the seasonlong treatment (Manske 1995). Herbage production was greater on the twice-over rotation treatment than on the seasonlong treatment. The twice-over rotation treatment produced an average of 33% to 45% more herbage during each growing-season month than did the seasonlong treatment (Manske 1995, 1996).

Onsager (2000) followed grasshopper numbers for five growing seasons on native rangeland areas managed with a seasonlong treatment or the twice-over rotation treatment. The average number of grasshopper days per square meter was 748 on the seasonlong treatment, considerably greater than the average of 229 on the twice-over rotation treatment. During the last two years of the study, a local grasshopper outbreak (figure 1) with an average density of 22.6 adult grasshoppers per square meter occurred on the seasonlong treatment. This population outbreak did not occur on the twice-over rotation treatment, which maintained an average of only 3.9 adult grasshoppers per square meter.

The seasonlong treatment decreased the vegetation cover and promoted grasshopper population increases. The twice-over rotation treatment enhanced the vegetation cover and suppressed grasshopper population increases.

Rangelands are complex ecosystems consisting of numerous interactive biotic (living) and abiotic (nonliving) components. The biotic components are the plants, soil microorganisms, and large grazing graminivores that have biological and physiological requirements. The abiotic components include the major and minor essential elements that have transformable characteristics between organic and inorganic forms. The major essential elements are carbon, hydrogen, nitrogen, and oxygen and the minor essential elements consist of seven macrominerals and ten microminerals. The abiotic components also include radiant energy from the sun. Numerous biological, geological, chemical, and atmospheric pathways transfer the major essential elements into and out of an ecosystem and numerous pathways transfer the minor essential elements out of an ecosystem. Rangeland ecosystems are functioning units of coacting biotic organisms interacting with the abiotic components and the environment. The complex of mechanisms and processes connected with these extensive interactions are the defoliation resistance mechanisms within and around grass plants and the biogeochemical processes within an ecosystem.

Grass plants, soil microorganisms, and large grazing graminivores coevolved and develop extensive interactions that permit grassland ecosystems to function effectively. The defoliation resistance mechanisms that developed within grass plants provide important biological and physiological processes so grass plants can produce greater herbage biomass that replaces lost leaf material, restore disrupted vital processes, and vegetatively reproduce secondary tillers from axillary buds that increase grass tiller density and reduce bareground areas. The soil microorganisms in the rhizosphere and the biogeochemical processes cycle large quantities of plant available essential elements between the organic and inorganic forms. Activation of the defoliation resistance mechanisms and the biogeochemical processes requires partial defoliation by grazing that removes about 25% to 33% of the aboveground leaf material of grass lead tillers between the 3.5 new leaf stage and the flower stage and results in greatly increased ecosystem productivity that is favorable for livestock production. Proactive management of the residuum vegetation structure of grasshopper habitat uses the ecosystem mechanisms and processes to increase aboveground herbage biomass, increase grass plant basal cover, and decrease bareground area creating habitat conditions unfavorable for pest grasshopper production.

The twice-over rotation system is effective in grasshopper management because the grazing treatment properly times defoliation to lead to greater plant density and herbage production and fewer open areas in the vegetation canopy cover. These plant community characteristics develop because the biologically effective twice-over rotation system coordinates grazing with grass growth stages and removes a small amount of leaf material from grass plants between the 3.5 new leaf stage and the flower stage. This timed defoliation stimulates plant processes and soil organism activity that enhance plant growth, and the resulting greater herbage biomass production leads to grassland habitat conditions unfavorable for grasshopper population increases.

Areas with habitat unfavorable to grasshoppers are those on which plant density is increased so that only a few small spots of bare ground occur and on which adequate herbage biomass remains after grazing periods so that the vegetation canopy is nearly closed. The improvement in the vegetation characteristics of rangeland managed with the twice-over rotation system reduces the amount of sunlight reaching the ground, increases the humidity, and lowers the temperature within the grasshopper habitat. In these grassland habitat conditions, grasshopper metabolic rates and growth rates slow and disease increases mortality rates among grasshoppers. These changes negatively affect the growth and survival of immature grasshoppers in the nymphal stages and result in reduced grasshopper numbers and in suppression of local grasshopper population outbreaks (Onsager 2000).

Producers can suppress potential grasshopper population outbreaks by implementing biologically effective grazing management that minimizes habitat favorable to the insects. Three management practices can be used to develop grassland habitat unfavorable for grasshopper outbreaks: (1) delaying the start of grazing until grasses have reached the 3.5 new leaf stage (early May for crested wheatgrass and smooth bromegrass and early June for native rangeland), (2) grazing native rangeland with a twice-over rotation management system that coordinates rotation dates with plant growth stages, and (3) grazing complementary forage types during the fall rather than grazing spring and summer pastures or haylands late in the season.

Implementing improved cultural management practices is not a quick fix to a major problem. Grazing management strategies that produce habitat unfavorable for grasshopper population outbreaks are a long-term solution to grasshopper problems and take three or more years to show substantial results. Pastures that are grazed using traditional management practices and that have had problems with increased grasshopper numbers need a change of management treatments to biologically effective grazing management practices that stimulate plant mechanisms and ecosystem processes to increase plant density and vegetation canopy.

The twice-over rotation system is a biologically effective grazing management treatment that has the three attributes needed to deter grasshopper outbreaks in the Northern Plains. The twice-over rotation grazing system: (1) deliberately varies the time and intensity of defoliation from year to year, (2) controllably enhances vegetation shading canopy during critical portions of grasshopper life cycles, and (3) reduces and almost eliminates bare soil areas.

Pestiferous rangeland grasshopper population numbers in the Northern Plains can be held at tolerable low densities by proactive management of the grasshopper habitat by using the recently discovered grasshopper biology and population dynamics and the technologies for activation of the defoliation resistance mechanisms and the biogeochemical processes.

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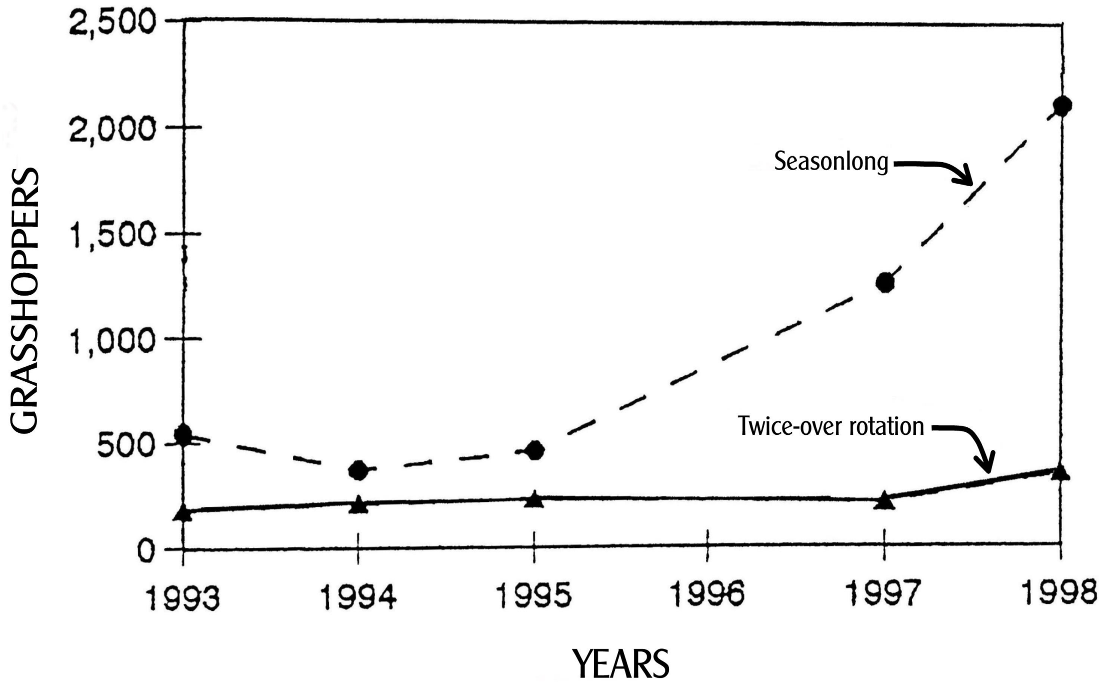


Fig. 1. Grasshopper population outbreak occurring on the seasonlong treatment during 1997 and 1998 but not occurring on the twice-over rotation treatment. Grasshopper abundance reported as grasshopper days per square meter, data from Onsager 2000.

## Literature Cited


**Belovsky, G.E., M.A. Brusven, D.J. Fielding, and L. Manske. 2000.** Grasshopper habitat manipulation. United States Department of Agriculture, Animal and Plant Inspection Service, Grasshopper Integrated Pest Management User Handbook, Technical Bulletin No. 1809, Washington, DC. p.VII.15-1-VII.15-5.

**Lockwood, J.A., M.J. Brewer, and S.P. Schell. 1996.** Treating localized hot-spots of rangeland grasshoppers: A preventative strategy with promise. United States Department of Agriculture, Animal and Plant Health Inspection Service, Grasshopper Integrated Pest Management User Handbook, Technical Bulletin No. 1809, Washington, DC. p.II.10-1-II.10-8.

**Manske, L.L. 1995.** Modification to native range vegetation by grazing management to affect grasshopper populations, 1993-1994. NDSU Dickinson Research Extension Center. Range Research Report DREC 95-1006. Dickinson, ND. 12p.

**Manske, L.L. 1996.** Beneficial changes of rangeland through proper grazing. United States Department of Agriculture, Animal and Plant Inspection Service, Grasshopper Integrated Pest Management User Handbook, Technical Bulletin No. 1809, Washington, DC. p.V.7-1-V.7-7.

**Manske, L.L., and J.A. Onsager. 1996.** Grasshopper populations can be reduced by grazing management. Proceedings of the National Grasshopper Management Board 1996 Annual Meeting. Rapid City, SD. p. 14-15.

**Onsager, J.A. 1996.** The importance of grazing strategies to grasshopper management: an introduction. United States Department of Agriculture, Animal and Plant Health Inspection Service, Grasshopper Integrated Pest Management User Handbook, Technical Bulletin No. 1809, Washington, DC. p.V.1-1-V.1-3.

**Onsager, J.A. 2000.** Suppression of grasshoppers in the Great Plains through grazing management. Journal of Range Management 53:592-602.

**Stelljes, K.B. 1996.** IPM targets grasshoppers. Agricultural Research. USDA-ARS, Washington, DC. Vol.44:4-10.

# Effects of Partial Defoliation

# Effects of Grazing Management Treatments on Rangeland Vegetation

Llewellyn L. Manske PhD
Range Scientist
North Dakota State University
Dickinson Research Extension Center

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## Introduction

Grazing is not simply the removal of leaf material from grass plants. The effects of defoliation of leaf material by grazing are complex. Different grazing management treatments cause diverse changes in plant growth, and these changes affect the quantity and quality of the aboveground herbage biomass produced on grasslands. Grazing can change plant species composition, manipulate some plant and ecosystem processes, and alter levels and rates of plant growth.

The timing and severity of grazing determine whether detrimental or beneficial effects occur. Repeated heavy grazing removes a great amount of the leaf area and causes long-term reductions in the total quantity of herbage produced. Early grazing--grazing before the grass tillers have reached the third new leaf stage--and late grazing--grazing during the fall, after the end of the growing season--both reduce herbage biomass on grasslands. In contrast, grazing that is coordinated with grass growth stages is beneficial to plant growth mechanisms and ecosystem processes and stimulates greater herbage production.

The purpose of this study is to document and compare herbage biomass production, plant basal cover, and vegetative tiller development on native rangeland pastures of grazing management systems during the grazing season.

## Procedure

This study was conducted at the NDSU Dickinson Research Extension Center, located in western North Dakota, U.S.A. (47°14'N.lat., 102°50'W.long.). Soils are primarily Typic Haploborolls. Mean annual temperature is 42.2°F (5.7°C). Average annual precipitation is 16.6 inches (420.9 mm). The growing-season precipitation (April to October) is 14.0 inches (356.7 mm), 85.0% of the annual precipitation (Manske 2003). The native rangeland vegetation is the Wheatgrass-Needlegrass Type (Barker and Whitman 1988) of the mixed grass prairie. The dominant species are western wheatgrass, needle and thread, blue grama, and threadleaf sedge.

Plant growth data were collected on permanent plots organized in a paired-plot design. Each of the replicated treatments was stratified on the basis of three range sites (sandy, shallow, and silty). Samples from the grazed treatments were collected on both grazed quadrats and ungrazed (protected with cages) quadrats and exclosures. Aboveground herbage biomass was collected by the standard clipping method (Cook and Stubbendieck 1986) on 7 sampling dates from May to October. Material was sorted by biotype categories (cool-season grasses, warm-season grasses, sedge, forb, standing dead, and litter) and oven dried. Plant species composition was determined during peak growth by the ten-pin point frame method (Cook and Stubbendieck 1986) between mid July and mid August. Grass plant tiller development in response to timing and severity of grazing was evaluated for 2 years following a defoliation treatment. These data were collected on individually marked tillers of western wheatgrass in microplots within exclosures in pastures of long-term grazing management treatments. The time of defoliation was mid June and the severity of defoliation was 50%, 25%, or 0%. A standard paired plot t-test was used to analyze differences between means (Mosteller and Rourke 1973).

Plant growth data were collected on native rangeland grazing treatments and a nongrazed treatment involved in pasture research projects. The stocking rates of the grazing management treatments were determined for proper full use of the forage produced on the pastures. The long-term nongrazed treatment had not been grazed, mowed, or burned for more than 30 years prior to the start of data collection. The 6.0-month seasonlong treatment native rangeland pasture was grazed by cow-calf pairs for 183 days, from mid May to mid November. The 4.5-month seasonlong treatment native rangeland pasture was grazed by cow-calf pairs for 135 days, from early June to mid October. The twice-over rotation treatment native rangeland pastures were grazed by cow-calf pairs for 135 days, from early June to mid October. Each of the three pastures was grazed for two periods, one period of 15 days between early June and mid July (third-leaf stage to flowering stage), followed by a second period of 30 days after mid July and prior to mid October.

## Results

Herbage biomass was greatest on the twice-over rotation treatment (table 1, figure 1). The measurement of the amount of herbage standing after each grazing period does not include the amount of vegetation removed by livestock during the grazing period. The amount of herbage remaining on pastures following grazing was significantly greater in July, August, and September on the twice-over rotation treatment than on the seasonlong treatment. The seasonlong treatment averaged 29% less herbage standing after grazing than the twice-over rotation treatment. The quantity of herbage biomass remaining after grazing on the twice-over rotation treatment was greater than the current year's herbage growth on the long-term nongrazed treatment during the entire growing season; however, during August, the herbage remaining after grazing on the twice-over rotation treatment was not significantly different from the peak herbage on the nongrazed treatment. An average of 15% more herbage remained standing after each grazing period on the twice-over rotation treatment than the amount that grew on the nongrazed treatment. The seasonlong treatment averaged 8% less herbage standing after grazing than the amount that grew on the long-term nongrazed treatment. The amount of herbage remaining standing at the end of the grazing season on the twice-over rotation treatment was significantly greater than the herbage remaining on the nongrazed and seasonlong treatments. The greater amount of photosynthetic leaf area of the herbage remaining on the twice-over rotation treatment in mid October, at the end of the growing season, was beneficial for the continued functioning of the grassland ecosystem at a higher production level.

Grass basal cover (table 2) was greatest on the twice-over rotation treatment. Grass basal cover was 25% greater on the twice-over rotation treatment than on the seasonlong treatment. Sedge basal cover was 4% greater on the seasonlong treatment than on the twice-over rotation treatment. Forb basal cover was 36% less on the twice-over rotation treatment than on the seasonlong treatment. The greater number of forbs on the seasonlong treatment was primarily less desirable plants, both introduced and native. Most undesirable and less desirable plants are not very competitive and are not the cause of pasture problems, but they are symptoms indicating that problems exist. These plants are opportunistic and can grow in the bare spots of plant communities that are below their potential plant density.

The total plant basal cover on the twice-over rotation treatment was 9.2% greater than that on the seasonlong treatment and 30.2% greater than that on the nongrazed treatment. The relative percent composition of the plant communities (table 3) on the twice-over rotation treatment consisted of 14% more grass, 14% less sedge, and 40% less forbs and shrubs than composition of the seasonlong treatment plant communities. The average percent of ground not covered by vegetation was lowest on the twice-over rotation treatment (4.8%), followed by the seasonlong treatment (7.0%) and the nongrazed treatment (12.1%).

The greatest number of western wheatgrass tillers per square meter developed on the twice-over rotation treatment (table 4). The tiller density on the twice-over rotation treatment was 70.0% greater than that on the 6.0-month seasonlong treatment and 183.3% greater than that on the 4.5-month seasonlong treatment. The defoliation treatment that stimulated the greatest number of tillers was 25% removal of leaf material in mid June. The greatest number of stimulated tillers grew on the twice-over rotation treatment. The defoliation treatment that removed 25% of the leaf material in mid June on the twice-over rotation grazing treatment produced 123.8% more tillers than the same defoliation treatment on the 6.0-month seasonlong grazing treatment and 193.8% more tillers than that on the 4.5-month seasonlong grazing treatment. The defoliation treatment that removed 50% of the leaf material in mid June tended to suppress tiller numbers below the number of tillers produced by plants that had no defoliation treatment for two years on all three grazing treatments.

## Discussion

Grazing periods that are coordinated with grass growth stages activate the defoliation resistance mechanisms that grass plants developed in response to a long history of grazing. Properly timed grazing that removes only a small portion, about 25% to 33%, of the leaf material from grasses that are between the 3.5 new leaf stage and the flower stage triggers the beneficial biological processes that increase the symbiotic activity of soil organisms in the rhizosphere and stimulate vegetative reproduction of grasses by secondary tiller development from axillary tiller buds located on the plant crown. The proliferation of grass tiller development fills in soil bare areas, reducing the less desirable plants and increasing grass density and grass growth to produce an average of 45% greater herbage biomass. The increase of herbage biomass permits an increase in stocking rates. The stocking rate on the native rangeland pastures managed by the twice-over rotation treatment was 40% greater than the stocking rate on the native rangeland of the 4.5-month seasonlong treatment and 90% greater than the stocking rate on the native rangeland of the 6.0-month seasonlong treatment.

The defoliation resistance mechanisms do not function at full capacity following a single stimulation event. Grass tiller numbers and herbage biomass usually rise in increasing increments in grassland ecosystems for about 3 to 5 years following implementation of a biologically effective twice-over rotation system. After the ecosystem's biogeochemical cycles are functioning at elevated levels and vegetative reproduction by tillering occurs at enhanced rates, the momentum of these activities will not stop immediately upon suspension of stimulation from defoliation at appropriate times and severities but will decrease in stages. Maintaining healthy grassland ecosystem performance at sustainable high levels requires long-term biologically effective grazing management that places priorities on meeting the biological requirements of the plants and on facilitating ecological processes.

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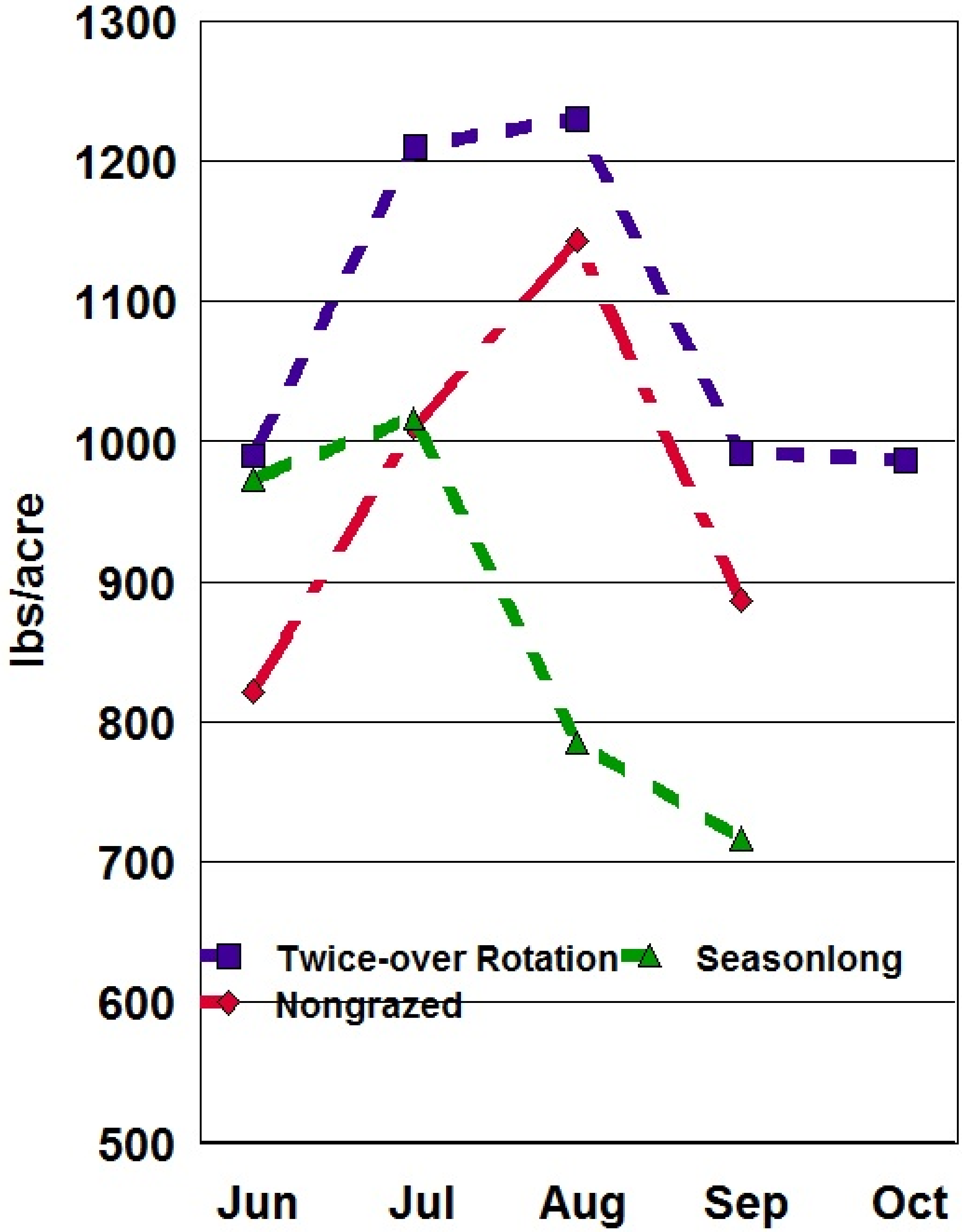


Fig 1.  Herbage biomass remaining after monthly grazing periods.

Table 1. Mean herbage biomass in lbs/ac remaining after monthly grazing periods.

| | Grazing Periods | | | | |
|---|---|---|---|---|---|
| Grazing Treatments | Jun | Jul | Aug | Sep | Oct |
| Nongrazed | 822a | 1010a | 1144a | 888a | - |
| Seasonlong | 974a | 1017a | 785b | 717a | - |
| Twice-over rotation | 990a | 1211b | 1231a | 993b | 987 |

Means of same column followed by the same letter are not significantly different (P<0.05).

Table 2. Mean percent basal cover.

| | Grazing Treatments | | |
|---|---|---|---|
| Plant Type | Seasonlong | Twice-over rotation | % Difference |
| Grass | 14.7 | 18.6 | +25.2 |
| Sedge | 7.7 | 7.6 | -3.8 |
| Forb | 3.8 | 2.4 | -35.9 |
| Shrub | 0.1 | 0.1 | - |

Table 3. Mean relative percent composition of plant communities.

| | Grazing Treatments | | |
|---|---|---|---|
| Plant Type | Seasonlong | Twice-over rotation | % Difference |
| Grass | 55.1 | 63.2 | +14.1 |
| Sedge | 30.6 | 28.0 | -13.6 |
| Forb and Shrub | 14.5 | 8.7 | -39.6 |

Table 4. Number of western wheatgrass tillers per square meter two years after defoliation treatment.

| | Defoliation Treatments | | |
|---|---|---|---|
| Grazing Treatments | No Defoliation for 2 years | mid June 25% | mid June 50% |
| 6.0-m Seasonlong | 626.5 | 657.9 | 563.9 |
| 4.5-m Seasonlong | 375.9 | 501.2 | 344.6 |
| Twice-over rotation | 1065.1 | 1472.3 | 908.5 |

## Literature Cited

**Barker, W.T., and W.C. Whitman. 1988.** Vegetation of the Northern Great Plains. Rangelands 10:266-272.

**Cook, C.W., and J. Stubbendieck. 1986.** Range research: basic problems and techniques. Society for Range Management, Denver, CO. 317p.

**Manske, L.L. 2003.** Ombrothermic interpretation of range plant water deficiency from temperature and precipitaiton data collected at the Ranch Headquarters of the Dickinson Research Extension Center in western North Dakota, 1982-2002. NDSU Dickinson Research Extension Center. Range Research Report DREC 03-1019f. Dickinson, ND. 17p.

**Mosteller, F., and R.E.K. Rourke. 1973.** Sturdy Statistics. Addison-Wesley Publishing Co., MA. 395p.

# Grazing Treatment Effects on Vegetative Tillering and Soil Rhizospheres of Western Wheatgrass

Michelle M. Gorder[1], Llewellyn L. Manske[2], and Tobias L. Stroh[1]
[1]Dickinson State University, Department of Agriculture and Technical Studies
[2]North Dakota State University, Dickinson Research Extension Center
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**Summary**

This investigation improved the understanding of grazing treatment effects on the stimulation of grass defoliation resistance mechanisms. The study explored the effects from three grazing treatments and a long-term nongrazed control on grass vegetative tiller development from axillary buds and on the activity level of soil microorganisms in the rhizosphere. The results included three significant findings: the grazing treatment developed to stimulate the defoliation resistance mechanisms increased tiller density per square meter, rhizosphere volume per plant, and rhizosphere volume per cubic meter of soil.

**Introduction**

An incomplete understanding of the interrelated processes within grassland ecosystems is the main reason for the limited effectiveness of traditional management practices. A better understanding of the complex biological and ecological grassland processes will advance the development of effective grazing management strategies.

Grazing effects are often simplistically perceived to be just the removal of leaf material from grass plants. However, defoliation by grazing produces complex effects on grass plants. Different grazing management treatments cause diverse changes in plant growth, plant density, and the herbage biomass produced on grasslands (Manske 2003a). Traditional grazing management practices result in encumbered grassland ecosystems that produce at less-than-potential levels. These antiquated practices are not based on the biological requirements of plants or on the biogeochemical processes in the ecosystem and need to be replaced with effective strategies that improve grassland health and productivity. Biologically effective management strategies, such as the 4.5-month twice-over rotation system, produce advantageous biological effects by coordinating grazing with specific phenological growth stages to manipulate the defoliation resistance mechanisms that grass plants developed during their coevolution with herbivores (Manske 1994). Two defoliation resistance mechanisms of primary concern to grassland managers are grass vegetative reproduction by secondary tiller development from axillary buds and symbiotic soil organism activity in the rhizosphere.

Vegetative shoots are produced from a main shoot or lead tiller by vegetative reproduction, the physiological process of tillering (Manske 1998). Tillering is the development of a shoot from vertical growth of an axillary bud (Dahl 1995), and each tiller is a complete unit with roots, stem, and leaves. Defoliation stimulates tillering by reducing the influence of apical dominance, the physiological process by which the apical meristem and young leaves of a lead tiller exert hormonal regulation of axillary bud growth that inhibits development of vegetative tillers (Briske 1991, Murphy and Briske 1992, Briske and Richards 1994, Briske and Richards 1995, Manske 1996b). Stimulation of the tillering process in grass plants results in increased plant density and greater quantity and quality of aboveground herbage production (Manske 2003a).

The soil rhizosphere around perennial grass roots is the zone where a symbiotic relationship occurs between the roots of plants and microorganisms living in the soil. The rhizosphere organisms are bacteria, protozoa, nematodes, mites, small insects, and fungi. These organisms interact in a complex trophic web that is critical for energy and nutrient flow in grassland ecosystems (Manske and Caesar-TonThat 2002). Defoliation beneficially stimulates soil organism activity in the rhizosphere by increasing the amount of carbon compounds released from grass roots into the rhizosphere. Increased exudation of sugars, amino acids, glycosides, and other compounds from the roots of grass plants increases microorganism activity (Curl and Truelove 1986, Whipps 1990, Campbell and Greaves 1990). Bacterial growth in the rhizosphere is stimulated by the presence of simple carbon compounds from the exudates (Elliot 1978, Anderson *et al.* 1981, Curl and Truelove 1986, Whipps 1990). Protozoa and nematodes graze increasingly on the proliferating bacteria (Curl and Truelove 1986) and accelerate the biogeochemical cycling processes (Coleman *et al.* 1983). The activity of microbes in the rhizosphere increases the amount of nutrients available for plant growth (Allen and Allen 1990). Increased activity of rhizosphere fungi also benefits plant growth. Rhizosphere fungi are primarily vesicular-arbuscular mycorrhizae (VAM) that form endomycorrhiza in which the vesicles, arbuscules, and hyphae of the fungus enter the cells and tissue of the host plant (Harley and Smith 1983). The symbiotic function of endomycorrhizal fungi in grassland plant rhizospheres is the nitrification of ammonia and the enhancement of the absorption of phosphorus, other mineral nutrients, and water (Moorman and Reeves 1979, Harley and Smith 1983, Allen and Allen 1990, Box and Hammond 1990, Marschner 1992, Manske 1996). Stimulation of the activity of rhizosphere organisms results in increased conversion of organic nitrogen into mineral nitrogen and in greater availability of water, minerals, and nutrients for the grass plants.

Both the tillering process and soil rhizosphere activity can be stimulated by grazing management that removes a small amount of leaf material while the plant is between the three and a half new leaf stage and flower growth stage (Manske 1999b). Grazing grass plants prior to the three and a half new leaf stage negatively affects grass growth. Early seasonal growth of grass plants depends on carbohydrates stored in the roots, rhizomes, and stem bases (Trlica 1977), and prematurely grazed plants are unable to replenish adequate amounts of carbohydrates to support active growth (Coyne *et al.* 1995, Manske 1999a). Starting grazing after the three and a half new leaf stage and before the flower stage allows plants to establish sufficient leaf area to produce adequate photosynthetic assimilates to meet leaf growth requirements and allows all leaf bud primordia in the apical meristem to develop into leaf buds (Manske 1998). Little evidence has been found to suggest that defoliation after the flower stage has beneficial stimulatory effects on grass growth (Manske 2000).

The objectives of this research project were to investigate the two primary defoliation resistance mechanisms by evaluating the effects from four management treatments on the response of western wheatgrass plants (*Agropyron smithii)* through comparison of quantitative differences in (1) the number of tillers per square meter and (2) the amount of soil rhizosphere activity as measured by the volume of rhizosphere in a known volume of soil.

**Procedure**

This project was conducted in 2002 at the NDSU Dickinson Research Extension Center ranch, located near the Knife River. The Ranch Headquarters is 20 miles north of Dickinson, in western North Dakota, U.S.A. (47° 14' N. lat., 102° 50' W. long.).

*Treatments*

The four treatments in this experiment were (1) 4.5-month twice-over rotation system (4.5-m TOR), (2) 4.5-month seasonlong (4.5-m SL), (3) 6.0-month seasonlong (6.0-m SL), and (4) long-term nongrazed control (NG). Livestock on the 4.5-month twice-over rotation management treatment followed a double rotation sequence through three native range pastures for 4.5 months (135 days) from early June until mid October. Each pasture was grazed for two periods, a stimulation period of about 15 days of grazing between early June and mid July (when grasses were in the three and a half new leaf stage to anthesis phenophase), followed by a harvest period of about 30 days of grazing after mid July and prior to mid October. The first pasture grazed in the sequence was the last pasture grazed the previous year. Sample pasture #1 (4.5-m TOR) was grazed in 2001 from 13 June to 28 June during the second stimulation period and again from 13 August to 11 September during the harvest period. In 2002 it was grazed from 27 June to 12 July during the third stimulation period and again from 11 September to 10 October during the harvest period. Livestock on the 4.5-month seasonlong management treatment grazed one native range pasture for 4.5 months (135 days) from early June until mid October. Sample pasture #11 (4.5-m SL) was grazed in 2001 from 30 May to 11 October and in 2002 from 29 May to 10 October. Livestock on the 6.0-month seasonlong management treatment grazed one native range pasture for 6.0 months (183 days) from mid May until mid November. Sample pasture #7 (6.0-m SL) was grazed in 2001 from 9 May until 8 November and in 2002 from 9 May until 7 November. The long-term nongrazed (NG) management treatment had not been grazed, mowed, or burned for more than 30 years before the initiation of these research treatments.

*Field Sample Collection Procedure*

Replicated plant and soil samples were collected monthly. The collection dates were 25 June, 26 July, 30 August, 6 September, and 30 September. Field samples collected 30 August and 6 September were analyzed as one sample period. Eight samples were collected each period: two representative replications of western wheatgrass (*Agropyron smithii*) with an intact soil core from silty range sites on each of the four defoliation treatments. Plastic PVC pipe 3 inches (7.62 cm) in diameter and 4 inches (10.16 cm) long was forced into sample site soil. Intact soil-plant cores and pipe were excavated and transported to the laboratory.

*Laboratory Procedure*

The basic research unit was the western wheatgrass plant. Tillers of each plant were categorized as lead, secondary, or fall types. The densities of the lead tillers, of the secondary and fall tillers, and of the total of all tillers were determined per square meter of soil surface for each sample period. The soil matrix of collected soil cores was carefully removed from between the rhizospheres around the roots of western wheatgrass plants. The roots and rhizospheres of other plant species were separated from the soil cores and discarded. The western wheatgrass rhizospheres were sprayed with a clear acrylic coating to prevent damage during further handling. The length and diameter of the rhizosphere around each root of every plant, including associated tillers, were measured in inches with a vernier caliper. The English measurements were converted to metric system values. During the process of extraction, some rhizospheres were damaged and small segments were detached from the root surface. The length measurements of damaged rhizospheres were the length of the root, including the regions of detached rhizosphere segments. The length and diameter measurements were used to determine the volume of the rhizosphere around each root. Data were analyzed on a per-plant basis, as a total of all plants per replication, and as a mean of the two replications per sample period. Differences between means of treatments were analyzed by a standard paired-plot t-test (Mosteller and Rourke 1973).

**Results**

*Precipitation*

Precipitation in 2002 (table 1) was greater than normal (134.21% LTM) and the growing season was categorized as wet. June, July, and August were wet months (>125% of LTM). September and October had water deficiencies (< 75% of LTM), and plants experienced water stress during September (Manske 2003b).

*Tiller Density of Western Wheatgrass*

The 4.5-m TOR treatment had greater numerical total tiller density for each sample period than the other treatments (table 2, figure 1). The mean total tiller density across the four monthly sample periods (June to September) was significantly greater ($P<0.05$) on the 4.5-m TOR treatment than on the 4.5-m SL, 6.0-m SL, and long-term nongrazed treatments. The mean total tiller density on the 4.5-m SL, 6.0-m SL, and long-term nongrazed treatments did not differ ($P<0.05$). The total tiller density on the 4.5-m TOR treatment was significantly greater ($P< 0.05$) than that on the 4.5-m SL and 6.0-m SL treatments during June, August, and September and greater ($P< 0.05$) than that on the long-term nongrazed treatment during June (table 2).

Lead tiller density (table 2, figure 2) on the 4.5-m TOR treatment was significantly greater ($P<0.05$) than that on the 4.5-m SL and 6.0-m SL treatments during June and September and greater ($P<0.05$) than that on the long-term nongrazed treatment during September.

Secondary tiller density (table 2, figure 3), including the fall tillers, was significantly greater ($P<0.05$) on the 4.5-m TOR treatments than on the 4.5-m SL treatment during June, July, and August and greater ($P<0.05$) on the 4.5-m TOR treatment than on the 6.0-m SL and long-term nongrazed treatments during June and August.

Sample pasture #1 of the 4.5-m TOR treatment was grazed in 2001 during the second stimulation period, mid June to late June. This is the period when light defoliation of western wheatgrass promotes the greatest increase in tiller numbers by stimulating vegetative reproduction processes. Western wheatgrass tiller density on the 4.5-m TOR treatment was significantly greater ($P<0.05$) than that on the 4.5-m SL, 6.0-m SL, and nongrazed treatments in June of 2002 (table 2, figure 1). In 2002, sample pasture #1 of the 4.5-m TOR treatment was grazed during the third stimulation period, early July to mid July. Western wheatgrass secondary tiller density on the 4.5-m TOR treatment was significantly greater ($P< 0.05$) than that on the 4.5-m SL, 6.0-m SL, and nongrazed treatments during August (table 2). Total tiller density on the 4.5-m TOR treatments was significantly greater ($P< 0.05$) than that on the 4.5-m SL and 6.0-m SL treatments during August and September (table 2).

*Rhizosphere Volume per Plant*

The rhizosphere volume per plant varied considerably during June and July, with little difference among treatments. Following the stimulation grazing period from early July to mid July, the rhizosphere volume per plant on sample pasture #1 of the 4.5-m TOR treatment greatly increased. The rhizosphere volume per plant (table 3, figure 4) on the 4.5-m TOR treatment was significantly greater ($P< 0.05$) than that on the 4.5-m SL and 6.0-m SL treatments in August and September and greater ($P< 0.05$) than that on the nongrazed treatment in September.

*Total Rhizosphere Volume*

The rhizosphere volume per cubic meter of soil was not different ($P< 0.05$) among treatments during June (table 4). Following the stimulation grazing period from early July to mid July on the 4.5-m TOR treatment, the total rhizosphere volume per cubic meter of soil (table 4, figure 5) on that treatment was significantly greater ($P< 0.05$) than that on the 4.5-m SL and 6.0-m SL treatments during July, August, and September and greater ($P< 0.05$) than that on the nongrazed treatments during August and September.

**Discussion**

This study measured tiller density and rhizosphere volume on four management treatments across one growing season. This relatively small data set revealed important biological differences among the grazing management treatments.

The twice-over rotation system is designed to match defoliation periods with grass phenological stages of growth when the defoliation resistance mechanisms can be stimulated. The two primary mechanisms are vegetative tillering from axillary buds and activity of symbiotic soil organisms in the rhizosphere.

Stimulation of vegetative reproduction from the twice-over rotation grazing treatment during the previous year increased western wheatgrass tiller density. The increase carried over through the winter and resulted in greater tiller density on that treatment than on the other treatments in June of the study year. The tiller stimulation that resulted from the twice-over rotation grazing treatment during the year of the study increased the western wheatgrass tiller density so that it was greater on that biologically effective treatment than on the other grazing treatments during the entire later portion of the growing season.

The activity of symbiotic soil organisms, as indicated by the volume of the rhizosphere, increased on the twice-over rotation system following defoliation during the stimulation grazing period, which occurred on the sample area from early July to mid July in 2002. The rhizosphere volume per plant significantly increased on the twice-over rotation treatment following the stimulation grazing period, and the total rhizosphere volume in the soil increased following the stimulation period and remained significantly greater during the remainder of the growing season.

**Conclusion**

Grazing management strategies that are designed to stimulate grass defoliation resistance mechanisms meet the biological requirements of plants and enhance the biogeochemical processes in grassland ecosystems. Stimulation of these biological and ecological mechanisms increases the vegetative tillering process and the rhizosphere organism activity. Traditional management practices that are designed for other priorities than to meet plant requirements or enhance ecosystem processes impede the function of defoliation resistance mechanisms. Inhibition of these mechanisms reduces the development of grass vegetative tillers and the activity of rhizosphere organisms.

Acknowledgment

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Table 1. Precipitation in inches for growing-season months at Ranch Headquarters DREC, North Dakota.

| | Apr | May | Jun | Jul | Aug | Sep | Oct | Growing Season |
|---|---|---|---|---|---|---|---|---|
| Long-term mean | 1.41 | 2.04 | 3.36 | 2.75 | 1.85 | 1.39 | 1.24 | 14.04 |
| 2002 | 1.14 | 2.18 | 5.40 | 4.27 | 4.24 | 0.74 | 0.88 | 18.85 |
| % of LTM | 80.85 | 106.86 | 160.71 | 155.27 | 229.19 | 53.24 | 70.97 | 134.21 |

Table 2. Tiller density of western wheatgrass per square meter.

| | Tiller Types | June | July | August | September |
|---|---|---|---|---|---|
| 4.5-m TOR | Lead | 1206.043a | 657.842a | 712.662a | 986.763a |
| | Secondary | 1206.042m | 548.202m | 1260.864m | 438.562m |
| | Total | 2412.087x | 1206.043x | 1973.526x | 1425.324x |
| | | | | | |
| 4.5-m SL | Lead | 548.202b | 548.202a | 493.382a | 548.202b |
| | Secondary | 0.0n | 109.641n | 274.101n | 109.641m |
| | Total | 548.202y | 657.842x | 767.482y | 657.842y |
| | | | | | |
| 6.0-m SL | Lead | 438.561b | 328.921a | 328.921a | 438.562b |
| | Secondary | 328.921o | 219.281mn | 493.382n | 328.922m |
| | Total | 767.482y | 548.202x | 822.303y | 767.482y |
| | | | | | |
| Nongrazed | Lead | 438.562ab | 328.921a | 712.663a | 438.561b |
| | Secondary | 109.641no | 219.281mn | 164.461n | 767.483m |
| | Total | 548.202y | 548.202x | 877.123xy | 1206.044x |

Means in the same column and followed by the same letter are not significantly different (P<0.05)

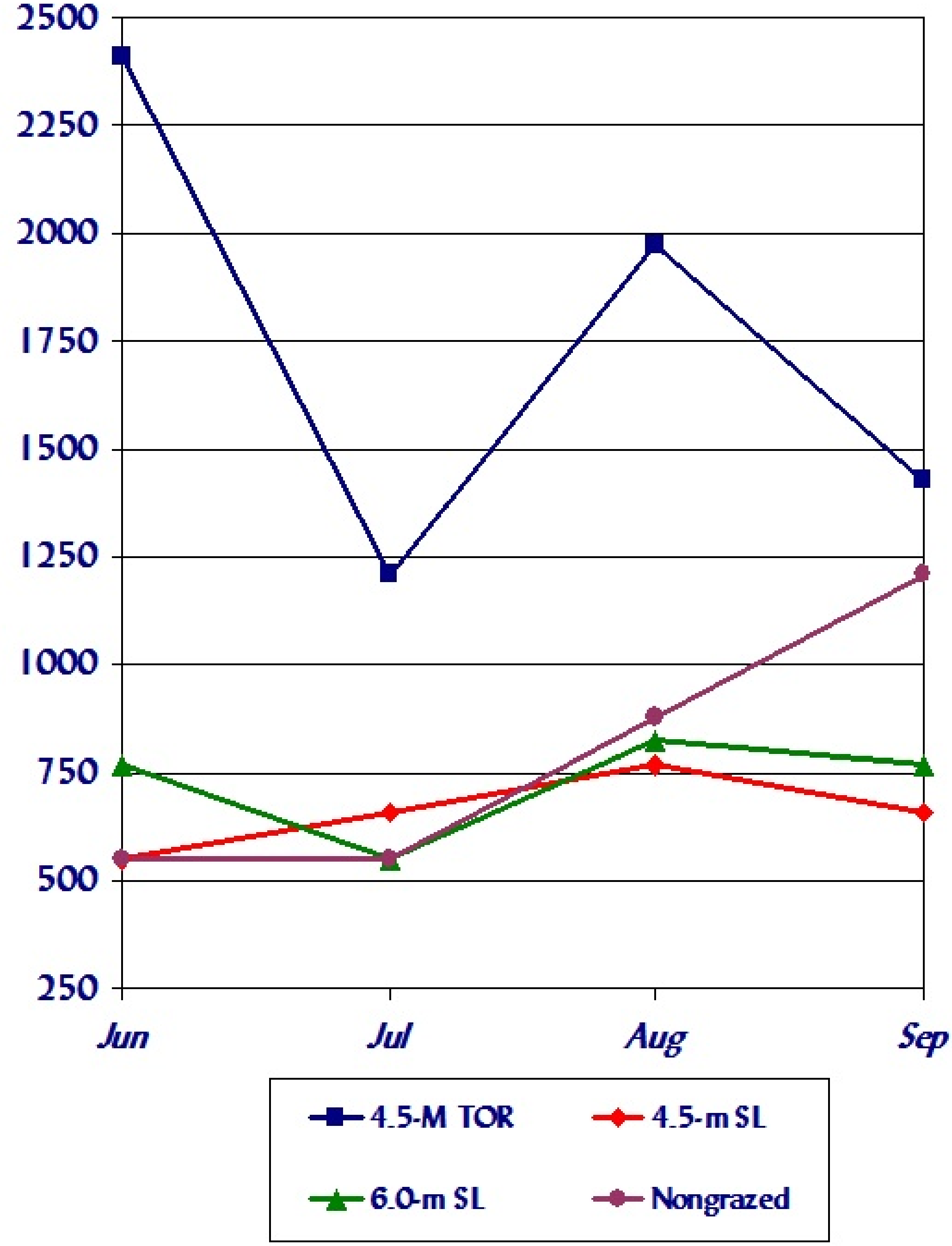


*Figure 1. Total tiller density of western wheatgrass per square meter*

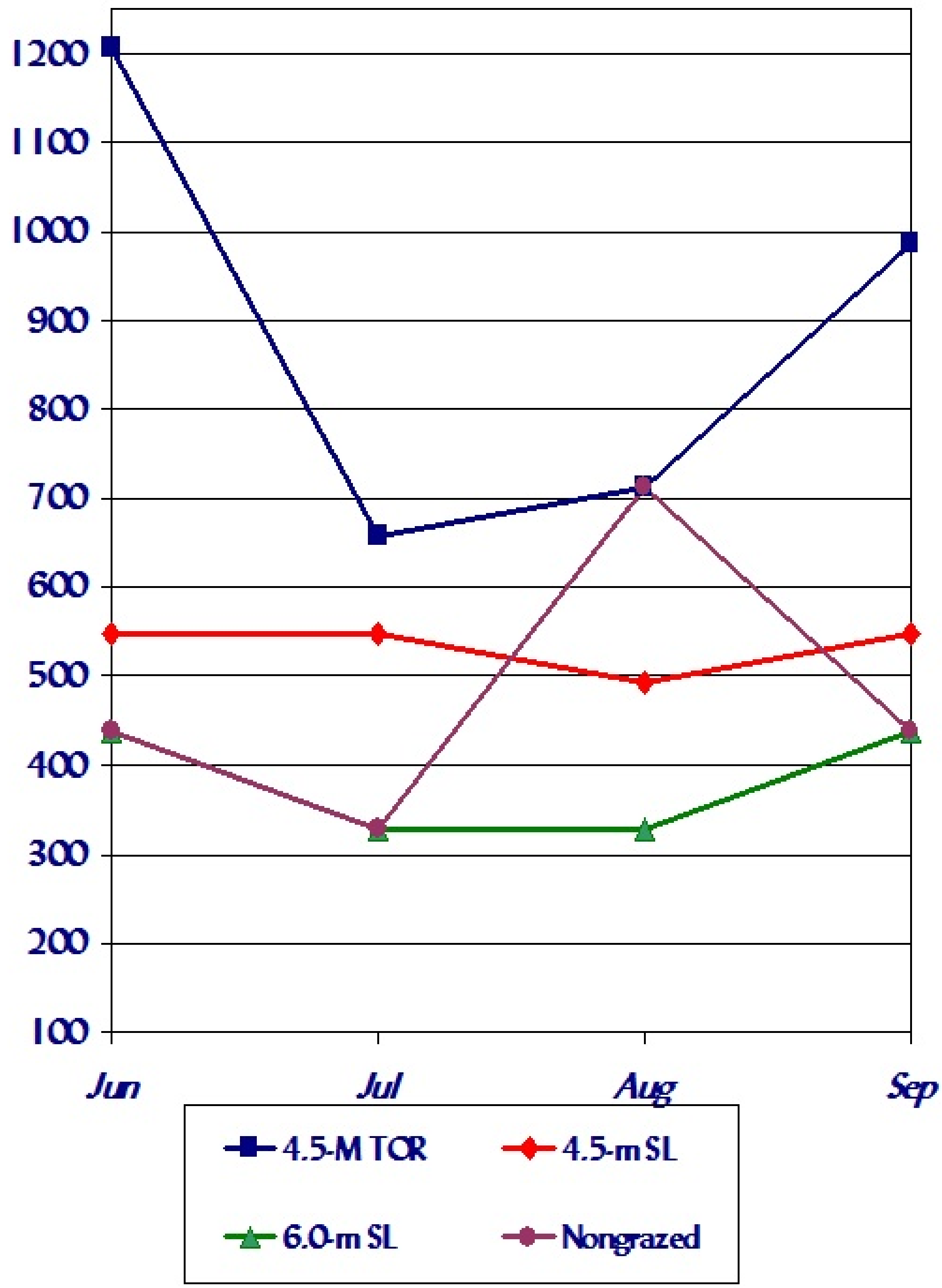


*Figure 2. Lead Tiller Density of western wheatgrass per square meter*

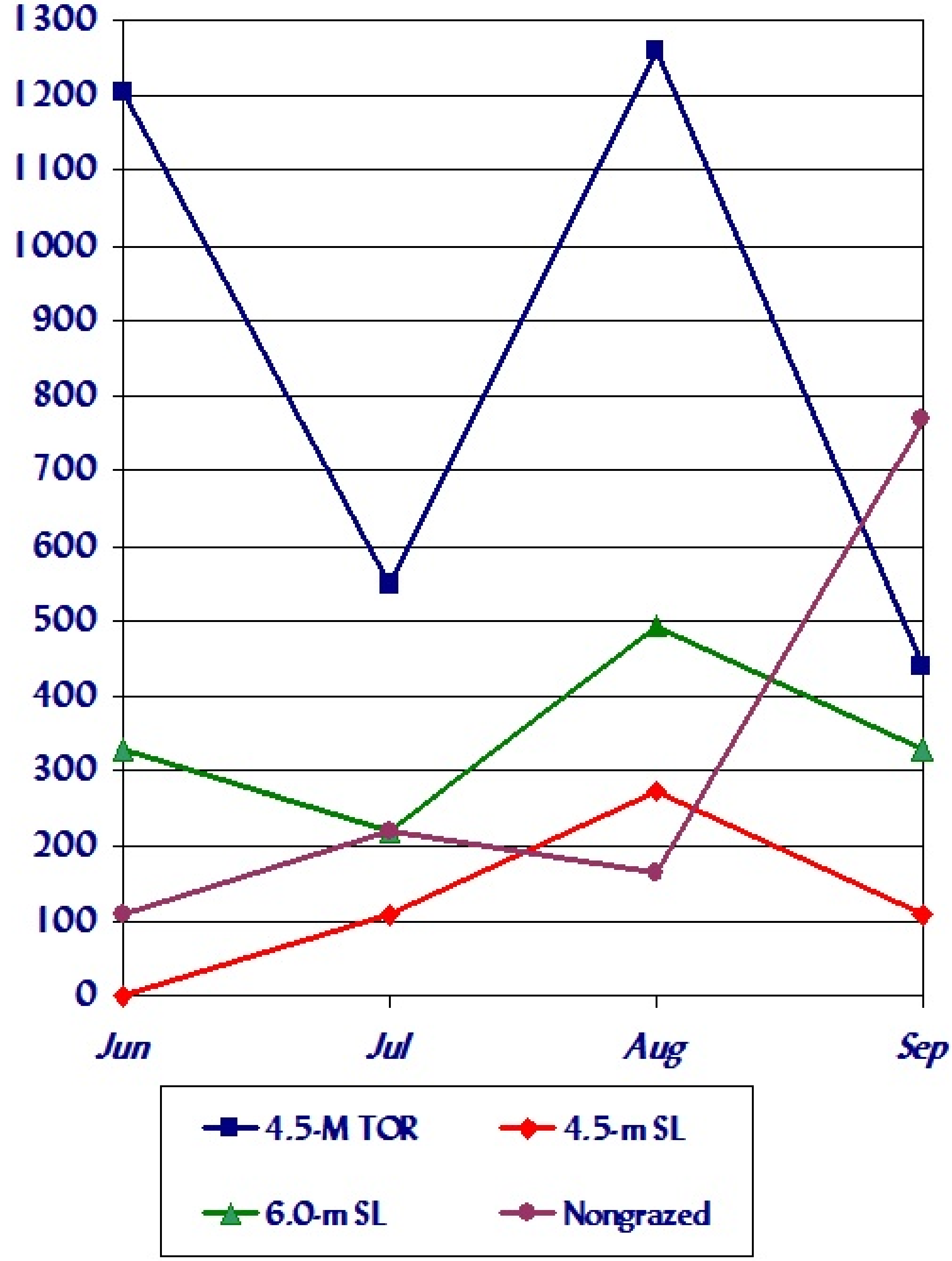


*Figure 3. Secondary Tiller Density of western wheatgrass per square meter*

Table 3. Rhizosphere volume ($cm^3$) per grass plant.

| | June | July | August | September |
|---|---|---|---|---|
| 4.5-m TOR | 0.270a | 0.491a | 1.113a | 1.192a |
| | | | | |
| 4.5-m SL | 0.367ab | 0.139b | 0.511b | 0.418b |
| | | | | |
| 6.0-m SL | 0.629ab | 0.369ab | 0.327c | 0.113c |
| | | | | |
| Nongrazed | 0.425b | 1.032a | 0.385abc | 0.341bc |

Means in the same column and followed by the same letter are not significantly different ($P<0.05$)

Table 4. Rhizosphere volume ($cm^3$) per cubic meter of soil.

| | June | July | August | September |
|---|---|---|---|---|
| 4.5-m TOR | 3214.748a | 3867.542a | 7183.271a | 6586.063a |
| | | | | |
| 4.5-m SL | 1800.931a | 642.209b | 1963.017b | 1802.973b |
| | | | | |
| 6.0-m SL | 1695.208a | 1087.083b | 1128.077b | 658.292c |
| | | | | |
| Nongrazed | 1725.236a | 2804.612a | 2391.966b | 2438.473b |

Means in the same column and followed by the same letter are not significantly different ($P<0.05$)

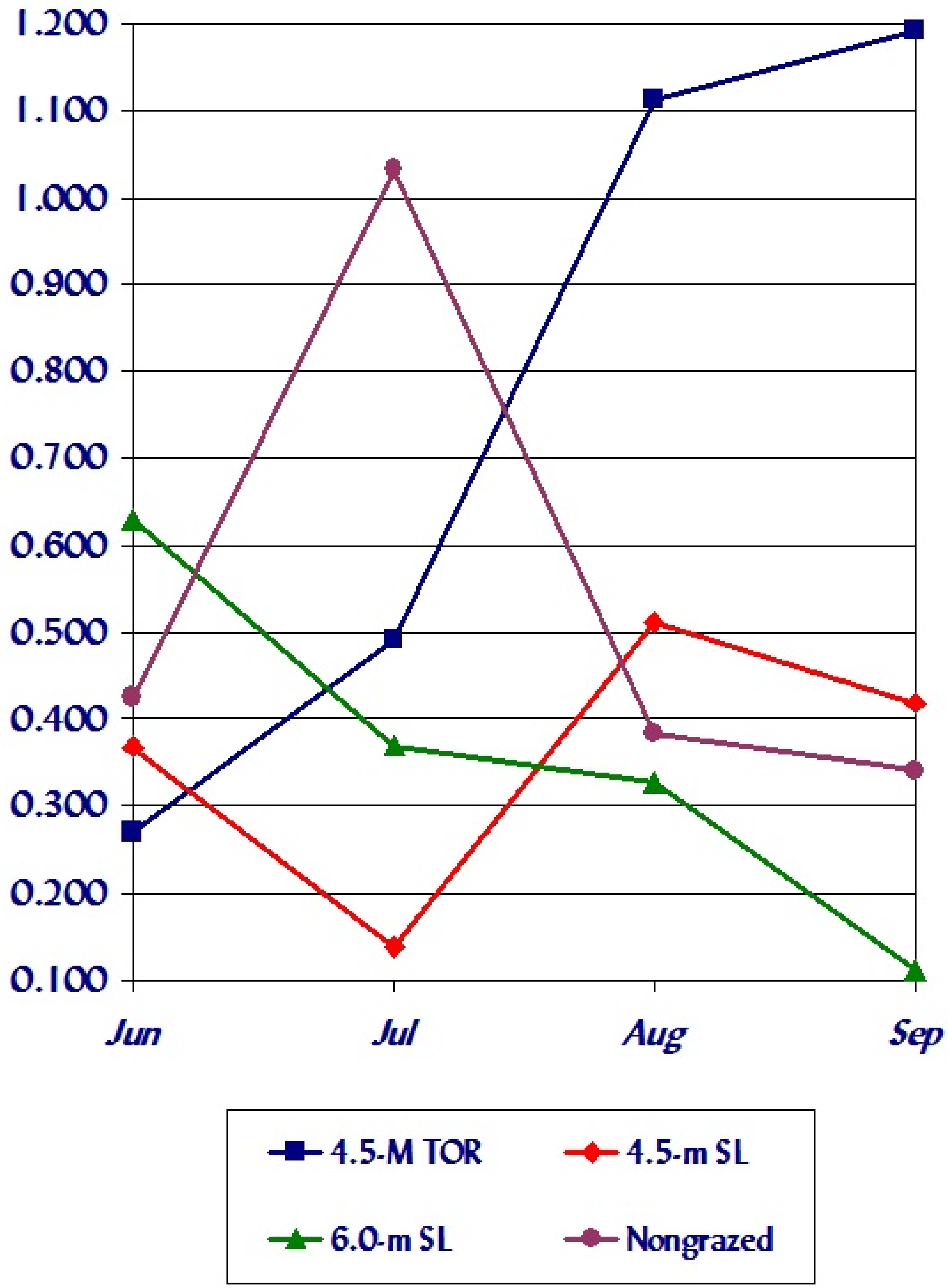


*Figure 4. Rhizosphere volume ($cm^3$) per grass plant*

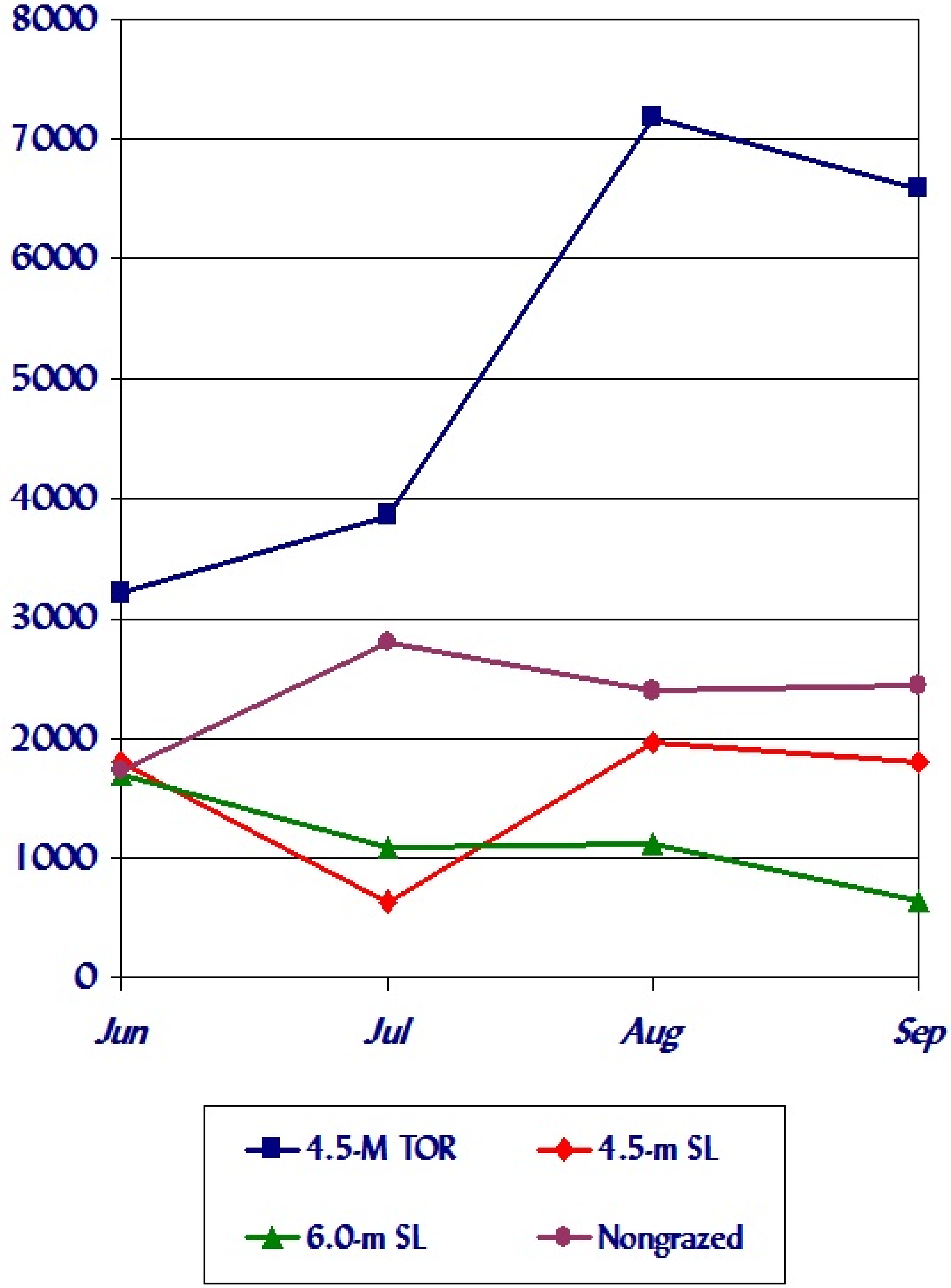


*Figure 5. Rhizosphere volume ($cm^3$) per cubic meter of soil*

## Literature Cited


**Allen, E.B., and M.F. Allen. 1990.** The mediation of competition by mycorrhizae in successional and patchy environments. p. 307-389. *in* J.B. Grace and D. Tilman (eds.). Perspectives on plant competition. Academic Press Inc., San Diego, CA.

**Anderson, R.V., D.C. Coleman, C.V. Cole, and E.T. Elliott. 1981.** Effect of the nematodes Acrobeloides sp. and Mesodiplogaster lheritieri on substrate utilization and nitrogen and phosphorus mineralization in soil. Ecology 62:549-555.

**Box, J.E., and L.C. Hammond. 1990.** Rhizosphere dynamics. Westview Press, Boulder, CO.

**Briske, D.D. 1991.** Developmental morphology and physiology of grasses. p. 85-108. *in* R.K. Heitschmidt and J. W. Stuth (eds.). Grazing management: an ecological perspective. Timber Press, Portland, OR.

**Briske, D.D., and J.H. Richards. 1994.** Physiological responses of individual plants to grazing: current status and ecological significance. p. 147-176. *in* M. Vavra, W.A. Laycock, and R.D. Pieper (eds.). Ecological implications of livestock herbivory in the west. Soc. for Range Manage., Denver, CO.

**Briske, D.D., and J.H. Richards. 1995.** Plant responses to defoliation: a physiological, morphological and demographic evaluation. p. 635-710. *in* D.J. Bedunah and R.E. Sosebee (eds.). Wildland plants: physiological ecology and developmental morphology. Soc. for Range Manage., Denver, CO.

**Campbell, R., and M.P. Greaves. 1990.** Anatomy and community structure of the rhizosphere. p. 11-34. *in* J.M. Lynch (ed.). The rhizosphere. John Wiley and Sons, New York, NY.

**Coleman, C.D., C.P.P. Reid, and C.V. Cole. 1983.** Biological strategies of nutrient cycling in soil ecosystems. Adv. Ecol. Res. 13:1-55.

**Coyne, P.I., M.J. Trlica, and C.E. Owensby. 1995.** Carbon and nitrogen dynamics in range plants. p. 59-167. *in* D.J. Bedunah and R.E. Sosebee (eds.). Wildland plants: physiological ecology and developmental morphology. Soc. for Range Manage., Denver, CO.

**Curl, E.A., and B. Truelove. 1986.** The rhizosphere. Springer-Verlag, New York, NY.

**Dahl, B.E. 1995.** Developmental morphology of plants. p. 22-58. *in* D.J. Bedunah and R.E. Sosebee (eds.). Wildland plants: physiological ecology and developmental morphology. Soc. for Range Manage., Denver, CO.

**Elliot, E.T. 1978.** Carbon, nitrogen and phosphorus transformations in gnotobiotic soil microcosms. M.S. Thesis, Department of Agronomy, Colorado State University, Ft. Collins, CO.

**Harley, J.L., and S.E. Smith. 1983.** Mycorrhizal symbiosis. Academic Press, New York, NY.

**Manske, L.L. 2003a.** Effects of grazing management treatments on rangeland vegetation. NDSU Dickinson Research Extension Center. Range Research Report DREC 03-3027. Dickinson, ND. 6p.

**Manske, L.L. 2003b.** Ombrothermic interpretation of range plant water deficiency from temperature and precipitation data at the Ranch Headquarters of the Dickinson Research Extension Center in western North Dakota, 1982-2002. NDSU Dickinson Research Extension Center. Range Research Report DREC 03-1019f. Dickinson, ND. 17p.

**Manske, L.L., and T.C. Caesar-TonThat. 2002.** Grazing management effects on rhizosphere fungi. NDSU Dickinson Research Extension Center. Range Research Report DREC 02-1041. Dickinson, ND. 10p.

**Manske, L.L. 2000.** Management of Northern Great Plains prairie based on biological requirements of the plants. NDSU Dickinson Research Extension Center. Range Research Report DREC 00-1028. Dickinson, ND. 12p.

**Manske, L.L. 1999a.** Defoliation applied at some phenological growth stages negatively affects grass plants. NDSU Dickinson Research Extension Center. Summary Range Management Report DREC 99-3013. Dickinson, ND. 4p.

**Manske, L.L. 1999b.** Can native prairie be sustained under livestock grazing? p. 99-108. *in* J. Thorpe, T.A. Steeves, and M. Gallop (eds.). Proceedings of the Fifth Prairie Conservation and Endangered Species Conference, Provincial Museum of Alberta. Natural History Occasional Paper No. 24. Edmonton, Alberta.

**Manske, L.L. 1998.** General description of grass growth and development and defoliation resistance mechanisms. NDSU Dickinson Research Extension Center. Range Management Report DREC 98-1022. Dickinson, ND. 12p.

**Manske, L.L. 1996.** Adaptive tolerance mechanisms in grass plants. p. 97-99. *in* Z. Abouguendia (ed.). Total ranch management in the Northern Great Plains. Grazing and Pasture Technology Program, Saskatchewan Agriculture and Food. Regina, Saskatchewan, Canada.

**Manske, L.L. 1994.** Grazing management for Northern Great Plains rangelands. NDSU Dickinson Research Extension Center. Range Research Report DREC 94-1004. Dickinson, ND. 11p.

**Marschner, H. 1992.** Nutrient dynamics at the soil-root interface (Rhizosphere). p. 3-12. *in* D.J. Read, D.H. Lewis, A.H. Fitter, and I.J. Alexander (eds.). Mycorrhizas in ecosystems. C.A.B. International, Wallingford, U.K.

**Moorman, T., and F.B. Reeves. 1979.** The role of endomycorrhizae in revegetation practices in the semi-arid west. II. A bioassay to determine the effect of land disturbance on endomycorrhizal populations. American Journal of Botany 66:14-18.

**Mosteller, F., and R.E.K. Rourke. 1973.** Sturdy Statistics. Addison-Wesley Publishing Co., MA. 395p.

**Murphy, J.S., and D.D. Briske. 1992.** Regulation of tillering by apical dominance: chronology, interpretive value, and current perspectives. J. Range Manage. 45:419-429.

**Trlica, M.J. 1977.** Distribution and utilization of carbohydrate reserves in range plants. p. 73-97. *in* R.E. Sosebee (ed.). Range plant physiology. Range Sci. Ser. No. 4. Soc. for Range Manage., Denver, CO.

**Whipps, J.M. 1990.** Carbon economy. p. 59-97. *in* J.M. Lynch (ed.). The rhizosphere. John Wiley and Sons, New York, NY.

# Grass Vegetative Tillering Responses to Partial Defoliation

Llewellyn L. Manske PhD
Research Professor of Range Science
North Dakota State University
Dickinson Research Extension Center
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Management of grassland ecosystems has customarily been applied from the perspective of the "use" of the grassland creating conflict among competing user groups and imposing antagonistic effects on grassland plants and soil organisms that cause degradation of biogeochemical processes, reduction of available mineral nitrogen, reduction of grass tiller density, and reduction of grassland productivity (Manske 2007a). Management strategies that place priority with the living components of the ecosystem meet the biological requirements of grassland plants and soil organisms, and are beneficial for biogeochemical processes, thereby increasing soil mineral nitrogen and enhancing health and productivity of grassland ecosystems (Manske 2007b).

Implementation of biologically effective management strategies that are beneficial for grassland ecosystems requires knowledge of grass plant responses to defoliation resulting from activation of the defoliation resistance mechanisms developed in grass plants during coevolution with herbivores (McNaughton 1979, 1983; Coleman et al. 1983; Briske 1991; Briske and Richards 1995; Manske 1999). The defoliation resistance mechanisms help grass tillers withstand and recover from partial defoliation by grazing and are: herbivore-induced compensatory physiological processes (McNaughton 1979, 1983; Briske 1991); stimulation of vegetative reproduction of secondary tillers from axillary buds (Mueller and Richards 1986, Richards et al. 1988, Murphy and Briske 1992, Briske and Richards 1994, Briske and Richards 1995); and stimulation of rhizosphere organism activity and the increased conversion of inorganic nitrogen from soil organic nitrogen (Coleman et al. 1983, Ingham et al. 1985). The defoliation resistance mechanisms not only permit grass plants to tolerate defoliation but to benefit from partial defoliation by grazing at vegetative phenological growth stages.

Compensatory physiological processes within grass plants enable rapid recovery of defoliated tillers through: increased growth rates of replacement leaves and shoots that produces larger leaves with greater mass (Langer 1972, Briske and Richards 1995); increased photosynthetic capacity of remaining mature leaves and rejuvenated portions of older leaves not completely senescent (Atkinson 1986, Briske and Richards 1995); and increased allocation of carbon and nitrogen from remaining leaf and shoot tissue, not from material stored in the roots (Richards and Caldwell 1985, Briske and Richards 1995, Coyne et al. 1995).

Vegetative reproduction by tillering is the asexual process of growth and development of tillers from axillary buds (Dahl 1995). The meristematic activity in axillary buds and the subsequent development of vegetative secondary tillers is regulated by auxin, a growth-inhibiting hormone produced in the apical meristem and young developing leaves of lead tillers (Briske and Richards 1995). Auxin interferes with the metabolic function of cytokinin, a growth hormone (Briske and Richards 1995). Partial defoliation temporarily reduces the production of the blockage hormone, auxin (Briske and Richards 1994). This abrupt reduction of plant auxin in the lead tiller allows for cytokinin synthesis or utilization in multiple axillary buds, stimulating the development of vegetative tillers (Murphy and Briske 1992, Briske and Richards 1994).

The rhizosphere is the narrow zone of soil around active roots of perennial grassland plants and is comprised of bacteria, protozoa, nematodes, springtails, mites, endomycorrhizal fungi (Anderson et al. 1981, Curl and Truelove 1986) and ectomycorrhizal fungi (Caesar-TonThat et al. 2001, Manske and Caesar-TonThat 2003). Active rhizosphere organisms are required in grassland ecosystems for the conversion of plant usable inorganic nitrogen from soil organic nitrogen. Rhizosphere organism biomass and activity are limited by access to simple carbon chains (Curl and Truelove 1986) because the microflora trophic levels lack chlorophyll and have low carbon (energy) content. Partial defoliation of grass plants at vegetative phenological growth stages by large grazing herbivores causes greater quantities of exudates containing simple carbon compounds to be released through the plant roots into the rhizosphere (Hamilton and Frank 2001). With the increase in availability of carbon compounds in the rhizosphere, activity of the microorganisms increases (Anderson et al. 1981, Curl and Truelove 1986, Whipps 1990). The increase in rhizosphere organism activity causes an increase in microorganism biomass and an increase in rhizosphere volume (Gorder, Manske, and Stroh 2004). The elevated rhizosphere organism activity caused by the increase in available carbon compounds results in a greater quantity of organic nitrogen converted into inorganic nitrogen (Coleman et al. 1983, Klein et al. 1988, Burrows and Pfleger 2002, Rillig et al. 2002, Bird et al. 2002, Driver et al. 2005). The increase in inorganic nitrogen available to defoliated grass plants allows the plant to recover more quickly from defoliation, to accelerate the growth rate, to increase vegetative tiller development from axillary buds, and to increase the total herbage biomass production (Manske 1999, 2003). However, a mineral nitrogen deficiency with less than 100 lbs/ac available causes a decrease in plant water (precipitation) use efficiency that results in a 49.6% reduction in herbage production (Wight and Black 1972, 1979).

The defoliation resistance mechanisms do not function automatically and they do not start and stop instantaneously; they must be activated annually by seasonable partial defoliation by grazing of grass tillers during phenological growth between the three and a half new leaf stage and the flower (anthesis) stage (Manske 1999). The percentage of leaf material needed to be removed by grazing from the grass tillers to activate the defoliation resistance mechanisms is not completely understood. The goal of this project was to evaluate grass vegetative tiller responses to partial defoliation to improve the scientific understanding of the use of grazing to activate the defoliation resistance mechanisms. This research project was funded by North Dakota State Board of Agricultural Research and Education (SBARE) and conducted at the Dickinson Research Extension Center in southwestern North Dakota during 2000 and 2001. This project compared the differences in vegetative tiller development as responses to partial defoliation of tillers with 25% and 50% leaf material removed and to nondefoliation of tillers of western wheatgrass growing on silty range sites managed with three different grazing treatments.

**Study Area**

The native rangeland study sites were on the Dickinson Research Extension Center ranch, operated by North Dakota State University and located 20 miles north of Dickinson, in southwestern North Dakota, U.S.A. (47° 14' N. lat., 102° 50' W. long.).

Soils were primarily Typic Haploborolls. Long-term mean annual temperature was 42.4° F (5.8° C). January was the coldest month, with a mean temperature of 14.6° F (-9.7° C). July and August were the warmest months, with mean temperatures of 69.8° F (21.0° C) and 68.8° F (20.4° C), respectively. Long-term annual precipitation was 16.69 inches (423.96 mm). The amount of precipitation received during the growing season (April to October) was 13.90 inches (353.08 mm), 83.28% of annual precipitation (Manske 2009a).

The native rangeland vegetation was the Wheatgrass-Needlegrass Type (Barker and Whitman 1988, Shiflet 1994) of the mixed grass prairie. The dominant native range grasses were western wheatgrass (*Agropyron smithii*) (*Pascopyrum smithii*), needle and thread (*Stipa comata*) (*Hesperostipa comata*), blue grama (*Bouteloua gracilis*), and threadleaf sedge (*Carex filifolia*).

The study sites were managed with three different grazing strategies. The 6.0-month seasonlong management strategy started in mid May. Livestock grazed a single native range pasture for 183 days, until mid November. The 4.5-month seasonlong management strategy started in early June. Livestock grazed a single native range pasture for 137 days, until mid October. The 4.5-month twice-over rotation management strategy started in early June, when livestock were moved to one of three native range pastures. Livestock remained on native range for 137 days, grazing each pasture for two periods, one 15-day period between 1 June and 15 July (when lead tillers of grasses were between the three and a half new leaf stage and flower stage) and one 30-day period after 15 July and prior to mid October. The first pasture grazed in the sequence was the last pasture grazed the previous year.

**Procedures**

Three study site exclosures were established on native rangeland silty range sites with livestock grazing controlled by three different management strategies: 6.0-month seasonlong (6.0 m SL), 4.5-month seasonlong (4.5 m SL), and 4.5-month twice-over rotation (4.5 m TOR). The silty range sites were located on gently sloping upland terrace landscape positions with deep fine sandy loam soils. Sites with near 10 inch (25 cm) surface horizon depth were reconnoitered prior to the start of the study, however, the exclosure construction crew relocated the 4.5 m SL site to a more level grade but with a shallower surface horizon depth. The depths of the surface horizon on the study sites of the 6.0 m SL, 4.5 m SL, and 4.5 m TOR management strategies were 9.6 inches (24.4 cm), 8.1 inches (20.6 cm), and 9.8 inches (24.5 cm), respectively. The surface horizon of the soil on the 4.5 m SL management strategy was significantly shallower than that on the 6.0 m SL and 4.5 m TOR management strategies.

Within each exclosure, 21 microplots were located and seven randomly selected microplots were assigned to each of the three defoliation treatments. Grass tillers within each microplot were separated from the surrounding plant community by inserting into the sample site soil a PVC conduit barrier with a 3 inch (7.62 cm) diameter and 6 inch (15.24 cm) depth that was open at both ends. The PVC barriers prevented lateral movement of soil water, consequently, the only source of soil water in the microplots was precipitation.

Every western wheatgrass tiller within each microplot was individually identified with a distinguishing loop of colored wire that encircled the tiller at its base. New tillers were identified with different colored wire loops as they developed and carry over tillers were remarked at the start of the second year.

The western wheatgrass tillers were categorized as lead tillers, rhizome tillers, crown tillers, or fall tillers during data collection according to biological characteristics observed and relative position in the microplot. However, not all of the tillers classified as lead tillers were actually dominant tillers; some were subordinate secondary tillers. The tillers classified as rhizome tillers, crown tillers, or fall tillers were the type of tiller as classified, however, not all of these tillers were subordinate secondary tillers; some were actually lead tillers. Differentiation of tillers into distinguishable categories of dominant lead tillers and subordinate secondary tillers is not clear-cut. There appears to be a continuum of hierarchical levels within the tiller population from greatest dominance to lowest subordinate.

With the power of hindsight, the study tillers were divided into two synthetic groups based on relative rates of growth and development. Tillers with seemingly rapid or unimpeded growth were reclassified as lead tillers, and tillers with obviously inhibited growth and development were reclassified as secondary tillers. The lead tillers were subdivided into tillers that developed into sexually reproductive flower stages (reproductive lead tillers) and tillers that remained vegetative at the end of the growing season (vegetative lead tillers). The secondary tillers with inhibited growth rates were subdivided into tillers that remained vegetative at the end of the growing season (slow growth secondary tillers) and tillers that terminated growth during the growing season (early senescent secondary tillers). Tillers that were initiated between mid August and mid October were classified as fall tillers. Vegetative tillers with intact apical meristem tissue that survived the winter period and continued growth and development during the next growing season were classified as carry over tillers.

The defoliation treatments with 25% and 50% of the tiller leaf material removed were based on actual observed livestock grazing patterns and a control of no defoliation were applied to the western wheatgrass tillers in the microplots located in each of the three exclosures during 22 June of the first year. The resulting three study treatments were: A) no defoliation, control, B) defoliation, mid June-25%, and C) defoliation, mid June-50%. Each of the three defoliation treatments were conducted on three different grazing management strategies: 6.0-month seasonlong (6.0 m SL), 4.5-month seasonlong (4.5 m SL), and 4.5-month twice-over rotation (4.5 m TOR).

All western wheatgrass tillers within each of the seven replicated microplots received the same defoliation treatment. Defoliation treatment clip heights were based on percent height-weight data determined during the week before the date of the defoliation treatment from 40 typical tillers collected at ground level from near the study areas. The typical tillers were cut into segments of 1.0 inch (2.5 cm) height increments from the base upwards. The height increments were oven dried and weighed separately. Percent of mean total tiller weight was determined for each height increment. The height of the tillers in each microplot was measured and the appropriate proportion of height equal to 25% or 50% of the typical tillers weight was removed from each microplot tiller. The height of the tillers in each microplot was remeasured and a post defoliation tiller height was determined for each microplot (table 1).

Data collection began in early May and continued into October for two years (2000 and 2001). Sample periods occurred weekly during the first year and biweekly during the second year. The data collected for each tiller included number of leaves produced, phenological growth stage, and height of tallest leaf. New tillers were added to the data set as they developed during the growing season or early fall. A standard paired-plot t-test was used to analyze differences among means (Mosteller and Rourke 1973).

Table 1. Defoliation treatment tiller height before and after removal of 25% or 50% of tiller weight.

| Date Treatment | Management Strategy | Pretreatment Height cm | Post treatment Height cm | Removed Height cm | Percent Height Removed % |
|---|---|---|---|---|---|
| Mid June | | | | | |
| June 25% | 6.0 m SL | 15.8 | 12.6 | 3.2 | 20.2 |
| | 4.5 m SL | 13.6 | 10.9 | 2.7 | 19.9 |
| | 4.5 m TOR | 14.1 | 11.3 | 2.8 | 19.9 |
| | mean | 14.5 | 11.6 | 2.9 | 20.0 |
| June 50% | 6.0 m SL | 15.4 | 9.2 | 6.2 | 40.2 |
| | 4.5 m SL | 14.9 | 9.0 | 5.9 | 39.4 |
| | 4.5 m TOR | 17.4 | 10.4 | 7.0 | 40.1 |
| | mean | 15.9 | 9.6 | 6.4 | 39.9 |

**Results**

The basic design of this study was intended to test a simple straight forward treatment-response relationship between a defoliation event and the grass tiller reaction. However, the western wheatgrass tillers on the three grazing management strategies did not respond similarly to each of the defoliation treatments, disclosing that stimulation of the defoliation resistance mechanisms that help grass tillers withstand and recover from partial defoliation was not simple and was influenced by additional conditions or other factors. Activation of the physiological processes within the grass plants and the biogeochemical processes within the grassland ecosystem that provide resistance to defoliation depend on complex interactions among grazing animals, grass plants, and rhizosphere soil organisms (Manske 2007b).

The quantity of vegetative tiller development in grassland ecosystems and the rate of tiller growth and recovery following partial defoliation are affected by hierarchical dominant tiller regulation, by growing season environmental variables, and by availability of essential elements (Briske and Richards 1995, Manske 1998). Stimulation of vegetative tiller development from axillary buds requires the reduction of the inhibiting hormone, auxin, and growth and development of stimulated vegetative tillers requires procurement of sufficient quantities of essential elements from the surrounding environment. The major elements needed by grass plants are hydrogen, carbon, and nitrogen. The hydrogen comes from soil water ($H_20$) absorbed through the roots and distributed throughout the plant within the xylem vascular tissue. The source of carbon is atmospheric carbon dioxide ($C0_2$). Plants capture and fix carbon with the hydrogen from soil water during the process of photosynthesis which converts radiant energy from sunlight into chemical energy. The assimilated carbon is combined in several ways to form various types of sugars and starches that collectively are carbohydrates ($CH_20$). The source of nitrogen is inorganic nitrogen ($N0_3$) mineralized from soil organic nitrogen by rhizosphere organisms. This available mineral nitrogen is transferred from the rhizosphere through the endomycorrhizal fungi to the roots of the host grass plant and is than preferentially moved up to the active axillary bud meristmatic tissue shortly after stimulation by the growth hormone, cytokinin. Phosphorus and minor mineral nutrients are absorbed by grass plant roots from soil with assistance from rhizosphere endomycorrhizal fungi (Manske 2007b).

The amount of vegetative tiller growth and development on grassland ecosystems is not limited by the availability of radiant energy from the sun or by the availability of atmospheric carbon dioxide and these two essential elements were not quantified. The environmental variables of temperature and precipitation were determined for the study area, and the resource availability of mineral nitrogen and the volume of the rhizosphere were determined for the silty range sites on the three grazing management strategies, 6.0 m SL, 4.5 m SL, and 4.5 m TOR.

The average monthly temperature and monthly precipitation data for 1999 to 2001 collected from the Dickinson Research Extension Center ranch were used to characterize growing-season conditions and to identify water-deficiency months. The ombrothermic diagram (figure 1) developed through use of the ombrothermic graph technique reported by Emberger et al. (1963) identified monthly periods with water-deficiency conditions. Water-deficiency periods are indicated when the monthly precipitation data bar drops below the mean monthly temperature data curve. During water-deficiency periods perennial plants experience water stress, a condition that results when plants are unable to absorb adequate water to match the transpiration rate. Water-deficiency periods lasting for a month place plants under water stress severe enough to reduce herbage biomass production. During fall, average monthly temperatures are near or below freezing (32°F, 0°C), and most grass leaves are senescent and contain only a small amount of green tissue; however, plant growth continues at low levels.

The precipitation during the growing seasons of 2000 and 2001 was normal (table 2). During 2000 and 2001, 14.99 inches (107.84% of LTM) and 16.40 inches (117.98% of LTM) of precipitation were received, respectively. August of 2000 was a wet month and received 158.38% of LTM precipitation. April, May, June, July, and October received normal precipitation at 90.00%, 79.17%, 116.36%, 113.99%, and 109.77% of LTM. September was a dry month and received 79.56% of LTM precipitation. Perennial plants were under water stress conditions during September, 2000 (figure 1) (Manske 2009a). April, June, July, and September of 2001 were wet months and each received 192.86%, 196.30%, 200.41%, and 141.61% of LTM precipitation, respectively. May was a very dry month and received 22.08% of LTM precipitation. August and October were extremely dry months and received no precipitation. Perennial plants were under water stress conditions during May, August, and October, 2001 (figure 1) (Manske 2009a).

The availability of water, which is essential in physiological processes, does not limit herbage production on grassland ecosystems to the extent that mineral nitrogen availability does (Wight and Black 1972). Available soil mineral nitrogen is the major herbage growth limiting factor in Northern Plains rangelands (Wight and Black 1979). Available mineral nitrogen was determined from four replicated field soil core samples collected to a depth of 6 inches during mid June from silty range sites in each of the three grazing management strategies at the start of the seventh year of the grazing treatment study. Subsamples of field soil cores were analyzed for total incubated mineralizable nitrogen (N) using procedures outlined by Keeney (1982) and Keeney and Nelsen (1982). The available mineral nitrogen was 178, 77, and 62 lbs/acre-foot on the 4.5 m TOR, 4.5 m SL, and 6.0 m SL management strategies, respectively (table 3) (Manske 2008, 2009b). The quantity of soil mineral nitrogen at the exclosure sites of the 4.5 m SL and 6.0 m SL management strategies were well below 100 lbs/ac. All mineral nitrogen values for the three management strategies were significantly different from each other (table 3).

The rhizosphere volume, which reflects the activity and biomass levels of soil microorganisms, was determined from length and diameter measurements of the rhizosphere soil cylinder around each root of every western wheatgrass tiller located in two replicated soil cores of 3 inches in diameter and 4 inches deep collected during June, July, August, and September from silty range sites in each of the three grazing management strategies during 2002 (Gorder, Manske, and Stroh 2004). The seasonal mean rhizosphere volume was 227, 68, and 50 $ft^3$/acre-foot on the 4.5 m TOR, 4.5 m SL, and 6.0 m SL management strategies, respectively (table 3) (Manske 2008). The rhizosphere volume on the 4.5 m SL and 6.0 m SL management strategies were not significantly different and the rhizosphere volume on both the seasonlong management strategies were significantly less than the rhizosphere volume on the 4.5 m TOR management strategy (table 3).

Tiller Dynamics

Control Treatment

The first year on the control treatment of the 6.0 month seasonlong management strategy (table 4a) started in early May with 469.9 /$m^2$ vegetative tillers including 344.6 /$m^2$ lead tillers and 125.3 /$m^2$ secondary tillers. An unknown quantity of these tillers were carry over tillers from the previous growing season. Vegetative reproduction produced 0.0 /$m^2$ tillers during the first growing season with 0.0 /$m^2$ initiated during May and 0.0 /$m^2$ initiated during mid season. A total of 469.9 /$m^2$ different tillers were present during the first growing season. During mid season, 219.3 /$m^2$ lead tillers developed into reproductive flowering stages (46.7% of the tiller population). Before reaching maturity, 31.3 /$m^2$ vegetative tillers terminated. Between mid August and mid October, 219.3 /$m^2$ fall tillers developed. During mid October, 438.6 /$m^2$ live vegetative tillers remained, of which, 125.3 /$m^2$ were lead tillers, 94.0 /$m^2$ were secondary tillers, and 219.3 /$m^2$ were fall tillers. During the winter period, 0.0 /$m^2$ tillers terminated. The second year on the control treatment (table 4b) started in early May with 783.2 /$m^2$ vegetative tillers including 501.2 /$m^2$ lead tillers and 281.9 /$m^2$ secondary tillers, of which, 438.6 /$m^2$ were carry over tillers and 344.6 /$m^2$ were early spring initiated tillers; there were 313.3 /$m^2$ more tillers than during May of the first growing season. Vegetative reproduction produced 31.3 /$m^2$ tillers during the second growing season with 0.0 /$m^2$ initiated during May and 31.3 /$m^2$ initiated during mid season. A total of 814.5 /$m^2$ different tillers were present during the second growing season; there were 344.6 /$m^2$ more total tillers than during the first growing season. During mid season, 156.6 /$m^2$ lead tillers developed into reproductive flowering stages (19.2% of the tiller population). Before reaching maturity, 250.6 /$m^2$ vegetative tillers terminated. Between mid August and mid October, 313.3 /$m^2$ fall tillers developed. During mid October, 720.5 /$m^2$ live vegetative tillers remained, of which, 219.3 /$m^2$ were lead tillers, 188.0 /$m^2$ were secondary tillers, and 313.3 /$m^2$ were fall tillers; there were 281.9 /$m^2$ more live vegetative tillers than during mid October of the first growing season.

The first year on the control treatment of the 4.5 month seasonlong management strategy (table 4a) started in early May with 281.9 /$m^2$ vegetative tillers including 188.0 /$m^2$ lead tillers and 94.0 /$m^2$ secondary tillers. An unknown quantity of these tillers were carry over tillers from the previous growing season. Vegetative reproduction produced 0.0 /$m^2$ tillers during the first growing season with 0.0 /$m^2$ initiated during May and 0.0 /$m^2$ initiated during mid season. A total of 281.9 /$m^2$ different tillers were present during the first growing season. During mid season, 94.0 /$m^2$ lead tillers developed into reproductive flowering stages (33.3% of the tiller population). Before reaching maturity, 62.7 /$m^2$ vegetative tillers terminated. Between mid August and mid October, 94.0 /$m^2$ fall tillers developed. During mid October, 219.3 /$m^2$ live vegetative tillers remained, of which, 94.0 /$m^2$ were lead tillers, 31.3

/m$^2$ were secondary tillers, and 94.0 /m$^2$ were fall tillers. During the winter period, 0.0 /m$^2$ tillers terminated. The second year on the control treatment (table 4b) started in early May with 407.2 /m$^2$ vegetative tillers including 219.3 /m$^2$ lead tillers and 188.0 /m$^2$ secondary tillers, of which, 219.3 /m$^2$ were carry over tillers and 188.0 /m$^2$ were early spring initiated tillers; there were 125.3 /m$^2$ more tillers than during May of the first growing season. Vegetative reproduction produced 125.3 /m$^2$ tillers during the second growing season with 31.3 /m$^2$ initiated during May and 94.0 /m$^2$ initiated during mid season. A total of 532.5 /m$^2$ different tillers were present during the second growing season; there were 250.6 /m$^2$ more total tillers than during the first growing season. During mid season, 31.3 /m$^2$ lead tillers developed into reproductive flowering stages (5.9% of the tiller population). Before reaching maturity, 188.0 /m$^2$ vegetative tillers terminated. Between mid August and mid October, 156.6 /m$^2$ fall tillers developed. During mid October, 469.9 /m$^2$ live vegetative tillers remained, of which, 219.3 /m$^2$ were lead tillers, 94.0 /m$^2$ were secondary tillers, and 156.6 /m$^2$ were fall tillers; there were 250.6 /m$^2$ more live vegetative tillers than during mid October of the first growing season.

The first year on the control treatment of the 4.5 month twice-over rotation management strategy (table 4a) started in early May with 877.1 /m$^2$ vegetative tillers including 626.5 /m$^2$ lead tillers and 250.6 /m$^2$ secondary tillers. An unknown quantity of these tillers were carry over tillers from the previous growing season. Vegetative reproduction produced 62.7 /m$^2$ tillers during the first growing season with 31.3 /m$^2$ initiated during May and 31.3 /m$^2$ initiated during mid season. A total of 939.8 /m$^2$ different tillers were present during the first growing season. During mid season, 344.6 /m$^2$ lead tillers developed into reproductive flowering stages (36.7% of the tiller population). Before reaching maturity, 250.6 /m$^2$ vegetative tillers terminated. Between mid August and mid October, 250.6 /m$^2$ fall tillers developed. During mid October, 595.2 /m$^2$ live vegetative tillers remained, of which, 219.3 /m$^2$ were lead tillers, 125.3 /m$^2$ were secondary tillers, and 250.6 /m$^2$ were fall tillers. During the winter period, 31.3 /m$^2$ tillers terminated. The second year on the control treatment (table 4b) started in early May with 1033.8 /m$^2$ vegetative tillers including 626.5 /m$^2$ lead tillers and 407.2 /m$^2$ secondary tillers, of which, 563.9 /m$^2$ were carry over tillers and 469.9 /m$^2$ were early spring initiated tillers; there were 156.6 /m$^2$ more tillers than during May of the first growing season. Vegetative reproduction produced 250.6 /m$^2$ tillers during the second growing season with 125.3 /m$^2$ initiated during May and 125.3 /m$^2$ initiated during mid season. A total of 1284.4 /m$^2$ different tillers were present during the second growing season; there were 344.6 /m$^2$ more total tillers than during the first growing season. During mid season, 375.9 /m$^2$ lead tillers developed into reproductive flowering stages (29.3% of the tiller population). Before reaching maturity, 438.6 /m$^2$ vegetative tillers terminated. Between mid August and mid October, 188.0 /m$^2$ fall tillers developed. During mid October, 657.8 /m$^2$ live vegetative tillers remained, of which, 250.6 /m$^2$ were lead tillers, 219.3 /m$^2$ were secondary tillers, and 188.0 /m$^2$ were fall tillers; there were 62.7 /m$^2$ more live vegetative tillers than during mid October of the first growing season.

Mid June 25% Treatment

The first year on the mid June 25% defoliation treatment of the 6.0 month seasonlong management strategy (table 4a) started in early May with 469.9 /m$^2$ vegetative tillers including 375.9 /m$^2$ lead tillers and 94.0 /m$^2$ secondary tillers. An unknown quantity of these tillers were carry over tillers from the previous growing season. Vegetative reproduction produced 62.7 /m$^2$ tillers during the first growing season with 62.7 /m$^2$ initiated during May and 0.0 /m$^2$ initiated during mid season. A total of 532.5 /m$^2$ different tillers were present during the first growing season. During mid season, 94.0 /m$^2$ lead tillers developed into reproductive flowering stages (17.7% of the tiller population). Before reaching maturity, 31.3 /m$^2$ vegetative tillers terminated. Between mid August and mid October, 125.3 /m$^2$ fall tillers developed. During mid October, 532.5 /m$^2$ live vegetative tillers remained, of which, 188.0 /m$^2$ were lead tillers, 219.3 /m$^2$ were secondary tillers, and 125.3 /m$^2$ were fall tillers. During the winter period, 62.7 /m$^2$ tillers terminated. The second year on the mid June 25% defoliation treatment (table 4b) started in early May with 501.2 /m$^2$ vegetative tillers including 438.6 /m$^2$ lead tillers and 62.7 /m$^2$ secondary tillers, of which, 469.9 /m$^2$ were carry over tillers and 31.3 /m$^2$ were early spring initiated tillers; there were 31.3 /m$^2$ more tillers than during May of the first growing season. Vegetative reproduction produced 94.0 /m$^2$ tillers during the second growing season with 0.0 /m$^2$ initiated during May and 94.0 /m$^2$ initiated during mid season. A total of 595.2 /m$^2$ different tillers were present during the second growing season; there were 62.7 /m$^2$ more total tillers than during the first growing season. During mid season, 188.0 /m$^2$ lead tillers developed into reproductive flowering stages (31.6% of the tiller population). Before reaching maturity, 94.0 /m$^2$ vegetative tillers terminated. Between mid August and mid October, 469.9 /m$^2$ fall tillers developed. During mid October, 783.2 /m$^2$ live vegetative tillers remained, of which, 219.3 /m$^2$ were lead tillers, 94.0 /m$^2$ were secondary tillers, and 469.9 /m$^2$ were fall tillers; there were 250.6 /m$^2$ more live vegetative tillers than during mid October of the first growing season.

The first year on the mid June 25% defoliation treatment of the 4.5 month seasonlong management strategy (table 4a) started in early May with 438.6 /m$^2$ vegetative tillers including 250.6 /m$^2$ lead tillers and 188.0 /m$^2$ secondary tillers. An unknown quantity of these tillers were carry over tillers from the previous growing season. Vegetative reproduction produced 31.3 /m$^2$ tillers during the first growing season with 0.0 /m$^2$ initiated during May and 31.3 /m$^2$ initiated during mid season. A total of 469.9 /m$^2$ different tillers were present during the first growing season. During mid season, 94.0 /m$^2$ lead tillers developed into reproductive flowering stages (20.0% of the tiller population). Before reaching maturity, 156.6 /m$^2$ vegetative tillers terminated. Between mid August and mid October, 125.3 /m$^2$ fall tillers developed. During mid October, 344.6 /m$^2$ live vegetative tillers remained, of which, 62.7 /m$^2$ were lead tillers, 156.6 /m$^2$ were secondary tillers, and 125.3 /m$^2$ were fall tillers. During the winter period, 0.0 /m$^2$ tillers terminated. The second year on the mid June 25% defoliation treatment (table 4b) started in early May with 344.6 /m$^2$ vegetative tillers including 219.3 /m$^2$ lead tillers and 125.3 /m$^2$ secondary tillers, of which, 344.6 /m$^2$ were carry over tillers and 0.0 /m$^2$ were early spring initiated tillers; there were 94.0 /m$^2$ fewer tillers than during May of the first growing season. Vegetative reproduction produced 188.0 /m$^2$ tillers during the second growing season with 62.7 /m$^2$ initiated during May and 125.3 /m$^2$ initiated during mid season. A total of 532.5 /m$^2$ different tillers were present during the second growing season; there were 62.7 /m$^2$ more total tillers than during the first growing season. During mid season, 125.3 /m$^2$ lead tillers developed into reproductive flowering stages (23.5% of the tiller population). Before reaching maturity, 156.6 /m$^2$ vegetative tillers terminated. Between mid August and mid October, 125.3 /m$^2$ fall tillers developed. During mid October, 375.9 /m$^2$ live vegetative tillers remained, of which, 188.0 /m$^2$ were lead tillers, 62.7 /m$^2$ were secondary tillers, and 125.3 /m$^2$ were fall tillers; there were 31.3 /m$^2$ more live vegetative tillers than during mid October of the first growing season.

The first year on the mid June 25% defoliation treatment of the 4.5 month twice-over rotation management strategy (table 4a) started in early May with 971.1 /m$^2$ vegetative tillers including 595.2 /m$^2$ lead tillers and 375.9 /m$^2$ secondary tillers. An unknown quantity of these tillers were carry over tillers from the previous growing season. Vegetative reproduction produced 62.7 /m$^2$ tillers during the first growing season with 31.3 /m$^2$ initiated during May and 31.3 /m$^2$ initiated during mid season. A total of 1033.8 /m$^2$ different tillers were present during the first growing season. During mid season, 156.6 /m$^2$ lead tillers developed into reproductive flowering stages (15.1% of the tiller population). Before reaching maturity, 407.2 /m$^2$ vegetative tillers terminated. Between mid August and mid October, 344.6 /m$^2$ fall tillers developed. During mid October, 814.5 /m$^2$ live vegetative tillers remained, of which, 313.3 /m$^2$ were lead tillers, 156.6 /m$^2$ were secondary tillers, and 344.6 /m$^2$ were fall tillers. During the winter period, 188.0 /m$^2$ tillers terminated. The second year on the mid June 25% defoliation treatment (table 4b) started in early May with 1096.4 /m$^2$ vegetative tillers including 845.8 /m$^2$ lead tillers and 250.6 /m$^2$ secondary tillers, of which, 626.5 /m$^2$ were carry over tillers and 469.9 /m$^2$ were early spring initiated tillers; there were 125.3 /m$^2$ more tillers than during May of the first growing season. Vegetative reproduction produced 188.0 /m$^2$ tillers during the second growing season with 156.6 /m$^2$ initiated during May and 31.3 /m$^2$ initiated during mid season. A total of 1284.4 /m$^2$ different tillers were present during the second growing season; there were 250.6 /m$^2$ more total tillers than during the first growing season. During mid season, 188.0 /m$^2$ lead tillers developed into reproductive flowering stages (14.6% of the tiller population). Before reaching maturity, 281.9 /m$^2$ vegetative tillers terminated. Between mid August and mid October, 219.3 /m$^2$ fall tillers developed. During mid October, 1033.8 /m$^2$ live vegetative tillers remained, of which, 657.8 /m$^2$ were lead tillers, 156.6 /m$^2$ were secondary tillers, and 219.3 /m$^2$ were fall tillers; there were 219.3 /m$^2$ more live vegetative tillers than during mid October of the first growing season.

Mid June 50% Treatment

The first year on the mid June 50% defoliation treatment of the 6.0 month seasonlong management strategy (table 4a) started in early May with 563.9 /m$^2$ vegetative tillers including 438.6 /m$^2$ lead tillers and 125.3 /m$^2$ secondary tillers. An unknown quantity of these tillers were carry over tillers from the previous growing season. Vegetative reproduction produced 62.7 /m$^2$ tillers during the first growing season with 31.3 /m$^2$ initiated during May and 31.3 /m$^2$ initiated during mid season. A total of 626.5 /m$^2$ different tillers were present during the first growing season. During mid season, 156.6 /m$^2$ lead tillers developed into reproductive flowering stages (25.0% of the tiller population). Before reaching maturity, 62.7 /m$^2$ vegetative tillers terminated. Between mid August and mid October, 188.0 /m$^2$ fall tillers developed. During mid October, 595.2 /m$^2$ live vegetative tillers remained, of which, 219.3 /m$^2$ were lead tillers, 188.0 /m$^2$ were secondary tillers, and 188.0 /m$^2$ were fall tillers. During the winter period, 156.6 /m$^2$ tillers terminated. The second year on the mid June 50% defoliation treatment (table 4b) started in early May with 469.9 /m$^2$ vegetative tillers including 407.2 /m$^2$ lead tillers and 62.7 /m$^2$ secondary tillers, of which, 438.6 /m$^2$ were carry over tillers and 31.3 /m$^2$ were early spring initiated tillers; there were 94.0 /m$^2$ fewer tillers than during May of the first growing season. Vegetative reproduction produced 156.6 /m$^2$ tillers during the second growing season with 125.3 /m$^2$ initiated during May and 31.3 /m$^2$ initiated during mid season. A total of 626.5 /m$^2$ different tillers were present during the second growing season; there were the same number of total tillers as during the first growing season. During mid season, 125.3 /m$^2$ lead tillers developed into reproductive flowering stages (20.0% of the tiller population). Before reaching maturity, 94.0 /m$^2$ vegetative tillers terminated. Between mid August and mid October, 313.3 /m$^2$ fall tillers developed. During mid October, 720.5 /m$^2$ live vegetative tillers remained, of which, 375.9 /m$^2$ were lead tillers, 31.3 /m$^2$ were secondary tillers, and 313.3 /m$^2$ were fall tillers; there were 125.3 /m$^2$ more live vegetative tillers than during mid October of the first growing season.

The first year on the mid June 50% defoliation treatment of the 4.5 month seasonlong management strategy (table 4a) started in early May with 375.9 /m$^2$ vegetative tillers including 281.9 /m$^2$ lead tillers and 94.0 /m$^2$ secondary tillers. An unknown quantity of these tillers were carry over tillers from the previous growing season. Vegetative reproduction produced 0.0 /m$^2$ tillers during the first growing season with 0.0 /m$^2$ initiated during May and 0.0 /m$^2$ initiated during mid season. A total of 375.9 /m$^2$ different tillers were present during the first growing season. During mid season, 62.7 /m$^2$ lead tillers developed into reproductive flowering stages (16.7% of the tiller population). Before reaching maturity, 125.3 /m$^2$ vegetative tillers terminated. Between mid August and mid October, 156.6 /m$^2$ fall tillers developed. During mid October, 344.6 /m$^2$ live vegetative tillers remained, of which, 125.3 /m$^2$ were lead tillers, 62.7 /m$^2$ were secondary tillers, and 156.6 /m$^2$ were fall tillers. During the winter period, 125.3 /m$^2$ tillers terminated. The second year on the mid June 50% defoliation treatment (table 4b) started in early May with 250.6 /m$^2$ vegetative tillers including 156.6 /m$^2$ lead tillers and 94.0 /m$^2$ secondary tillers, of which, 219.3 /m$^2$ were carry over tillers and 31.3 /m$^2$ were early spring initiated tillers; there were 125.3 /m$^2$ fewer tillers than during May of the first growing season. Vegetative reproduction produced 94.0 /m$^2$ tillers during the second growing season with 62.7 /m$^2$ initiated during May and 31.3 /m$^2$ initiated during mid season. A total of 344.6 /m$^2$ different tillers were present during the second growing season; there were 31.3 /m$^2$ fewer total tillers than during the first growing season. During mid season, 94.0 /m$^2$ lead tillers developed into reproductive flowering stages (27.3% of the tiller population). Before reaching maturity, 94.0 /m$^2$ vegetative tillers terminated. Between mid August and mid October, 219.3 /m$^2$ fall tillers developed. During mid October, 375.9 /m$^2$ live vegetative tillers remained, of which, 156.6 /m$^2$ were lead tillers, 0.0 /m$^2$ were secondary tillers, and 219.3 /m$^2$ were fall tillers; there were 31.3 /m$^2$ more live vegetative tillers than during mid October of the first growing season.

The first year on the mid June 50% defoliation treatment of the 4.5 month twice-over rotation management strategy (table 4a) started in early May with 720.5 /m$^2$ vegetative tillers including 595.2 /m$^2$ lead tillers and 125.3 /m$^2$ secondary tillers. An unknown quantity of these tillers were carry over tillers from the previous growing season. Vegetative reproduction produced 62.7 /m$^2$ tillers during the first growing season with 62.7 /m$^2$ initiated during May and 0.0 /m$^2$ initiated during mid season. A total of 783.2 /m$^2$ different tillers were present during the first growing season. During mid season, 219.3 /m$^2$ lead tillers developed into reproductive flowering stages (28.0% of the tiller population). Before reaching maturity, 250.6 /m$^2$ vegetative tillers terminated. Between mid August and mid October, 344.6 /m$^2$ fall tillers developed. During mid October, 657.8 /m$^2$ live vegetative tillers remained, of which, 219.3 /m$^2$ were lead tillers, 94.0 /m$^2$ were secondary tillers, and 344.6 /m$^2$ were fall tillers. During the winter period, 219.3 /m$^2$ tillers terminated. The second year on the mid June 50% defoliation treatment (table 4b) started in early May with 689.2 /m$^2$ vegetative tillers including 563.9 /m$^2$ lead tillers and 125.3 /m$^2$ secondary tillers, of which, 438.6 /m$^2$ were carry over tillers and 250.6 /m$^2$ were early spring initiated tillers; there were 31.3 /m$^2$ fewer tillers than during May of the first growing season. Vegetative reproduction produced 250.6 /m$^2$ tillers during the second growing season with 156.6 /m$^2$ initiated during May and 94.0 /m$^2$ initiated during mid season. A total of 939.8 /m$^2$ different tillers were present during the second growing season; there were

156.6 /m$^2$ more total tillers than during the first growing season. During mid season, 281.9 /m$^2$ lead tillers developed into reproductive flowering stages (30.0% of the tiller population). Before reaching maturity, 156.6 /m$^2$ vegetative tillers terminated. Between mid August and mid October, 344.6 /m$^2$ fall tillers developed. During mid October, 845.8 /m$^2$ live vegetative tillers remained, of which, 438.6 /m$^2$ were lead tillers, 62.7 /m$^2$ were secondary tillers, and 344.6 /m$^2$ were fall tillers; there were 188.0 /m$^2$ more live vegetative tillers than during mid October of the first growing season.

Tiller Density

The number of total different tillers present were significantly greater during the first and second years on the control, and June 25% treatments of the 4.5 m TOR management strategy (tables 4a and 4b). The number of total different tillers were significantly lower during the first year on the control, and June 50% treatments and during the second year on the June 50% treatment of the 4.5 m SL management strategy (tables 4a and 4b). On the 6.0 m SL management strategy, the number of total different tillers were intermediate during the first and second years on the control, June 25%, and June 50% treatments (tables 4a and 4b).

Monthly tiller densities, consisting of lead tillers, secondary tillers, and, from mid August to mid October, fall tillers, were greater during both years on all treatments of the 4.5 m TOR management strategy; were lower on all treatments of the 4.5 m SL management strategy; and were intermediate on all treatments of the 6.0 m SL management strategy (figures 2, 3, and 4).

Monthly tiller densities of the 4.5 m SL management strategy were lower on the control treatment than those on the June 50% treatment during the first growing season and were greater on the control treatment than those on the June 50% treatment during the second growing season; densities were lower on the control treatment than those on the June 25% treatment during the first growing season and were the same on the control and June 25% treatments during the second growing season; and densities were greater on the June 25% treatment than those on the June 50% treatment during the first and second growing seasons (figures 2, 3, and 4 and table 5).

Monthly tiller densities of the 6.0 m SL management strategy were lower on the control treatment than those on the June 50% treatment during the first growing season and were greater on the control treatment than those on the June 50% treatment during the second growing season; densities were lower on the control treatment than those on the June 25% treatment during the first growing season and were the greater on the control treatment than those on the June 25% treatments during the second growing season; and densities were lower on the June 25% treatment than those on the June 50% treatment during the first and second growing seasons (figures 2, 3, and 4 and table 5).

Monthly tiller densities of the 4.5 m TOR management strategy were greater on the control treatment than those on the June 50% treatment during the first and second growing seasons; densities were lower on the control treatment than those on the June 25% treatment during the first and second growing seasons; and densities were greater on the June 25% treatment than those on the June 50% treatment during the first and second growing seasons (figures 2, 3, and 4 and table 5).

Mean monthly tiller densities were significantly greater during the first and second years on the control, June 25%, and June 50% treatments of the 4.5 m TOR management strategy (table 5). Mean monthly densities were significantly lower during the first and second years on the control, June 25%, and June 50% treatments of the 4.5 m SL management strategy (table 5).

The change in mean monthly tiller densities from the first year to the second year were not significantly different on the control, and June 50% treatments of the 6.0 m SL, 4.5 m SL, and 4.5 m TOR management strategies and on the June 25% treatments of the 6.0 m SL and 4.5 m SL management strategies (table 5). Mean monthly tiller densities increased significantly during the second year on the June 25% treatment of the 4.5 m TOR management strategy (table 5).

The total tiller density for the combined first and second years, excluding the carry over tillers during the second year, were significantly greater on the June 25% treatment of the 4.5 m TOR management strategy; and were significantly lower on the control, June 25%, and June 50% treatments of the 4.5 m SL management strategy (table 6). The total two year tiller densities were intermediate on the control, June 25%, and June 50% treatments of the 6.0 m SL management strategy and on the control and June 50% treatments of the 4.5 m TOR management strategy (table 6).

The 6.0 m SL, 4.5 m SL, and 4.5 m TOR grazing management strategies had been operational prior to the start of this defoliation study for 12 years, 14 years, and 17 years, respectively. The effects from these grazing management strategies would have been established within the respective ecosystems at some proportion related the length of operational time. The quantities of tillers were significantly or numerically greater on all treatments of the 4.5 m TOR management strategy during both years. The quantities of tillers were significantly or numerically lower on all treatments of the 4.5 m SL management strategy. The quantity of tillers on all treatments of the 6.0 m SL management strategy were usually intermediate. The greater quantity of tillers on the 4.5 m TOR management strategy developed because of the significantly greater quantities of available soil mineral nitrogen that resulted from the greater soil organism activity in the significantly larger rhizosphere volume (table 3). The low quantity of tillers produced on the 4.5 m SL management strategy resulted because of the low quantities of soil mineral nitrogen, the low rhizosphere volume, and the effects from the soil characteristics related to the significantly shallower surface horizon depth. The quantity of tillers on the 6.0 m SL management strategy were lower than the tiller densities on the 4.5 m TOR management strategy because of the lower quantities of soil mineral nitrogen and lower rhizosphere volume, and would be expected to be lower than those on the 4.5 m SL management strategy had both seasonlong management strategies had similar duration of operation and surface horizon depth.

Tiller Initiation

The total number of tillers initiated through vegetative reproduction from axillary buds were numerically greater on the control, June 25%, and June 50% treatments of the 4.5 m TOR management strategy; and were significantly lower on the control, June 25%, and June 50% treatments of the 4.5 m SL management strategy (table 7). Vegetatively reproduced tillers were intermediate on all treatments of the 6.0 m SL management strategy (table 7). No seedlings were encountered during this study.

The number of vegetative tillers stimulated per lead tiller present at the time of defoliation treatment were numerically greater on the June 25%, and June 50% treatments of the 4.5 m TOR management strategy; were numerically lower on the June 25% and June 50% treatments of the 4.5 m SL management strategy; and were intermediate on the June 25%, and June 50% treatment of the 6.0 m SL management strategy (table 7).

Significantly greater numbers of vegetative tillers were stimulated per lead tiller on the June 25% treatment than on the control treatment and numerically fewer tillers were stimulated per lead tiller on the June 50% treatment than on the control treatment of the 4.5 m TOR management strategy. Numerically fewer tillers were stimulated on the June 25%, and June 50% treatments than on the control treatment of the 4.5 m SL management strategy; and numerically fewer tillers were stimulated on the June 25%, and June 50% treatments than on the control treatment of the 6.0 m SL management strategy (table 7). The defoliated tillers on the June 25% and June 50% treatments of the traditional 6.0 m SL and 4.5 m SL management strategies produced 125.3/$m^2$ and 156.7/$m^2$, and 94.0/$m^2$ and 62.7/$m^2$ fewer vegetative tillers than were produced by undefoliated tillers on the respective control treatments. The defoliated tillers on the June 25% and June 50% treatments of the 4.5 m TOR management strategy produced 62.7/$m^2$ and 31.3/$m^2$ more vegetative tillers respectively than were produced by undefoliated tillers on the control treatment.

The total number of initiated vegetative tillers was lower on the treatments of the 4.5 m SL and 6.0 m SL management strategies than the number of initiated tillers on the treatments of the 4.5 m TOR management strategy because of the significantly lower soil mineral nitrogen, and the significantly lower volume of rhizosphere on the two seasonlong management strategies. The number of stimulated vegetative tillers per lead tiller on all defoliation treatments of the 4.5 m SL and 6.0 m SL management strategies was lower than the number of tillers that developed on the respective control treatments because the defoliated tillers were unable to recover fully from the single event defoliation treatment as a result of the insufficient quantities of soil mineral nitrogen inhibiting the compensatory physiological processes within the grass plants on the two seasonlong management strategies. The defoliated tillers on the June 50% treatment of the 4.5 m TOR management strategy recovered to slightly less than full pretreatment condition and produced slightly fewer tillers per lead tiller than were produced on the control treatment.

The defoliated tillers on the June 25% treatment of the 4.5 m TOR management strategy fully recovered from the defoliation treatments and produced more vegetative tillers per lead tiller than were produced on the control treatment. The significantly larger rhizosphere volume and the significantly greater quantities of available soil mineral nitrogen on the 4.5 m TOR management strategy were the essential resources that permitted grass tillers to fully recover by the compensatory physiological processes within the grass plants, to support vegetative tiller growth from several axillary buds, and to increase herbage production following defoliation treatments.

Vegetative tillers initiated during early spring were significantly greater on the control, and June 25% treatments of the 4.5 m TOR management strategy than on the defoliation treatments of the two seasonlong management strategies (table 8). Vegetative tillers initiated during May were significantly greater on the June 25% and June 50% treatments of the 4.5 m TOR management strategy than on the defoliation treatments of the two seasonlong management strategies (table 8). The vegetative tillers initiated during early spring and during May appear to be more closely related to the management and conditions of the previous growing season than to those of the current growing season. Vegetative tillers initiated during mid season were significantly greater on the June 25% treatment of the 4.5 m SL management strategy and were significantly greater on the control treatment of the 4.5 m TOR management strategy (table 8). Greater numbers of vegetative tillers were initiated during early spring and May on the treatments of the 4.5 m TOR management strategy than were initiated on the treatments of the 4.5 m SL and 6.0 m SL management strategies showing that grass plants on the 4.5 m TOR management strategy were in better condition and had access to carbohydrates and essential mineral nitrogen in much greater quantities than were available to grass plants on the 4.5 m SL and 6.0 m SL management strategies. The mid season vegetative tiller initiation period occurred simultaneously with the high resource demand period in which the dominant reproductive lead tillers progressed through the flower stages and produced seeds. Greater numbers of lead tillers flowered and greater numbers of vegetative tillers were maintained during mid season on the treatments of the 4.5 m TOR management strategy than flowered and were maintained on the treatments of the 4.5 m SL and 6.0 m SL management strategies showing that the grass plants on the 4.5 m TOR management strategy were in better condition and had access to greater quantities of essential mineral nitrogen than the grass plants on the 4.5 m SL and 6.0 m SL management strategies.

Vegetative tillers initiated as fall tillers during mid August to mid October were numerically greater than 550.0/$m^2$ on the June 25% treatment of the 6.0 m SL management strategy and on the June 25% and June 50% treatments of the 4.5 m TOR management strategy (table 8). Vegetative tillers initiated during fall season were significantly lower on the control, and June 25% treatments of the 4.5 m SL management strategy (table 8). Greater numbers of vegetative tillers were initiated as fall tillers than were initiated during early spring and May on all treatments of the 6.0 m SL and 4.5 m SL management strategies (table 8). A greater percentage of the total vegetative tillers were initiated during mid August to mid October as fall tillers on all treatments of the 6.0 m SL and 4.5 m SL management strategies than the percent of total vegetative tillers initiated as fall tillers on the respective treatments of the 4.5 m TOR management strategy (table 8). The fall tiller initiation period, mid August to mid October, started after the lead tillers had completed most of their active growth and occurred simultaneously with the winter hardening process of perennial grasses. Young vegetative tillers on the 4.5 m SL and 6.0 m SL management strategies appeared to have lower competition for essential elements during this late season period than during the other vegetative tiller initiation periods.

The greatest number of total vegetative tillers initiated from axillary buds on the 4.5 m SL, 6.0 m SL, and 4.5 m TOR management strategies were 563.9 /$m^2$ tillers on the control treatment, 908.5 /$m^2$ tillers on the control treatment, and 11284.4 /$m^2$ tillers on the June 25% treatment, respectively. The lowest number of total vegetative tillers initiated on the 4.5 m SL, 6.0 m SL, and 4.5 m TOR management strategies were 469.9 /$m^2$ tillers on the June 25% treatment, 751.8 /$m^2$ tillers on the June 50% treatment, and 1221.7 /$m^2$ tillers on the control treatment, respectively (table 8). The lowest number of vegetative tillers initiated on the treatments of the 4.5 m TOR management strategy (1221.7 /$m^2$ tillers) was greater than the greatest number of vegetative tillers initiated on the treatments of the 4.5 m SL (563.9 /$m^2$ tillers) and 6.0 m SL (908.5 /$m^2$ tillers) management strategies (table 8). All of the treatments of the 4.5 m TOR management strategy initiated more vegetative tillers during the growing season than all the treatments of the 4.5 m SL and 6.0 m SL management strategies because of the greater quantities of available essential soil mineral nitrogen that resulted from the greater soil organism activity in the larger rhizosphere volume on the 4.5 m TOR management strategy.

Tiller Termination

The number of total tillers terminated during the growing season were significantly greater on the control treatment and numerically greater on the June 25%, and June 50% treatments of the 4.5 m TOR management strategy; were significantly lower on the control treatment and numerically lower on the June 25%, and June 50% treatments of the 4.5 m SL management strategy; and were intermediate on all treatments of the 6.0 m SL management strategy (table 9). The mean percent of the tiller population terminated was 54.0%. Percent termination of the tiller population was lowest (50.1%) on the June 25% treatments. There was no significant differences in the percent of total tillers that terminated among all the treatments of the 6.0 m SL, 4.5 m SL, and 4.5 m TOR management strategies.

The number of lead tillers terminated after flowering was significantly greater on the control, and June 50% treatments of the 4.5 m TOR management strategy; was significantly lower on the control, and June 50% treatments and numerically lower on the June 25% treatment of the 4.5 m SL management strategy; and was intermediate on all treatments of the 6.0 m SL management strategy (table 9). The percent of the tiller population that produced flower stages was around 28.5% on the control treatments and around 21.9% on the defoliation treatments, with a mean of 20.4% during the first year and a mean of 23.5% during the second year. The number of lead tillers terminated after flowering was a significantly high percentage of the total tiller population on the control treatment of the 4.5 m TOR management strategy. The number of lead tillers terminated after flowering was a significantly low percentage of the total tiller population on the control treatment of the 4.5 m SL management strategy and on the June 25% treatment of the 4.5 m TOR management strategy.

The number of vegetative tillers terminated before reaching maturity during the mid and fall season was numerically greater on the June 25% treatment of the 4.5 m TOR management strategy, and was significantly lower on the June 25% treatment of the 6.0 m SL management strategy (table 9). The greatest percent of the tiller population terminated during the early season was on the control and June 25% treatments of the 4.5 m TOR management strategy. The greatest percent of the tiller population terminated during the mid and fall season was on the control and June 25% treatments of the 4.5 m SL management strategy. The lowest percent of the tiller population terminated during the mid and fall season was on June 25% and the June 50% treatments of the 6.0 m SL management strategy. The lowest percent of the tiller population terminated during the winter period was on the June 25% treatment of the 4.5 m SL management strategy and on the control treatments of the 6.0 m SL, 4.5 m SL, and 4.5 m TOR management strategies (table 9).

The relationships among the numbers of tillers terminated on the management strategies were similar to the relationships among the total tiller densities on the management strategies with greater numbers on the treatments of the 4.5 m TOR management strategy, intermediate numbers on the treatments of the 6.0 m SL management strategy, and lower numbers on the treatments of the 4.5 m SL management strategy. Termination of lead tillers after reaching flowering stages occurred systematically because the apical meristem tissue was depleted during the process of inflorescence production. Termination of secondary tillers before reaching maturity most likely resulted from insufficient quantities of essential resources reaching those tillers. The allocation of essential elements and photosynthetic products to some tillers and not to other tillers required a controlling process and an hierarchical differentiation of tillers into categories.

Tiller Leaf Height

Mean tiller leaf height of the reproductive lead tillers was 17.5 cm during the first year and 25.0 cm during the second year with increases in leaf height on all treatments the second year. The mean monthly reproductive lead tiller leaf heights were not significantly different among the 6.0 m SL, 4.5 m SL, and 4.5 m TOR management strategies on all treatments during the first and second years, respectively. Mean tiller leaf height of the vegetative lead tillers was 13.6 cm during the first year and 19.7 cm during the second year with increases in leaf height on all treatments the second year. The mean monthly vegetative lead tiller leaf heights were not significantly different among the 6.0 m SL, 4.5 m SL, and 4.5 m TOR management strategies on all treatments during the first and second years, respectively.

Mean tiller leaf height of the slow growth secondary tillers was 7.9 cm during the first year and 11.9 cm during the second year with increases in leaf height on all treatments the second year. The mean monthly slow growth secondary tiller leaf heights were not significantly different among the 6.0 m SL, 4.5 m SL, and 4.5 m TOR management strategies on all treatments during the first and second years, respectively. Mean tiller leaf height of the early senescent secondary tillers was 4.5 cm during the first year and 7.6 cm during the second year with increases in leaf height on all treatments the second year. The mean monthly early senescent secondary tiller leaf heights were not significantly different among the 6.0 m SL, 4.5 m SL, and 4.5 m TOR management strategies on all treatments during the first and second years, respectively.

Grazing management strategy and defoliation treatment did not appear to affect tiller leaf height. Mean tiller leaf height was affected by the relative hierarchical dominance of the tiller categories and by the greater precipitation during June and July of the second year. Both tiller density and tiller leaf height affect the quantity of herbage biomass production. When leaf heights are similar, the management strategy that supports the greatest tiller density will produce the greatest quantity of herbage biomass.

Tiller Growth and Development

Vegetative tillers did not all develop at the same rate. Rates of tiller growth and development were regulated by hormones and availability of essential elements. The dominant tillers with rapid or unimpeded growth were the reproductive lead tillers and vegetative lead tillers and the subordinate tillers with slow or inhibited growth were the slow growth secondary tillers and early senescent secondary tillers.

The reproductive lead tillers had the fastest rate of growth and development. They started with two or three leaves in early May and reached the early flower stages around mid June. Reproductive lead tiller development was significantly rapid on the June 50% treatment of the 6.0 m SL management strategy during the first and second years, and was significantly slower on the June 25% treatment of the 6.0 m SL management strategy during the first year and on the control treatment of the 4.5 m SL management strategy during the second year.

Mean percent of the tiller population to develop into reproductive flower stages on the 6.0 m SL, 4.5 m SL, and 4.5 m TOR management strategies were 23.7%, 18.9%, and 25.0%, respectively, and were not significantly different. The percent of tillers at flower stages were significantly greater on the control treatments of the 6.0 m SL, 4.5 m SL, and 4.5 m TOR management strategies during the first year. The defoliation treatments reduced the number of tillers that developed into flower stages by around 38.5%. Greater numbers of tillers developed into flower stages during the second year than during the first year on all defoliation treatments of the 6.0 m SL, 4.5 m SL, and 4.5 m TOR management strategies, except on the June 50% treatment of the 6.0 m SL management strategy.

The length of the annual flowering period was affected by the availability of essential elements. The flower period started shortly after 15 June during the first year and was completed by late June on the control and June 50% treatments of the 6.0 m SL management strategy and on all treatments of the 4.5 m SL management strategy; was completed by mid July on the June 25% treatment of the 4.5 m TOR management strategy; and was completed by mid or late August on the June 25% treatment of the 6.0 m SL management strategy and on the control, and June 50% treatments of the 4.5 m TOR management strategy.

The flower period started shortly after 21 June during the second year and was completed by mid July on all treatments of the 6.0 m SL management strategy and on the control treatment of the 4.5 m SL management strategy; and was completed by mid August on the June 25%, and June 50% treatments of the 4.5 m SL management strategy, and on all treatments of the 4.5 m TOR management strategy.

The flower periods were extended beyond early August during the first year on one treatment of the 6.0 m SL management strategy and on two treatments of the 4.5 m TOR management strategy, and during the second year on two treatments of the 4.5 m SL management strategy, and on three treatments of the 4.5 m TOR management strategy.

The precipitation for June and July during the first year was 115.34% of the LTM (long-term mean) and during the second year was 198.06% of the LTM (table 2). The additional 5.56 inches of precipitation during the second year contributed to the extended length of the flowering periods and to the increased number of tillers that developed into flower stages on the treatments of the 6.0 m SL, 4.5 m SL, and 4.5 m TOR management strategies. The quantity of soil mineral nitrogen available on the 4.5 m TOR management strategy was significantly greater than that on the 6.0 m SL and 4.5 m SL management strategies (table 3). The increase in mineral nitrogen resulted from the increased soil microorganism activity in the significantly greater rhizosphere volume on the 4.5 m TOR management strategy (table 3). The greater quantity of mineral nitrogen and greater volume of the rhizosphere on the

4.5 m TOR management strategy contributed to the greater number of tillers developing flower stages and the longer flowering periods during both years.

The vegetative lead tillers had the second fastest rate of growth and development. They started with one, two, or three leaves in early May and reached the fifth leaf stage by early June and the sixth leaf stage by early July. Vegetative lead tiller development was significantly rapid on the control treatment of the 6.0 m SL management strategy during the first and second years, and was significantly slower on the June 50% treatment of the 4.5 m SL management strategy during the second year.

The slow growth secondary tillers and early senescent secondary tillers were the subordinate tillers and had very slow growth rates. The secondary tillers remained at the second and third leaf stages for more than half of the growing season. After the majority of the reproductive lead tillers had reached the anthesis (flower) stage, a few of the secondary tillers advanced to the fourth and sometimes the fifth leaf stages. Slow growth secondary tiller development was relatively slow on all treatments. Early senescent secondary tillers usually terminated before mid August. Growth and development of early senescent tillers was slow on all treatments.

Vegetatively reproduced tillers with three leaves or less were not independent and relied on allocation of essential elements and photosynthetic products from lead tillers. The four leaf stage appeared to be a transition phase between dependence on and independence from other tillers. After the development of the fifth or sixth leaf, vegetatively initiated tillers appeared to be able to procure essential elements independently and possibly could control distribution of essential elements and photosynthetic products to subordinate tillers; indicating that vegetatively produced tillers do not achieve independence from dominant tiller regulation of growth until after development of adequate mature leaf area and root system.

**Discussion**

Growth and development of grass tillers were affected by availability of essential elements and required energy from sunlight, carbon from atmospheric carbon dioxide, hydrogen from soil water, and nitrogen from soil inorganic nitrogen. Radiant energy from sunlight is usually available in sufficient amounts on rangelands (Wight and Black 1972), even after the reductions in energy due to ambient cloud cover. Availability of sunlight can be a limiting factor in areas where taller woody plants shade the grassland community (Kochy and Wilson 2000). Atmospheric carbon dioxide is readily available on rangelands and carbon is not a limiting factor for grass plants (Wight and Black 1972). Hydrogen from soil water is readily available on rangelands during some periods of the growing season with various degrees of deficiency during other periods, and soil water can be a limiting factor during periodic drought conditions (Manske 2009a). The availability of soil water, which is an essential requirement for plant growth and has a dominant role in physiological processes, does not limit herbage production on rangeland ecosystems to the extent that mineral nitrogen availability does (Wight and Black 1972). Available soil mineral nitrogen is the major limiting factor on native rangeland (Wight and Black 1979). The rate of mineralization of soil organic nitrogen by rhizosphere organisms determines the quantity of mineral nitrogen available on grasslands (Manske 2008, 2009b). Soil mineral nitrogen available at amounts of less than 100 lbs/ac causes nitrogen deficiencies that limit plant physiological processes and production of herbage (Wight and Black 1972). Deficiencies of mineral nitrogen decrease grass plant soil water use efficiency and cause the weight of herbage produced per inch of precipitation received to be reduced an average of 49.6% below the quantity of herbage produced per inch of precipitation on grasslands with sufficient available mineral nitrogen at 100 lbs/ac or greater (Wight and Black 1979).

Growth and development of grass tillers were affected by grazing because defoliation removes vital leaf material from the plant, disrupts photosynthesis and physiological processes throughout the plant, alters the microclimate around the plant, and changes the soil environment affecting soil organism activity. Grass plants developed defoliation resistance mechanisms in response to grazing during the period of coevolution with herbivores. The defoliation resistance mechanisms help grass tillers withstand and recover from partial defoliation. The defoliation resistance mechanisms consist of three major components that are: compensatory physiological processes within grass plants, vegetative reproduction of secondary tillers from axillary buds, and symbiotic rhizosphere organism activity and the associated conversion of inorganic nitrogen from soil organic nitrogen (Manske 2007b).

Different grazing management strategies produce different effects on grassland ecosystems as a result of the variations with the timing and severity of defoliation events. Depending on the degree of foliage removal and phenological growth stage of the grass tillers, the effects from defoliation can be beneficial or antagonistic to the defoliation resistance mechanisms and to the rate of mineralization of soil organic nitrogen into mineral nitrogen by rhizosphere organisms. Low rates of mineralization occur on grasslands managed with traditional grazing management strategies (Wight and Black 1972). The quantity of available mineral nitrogen on traditionally managed grasslands ranges from a low of 31 lbs/ac on deferred management strategies up to 77 lbs/ac on moderately stocked 4.5 month seasonlong management strategies (Manske 2008, 2009b). High rates of mineralization with mineral nitrogen available at quantities from 164 lbs/ac to 199 lbs/ac can be obtained on grasslands managed with the twice-over rotation management strategy (Manske 2008, 2009b).

The quantity of total tillers present during the growing season was greatest on the 4.5 m TOR management strategy because of the greater quantities of available mineral nitrogen resulting from the increased soil microorganism activity in the larger rhizosphere volume. The quantity of total tillers was intermediate on the 6.0 m SL management strategy because the quantities of available mineral nitrogen and rhizosphere volume were lower than those on the 4.5 m TOR management strategy. The quantity of total tillers was lowest on the 4.5 m SL management strategy because of the low quantities of available mineral nitrogen, the low rhizosphere volume, and the shallower surface soil horizon depth.

Grass plants reproduce by two methods; sexually by seeds developing into seedlings and vegetatively by tillers developing from axillary buds. Seedlings are rare on rangeland ecosystems. Stimulation of vegetative tiller development from axillary buds requires the reduction of the inhibiting hormone, auxin, through partial defoliation of lead tiller leaf area while the tillers are in vegetative growth stages, and requires the availability of sufficient quantities of the essential elements for growth and development of the initiated tillers. All the treatments of the 4.5 m TOR management strategy initiated more vegetative tillers from axillary buds during the growing season than all the treatments of the 4.5 m SL and 6.0 m SL management strategies because of the greater quantities of available mineral nitrogen. The lowest number of vegetative tillers initiated on the 4.5 m TOR management strategy was on the control treatment and was greater than the number of tillers initiated on any of the treatments of the 4.5 m SL and 6.0 m SL management strategies.

Greater numbers of vegetative tillers were stimulated per lead tiller on the June 25% defoliation treatment of the 4.5 m TOR management strategy than vegetative tillers per lead tiller on the control treatment. The increased soil organism activity in the large rhizosphere volume and the great quantities of available mineral nitrogen above 100 lbs/ac were the essential resources that permitted the partially defoliated tillers to fully recover, to develop more vegetative tillers per lead tiller, and to increase production following defoliation treatments. The June 25% defoliation treatment of the 4.5 m TOR management strategy had greater numbers of tillers during the first and second growing seasons, greater two year total numbers of tillers, and greater numbers of live tillers in mid October of the second growing season than those on the June 50% treatment. Fewer vegetative tillers were stimulated per lead tiller on the June 50% treatment of the 4.5 m TOR management strategy than on the control treatment because the defoliated tillers recovered to slightly less than full pretreatment condition and produced slightly fewer tillers per lead tiller than were produced on the control treatment.

Lower numbers of vegetative tillers were stimulated per lead tiller on the defoliation treatments of the 4.5 m SL and 6.0 m SL management strategies than vegetative tillers per lead tiller on the respective control treatments. The partially defoliated tillers were unable to recover fully from the single event defoliation treatments as a result of the significantly insufficient quantities of available mineral nitrogen on the two traditional seasonlong management strategies.

The numbers of vegetative tillers initiated during the early spring, during May, and during the mid season periods of the growing season were greater on the 4.5 m TOR management strategy than on the 4.5 m SL and 6.0 m SL management strategies. The greater numbers of vegetative tillers initiated during early spring and May showed that the grass plants on the 4.5 m TOR management strategy were in better condition and had access to carbohydrates and essential mineral nitrogen in much greater quantities than were available to grass plants on the 4.5 m SL and 6.0 m SL management strategies. The mid season period occurred simultaneously with the high resource demand period in which the dominant reproductive lead tillers progressed through the flowering stages and produced seeds. The greater numbers of vegetative tillers maintained during mid season showed that the grass plants on the 4.5 m TOR management strategy were in better condition and had access to essential mineral nitrogen in much greater quantities than were available to grass plants on the 4.5 m SL and 6.0 m SL management strategies.

Greater numbers of vegetative tillers were initiated during mid August to mid October as fall tillers than were initiated during early spring and May on the 4.5 m SL and 6.0 m SL management strategies. A greater percent of the total vegetative tillers stimulated were initiated during mid August to mid October as fall tillers on the 4.5 m SL and 6.0 m SL management strategies than the percent of total vegetative tillers initiated as fall tillers on the respective treatments of the 4.5 m TOR management strategy. The fall tiller initiation period, mid August to mid October, started after the lead tillers had completed most of their active growth and occurred simultaneously with the winter hardening process of perennial grasses. There appeared to be lower competition for essential elements during this late season period than during the other vegetative tiller initiation periods, giving the young initiated vegetative tillers access to a greater proportion of the significantly lower quantities of available mineral nitrogen on the 4.5 m SL and 6.0 m SL management strategies.

The total number of tillers terminated during the growing season was greatest on the 4.5 m TOR management strategy, intermediate on the 6.0 m SL management strategy, and lowest on the 4.5 m SL management strategy, which was the same relationship as with the total number of tillers present during the growing season. The mean percent of the tiller population that terminated was 54% and was not different among the management strategies.

The number of lead tillers terminated after flowering was greatest on the 4.5 m TOR management strategy, intermediate on the 6.0 m SL management strategy, and lowest on the 4.5 m SL management strategy. Tillers usually produced vegetative growth during the first growing season and developed into flower stages during the second growing season. Tillers rarely reached flowering stages during the initiation growing season. Termination of lead tillers after reaching the flowering stages occurred because the apical meristem tissue was depleted during the production of the inflorescence. The percent of the tiller population that produced flower stages was around 28.5% on the control treatments. The defoliation treatments did not remove the apical meristem from any tillers, however, the percent of the tiller population reaching flowering stages was reduced during two growing seasons to around 21.9%.

The number of vegetative tillers terminated before reaching maturity was greatest on the 4.5 m TOR management strategy and was lower on the 4.5 m SL and 6.0 m SL management strategies. The greatest percent of the tiller population terminated during the early season was on the control and June 25% treatments of the 4.5 m TOR, during the mid and fall season was on the control and June 25% treatments of the 4.5 m SL, and during the winter period was on the June 50% treatments of the 6.0 m SL, 4.5 m SL, and 4.5 m TOR management strategies. The lowest percent of the tiller population terminated during the early season was on the control, June 25%, and June 50% treatments of the 6.0 m SL and 4.5 m SL, during the mid and fall season was on the June 25% and June 50% treatments of the 6.0 m SL, and during the winter period was on the June 25% treatment of the 4.5 m SL on the control treatments of the 6.0 m SL, 4.5 m SL, and 4.5 m TOR management strategies.

The quantity of available essential elements determined the quantity of tillers that could be sustained on each grazing management strategy with the greatest tiller densities, intermediate densities, and the lowest densities on the 4.5 m TOR, 6.0 m SL, and 4.5 m SL management strategies, respectively. More tillers were initiated than could be supported by the available quantity of essential elements. Some of the lower subordinate tillers terminated before reaching maturity as a result of not receiving sufficient resources. Allocation of essential elements to some tillers and not to other tillers would require a controlling process with a continuum of hierarchical differentiation of tillers into dominant and subordinate levels and would indicate that vegetatively reproduced tillers did not achieve independence at phenological growth stages of three leaves or less, that the fourth leaf stage was a transition phase, and that with the development of the fifth or sixth leaf the tillers could procure essential elements independently and possibly could control distribution of essential elements and photosynthetic products to subordinate secondary tillers.

Tiller leaf height did not appear to be affected by grazing management strategy or by defoliation treatment, however, tiller growth and development were strongly affected by the relative hierarchical dominance level of the tiller categories and by the greater precipitation received during June and July of the second year. The dominant lead tillers had greater leaf height and had rapid or unimpeded growth and development. The subordinate secondary tillers had shorter leaf height and had slow or inhibited growth and development. The tiller leaf height increased on all tiller categories during the second year which received 5.56 inches of precipitation during June and July greater than was received during the first year. The reproductive lead tillers started with two or three leaves in early May and reached the early flower stages around mid June. The vegetative lead tillers started with one to three leaves in early May and reached the fifth leaf stage by early June and the sixth leaf stage by early July. The secondary tillers developed relatively slow and remained at the second and third leaf stages for more than half of the growing season. After the majority of the lead tillers had completed most of the active growth, a few of the secondary tillers advanced to the fourth and fifth leaf stages. Some secondary tillers terminated before mid August as a result of not receiving sufficient quantities of essential elements or photosynthetic products. The surviving vegetative lead tillers, slow growth secondary tillers, and initiated fall tillers did not terminate at the end of the growing season; the tillers with intact apical meristems became carry over tillers and continued growth and development during the next growing season, and it appears likely that some vegetative tillers would continue active growth into the third growing season.

The grass plants on the 6.0 m SL, 4.5 m SL, and 4.5 m TOR management strategies did not respond similarly to identical timing and severity defoliation treatments because the defoliation by grazing during the previous growing seasons caused differential effects to the defoliation resistance mechanisms and to the rates of mineralization of soil organic nitrogen on the three management strategies.

Grass plant responses to defoliation were negative on the traditional 4.5 m SL and 6.0 m SL management strategies because the timing and severity of grass tiller defoliation was antagonistic to rhizosphere organism activity resulting in insufficient quantities of available mineral nitrogen that inhibited the defoliation resistance mechanisms from functioning at restorative levels causing incomplete recovery of partially defoliated grass tillers, decreased numbers of vegetatively initiated tillers, low grass tiller densities, and decreased quantities of herbage production.

Grass plant responses to defoliation were positive on the 4.5 m TOR management strategy because the timing and severity of grass tiller defoliation was beneficial to rhizosphere organism activity resulting in great quantities of available mineral nitrogen above 100 lbs/ac that permitted the defoliation resistance mechanisms to function at elevated levels causing full recovery of partially defoliated grass tillers, increased numbers of vegetatively initiated tillers, high grass tiller densities, and increased quantities of herbage production.

Grass plant responses to defoliation were positive or negative depending on the quantity of soil mineral nitrogen and whether the available mineral nitrogen was greater than or less than 100 lbs/ac, respectively.

The defoliation resistance mechanisms are activated following removal of a portion of the leaf material. The defoliation resistance mechanisms, however, do not function at full capacity following a single defoliation event. The functionality of the various processes increase in increments over several years with annually repeated partial defoliation occurring during vegetative phenological growth stages. Successful fulfillment of the defoliation resistance mechanisms requires availability of sufficient quantities of the essential elements and requires sufficient periods of time without further disruption to develop and perform all specific steps for each process. The compensatory physiological processes within the grass plants and the processes for vegetative reproduction of secondary tillers from axillary buds cannot function at elevated levels until the biogeochemical processes of nutrient cycling within the ecosystem that require rhizosphere organism activity are functioning at elevated levels with soil mineral nitrogen available at 100 lbs/ac or greater.

**Summary**

Northern Plains ranchers who implemented the biologically effective twice-over rotation management strategy found that it required three to five years before grass tiller density increased significantly. An intensive timing and severity defoliation treatment study was conducted with western wheatgrass to determine treatments that activated vegetative reproduction of tillers from axillary buds. Two defoliation treatments and a control with seven microplots each were established on silty range sites in 6.0 month seasonlong (6.0 m SL), 4.5 month seasonlong (4.5 m SL), and 4.5 month twice-over rotation (4.5 m TOR) management strategies. Mean annual tiller densities on the control treatments were 532.6 $/m^2$, 908.5 $/m^2$, and 1331.4 $/m^2$; on the June 25% treatments were 626.5 $/m^2$, 861.5 $/m^2$, and 1441.0 $/m^2$; and on the June 50% treatments were 548.2 /m$^2$, 877.2 /m$^2$, and 1206.1 /m$^2$ of the 4.5 m SL, 6.0 m SL, and 4.5 m TOR management strategies, respectively. Fewer vegetative tillers were maintained on the control treatment than on the June 25% and June 50% treatments of the 4.5 m SL management strategy. Fewer vegetative tillers were produced on the June 25% and June 50% treatments than on the control treatment of the 6.0 m SL management strategy. Fewer vegetative tillers were maintained on the June 50% treatment than on the control treatment of the 4.5 m TOR management strategy and greater numbers of vegetative tillers were produced on the June 25% treatment than on the control treatment of the 4.5 m TOR management strategy. Removal of 25% of the leaf material from grass tillers between the three and a half new leaf stage and the flower stage produces the greatest number of vegetative tillers from axillary buds when soil mineral nitrogen is available at quantities greater than 100 lbs/ac. Twenty five percent removal of leaf weight during vegetative growth stages also removed sufficient quantities of the growth-inhibiting hormone, auxin, permitting synthesis or utilization of the growth hormone, cytokinin, in the axillary buds, and activating the asexual process of vegetative production of tillers. On the June 25% treatment of the 4.5 m TOR management strategy there was adequate quantities of available mineral nitrogen and the remaining 75% leaf weight had sufficient leaf area to fix carbon at adequate quantities for growth and development of the tillers from the activated axillary buds. On the June 25% treatments of the 6.0 m SL and 4.5 m SL management strategies, the process of vegetative tiller production was activated by the defoliation treatment, however, the required quantity of mineral nitrogen was not available for growth and development of the tillers. On the June 50% treatment of the 4.5 m TOR management strategy, the defoliation treatment activated the process of vegetative tillering, adequate quantities of mineral nitrogen was available, however, the remaining 50% leaf area could not supply adequate quantities of fixed carbon causing fewer tillers to develop. On the June 50% treatments of the 6.0 m SL and 4.5 m SL management strategies, the vegetative tillering process was activated, however, adequate quantities of mineral nitrogen and fixed carbon were not available. On the control treatments of the 6.0 m SL, 4.5 m SL and 4.5 m TOR management strategies, because there was no defoliation treatment, the process of vegetative tiller production was not activated, however, some vegetative tillers were produced; these processes do not stop instantaneously, the quantity of vegetative tillers would decrease at the rates the respective decrease in available mineral nitrogen and fixed carbon down to producing one vegetative tiller per lead tiller and then the number of lead tillers would soon be reduced. These processes do not start instantaneously either, it has been taking three to five years with annual removal of 25% of the leaf material during vegetative growth stages before the tiller numbers increase adequately. The soil rhizosphere organisms need to increase in biomass and activity before they can mineralize 100 lbs/ac of organic nitrogen. The increase in rhizosphere organisms requires an increase in the quantity of exudated short chain carbon energy from the grass plants, which requires annual removal of 25% of the leaf material during vegetative growth stages.

The seasonal mean rhizosphere volume was 50 ft$^3$/ac and 68 ft$^3$/ac and the available soil mineral nitrogen was 62 lbs/ac and 77 lbs/ac on the traditional 6.0 m SL and 4.5 m SL management strategies, respectively. The compensatory physiological processes that enable rapid recovery of defoliated tillers and the processes for vegetative reproduction of secondary tillers from axillary buds were not fully activated on the 6.0 m SL and 4.5 m SL management strategies because the timing and severity of grass tiller defoliation was antagonistic to rhizosphere organism activity causing insufficient quantities of available mineral nitrogen that resulted in incomplete recovery of defoliated tillers, decreased vegetative tillers from axillary buds, low tiller densities, and decreased herbage production.

The seasonal mean rhizosphere volume was 227 ft$^3$/ac and the available soil mineral nitrogen was 178 lbs/ac on the biologically effective 4.5 m TOR management strategy. The defoliation resistance mechanisms functioned at elevated levels on the 4.5 m TOR management strategy because the timing and severity of grass tiller defoliation was beneficial to rhizosphere organism activity causing great quantities of available mineral nitrogen that resulted in full recovery of defoliated tillers, increased vegetative tillers from axillary buds, high tiller densities, and increased herbage production.

Wight and Black (1979) found that activation of the processes for grass plant water use efficiency required 100 lbs/ac or greater soil mineral nitrogen. This study found that activation of the components of the defoliation resistance mechanisms that help grass tillers withstand and recover from defoliation and that produce vegetative tillers from axillary buds required 100 lbs/ac or greater soil mineral nitrogen. Stimulation of increased rhizosphere organism activity and increased mineralization of soil organic nitrogen into mineral nitrogen available at 100 lbs/ac or greater must occur before the other beneficial components of the defoliation resistance mechanisms can be fully activated.

Acknowledgment

I am grateful to Sheri Schneider for assistance in the production of this manuscript and for development of the tables and figures.

Table 2. Precipitation in inches for growing-season months and the annual total precipitation for 1999-2001, DREC Ranch, Manning, North Dakota.

| | Apr | May | Jun | Jul | Aug | Sep | Oct | Growing Season | Annual Total |
|---|---|---|---|---|---|---|---|---|---|
| Long-term mean | | | | | | | | | |
| 1982-2008 | 1.40 | 2.40 | 3.24 | 2.43 | 1.73 | 1.37 | 1.33 | 13.90 | 16.69 |
| 1999 | 1.10 | 4.93 | 1.59 | 1.80 | 2.70 | 2.40 | T | 14.52 | 15.56 |
| % of LTM | 78.57 | 205.42 | 49.07 | 74.07 | 156.07 | 175.18 | 0.00 | 104.46 | 93.23 |
| 2000 | 1.26 | 1.90 | 3.77 | 2.77 | 2.74 | 1.09 | 1.46 | 14.99 | 20.23 |
| % of LTM | 90.00 | 79.17 | 116.36 | 113.99 | 158.38 | 79.56 | 109.77 | 107.84 | 121.21 |
| 2001 | 2.70 | 0.53 | 6.36 | 4.87 | 0.00 | 1.94 | 0.00 | 16.40 | 18.03 |
| % of LTM | 192.86 | 22.08 | 196.30 | 200.41 | 0.00 | 141.61 | 0.00 | 117.98 | 108.03 |
| 1999-2001 | 1.69 | 2.45 | 3.91 | 3.15 | 1.81 | 1.81 | 0.49 | 15.30 | 17.94 |
| % of LTM | 120.71 | 102.08 | 120.68 | 129.63 | 104.62 | 132.12 | 36.84 | 110.07 | 107.49 |

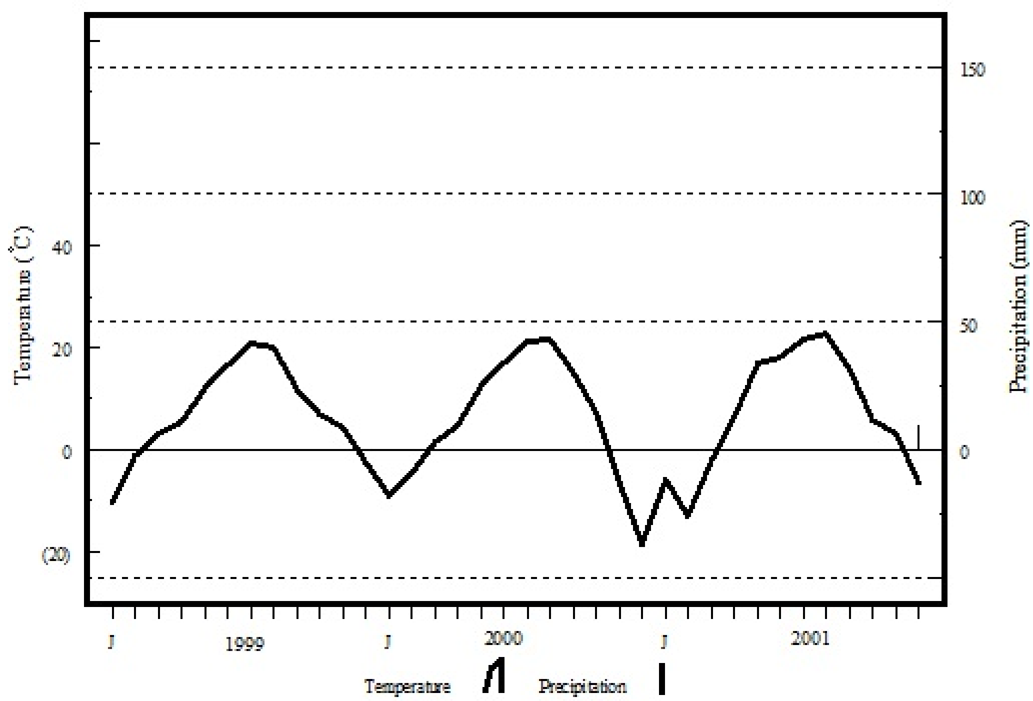


Fig. 1. Ombrothermic diagram of 1999-2001 mean monthly temperature and monthly precipitation at DREC Ranch, Manning, North Dakota.

Table 3. Mineral nitrogen and rhizosphere volume for grazing management strategies.

| Grazing Management Strategy | Mineral Nitrogen lbs/acre-foot | Rhizosphere Volume $ft^3$/acre-foot |
|---|---|---|
| 6.0-m Seasonlong | 62c | 50z |
| 4.5-m Seasonlong | 77b | 68z |
| 4.5-m Twice-over Rotation | 178a | 227x |

Means in the same column and followed by the same letter are not significantly different (P<0.05).
Data from Manske 2008, 2009b.

Table 4a. Density per square meter of tiller types on the defoliation treatments of the management strategies during the first growing season.

| Treatment Management Strategy | Live tillers early May #/m² | New tillers first season #/m² | Total first season tillers #/m² | Tillers at flower stages #/m² | Dead tillers first season #/m² | Live tillers fall #/m² | New fall tillers #/m² | Total live tillers mid October #/m² | Dead tillers winter period #/m² |
|---|---|---|---|---|---|---|---|---|---|
| Control | | | | | | | | | |
| 6.0 m SL | 469.9b | 0.0c | 469.9b | 219.3b | 31.3c | 219.3b | 219.3b | 438.6b | 0.0c |
| 4.5 m SL | 281.9c | 0.0c | 281.9c | 94.0b | 62.7b | 125.3c | 94.0c | 219.3c | 0.0c |
| 4.5 m TOR | 877.1a | 62.7b | 939.8a | 344.6a | 250.6b | 344.6b | 250.6b | 595.2b | 31.3b |
| June 25% | | | | | | | | | |
| 6.0 m SL | 469.9b | 62.7b | 532.5b | 94.0b | 31.3c | 407.2b | 125.3b | 532.5b | 62.7b |
| 4.5 m SL | 438.6b | 31.3b | 469.9b | 94.0b | 156.6b | 219.3b | 125.3b | 344.6b | 0.0c |
| 4.5 m TOR | 971.1a | 62.7b | 1033.8a | 156.6b | 407.2a | 469.9b | 344.6b | 814.5b | 188.0b |
| June 50% | | | | | | | | | |
| 6.0 m SL | 563.9b | 62.7b | 626.5b | 156.6b | 62.7b | 407.2b | 188.0b | 595.2b | 156.6b |
| 4.5 m SL | 375.9c | 0.0c | 375.9c | 62.7b | 125.3b | 188.0b | 156.6b | 344.6b | 125.3b |
| 4.5 m TOR | 720.5a | 62.7b | 783.2b | 219.3b | 250.6b | 313.3b | 344.6b | 657.8b | 219.3b |

Means in the same column and followed by the same letter are not significantly different ($P<0.05$).

Table 4b. Density per square meter of tiller types on the defoliation treatments of the management strategies during the second growing season.

| Treatment Management Strategy | Carry over tillers #/m² | New tillers early spring #/m² | Live tillers early May #/m² | New tillers second season #/m² | Total second season tillers #/m² | Tillers at flower stages #/m² | Dead tillers second season #/m² | Live tillers fall #/m² | New fall tillers #/m² | Total live tillers mid October #/m² |
|---|---|---|---|---|---|---|---|---|---|---|
| Control | | | | | | | | | | |
| 6.0 m SL | 438.6b | 344.6b | 783.2b | 31.3c | 814.5b | 156.6b | 250.6b | 407.2b | 313.3b | 720.5b |
| 4.5 m SL | 219.3c | 188.0b | 407.2b | 125.3b | 532.5b | 31.3c | 188.0b | 313.3b | 156.6b | 469.9b |
| 4.5 m TOR | 563.9b | 469.9a | 1033.8a | 250.6a | 1284.4a | 375.9a | 438.6a | 469.9b | 188.0b | 657.8b |
| June 25% | | | | | | | | | | |
| 6.0 m SL | 469.9b | 31.3b | 501.2b | 94.0c | 595.2b | 188.0b | 94.0b | 313.3b | 469.9a | 783.2b |
| 4.5 m SL | 344.6b | 0.0c | 344.6c | 188.0b | 532.5b | 125.3b | 156.6b | 250.6b | 125.3c | 375.9c |
| 4.5 m TOR | 626.5b | 469.9a | 1096.4a | 188.0b | 1284.4a | 188.0b | 281.9b | 814.5a | 219.3b | 1033.8a |
| June 50% | | | | | | | | | | |
| 6.0 m SL | 438.6b | 31.3b | 469.9b | 156.6b | 626.5b | 125.3b | 94.0b | 407.2b | 313.3b | 720.5b |
| 4.5 m SL | 219.3c | 31.3b | 250.6c | 94.0c | 344.6c | 94.0b | 94.0b | 156.6c | 219.3b | 375.9c |
| 4.5 m TOR | 438.6b | 250.6b | 689.2b | 250.6a | 939.8b | 281.9a | 156.6b | 501.2b | 344.6b | 845.8b |

Means in the same column and followed by the same letter are not significantly different ($P<0.05$).

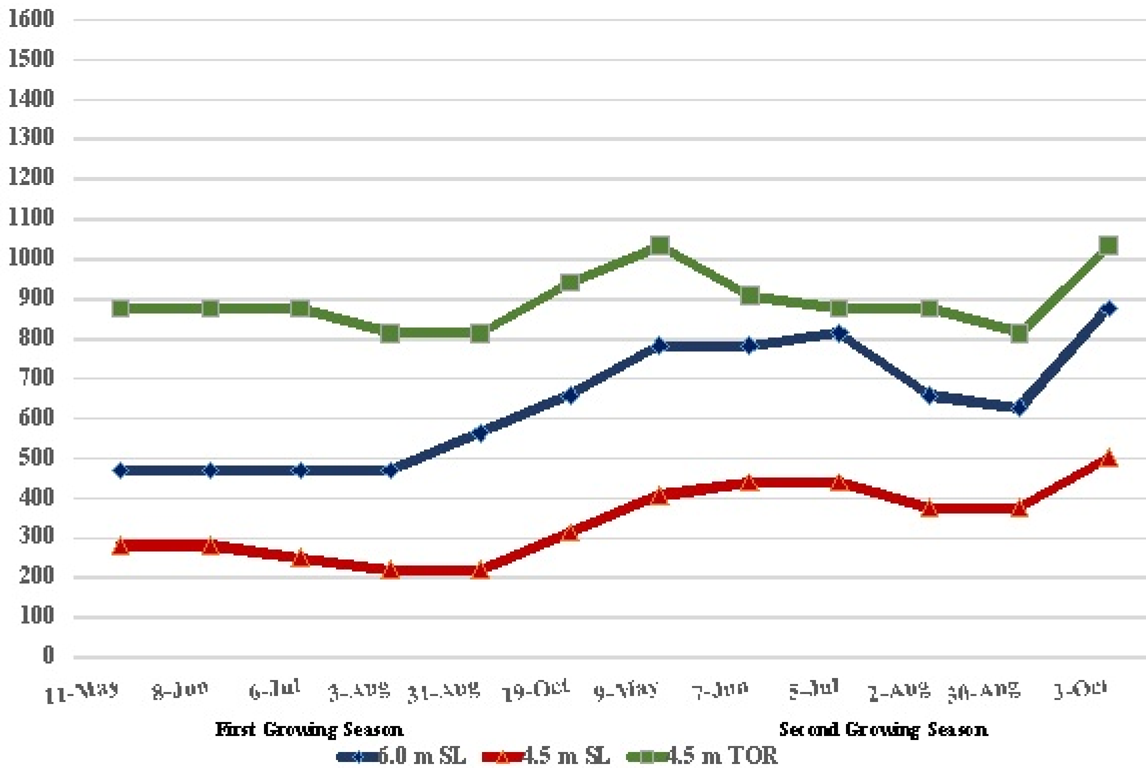


**Figure 2. Monthly tiller density per square meter on the control treatments during the first and second growing seasons.**

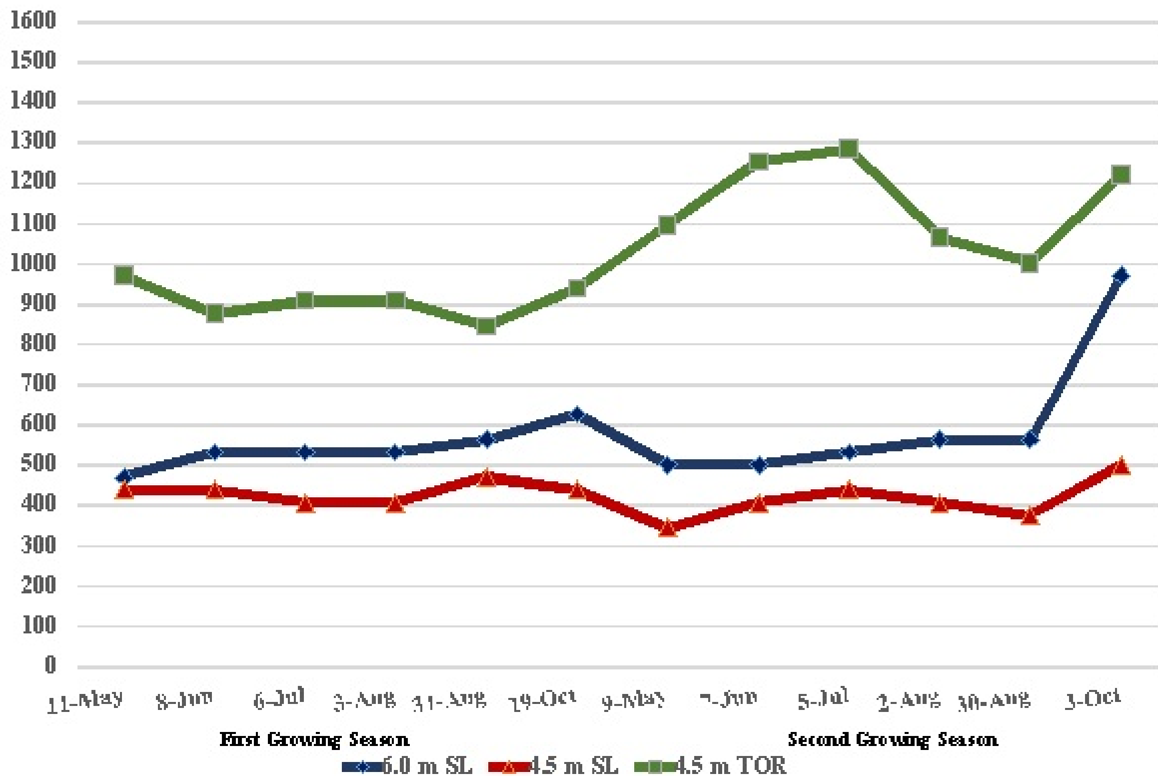


Figure 3. Monthly tiller density per square meter on the mid June 25% defoliation treatments during the first and second growing seasons.

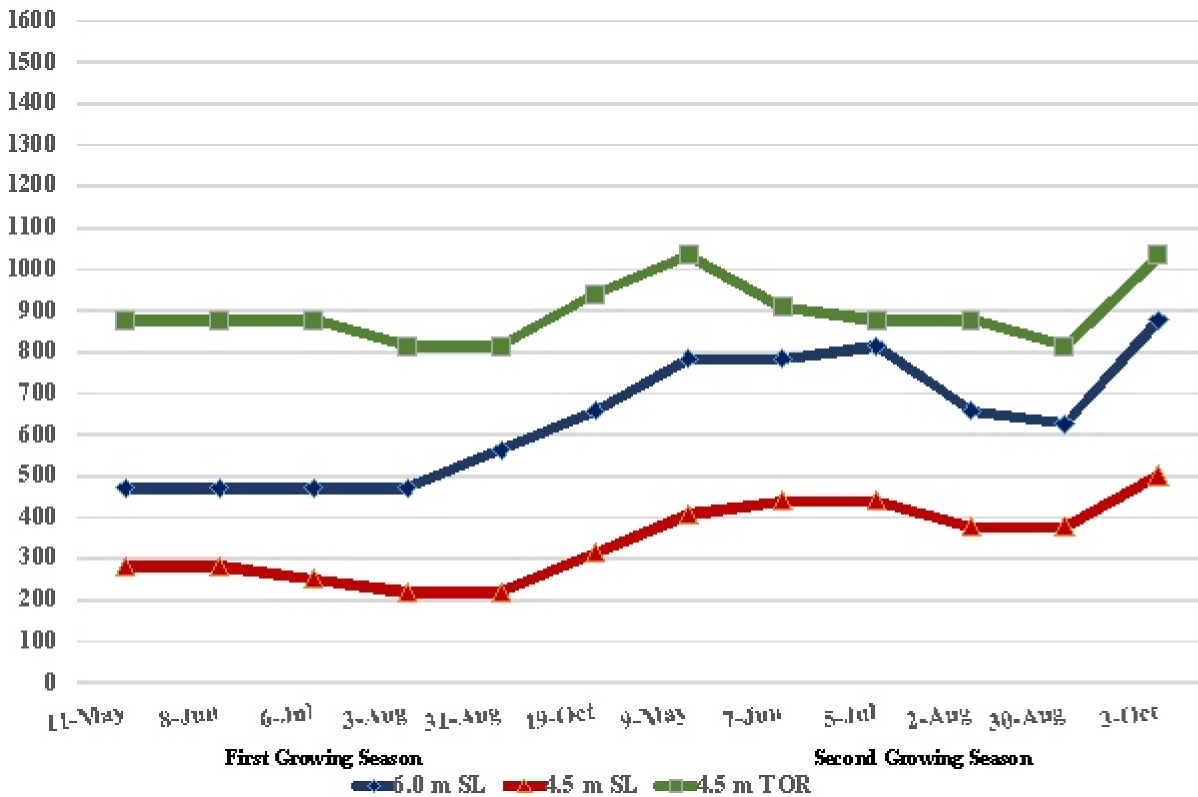


**Figure 4. Monthly tiller density per square meter on the mid June 50% defoliation treatments during the first and second growing seasons.**

Table 5. Mean monthly growing season tiller density (excluding the fall tillers) on the defoliation treatments of the management strategies.

| Treatment<br>Management<br>Strategy | First Growing Season<br>#/m$^2$ | Second Growing Season<br>#/m$^2$ | Change during Second Growing Season<br>#/m$^2$ |
|---|---|---|---|
| Control | | | |
| 6.0 m SL | 464.7b | 704.9b | +240.2b |
| 4.5 m SL | 245.4c | 391.6c | +146.2b |
| 4.5 m TOR | 814.5a | 892.8a | +78.3b |
| June 25% | | | |
| 6.0 m SL | 516.9b | 522.1b | +5.2b |
| 4.5 m SL | 402.0c | 391.6c | -10.4b |
| 4.5 m TOR | 824.9a | 1117.3a | +292.4a |
| June 50% | | | |
| 6.0 m SL | 584.8b | 543.0b | -41.8b |
| 4.5 m SL | 349.8c | 281.9c | -67.9b |
| 4.5 m TOR | 710.1a | 788.4a | +78.3b |

Means in the same column of each defoliation treatment and followed by the same letter are not significantly different (P<0.05).

Table 6. Density per square meter of total growing season tillers on the defoliation treatments of the management strategies.

| Treatment Management Strategy | First Growing Season Tillers #/m² | Fall Tillers First Year #/m² | Total Tillers First Year #/m² | Carry Over Tillers #/m² | Second Growing Season Tillers #/m² | Fall Tillers Second Year #/m² | Total Tillers Second Year #/m² | Two Year Total Tillers #/m² |
|---|---|---|---|---|---|---|---|---|
| Control | | | | | | | | |
| 6.0 m SL | 469.9b | 219.3b | 689.2b | 438.6b | 814.5b | 313.3b | 1127.7b | 1378.3b |
| 4.5 m SL | 281.9c | 94.0c | 375.9c | 219.3c | 532.5b | 156.6b | 689.2c | 845.8c |
| 4.5 m TOR | 939.8a | 250.6b | 1190.4b | 563.9b | 1284.4a | 188.0b | 1472.3b | 2098.8b |
| June 25% | | | | | | | | |
| 6.0 m SL | 532.5b | 125.3b | 657.8b | 469.9b | 595.2b | 469.9a | 1065.1b | 1253.0b |
| 4.5 m SL | 469.9b | 125.3b | 595.2b | 344.6b | 532.5b | 125.3c | 657.8c | 908.5c |
| 4.5 m TOR | 1033.8a | 344.6b | 1378.3a | 626.5b | 1284.4a | 219.3b | 1503.6b | 2255.5a |
| June 50% | | | | | | | | |
| 6.0 m SL | 626.5b | 188.0b | 814.5b | 438.6b | 626.5b | 313.3b | 939.8b | 1315.7b |
| 4.5 m SL | 375.9c | 156.6b | 532.5c | 219.3c | 344.6c | 219.3b | 563.9c | 877.1c |
| 4.5 m TOR | 783.2b | 344.6b | 1127.7b | 438.6b | 939.8b | 344.6b | 1284.4b | 1973.5b |

Means in the same column and followed by the same letter are not significantly different ($P<0.05$).

Table 7. Vegetative tillers developed per lead tiller on the defoliation treatments of the management strategies.

| Treatment<br>Management<br>Strategy | Density of Lead Tillers at Defoliation Treatment<br>#/m$^2$ | Density of Total Initiated Vegetative Tillers<br>#/m$^2$ | Number of Stimulated Vegetative Tillers per Lead Tiller<br># | Difference from Management Strategy Control |
|---|---|---|---|---|
| Control | | | | |
| 6.0 m SL | 344.6b | 908.5b | 2.64a | |
| 4.5 m SL | 188.0c | 563.9c | 3.00a | |
| 4.5 m TOR | 595.2b | 1221.7b | 2.05b | |
| June 25% | | | | |
| 6.0 m SL | 344.6b | 783.2b | 2.27b | -0.37b |
| 4.5 m SL | 250.6c | 469.9c | 1.88b | -1.12b |
| 4.5 m TOR | 563.9b | 1284.4b | 2.28b | +0.23a |
| June 50% | | | | |
| 6.0 m SL | 407.2b | 751.8b | 1.85b | -0.79b |
| 4.5 m SL | 281.9c | 501.2c | 1.78b | -1.22b |
| 4.5 m TOR | 626.5b | 1253.0b | 2.00b | -0.05b |

Means in the same column and followed by the same letter are not significantly different ($P<0.05$).

Table 8. Density per square meter and percent of total for tillers initiated through vegetative reproduction during periods of the growing season.

| Treatment Management Strategy | Seasonal Periods Early Spring #/m² | May #/m² | Mid Season #/m² | Fall Season #/m² | Total Initiated Tillers #/m² | Seasonal Periods Early Spring % | May % | Mid Season % | Fall Season % |
|---|---|---|---|---|---|---|---|---|---|
| Control | | | | | | | | | |
| 6.0 m SL | 344.6b | 0.0c | 31.3c | 532.5b | 908.5b | 37.9a | 0.0c | 3.5b | 58.6b |
| 4.5 m SL | 188.0b | 31.3c | 94.0b | 250.6c | 563.9c | 33.3b | 5.6c | 16.7b | 44.4b |
| 4.5 m TOR | 469.9a | 156.6b | 156.6a | 438.6b | 1221.7b | 38.5a | 12.8b | 12.8b | 35.9c |
| June 25% | | | | | | | | | |
| 6.0 m SL | 31.3b | 62.7b | 94.0b | 595.2b | 783.2b | 4.0b | 8.0b | 12.0b | 76.0a |
| 4.5 m SL | 0.0c | 62.7b | 156.6a | 250.6c | 469.9c | 0.0c | 13.3b | 33.3a | 53.3b |
| 4.5 m TOR | 469.9a | 188.0a | 62.7b | 563.9b | 1284.4b | 36.6a | 14.6b | 4.9b | 43.9c |
| June 50% | | | | | | | | | |
| 6.0 m SL | 31.3b | 156.6b | 62.7b | 501.2b | 751.8b | 4.2b | 20.8a | 8.3b | 66.7b |
| 4.5 m SL | 31.3b | 62.7b | 31.3c | 375.9b | 501.2c | 6.3b | 12.5b | 6.3b | 75.0a |
| 4.5 m TOR | 250.6b | 219.3a | 94.0b | 689.2b | 1253.0b | 20.0b | 17.5b | 7.5b | 55.0b |

Means in the same column and followed by the same letter are not significantly different ($P<0.05$).

Table 9. Density per square meter and percent of total for vegetative tillers terminated during periods of the growing season before reaching maturity and for lead tillers terminated after flowering.

| | Seasonal Periods | | | | Total Terminated Tillers | Seasonal Periods | | | |
|---|---|---|---|---|---|---|---|---|---|
| Treatment Management Strategy | Early Season #/m$^2$ | Mid and Fall Season #/m$^2$ | Flowering Lead Tillers #/m$^2$ | Winter Period #/m$^2$ | #/m$^2$ | Early Season % | Mid and Fall Season % | Flowering Lead Tillers % | Winter Period % |
| Control | | | | | | | | | |
| 6.0 m SL | 0.0b | 281.9b | 375.9b | 0.0c | 657.8b | 0.0b | 42.9b | 57.1a | 0.0c |
| 4.5 m SL | 0.0b | 250.6b | 125.3c | 0.0c | 375.9c | 0.0b | 66.7a | 33.3b | 0.0c |
| 4.5 m TOR | 281.9a | 407.2b | 720.5a | 31.3b | 1441.0a | 19.5a | 28.3b | 50.0b | 2.2c |
| June 25% | | | | | | | | | |
| 6.0 m SL | 0.0b | 125.3c | 281.9b | 62.7b | 469.9b | 0.0b | 26.7c | 60.0a | 13.3b |
| 4.5 m SL | 0.0b | 313.3b | 219.3b | 0.0c | 532.5b | 0.0b | 58.8a | 41.2b | 0.0c |
| 4.5 m TOR | 125.3a | 563.9b | 344.6b | 188.0b | 1221.7b | 10.3a | 46.2b | 28.2b | 15.3b |
| June 50% | | | | | | | | | |
| 6.0 m SL | 0.0b | 156.6b | 281.9b | 156.6b | 595.2b | 0.0b | 26.3c | 47.4b | 26.3b |
| 4.5 m SL | 0.0b | 219.3b | 156.6c | 125.3b | 501.2b | 0.0b | 43.8b | 31.2b | 25.0b |
| 4.5 m TOR | 31.3b | 375.9b | 501.2a | 219.3b | 1127.7b | 2.8b | 33.3b | 44.4b | 19.5b |

Means in the same column and followed by the same letter are not significantly different ($P<0.05$).

## Literature Cited


**Anderson, R.V., D.C. Coleman, C.V. Cole, and E.T. Elliott. 1981.** Effect of nematodes *Acrobeloides sp.* and *Mesodiplogaster lheritieri* on substrate utilization and nitrogen and phosphorus mineralization. Ecology 62:549-555.

**Atkinson, C.J. 1986.** The effect of clipping on net photosynthesis and dark respiration rates of plants from an upland grassland, with reference to carbon partitioning in *Festuca ovina.* Annals of Botany 58:61-72.

**Barker, W.T., and W.C. Whitman. 1988.** Vegetation of the Northern Great Plains. Rangelands 10:266-272.

**Bird, S.B., J.E. Herrick, M.M. Wander, and S.F. Wright. 2002.** Spatial heterogeneity of aggregate stability and soil carbon in semi-arid rangeland. Environmental Pollution 116:445-455.

**Briske, D.D. 1991.** Developmental morphology and physiology of grasses. p. 85-108. *in* R.K. Heitschmidt and J.W. Stuth (eds.). Grazing management: an ecological perspective. Timber Press, Portland, OR.

**Briske, D.D., and J.H. Richards. 1994.** Physiological responses of individual plants to grazing: current status and ecological significance. p. 147-176. *in* M. Vavra, W.A. Laycock, and R.D. Pieper (eds.). Ecological implications of livestock herbivory in the west. Society for Range Management, Denver, CO.

**Briske, D.D., and J.H. Richards. 1995.** Plant response to defoliation: a physiological, morphological, and demographic evaluation. p. 635-710. *in* D.J. Bedunah and R.E. Sosebee (eds.). Wildland plants: physiological ecology and developmental morphology. Society for Range Management, Denver, CO.

**Burrows, R.L., and F.L. Pfleger. 2002.** Arbuscular mycorrhizal fungi respond to increasing plant diversity. Canadian Journal of Botany 80:120-130.

**Caesar-TonThat, T.C., D.H. Branson, J.D. Reeder, and L.L. Manske. 2001.** Soil-aggregating basidiomycetes in the rhizosphere of grasses under two grazing management systems. Poster. American Society of Agronomy Annual Meeting. Charlotte, NC.

**Coleman, D.C., C.P.P. Reid, and C.V. Cole. 1983.** Biological strategies of nutrient cycling in soil ecosystems. Advances in Ecological Research 13:1-55.

**Coyne, P.I., M.J. Trlica, and C.E. Owensby. 1995.** Carbon and nitrogen dynamics in range plants. p. 59-167. *in* D.J. Bedunah and R.E. Sosebee (eds.). Wildland plants: physiological ecology and developmental morphology. Society for Range Management, Denver, CO.

**Curl, E.A., and B. Truelove. 1986.** The rhizosphere. Springer-Verlag, New York, NY.

**Dahl, B.E. 1995.** Developmental morphology of plants. p. 22-58. *in* D.J. Bedunah and R.E. Sosebee (eds.). Wildland plants: physiological ecology and developmental morphology. Society for Range Management, Denver, CO.

**Driver, J.D., W.E. Holben, and M.C. Rillig. 2005.** Characterization of glomalin as a hyphal wall component of arbuscular mycorrhizal fungi. Soil Biology and Biochemistry 37:101-106.

**Emberger, C., H. Gaussen, M. Kassas, and A. dePhilippis. 1963.** Bioclimatic map of the Mediterranean Zone, explanatory notes. UNESCO-FAO. Paris. 58p.

**Gorder, M.M., L.L. Manske, and T.L. Stroh. 2004.** Grazing treatment effects on vegetative tillering and soil rhizospheres of western wheatgrass. NDSU Dickinson Research Extension Center. Range Research Report DREC 04-1056. Dickinson, ND. 13p.

**Hamilton, E.W., and D.A. Frank. 2001.** Can plants stimulate soil microbes and their own nutrient supply? Evidence from a grazing tolerant grass. Ecology 82:2397-2402.

**Ingham, R.E., J.A. Trofymow, E.R. Ingham, and D.C. Coleman. 1985.** Interactions of bacteria, fungi, and the nemotode grazers: effects of nutrient cycling and plant growth. Ecological Monographs 55:119-140.

**Keeney, D.R. 1982.** Nitrogen - availability indices. p. 711-733. *in* R.H. Miller and D.R. Keeney (eds.). Methods of soil analysis. 2nd ed. American Society of Agronomy, Madison, WI.

**Keeney, D.R., and D.W. Nelson. 1982.** Nitrogen - inorganic forms. p. 643-698. *in* R.H. Miller and D.R. Keeney (eds.). Methods of soil analysis. 2nd ed. American Society of Agronomy, Madison, WI.

**Klein, D.A., B.A. Frederick, M. Biondini, and M.J. Trlica. 1988.** Rhizosphere microorganism effects on soluble amino acids, sugars, and organic acids in the root zone of *Agropyron cristatum, A. smithii,* and *Bouteloua gracilis*. Plant and Soil 110:19-25.

**Kochy, M., and S.D. Wilson. 2000.** Competitive effects of shrubs and grasses in prairie. Oikos 91:385-395.

**Langer, R.H.M. 1972.** How grasses grow. Edward Arnold, London, Great Britain.

**Manske, L.L. and T.C. Caesar-TonThat. 2003.** Increasing rhizosphere fungi and improving soil quality with biologically effective grazing management. NDSU Dickinson Research Extension Center. Summary Range Research Report DREC 03-3025. Dickinson, ND. 6p.

**Manske, L.L. 1998.** General description of grass growth and development and defoliation resistance mechanisms. NDSU Dickinson Research Extension Center. Range Management Report DREC 98-1022. Dickinson, ND. 12p.

**Manske, L.L. 1999.** Can native prairie be sustained under livestock grazing? p.99-108. *in* J. Thorpe, T.A. Steeves, and M. Gollop (eds.). Proceedings of the Fifth Prairie Conservation and Endangered Species Conference. Provincial Museum of Alberta. Natural History Occasional Paper No. 24. Edmonton, Alberta.

**Manske, L.L. 2003.** Effects of grazing management treatments on rangeland vegetation. NDSU Dickinson Research Extension Center. Summary Range Research Report DREC 03-3027. Dickinson, ND. 6p.

**Manske, L.L. 2007a.** Restoration of degraded prairie ecosystems. NDSU Dickinson Research Extension Center. Summary Range Management Report DREC 07-3045. Dickinson, ND. 6p.

**Manske, L.L. 2007b.** Biology of defoliation by grazing. NDSU Dickinson Research Extension Center. Range Management Report DREC 07-1067. Dickinson, ND. 25p.

**Manske, L.L. 2008.** Grazing and burning treatment effects on soil mineral nitrogen and rhizosphere volume. NDSU Dickinson Research Extension Center. Range Research Report DREC 08-1066b. Dickinson, ND. 15p.

**Manske, L.L. 2009a.** Ombrothermic interpretation of range plant water deficiency from temperature and precipitation data collected at the Ranch Headquarters of the Dickinson Research Extension Center in western North Dakota, 1982-2008. NDSU Dickinson Research Extension Center. Range Research Report DREC 09-1019l. Dickinson, ND. 17p.

**Manske, L.L. 2009b.** Enhancement of the nitrogen cycle improves native rangeland. NDSU Dickinson Research Extension Center. Summary Range Management Report DREC 09-3054. Dickinson, ND. 6p.

**McNaughton, S.J. 1979.** Grazing as an optimization process: grass-ungulate relationships in the Serengeti. American Naturalist 113:691-703.

**McNaughton, S.J. 1983.** Compensatory plant growth as a response to herbivory. Oikos 40:329-336.

**Mosteller, F., and R.E.K. Rourke. 1973.** Sturdy statistics. Addison-Wesley Publishing Co., MA. 395p.

**Mueller, R.J., and J.H. Richards. 1986.** Morphological analysis of tillering in *Agropyron spicatum* and *Agropyron desertorum.* Annals of Botany 58:911-921.

**Murphy, J.S., and D.D. Briske. 1992.** Regulation of tillering by apical dominance: chronology, interpretive value, and current perspectives. Journal of Range Management 45:419-429.

**Richards, J.H., and M.M. Caldwell. 1985.** Soluble carbohydrates, concurrent photosynthesis and efficiency in regrowth following defoliation: a field study with *Agropyron* species. Journal of Applied Ecology 22:907-920.

**Richards, J.H., R.J. Mueller, and J.J. Mott. 1988.** Tillering in tussock grasses in relation to defoliation and apical bud removal. Annals of Botany 62:173-179.

**Rillig, M.C., S.F. Wright, and V.T. Eviner. 2002.** The role of arbuscular mycorrhizal fungi and glomalin in soil aggregation: comparing effects of five plant species. Plant and Soil 238:325-333.

**Shiflet, T.N. (ed.). 1994.** Rangeland cover types. Society for Range Management. Denver, CO. 152p.

**Whipps, J.M. 1990.** Carbon economy. p. 59-97. *in* J.M. Lynch (ed.). The rhizosphere. John Wiley and Sons, New York, NY.

**Wight, J.R., and A.L. Black. 1972.** Energy fixation and precipitation use efficiency in a fertilized rangeland ecosystem of the Northern Great Plains. Journal of Range Management 25:376-380.

**Wight, J.R., and A.L. Black. 1979.** Range fertilization: plant response and water use. Journal of Range Management 32:345-349.

# Evaluation of the Defoliation Resistance Mechanisms Influence on Vegetative Tiller Initiation and Tiller Density

Llewellyn L. Manske PhD
Report DREC 10-1076
Range Scientist
North Dakota State University
Dickinson Research Extension Center

Defoliation of grass tillers removes leaf area terminating photosynthesis in those lost leaves and disrupts physiological processes in all remaining plant parts. Replacement of lost leaf material and restoration of biological processes are essential for grass tiller recovery. During the period of coevolution with herbivores, grass plants developed numerous biogeochemical processes that help grass tillers withstand and recover from defoliation (McNaughton 1979, 1983; Coleman et al. 1983; Briske 1991; Briske and Richards 1995; Manske 1999). These defoliation resistance mechanisms are comprised of three major components: compensatory physiological processes within plants (McNaughton 1979, 1983; Briske 1991); vegetative reproduction of secondary tillers from axillary buds (Mueller and Richards 1986, Richards et al. 1988, Murphy and Briske 1992, Briske and Richards 1994, Briske and Richards 1995); and symbiotic activity of rhizosphere organisms (Coleman et al. 1983, Ingham et al. 1985).

Compensatory physiological processes within grass plants enable rapid recovery of defoliated tillers through: increased growth rates of replacement leaves and shoots that produces larger leaves with greater mass (Langer 1972, Briske and Richards 1995); increased photosynthetic capacity of remaining mature leaves and rejuvenated portions of older leaves not completely senescent (Atkinson 1986, Briske and Richards 1995); and increased allocation of carbon and nitrogen from remaining leaf and shoot tissue, not from material stored in the roots (Richards and Caldwell 1985, Briske and Richards 1995, Coyne et al. 1995).

Vegetative reproduction by tillering is the asexual process of growth and development of secondary tillers from axillary buds (Dahl 1995). The meristematic activity in axillary buds and the subsequent development of vegetative secondary tillers is regulated by auxin, a growth-inhibiting hormone produced in the apical meristem and young developing leaves of lead tillers (Briske and Richards 1995). Auxin interferes with the metabolic function of cytokinin, a growth hormone (Briske and Richards 1995). Partial defoliation temporarily reduces the production of the blockage hormone, auxin (Briske and Richards 1994). This abrupt reduction of plant auxin in lead tillers allows for cytokinin synthesis or utilization in multiple axillary buds, stimulating the development of several vegetative tillers (Murphy and Briske 1992, Briske and Richards 1994).

The rhizosphere is the narrow zone of cylindrical soil around active roots of perennial grassland plants and is comprised of bacteria, protozoa, nematodes, springtails, mites, endomycorrhizal fungi (Anderson et al. 1981, Curl and Truelove 1986) and ectomycorrhizal fungi (Caesar-TonThat et al. 2001, Manske and Caesar-TonThat 2003). Active rhizosphere organisms are required in grassland ecosystems for the conversion of plant usable inorganic nitrogen from soil organic nitrogen. The greater the organism biomass and activity level, the greater the rhizosphere volume (Gorder, Manske, and Stroh 2004) and the greater the quantity of soil organic nitrogen mineralized into inorganic nitrogen (Coleman et al. 1983, Klein et al. 1988, Burrows and Pfleger 2002, Rillig et al. 2002, Bird et al. 2002, Driver et al. 2005).

The defoliation resistance mechanisms are complex and consist of numerous biogeochemical processes. Full activation of the compensatory physiological processes within grass plants and the asexual processes of vegetative reproduction of secondary tillers from axillary buds require mineral nitrogen to be available at 100 lbs/ac or greater (Manske 2009). However, the levels of activation of these processes are inconsistent when grass tillers are defoliated at various phenological growth stages and when various quantities of leaf material are removed. The functional levels of activation of the component processes of the defoliation resistance mechanisms are not the same on different grazing management strategies.

This project was conducted to evaluate the influence of the defoliation resistance mechanisms on vegetative secondary tiller initiation and on seasonal mean tiller type density per square meter following tiller defoliation treatments at two severities with 25% and 50% removal of current aboveground biomass on three different grazing management strategies.

## Study Area

The native rangeland study sites were on the Dickinson Research Extension Center ranch, operated by North Dakota State University and located 20 miles north of Dickinson, in southwestern North Dakota, U.S.A. (47° 14' N. lat., 102° 50' W. long.).

Soils were primarily Typic Haploborolls. Long-term mean annual temperature was 42.3° F (5.8° C). January was the coldest month, with a mean temperature of 14.5° F (-9.7° C). July and August were the warmest months, with mean temperatures of 69.6° F (20.9° C) and 68.6° F (20.3° C), respectively. Long-term annual precipitation was 16.73 inches (425.04 mm). The precipitation received during May, June, and July accounts for nearly 50% of the annual precipitation. The amount of precipitation received during the perennial plant growing season (April to October) was 13.94 inches (354.15 mm), 83.32% of annual precipitation (Manske 2010).

The precipitation during the growing seasons of 2000 and 2001 was normal (table 1). During 2000 and 2001, 14.99 inches (107.53% of LTM) and 16.40 inches (117.65% of LTM) of precipitation were received, respectively. August of 2000 was a wet month and received 161.18% of LTM precipitation. April, May, June, July, and October received normal precipitation at 90.00%, 79.17%, 115.29%, 112.60%, and 108.15% of LTM. September was a dry month and received 80.15% of LTM precipitation. Perennial plants were under water stress conditions during September, 2000 (Manske 2010). April, June, July, and September of 2001 were wet months and each received 192.86%, 194.50%, 197.97%, and 142.65% of LTM precipitation, respectively. May was a very dry month and received 22.08% of LTM precipitation. August and October were extremely dry months and received no precipitation. Perennial plants were under water stress conditions during May, August, and October, 2001 (Manske 2010).

The native rangeland vegetation was the Wheatgrass-Needlegrass Type (Barker and Whitman 1988, Shiflet 1994) of the mixed grass prairie. The dominant native range grasses were western wheatgrass (*Agropyron smithii*) (*Pascopyrum smithii*), needle and thread (*Stipa comata*) (*Hesperostipa comata*), blue grama (*Bouteloua gracilis*), and threadleaf sedge (*Carex filifolia*).

The study sites were managed with three different grazing strategies. The 6.0 month seasonlong management strategy started in mid May. Livestock grazed a single native range pasture for 183 days, until mid November. The 4.5 month seasonlong management strategy started in early June. Livestock grazed a single native range pasture for 137 days, until mid October. The 4.5 month twice-over rotation management strategy started in early June, when livestock were moved to one of three native range pastures. Livestock remained on native range for 137 days, grazing each pasture for two periods, one 15-day period between 1 June and 15 July (when lead tillers of grasses were between the third-leaf stage and flowering stage) and one 30-day period after 15 July (after secondary tillers of grasses reached the third-leaf stage) and prior to mid October. The first pasture grazed in the sequence was the last pasture grazed the previous year.

## Procedures

Three study site exclosures were established on native rangeland silty range sites with livestock grazing controlled by three different management strategies: 6.0 month seasonlong (6.0 m SL), 4.5 month seasonlong (4.5 m SL), and 4.5 month twice-over rotation (4.5 m TOR). Within each exclosure, 21 microplots were located and seven randomly selected microplots were assigned to each of the three defoliation treatments. A control treatment had no defoliation of the grass tillers. Two severity of defoliation treatments with 25% and 50% removal of current aboveground biomass were applied 22 June during the first year. Each western wheatgrass tiller within a microplot received the same defoliation treatment and was individually identified with a distinguishing loop of colored wire. At the end of the study, each western wheatgrass tiller was classified as reproductive lead tiller, vegetative lead tiller, or secondary tiller based on relative rates of growth and development during the growing season.

Data collection began in early May and continued into October for two years (2000 and 2001). Data for each tiller was collected weekly during the first year and biweekly during the second year. These collected data were reported by Manske (2009). Additional computations of the data were conducted for this report. The total number of secondary tillers initiated through vegetative reproduction from axillary buds during the two growing seasons were determined for each defoliation treatment on each of the three grazing management strategies. A seasonal mean tiller density per square meter was determined from the two year mean biweekly tiller densities per square meter data during May, June, and July for the reproductive lead tillers, vegetative lead tillers, secondary tillers, and total tillers on each of the three grazing management strategies. A standard paired-plot t-test was used to analyze differences among means (Mosteller and Rourke 1973).

**Results**

The western wheatgrass tillers on the three grazing management strategies responded differently to the partial defoliation treatments. The grass tillers on the 6.0 m SL and 4.5 m SL management strategies responded negatively to the defoliation treatments and the grass tillers on the 4.5 m TOR management strategy responded positively to the defoliation treatments.

Initiated Secondary Tillers

The defoliated tillers on the 6.0 m SL and 4.5 m SL management strategies produced fewer secondary tillers from axillary buds than were produced by undefoliated tillers on the respective control treatments during two grazing seasons. The defoliated tillers on the June 25% and June 50% treatments of the 6.0 m SL management strategy produced 125.3/m$^2$ and 156.6/m$^2$ fewer vegetative secondary tillers during two growing seasons, respectively, than the 908.5/m$^2$ vegetative secondary tillers produced from axillary buds during two growing seasons by the undefoliated tillers on the control treatment (table 2). The defoliated tillers on the June 25% and June 50% treatments of the 4.5 m SL management strategy produced 94.0/m$^2$ and 62.7/m$^2$ fewer vegetative secondary tillers during two growing seasons, respectively, then the 563.9/m$^2$ vegetative secondary tillers produced from axillary buds during two growing seasons by the undefoliated tillers on the control treatment (table 2).

The defoliated tillers on the 4.5 m TOR management strategy produced more secondary tillers from axillary buds than were produced by undefoliated tillers on the control treatment during two grazing seasons. The defoliated tillers on the June 25% and June 50% treatments of the 4.5 m TOR management strategy produced 62.7/m$^2$ and 31.3/m$^2$ more vegetative secondary tillers during two growing seasons, respectively, than the 1221.7/m$^2$ vegetative secondary tillers produced from axillary buds during two growing seasons by the undefoliated tillers on the control treatment (table 2).

The grass tillers responded differently to defoliation because of the different quantities of available mineral nitrogen resulting from the different quantities of rhizosphere organisms on the three grazing management strategies. The volume of the rhizospheres on the 6.0 m SL and 4.5 m SL management strategies were low at 1142.2 cm$^3$/m$^3$ and 1552.3 cm$^3$/m$^3$, respectively (table 3) (Manske 2009). The available mineral nitrogen on the 6.0 m SL management strategy was 62.0 lbs/ac (Manske 2009) and was 76.7 lbs/ac on the 4.5 m SL management strategy. The volume of the rhizosphere on the 4.5 m TOR management strategy was high at 5212.9/cm$^3$/m$^3$ (table 3) (Manske 2009). This large rhizosphere organism biomass and high activity levels on the 4.5 m TOR management strategy mineralized great quantities of soil organic nitrogen resulting in 177.8 lbs/ac of available mineral nitrogen (Manske 2009).

The low rhizosphere volume and low soil mineral nitrogen below 100 lbs/ac on the traditional 6.0 m SL and 4.5 m SL management strategies was an impairment resulting in negative responses from the grass tillers to the partial defoliation treatments. The number of secondary tillers initiated during two growing seasons through vegetative reproduction from axillary buds by the defoliated treatment tillers on the 6.0 m SL and 4.5 m SL management strategies was lower than the number of vegetative tillers initiated during two growing seasons by the undefoliated tillers on the respective control treatments because the defoliated tillers were unable to recover fully from the single event defoliation treatment as a consequence of insufficient quantities of soil mineral nitrogen preventing full activation of the compensatory physiological processes of the defoliation resistance mechanisms within the grass plants on the two traditional seasonlong management strategies (Manske 2009).

The high rhizosphere volume and high soil mineral nitrogen greater than 100 lbs/ac on the 4.5 m TOR management strategy was beneficial resulting in positive responses from the grass tillers to the partial defoliation treatments. The number of secondary tillers initiated during two growing seasons through vegetative reproduction from axillary buds by the defoliated treatment tillers on the 4.5 m TOR management strategy was greater than the number of vegetative secondary tillers initiated during two growing seasons by the undefoliated tillers on the control treatment. The defoliated tillers on the June 25% treatment fully recovered from the defoliation treatment because the adequate quantities of soil mineral nitrogen greater than 100 lbs/ac enabled full activation of the defoliation resistance mechanisms that completely replaced the lost leaf material, restored disrupted physiological processes, produced more vegetative secondary tillers per square meter, and developed more vegetative secondary tillers from axillary buds per lead tiller than were produced by undefoliated lead tillers on the control treatment (table 2) (Manske 2009). The greatest number of vegetative secondary tillers initiated from axillary buds were produced on the June 25% treatment of the 4.5 m TOR management strategy (table 2).

The defoliated tillers on the June 50% treatment of the 4.5 m TOR management strategy recovered to slightly less than full pretreatment condition. The large quantity of leaf area removed with 50% defoliation was not completely replaced by the fully activated defoliation resistance mechanism processes even with mineral nitrogen available at greater than 100 lbs/ac. The quantity of vegetative secondary tillers produced during two growing seasons by the less than fully recovered defoliated tillers on the June 50% treatment was less than the quantity of vegetative secondary tillers produced during two growing seasons by the fully recovered defoliated tillers on the June 25% treatment. The quantity of vegetative secondary tillers developed from axillary buds per lead tiller on the June 50% treatment was less than the quantity of vegetative secondary tillers developed per lead tiller by undefoliated tillers on the control treatment (Manske 2009).

The number of tillers initiated through vegetative reproduction from axillary buds during two growing seasons were greatest on the 4.5 m TOR management strategy, lowest on the 4.5 m SL management strategy, and intermediate on the 6.0 m SL management strategy (table 2), likewise, the mean number of total tillers per square meter during the May, June, and July seasonal period were greatest on the 4.5 m TOR management strategy, lowest on the 4.5 m SL management strategy, and intermediate on the 6.0 m SL management strategy (table 4).

Densities of Tiller Types

Mean total tiller density was significantly the greatest at 1049.4/m$^2$ on the June 25% treatment of the 4.5 m TOR management strategy as a result of the significantly greater vegetative lead tiller and secondary tiller densities (table 4, figure 1). Mean total tiller density was significantly the lowest at 342.0/m$^2$ on the control and June 50% treatments of the 4.5 m SL management strategy as a result of the significantly lower reproductive and vegetative lead tiller densities (table 4, figure 1). Mean total tiller densities were significantly lower on the June 25% treatment of the 6.0 m SL management strategy and on the June 50% treatment of the 4.5 m TOR management strategy and numerically lower on the June 50% treatment of the 6.0 m SL management strategy than on the respective control treatments. Mean total tiller densities were significantly greater on the June 25% treatments of the 4.5 m SL and 4.5 m TOR management strategies than on the respective control treatments (table 4, figure 1).

Mean reproductive lead tiller density was significantly the greatest at 352.5/m$^2$ on the control treatment of the 4.5 m TOR management strategy. Mean reproductive lead tiller density was significantly the lowest at 62.7/m$^2$ on the control treatment of the 4.5 m SL management strategy. The density of reproductive lead tillers was significantly lower on the June 25% and June 50% treatments of the 6.0 m SL and 4.5 m TOR management strategies than on the respective control treatments (table 4, figure 1). The quantities of reproductive lead tillers were greatly reduced on the June 25% and June 50% defoliation treatments during the first year. The greatest densities of reproductive lead tillers were on the respective control treatments of the 6.0 m SL, 4.5 m SL, and 4.5 m TOR management strategies with 46.7%, 33.3%, and 36.7% of the total tiller population developed into reproductive lead tillers, respectively. During the second year, the density of reproductive lead tillers on the June 25% and June 50% treatments increased slightly or remained about the same. The percentage of the tiller population that developed into reproductive lead tillers decreased during the second year on the control treatments. This reduction in the percent reproductive lead tillers on the control treatments was 58.8%, 82.3%, and 20.2% on the 6.0 m SL, 4.5 m SL, and 4.5 m TOR management strategies, respectively. Defoliation on the June 25% and June 50% treatments decreased the densities of reproductive lead tillers during the first growing season.

Mean vegetative lead tiller density was significantly the greatest at 543.0/m$^2$ on the June 25% treatment of the 4.5 m TOR management strategy. Mean vegetative lead tiller density was significantly the lowest on the control, June 25%, and June 50% treatments of the 4.5 m SL management strategy (table 4). The density of vegetative lead tillers was significantly greater on the June 25% and June 50% treatments of the 6.0 m SL and 4.5 m TOR management strategies and numerically greater on the June 25% and June 50% treatments of the 4.5 m SL management strategy than on the respective control treatments (table 4, figure 1). Defoliation on the June 25% and June 50% treatments increased the densities of vegetative lead tillers.

Mean secondary tiller density was the greatest at 334.2/m$^2$ on the June 25% treatment of the 4.5 m TOR management strategy. Mean secondary tiller density was the lowest at 99.2/$m^2$ on the June 50% treatment of the 4.5 m SL management strategy (table 4). The density of secondary tillers were significantly lower on the June 25% and June 50% treatments of the 6.0 m SL management strategy and on the June 50% treatment of the 4.5 m TOR management strategy and numerically lower on the June 50% treatment of the 4.5 m SL management strategy than on the respective control treatments (table 4, figure 1). Secondary tiller densities were not significantly different on the June 25% and June 50% treatments of the 6.0 m SL management strategy and on the control and June 50% treatments of the 4.5 m SL management strategy. Secondary tiller densities were greater on the June 25% treatments of the 4.5 m SL and 4.5 m TOR management strategies than on the respective control treatments. Defoliation on the June 25% treatment of the 6.0 m SL management strategy and on the June 50% treatments of the 6.0 m SL, 4.5 m SL, and 4.5 m TOR management strategies decreased secondary tiller densities. Defoliation on the June 25% treatments of the 4.5 m SL and 4.5 m TOR management strategies increased secondary tiller densities.

The defoliated tillers on the June 25% treatment of the 6.0 m SL management strategy and on the June 50% treatments of the 6.0 m SL, 4.5 m SL, and 4.5 TOR management strategies produced more vegetative lead tillers, fewer secondary tillers, and fewer total tillers than the undefoliated tillers produced on the respective control treatments. The reductions in the quantities of secondary tillers and total tillers on these defoliation treatments was not caused by damage to the grass tillers from the defoliation event, it was caused by the lack of full recovery of the leaf area and biogeochemical processes of the defoliated tillers. The two components of the defoliation resistance mechanisms that help defoliated tillers replace lost leaf material and recover disrupted physiological processes and that help secondary tillers develop vegetatively from axillary buds require mineral nitrogen to be available at a minimum of 100 lbs/ac for full activation (Manske 2009).

Mineral nitrogen on the 6.0 m SL and 4.5 m SL management strategies was available at quantities of less than 100 lbs/ac because the rhizosphere volume on these traditional management strategies was low (table 3), consequently the rates of mineralization of soil organic nitrogen were low, preventing full recovery of defoliated tillers and inhibiting vegetative development of axillary buds. Removal of 50% of the aboveground leaf biomass was also a contributing factor in the reductions of vegetatively reproduced secondary tillers (table 4, figure 1) resulting from insufficient quantities of available mineral nitrogen on the 6.0 m SL and 4.5 m SL management strategies. Replacement of the large quantity of leaf material removed with 50% defoliation required greater quantities of nutrient resources than were available on the two seasonlong management strategies. The defoliated tillers did not recover completely and only a few secondary tillers developed from axillary buds. The tillers with 50% leaf biomass removed did not recover to pretreatment condition on the 4.5 m TOR management strategy even with mineral nitrogen available at greater than 100 lbs/ac (Manske 2009) and the quantity of vegetatively produced secondary tillers was about half the quantity produced by undefoliated tillers on the control treatment.

The defoliated tillers on the June 25% treatments of the 4.5 m SL and 4.5 m TOR management strategies produced more vegetative lead tillers, more secondary tillers, and more total tillers than the undefoliated tillers produced on the respective control treatments. The large volume and high activity levels of rhizosphere organisms on the 4.5 m TOR management strategy provided mineral nitrogen at quantities greater than 100 lbs/ac. The two components of the defoliation resistance mechanisms that help defoliated tillers replace lost leaf material and recover disrupted physiological processes, and that help secondary tillers develop vegetatively from axillary buds were fully activated, resulting in full recovery of the tillers defoliated 25%, and in production of secondary tillers at quantities 20% greater than the quantities produced on the control treatment.

The rhizosphere volume on the 4.5 m SL management strategy was low (table 3) and mineral nitrogen was available at quantities of less than 100 lbs/ac, however, the defoliation resistance mechanisms were activated by the June 25% defoliation treatment sufficiently to provide partial recovery of the defoliated tillers and produce secondary tillers at quantities 18% greater than the quantities produced on the control treatment. The quantity of secondary tillers produced on the June 25% treatment of the 4.5 m SL management strategy was less than half the quantity of secondary tillers produced on the June 25% treatment of the 4.5 m TOR management strategy (table 4, figure 1).

The defoliated tillers on the June 25% and June 50% treatments of the 6.0 m SL, 4.5 m SL, and 4.5 m TOR management strategies all produced greater densities of vegetative lead tillers than were produced by the undefoliated tillers on the respective control treatments (table 4, figure 1). The numbers of vegetative lead tillers on the defoliation treatments were greater than the quantity of reproductive lead tillers reduced by the defoliation treatments; except on the June 25% treatment of the 6.0 m SL management strategy, the total number of lead tillers were 21/$m^2$ fewer than were on the control treatment. The number of total lead tillers on the June 50% treatments of the 6.0 m SL, 4.5 m SL, and 4.5 m TOR management strategies were 31.3/$m^2$, 33.9/$m^2$, and 28.7/$m^2$ greater, respectively, and on the June 25% treatments of the 4.5 m SL and 4.5 m TOR management strategies were 49.5/$m^2$ and 96.5/$m^2$ greater, respectively, than were produced on the respective control treatments. This increase in vegetative lead tiller densities on all of the partial defoliation treatments appears to be a residual effect resulting from the stimulation of the defoliation resistance mechanisms and most likely caused by the compensatory physiological processes within grass plants that function to increase photosynthetic capacity of remaining mature leaves and rejuvenate portions of older leaves not completely senescent (Atkinson 1986, Briske and Richards 1995).

**Discussion**

The defoliation resistance mechanisms are a complex assemblage of biogeochemical processes that involve intricate interactions among rhizosphere microorganisms, grass plants, and large grazing herbivores. The defoliation resistance mechanisms were developed during the coevolution of grass plants and large grazing herbivores and enable grass plants to replace lost leaf material, to restore disrupted physiological processes, and to vegetatively reproduce secondary tillers from axillary buds after partial defoliation. The defoliation resistance mechanisms function at variable levels of activation depending on the quantity of available mineral nitrogen in grassland ecosystem soil. When mineral nitrogen is available at 100 lbs/ac or greater, the defoliation resistance mechanisms function at full activation. When mineral nitrogen is available at less than 100 lbs/ac, the defoliation resistance mechanisms function at levels less than full activation (Manske 2009).

The quantity of available mineral nitrogen in grassland ecosystem soils is dependent on the rate of mineralization of soil organic nitrogen by rhizosphere organisms. The larger the rhizosphere volume and microorganism biomass, the greater the quantity of soil mineral nitrogen converted. Rhizosphere volume and microorganism biomass are limited by access to simple carbohydrates (Curl and Truelove 1986). Healthy grass plants capture and fix carbon during photosynthesis and produce carbohydrates in quantities greater than the amount needed for tiller growth and development (Coyne et al. 1995). Partial defoliation of grass tillers that removes about 25% of the aboveground leaf material at vegetative phenological growth stages between the 3.5 new leaf stage and the flower stage (Manske 2009) by large grazing herbivores causes greater quantities of exudates containing simple carbohydrates to be released from the grass tillers through the roots into the rhizosphere (Hamilton and Frank 2001). With the increase in availability of carbon compounds in the rhizosphere, the biomass and activity of the microorganisms increases (Anderson et al. 1981, Curl and Truelove 1986, Whipps 1990). The increase in rhizosphere organism biomass and activity results in greater rates of mineralization of soil organic nitrogen and greater quantities of available mineral nitrogen (Coleman et al. 1983, Klein et al. 1988, Burrows and Pfleger 2002, Rillig et al. 2002, Bird et al. 2002, Driver et al. 2005). Inorganic (mineral) nitrogen available in quantities of 100 lbs/ac or greater allows defoliated grass tillers full activation of the defoliation resistance mechanisms (Manske 2009). Full activation of the compensatory physiological processes within grass plants accelerates growth rates of replacement leaves and shoots and increases restoration of biological processes enabling rapid and complete recovery of partially defoliated tillers. Full activation of the asexual processes of vegetative reproduction of secondary tillers from axillary buds increases initiated tiller density during the grazing season (Manske 2007).

Mineral nitrogen was available at quantities less than 100 lbs/ac on the traditional 6.0 m SL and 4.5 m SL management strategies because the timing and severity of grass tiller defoliation decreased the quantities of carbon exudates and was antagonistic to rhizosphere organisms resulting in reduced rhizosphere volume, reduced organism biomass, and reduced rates of mineralization of soil organic nitrogen into mineral nitrogen. These deficiencies of mineral nitrogen in grassland ecosystems were expressed as negative responses from grass tillers to defoliation treatments because the defoliation resistance mechanisms functioned at reduced levels of less than full activation resulting in less than complete recovery of defoliated tillers, poor initiation of secondary tillers from axillary buds, and low densities of the tiller types causing reduced total tiller density, reduced herbage production, and slow deterioration of health in the grassland ecosystem.

Mineral nitrogen was available at quantities greater than 100 lbs/ac on the biological effective 4.5 m TOR management strategy because the timing and severity of grass tiller defoliation increased the quantities of carbon exudates and was beneficial to rhizosphere organisms resulting in expanded rhizosphere volume, enlarged organism biomass, and increased rates of mineralization of soil organic nitrogen into mineral nitrogen. These abundant quantities of mineral nitrogen in the grassland ecosystem were expressed as positive responses from grass tillers to defoliation treatments because the defoliation resistance mechanisms functioned at the high levels of full activation resulting in complete recovery or near complete recovery of defoliated tillers, initiation of enormous numbers of secondary tillers from axillary buds, and high densities of the tiller types causing increased total tiller density, increased herbage production, and restoration and then maintenance of health in the grassland ecosystem.

Full activation of the defoliation resistance mechanisms is necessary for rapid and complete recovery of defoliated tillers, for initiation of abundant quantities of secondary tillers from axillary buds, and for high densities of tiller types in grassland ecosystems. The defoliation resistance mechanisms require a large biomass of active rhizosphere organisms to convert soil organic nitrogen into mineral nitrogen at quantities of 100 lbs/ac or greater for full activation. The 4.5 month twice-over rotation (4.5 m TOR) management system is the only known grazing management strategy designed to meet the biological requirements of grass plants and rhizosphere organisms, to provide soil mineral nitrogen at quantities of 100 lbs/ac or greater, and to activate the defoliation resistance mechanisms at full functional levels.

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Table 1. Precipitation in inches for growing-season months and the annual total precipitation for 2000-2001, DREC Ranch, Manning, North Dakota.

| | Apr | May | Jun | Jul | Aug | Sep | Oct | Growing Season | Annual Total |
|---|---|---|---|---|---|---|---|---|---|
| Long-term mean | | | | | | | | | |
| 1982-2009 | 1.40 | 2.40 | 3.27 | 2.46 | 1.70 | 1.36 | 1.35 | 13.94 | 16.73 |
| 2000 | 1.26 | 1.90 | 3.77 | 2.77 | 2.74 | 1.09 | 1.46 | 14.99 | 20.23 |
| % of LTM | 90.00 | 79.17 | 115.29 | 112.60 | 161.18 | 80.15 | 108.15 | 107.53 | 120.92 |
| 2001 | 2.70 | 0.53 | 6.36 | 4.87 | 0.00 | 1.94 | 0.00 | 16.40 | 18.03 |
| % of LTM | 192.86 | 22.08 | 194.50 | 197.97 | 0.00 | 142.65 | 0.00 | 117.65 | 107.77 |
| 2000-2001 | 1.98 | 1.22 | 5.07 | 3.82 | 1.37 | 1.52 | 0.73 | 15.70 | 19.13 |
| % of LTM | 141.43 | 50.83 | 155.05 | 155.28 | 80.59 | 111.76 | 54.07 | 112.63 | 114.35 |

Table 2. Density per square meter of secondary tillers initiated from axillary buds through vegetative reproduction on three grazing management strategies during two growing seasons.

| | Grazing Management Strategy | | |
|---|---|---|---|
| | 6.0 m SL | 4.5 m SL | 4.5 m TOR |
| | Secondary Tiller Density | | |
| Defoliation Treatment | $\#/m^2$ | $\#/m^2$ | $\#/m^2$ |
| Control | 908.5 | 563.9 | 1221.7 |
| June 25% | 783.2 | 469.9 | 1284.4 |
| June 50% | 751.8 | 501.2 | 1253.0 |

Data from Manske 2009.

Table 3. Volume of rhizospheres on three grazing management strategies.

| | Grazing Management Strategy | | |
|---|---|---|---|
| | 6.0 m SL | 4.5 m SL | 4.5 m TOR |
| | Rhizosphere Volume | | |
| Volume | $cm^3/m^3$ | $cm^3/m^3$ | $cm^3/m^3$ |
| Rhizosphere | 1142.2 | 1552.3 | 5212.9 |

Data from Manske 2009.

Table 4. Seasonal mean tiller numbers and percentages per square meter on three defoliation treatments of three management strategies during May, June, and July.

| | 6.0 m SL | | 4.5 m SL | | 4.5 m TOR | |
|---|---|---|---|---|---|---|
| Treatment<br>Tiller Type | Tiller<br>Numbers | Tiller<br>Percentage | Tiller<br>Numbers | Tiller<br>Percentage | Tiller<br>Numbers | Tiller<br>Percentage |
| Control | | | | | | |
| Reproductive | 188.0 | 30.4 | 62.7 | 18.3 | 352.5 | 39.2 |
| Vegetative | 227.2 | 36.7 | 146.2 | 42.8 | 266.3 | 29.7 |
| Secondary | 203.6 | 32.9 | 133.1 | 38.9 | 279.3 | 31.1 |
| Total Tillers | 618.7 d | | 342.0 g | | 898.0 b | |
| June 25% | | | | | | |
| Reproductive | 141.0 | 27.1 | 99.2 | 23.9 | 172.3 | 16.4 |
| Vegetative | 253.2 | 48.8 | 159.2 | 38.4 | 543.0 | 51.7 |
| Secondary | 125.3 | 24.1 | 156.6 | 37.7 | 334.2 | 31.9 |
| Total Tillers | 519.5 e | | 415.1 f | | 1049.4 a | |
| June 50% | | | | | | |
| Reproductive | 135.8 | 23.6 | 78.3 | 22.9 | 235.0 | 29.7 |
| Vegetative | 310.7 | 54.1 | 164.5 | 48.1 | 412.5 | 52.1 |
| Secondary | 127.9 | 22.3 | 99.2 | 29.0 | 143.6 | 18.2 |
| Total Tillers | 574.3 d | | 342.0 g | | 791.0 c | |

Means followed by the same letter are not significantly different ($P<0.05$).

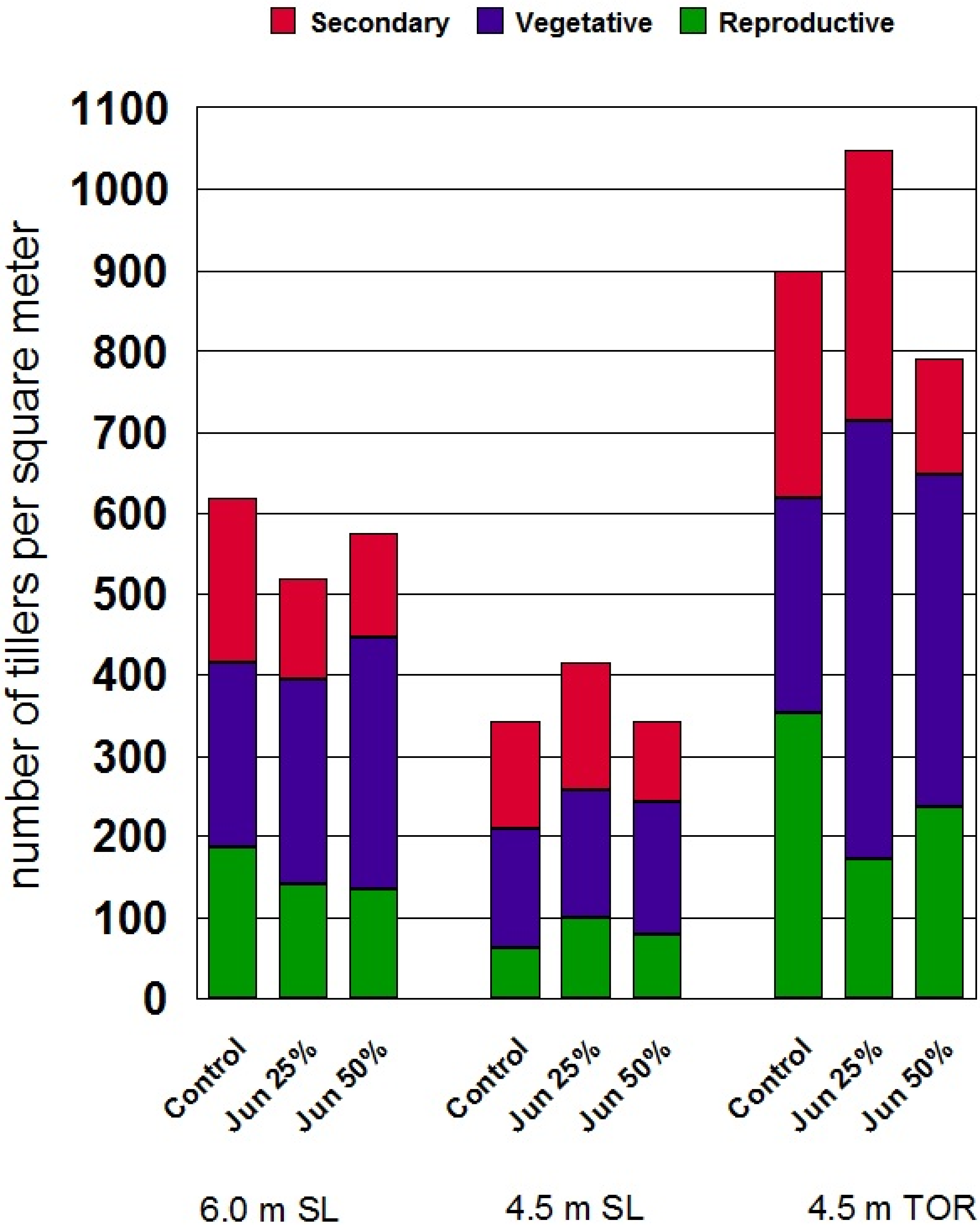


Figure 1. Seasonal mean tiller numbers per square meter on the three defoliation treatments of three management strategies.

## Literature Cited


**Anderson, R.V., D.C. Coleman, C.V. Cole, and E.T. Elliott. 1981.** Effect of nematodes *Acrobeloides sp.* and *Mesodiplogaster lheritieri* on substrate utilization and nitrogen and phosphorus mineralization. Ecology 62:549-555.

**Atkinson, C.J. 1986.** The effect of clipping on net photosynthesis and dark respiration rates of plants from an upland grassland, with reference to carbon partitioning in *Festuca ovina.* Annals of Botany 58:61-72.

**Barker, W.T., and W.C. Whitman. 1988.** Vegetation of the Northern Great Plains. Rangelands 10:266-272.

**Bird, S.B., J.E. Herrick, M.M. Wander, and S.F. Wright. 2002.** Spatial heterogeneity of aggregate stability and soil carbon in semi-arid rangeland. Environmental Pollution 116:445-455.

**Briske, D.D. 1991.** Developmental morphology and physiology of grasses. p. 85-108. *in* R.K. Heitschmidt and J.W. Stuth (eds.). Grazing management: an ecological perspective. Timber Press, Portland, OR.

**Briske, D.D., and J.H. Richards. 1994.** Physiological responses of individual plants to grazing: current status and ecological significance. p. 147-176. *in* M. Vavra, W.A. Laycock, and R.D. Pieper (eds.). Ecological implications of livestock herbivory in the west. Society for Range Management, Denver, CO.

**Briske, D.D., and J.H. Richards. 1995.** Plant response to defoliation: a physiological, morphological, and demographic evaluation. p. 635-710. *in* D.J. Bedunah and R.E. Sosebee (eds.). Wildland plants: physiological ecology and developmental morphology. Society for Range Management, Denver, CO.

**Burrows, R.L., and F.L. Pfleger. 2002.** Arbuscular mycorrhizal fungi respond to increasing plant diversity. Canadian Journal of Botany 80:120-130.

**Caesar-TonThat, T.C., D.H. Branson, J.D. Reeder, and L.L. Manske. 2001.** Soil-aggregating basidiomycetes in the rhizosphere of grasses under two grazing management systems. Poster. American Society of Agronomy Annual Meeting. Charlotte, NC.

**Coleman, D.C., C.P.P. Reid, and C.V. Cole. 1983.** Biological strategies of nutrient cycling in soil ecosystems. Advances in Ecological Research 13:1-55.

**Coyne, P.I., M.J. Trlica, and C.E. Owensby. 1995.** Carbon and nitrogen dynamics in range plants. p. 59-167. *in* D.J. Bedunah and R.E. Sosebee (eds.). Wildland plants: physiological ecology and developmental morphology. Society for Range Management, Denver, CO.

**Curl, E.A., and B. Truelove. 1986.** The rhizosphere. Springer-Verlag, New York, NY.

**Dahl, B.E. 1995.** Developmental morphology of plants. p. 22-58. *in* D.J. Bedunah and R.E. Sosebee (eds.). Wildland plants: physiological ecology and developmental morphology. Society for Range Management, Denver, CO.

**Driver, J.D., W.E. Holben, and M.C. Rillig. 2005.** Characterization of glomalin as a hyphal wall component of arbuscular mycorrhizal fungi. Soil Biology and Biochemistry 37:101-106.

**Gorder, M.M., L.L. Manske, and T.L. Stroh. 2004.** Grazing treatment effects on vegetative tillering and soil rhizospheres of western wheatgrass. NDSU Dickinson Research Extension Center. Range Research Report DREC 04-1056. Dickinson, ND. 13p.

**Hamilton, E.W., and D.A. Frank. 2001.** Can plants stimulate soil microbes and their own nutrient supply? Evidence from a grazing tolerant grass. Ecology 82:2397-2402.

**Ingham, R.E., J.A. Trofymow, E.R. Ingham, and D.C. Coleman. 1985.** Interactions of bacteria, fungi, and the nemotode grazers: effects of nutrient cycling and plant growth. Ecological Monographs 55:119-140.

**Klein, D.A., B.A. Frederick, M. Biondini, and M.J. Trlica. 1988.** Rhizosphere microorganism effects on soluble amino acids, sugars, and organic acids in the root zone of *Agropyron cristatum, A. smithii,* and *Bouteloua gracilis*. Plant and Soil 110:19-25.

**Langer, R.H.M. 1972.** How grasses grow. Edward Arnold, London, Great Britain.

**Manske, L.L. and T.C. Caesar-TonThat. 2003.** Increasing rhizosphere fungi and improving soil quality with biologically effective grazing management. NDSU Dickinson Research Extension Center. Summary Range Research Report DREC 03-3025. Dickinson, ND. 6p.

**Manske, L.L. 1999.** Can native prairie be sustained under livestock grazing? p.99-108. *in* J. Thorpe, T.A. Steeves, and M. Gollop (eds.). Proceedings of the Fifth Prairie Conservation and Endangered Species Conference. Provincial Museum of Alberta. Natural History Occasional Paper No. 24. Edmonton, Alberta.

**Manske, L.L. 2007.** Biology of defoliation by grazing. NDSU Dickinson Research Extension Center. Range Management Report DREC 07-1067. Dickinson, ND. 25p.

**Manske, L.L. 2009.** Grass plant responses to defoliation. NDSU Dickinson Research Extension Center. Range Research Report DREC 09-1074. Dickinson, ND. 47p.

**Manske, L.L. 2010.** Ombrothermic interpretation of range plant water deficiency from temperature and precipitation data collected at the Ranch Headquarters of the Dickinson Research Extension Center in western North Dakota, 1982-2009. NDSU Dickinson Research Extension Center. Range Research Report DREC 10-1019m. Dickinson, ND. 17p.

**McNaughton, S.J. 1979.** Grazing as an optimization process: grass-ungulate relationships in the Serengeti. American Naturalist 113:691-703.

**McNaughton, S.J. 1983.** Compensatory plant growth as a response to herbivory. Oikos 40:329-336.

**Mosteller, F., and R.E.K. Rourke. 1973.** Sturdy statistics. Addison-Wesley Publishing Co., MA. 395p.

**Mueller, R.J., and J.H. Richards. 1986.** Morphological analysis of tillering in *Agropyron spicatum* and *Agropyron desertorum.* Annals of Botany 58:911-921.

**Murphy, J.S., and D.D. Briske. 1992.** Regulation of tillering by apical dominance: chronology, interpretive value, and current perspectives. Journal of Range Management 45:419-429.

**Richards, J.H., and M.M. Caldwell. 1985.** Soluble carbohydrates, concurrent photosynthesis and efficiency in regrowth following defoliation: a field study with *Agropyron* species. Journal of Applied Ecology 22:907-920.

**Richards, J.H., R.J. Mueller, and J.J. Mott. 1988.** Tillering in tussock grasses in relation to defoliation and apical bud removal. Annals of Botany 62:173-179.

**Rillig, M.C., S.F. Wright, and V.T. Eviner. 2002.** The role of arbuscular mycorrhizal fungi and glomalin in soil aggregation: comparing effects of five plant species. Plant and Soil 238:325-333.

**Shiflet, T.N. (ed.). 1994.** Rangeland cover types. Society for Range Management. Denver, CO. 152p.

**Whipps, J.M. 1990.** Carbon economy. p. 59-97. *in* J.M. Lynch (ed.). The rhizosphere. John Wiley and Sons, New York, NY.

# Vegetative Forage Tiller Development in Response to Partial Defoliation

Llewellyn L. Manske PhD
Research Professor of Range Science
North Dakota State University
Dickinson Research Extension Center
Report DREC 14-1087

Partial defoliation of grass lead tillers at phenological growth stages between the three and a half new leaf stage and the flower (anthesis) stage is beneficial and activates the defoliation resistance mechanisms that enable rapid replacement of lost leaf material and recovery of disrupted physiological processes, that increase the asexual processes of vegetative reproduction of secondary tillers from axillary buds, and that increase the biomass and activity of symbiotic microorganisms of the rhizosphere resulting in increased quantities of soil organic nitrogen mineralized into inorganic nitrogen (Manske 2007). The results from activation of the defoliation resistance mechanisms are inconsistent on different grazing management strategies. Grass plant responses to partial defoliation can be positive or negative depending on the quantity of soil mineral nitrogen and whether the available mineral nitrogen is greater than or less than 100 lbs/ac, respectively (Manske 2009).

Defoliation of grass tillers before the 3.5 leaf stage is detrimental to the tiller and to the plant community (Manske 2007). Spring growth of carry over tillers from greenup until production of three and a half new leaves depends on carbohydrate reserves and on photosynthetic products from surviving portions of previous years leaves that have overwintered and regreened with chlorophyll (Coyne et al. 1995). Defoliation of grass tillers before the 3.5 leaf stage results in greatly reduced growth rates of herbage production (Coyne et al. 1995) causing decreased peak herbage biomass later in the growing season (Campbell 1952, Rogler et al. 1962, Manske 2000). Grass tillers have sufficient leaf area with 3.5 leaves to capture and fix carbon through photosynthesis at quantities adequate to meet growth and development needs and still provide short chain carbohydrates for exudation into the rhizosphere (Manske 2007). At the 3.5 leaf stage, all of the leaf primordia that will develop into leaves during that growing season have been produced on the apical meristem. Tillers that remain vegetative and carry over into the following growing season are able to continue production of leaf primordia. Reproductive lead tillers terminate leaf growth during the growing season that they produce a flower stalk. While reproductive lead tillers are between the 3 leaf stage and the 3.5 leaf stage, the apical meristems cease producing leaf primordia and commence producing flower primordia (Frank 1996, Frank et al. 1997). The previously produced leaf primordia continue to grow and develop. Evidence of flower stalk development can be observed externally at the boot stage. As the flower stalk develops in reproductive lead tillers, the fiber content increases and the percent crude protein, percent water, and digestibility decrease. Shortly after the flower (anthesis) stage, crude protein levels drop below 9.6%, the minimum requirements for a 1000 lb lactating cow (NRC 1996). Between the flower stage and the seed mature stage, crude protein levels decrease rapidly and drop below 7.8% by early August and drop below 6.2% in late August (Whitman et al. 1951, Manske 2008a). Vegetative tillers at leaf stages earlier than the 3.5 leaf stage and reproductive lead tillers at phenological stages advanced of the flower stage yield minuscule quantities of forage that have crude protein content at or above the nutrient requirements for lactating beef cattle. Grass tillers at vegetative growth stages between the 4 leaf stage and the flower (anthesis) stage provide the primary source of forage with crude protein quality at or above the nutrient requirements of lactating beef cows. The quantity of tillers between the 4 leaf stage and the flower stage directly effects the quantity of crude protein available for capture by grazing livestock, and in turn, the quantity of crude protein captured per acre is directly related to the quantity of pounds of calf weight produced per acre and inversely related to the cost per pound of calf weight produced (Manske 2008b). The quantity of forage tillers between the 4 leaf stage and the flower stage during the grazing season were affected by tiller type, grazing management strategy, and defoliation treatment.

This project was conducted to quantitatively determine the number of forage tillers between the four leaf stage and the flower (anthesis) stage that develop on three different grazing management strategies.

## Study Area

The native rangeland study sites were on the Dickinson Research Extension Center ranch, operated by North Dakota State University and located 20 miles north of Dickinson, in southwestern North Dakota, U.S.A. (47° 14' N. lat., 102° 50' W. long.).

Soils were primarily Typic Haploborolls. Long-term mean annual temperature was 42.3° F (5.8° C). January was the coldest month, with a mean temperature of 14.5° F (-9.7° C). July and August were the warmest months, with mean temperatures of 69.6° F (20.9° C) and 68.6° F (20.3° C), respectively. Long-term annual precipitation was 16.73 inches (425.04 mm). The precipitation received during May, June, and July accounts for nearly 50% of the annual precipitation. The amount of precipitation received during the perennial plant growing season (April to October) was 13.94 inches (354.15 mm), 83.32% of annual precipitation (Manske 2010).

The precipitation during the growing seasons of 2000 and 2001 was normal (table 1). During 2000 and 2001, 14.99 inches (107.53% of LTM) and 16.40 inches (117.65% of LTM) of precipitation were received, respectively. August of 2000 was a wet month and received 161.18% of LTM precipitation. April, May, June, July, and October received normal precipitation at 90.00%, 79.17%, 115.29%, 112.60%, and 108.15% of LTM, respectively. September was a dry month and received 80.15% of LTM precipitation. Perennial plants were under water stress conditions during September, 2000 (Manske 2010). April, June, July, and September of 2001 were wet months and each received 192.86%, 194.50%, 197.97%, and 142.65% of LTM precipitation, respectively. May was a very dry month and received 22.08% of LTM precipitation. August and October were extremely dry months and received no precipitation. Perennial plants were under water stress conditions during May, August, and October, 2001 (Manske 2010).

The native rangeland vegetation was the Wheatgrass-Needlegrass Type (Barker and Whitman 1988, Shiflet 1994) of the mixed grass prairie. The dominant native range grasses were western wheatgrass (*Agropyron smithii*) (*Pascopyrum smithii*), needle and thread (*Stipa comata*) (*Hesperostipa comata*), blue grama (*Bouteloua gracilis*), and threadleaf sedge (*Carex filifolia*).

The study sites were managed with three different grazing strategies. The 6.0 month seasonlong management strategy started in mid May. Livestock grazed a single native range pasture for 183 days, until mid November. The 4.5 month seasonlong management strategy started in early June. Livestock grazed a single native range pasture for 137 days, until mid October. The 4.5 month twice-over rotation management strategy started in early June, when livestock were moved to one of three native range pastures. Livestock remained on native range for 137 days, grazing each pasture for two periods, one 15-day period between 1 June and 15 July (when lead tillers of grasses were between the three and a half new leaf stage and flower stage) and one 30-day period after 15 July and prior to mid October. The first pasture grazed in the sequence was the last pasture grazed the previous year.

The volume of the rhizospheres on the 6.0 m SL and 4.5 m SL management strategies were low at 1142.2 $cm^3/m^3$ and 1552.3 $cm^3/m^3$**,** respectively (Manske 2009). The available mineral nitrogen on the 6.0 m SL management strategy was 62.0 lbs/ac (Manske 2009) and was 76.7 lbs/ac on the 4.5 m SL management strategy. The volume of the rhizosphere on the 4.5 m TOR management strategy was high at 5212.9 $cm^3/m^3$ (Manske 2009). Mineral nitrogen was available at high quantities of 177.8 lbs/ac on the 4.5 m TOR management strategy as a result of the large rhizosphere organism biomass and high activity levels that mineralized great quantities of soil organic nitrogen (Manske 2009). The soil depths of the surface horizon on the study sites of the 6.0 m SL, 4.5 m SL, and 4.5 m TOR management strategies were 9.6 inches (24.4 cm), 8.1 inches (20.6 cm), and 9.8 inches (25.4 cm), respectively. The surface horizon of the 4.5 m SL management strategy was significantly shallower than that of the 6.0 m SL and 4.5 m TOR management strategies (Manske 2009).

## Procedures

Three study site exclosures were established on native rangeland silty range sites with livestock grazing controlled by three different management strategies: 6.0 month seasonlong (6.0 m SL), 4.5 month seasonlong (4.5 m SL), and 4.5 month twice-over rotation (4.5 m TOR). Within each exclosure, 21 microplots were located and seven randomly selected microplots were assigned to each of the three defoliation treatments. A control treatment had no defoliation of the grass tillers. Two severity of defoliation treatments with 25% and 50% removal of current aboveground biomass were applied 22 June during the first year. Each western wheatgrass tiller within a microplot received the same defoliation treatment and was individually identified with a distinguishing loop of colored wire. At the end of the study, each western wheatgrass tiller was classified as reproductive lead tiller, vegetative lead tiller, or secondary tiller based on relative rates of growth and development during the growing season.

Data collection began in early May and continued into October for two years (2000 and 2001). Data for each tiller was collected weekly during the first year and biweekly during the second year. These collected data were reported by Manske (2009). For this report the number of leaves produced for western wheatgrass tillers were tabulated as the mean of two years for the control, June 25%, and June 50% treatments of the 6.0 m SL, 4.5 m SL, and 4.5 m TOR management strategies to determine the quantity and percent of phenological development of forage tillers between the 4 leaf and flower stages from reproductive lead tillers, vegetative lead tillers, and secondary tillers during the growing season. A standard paired-plot t-test was used to analyze differences among means (Mosteller and Rourke 1973).

**Results**

The three tiller types (reproductive lead tillers, vegetative lead tillers, and secondary tillers) did not develop leaves at the same rate and not all of the tillers within a tiller type developed leaves at the same time. Rates of tiller growth and development were regulated by hormones and availability of essential elements. The dominant tillers with rapid or unimpeded growth were the reproductive lead tillers and the vegetative lead tillers. The subordinate tillers with slow or inhibited growth were the secondary tillers.

Leaf Development Rates

The reproductive lead tillers had the fastest rate of growth and development (table 2a). Usually 5 to 8 leaves had developed when reproductive lead tillers reached the flower (anthesis) stage and no additional leaves were produced during development of flower stalk stages. Reproductive lead tillers that produced flower stalks early in the flower period had 5 to 6 leaves and tillers that produced flower stalks late in the flower period had 7 or 8 leaves. The reproductive lead tillers developed 1.3 leaves per tiller between early May and early June. The mean reproductive lead tiller was at the 4.5 leaf stage during early June. The period with the greatest rate of flower stalk development for the reproductive lead tillers occurred between early June and mid July. The reproductive lead tillers that did not produce flower stalks during early June to early July, produced 1.7 leaves per tiller. The reproductive lead tillers that did not produce flower stalks during early July to early August, produced 2.3 leaves per tiller. During early August, the mean reproductive lead tiller that had not yet produced a flower stalk was at the 8.5 leaf stage. The rate of leaf development of the reproductive lead tillers was not significantly different among the defoliation treatments of the three management strategies. However, the rate of leaf development was not uniform throughout the growing season. Spurts and lulls in tiller growth occurred during various biweekly periods on all of the treatments in an undetermined asymmetrical pattern that could not be directly related to defoliation treatment, grazing management strategy, or period precipitation.

The flower period started at the same general time on all defoliation treatments of the three management strategies. First flowers (anthesis) appeared on the reproductive lead tillers during early June, usually before 21 June, the summer solstice, the day with the longest daylight of nearly 16 hours. The length of the flower period differed greatly on the three management strategies. The end of the flower period occurred on the June 50% treatment of the 6.0 m SL management strategy in late June; occurred on the control treatment of the 6.0 m SL management strategy and on the control and June 25% treatments of the 4.5 m SL management strategy in mid July; occurred on the June 50% treatment of the 4.5 m SL management strategy and on the June 25% treatment of the 4.5 m TOR management strategy in late July; and occurred on the June 25% treatment of the 6.0 m SL management strategy and on the control and June 50% treatments of the 4.5 m TOR management strategy in mid August (table 2a).

The low quantity of mineral nitrogen of less than 100 lbs/ac and the low volume of rhizospheres on the 6.0 m SL and 4.5 m SL management strategies contributed to the shorter flowering periods on the traditional seasonlong grazing practices. The quantity of mineral nitrogen available at more than 100 lbs/ac and the larger volume of rhizosphere contributed to the longer flowering periods on the treatments of the 4.5 m TOR management strategy.

The vegetative lead tillers had the second fastest rate of growth and development (table 2b). The vegetative lead tillers developed 3.6 leaves in 3 months from the 3.0 leaf stage in early May to the 6.6 leaf stage in early August at an average rate of 0.6 leaves produced per biweekly period. An average of 1.0 leaf developed per tiller between early May and early June; an average of 1.5 leaves developed between early June and early July; and an average of 1.1 leaves developed between early July and early August. The mean vegetative lead tiller was at the 4.0 leaf stage during early June. The rate of leaf development of the vegetative lead tillers was not significantly different among the defoliation treatments of the three management strategies. The greatest rate of leaf development occurred on the control treatment of the 6.0 m SL management strategy and on the June 25% treatment of the 4.5 m TOR management strategy. The lowest rate of leaf development occurred on the control and June 50% treatments of the 4.5 m SL management strategy. The period with the greatest rate of leaf development for the vegetative lead tillers occurred between early June and early July. From early May to early July, the rate of leaf stage development was not significantly different between the reproductive lead tillers that had not produced flower stalks and the vegetative lead tillers.

The secondary tillers were the subordinate tillers and had very slow rates of growth and development (table 2c). The secondary tillers developed 1.2 leaves in 3 months from the 2.2 leaf stage in early May to the 3.4 leaf stage in early August at an average rate of 0.2 leaves produced per biweekly period. An average of 0.4 leaves developed per tiller between early May and early June; an average of 0.5 leaves developed between early June and early July; and an average of 0.2 leaves developed between early July and early August. The mean secondary tiller was at the 2.7 leaf stage during early June. During early July, the mean secondary tiller was at the 3.0 leaf stage on the 6.0 m SL and 4.5 m SL management strategies and at the 3.5 leaf stage on the 4.5 m TOR management strategy. The rate of leaf development of the secondary tillers was not significantly different among the defoliation treatments of the three management strategies.

Most of the growth in tiller leaf height and most of the development in tiller leaf stage by the reproductive lead tillers and the vegetative lead tillers occurred during May, June, and July. Goetz (1963) found that western wheatgrass lead tillers completed 100% of the growth in tiller leaf height and flower stalk height by the end of July. This rapid growth period corresponds with the period of greatest precipitation. The precipitation received during May, June, and July accounts for more than 50% of the annual precipitation (Manske 2010).

Forage Tillers

Forage tillers are that portion of grass tillers that provide nourishment for livestock. The grass tillers that do not have sufficient quantity or quality of nutrients are not forage tillers. Reproductive lead tillers are derived from carryover tillers are forage tillers between the 4 leaf stage and flower stage. Vegetative lead tillers derived from carryover tillers and from early spring initiated tillers are forage tillers between the 4 leaf and 10 leaf stages. Secondary tillers derived from growing season initiated tillers are forage tillers between the 4 leaf and 8 leaf stages. The numbers of forage tillers are greatly affected by grazing management practices.

Reproductive lead tillers composed 30% of the tiller population on the control treatment of the 6.0 m SL management strategy with 100% derived from carry over tillers. The number of reproductive lead tillers between the 4 leaf stage and the flower stage increased from 78.3/$m^2$ in early May to 188.0/$m^2$ in early June as tillers developed additional leaves, then decreased to 15.6/$m^2$ in early July and 0.0/$m^2$ in mid July as increasing numbers of tillers reached flower stages (table 3).

Vegetative lead tillers composed 37% of the tiller population on the control treatment of the 6.0 m SL management strategy with 88% derived from carry over tillers and 12% derived from early spring initiated tillers. The number of vegetative lead tillers between the 4 leaf stage and the 10 leaf stage increased from 47.0/$m^2$ in early May to 235.0/$m^2$ in early and mid June as tillers developed additional leaves, then decreased to 219.3/$m^2$ in mid July, 203.6/$m^2$ in early August, 188.0/$m^2$ in late August, and 172.3/$m^2$ in mid October as some tillers progressed through senescence (table 3).

Secondary tillers composed 33% of the tiller population on the control treatment of the 6.0 m SL management strategy with 100% derived from growing season initiated tillers. The number of secondary tillers between the 4 leaf stage and the 8 leaf stage remained at 0.0/$m^2$ during early and mid May, increased from 47.0/$m^2$ in early June to 78.3/$m^2$ in mid June and 125.3/$m^2$ in early July, then decreased slightly to 109.6/$m^2$ in mid July and early August, and increased to 141.0/$m^2$ in late August, and remained at 141.0/$m^2$ until mid October (table 3).

Growing season mean total tiller density was 689.2/$m^2$ on the control treatment of the 6.0 m SL management strategy. The number of total tillers between the 4 leaf stage and the flower stage increased from 125.3/$m^2$ in early May to 469.9/$m^2$ in early June, then decreased to 328.9/$m^2$ in mid July and 313.3/$m^2$ in early August, increased to 328.9/$m^2$ in late August, and remained at 313.3/$m^2$ in mid October (table 3, figure 1).

Reproductive lead tillers composed 27% of the tiller population on the June 25% treatment of the 6.0 m SL management strategy with 100% derived from carry over tillers. The number of reproductive lead tillers between the 4 leaf stage and the flower stage increased from 78.3/$m^2$ in early May to 125.3/$m^2$ in early June as tillers developed additional leaves, then decreased to 47.0/$m^2$ in early July, 15.6/$m^2$ in mid July, and 0.0/$m^2$ in late August as increasing numbers of tillers reached flower stages (table 3).

Vegetative lead tillers composed 49% of the tiller population on the June 25% treatment of the 6.0 m SL management strategy with 100% derived from carry over tillers. The number of vegetative lead tillers between the 4 leaf stage and the 10 leaf stage increased from 47.0/$m^2$ in early May to 188.0/$m^2$ in early June and 250.6/$m^2$ in mid June and early and mid July as tillers developed additional leaves, then decreased to 235.0/$m^2$ in early and late August, and 203.6/$m^2$ in mid October as some tillers progressed through senescence (table 3).

Secondary tillers composed 24% of the tiller population on the June 25% treatment of the 6.0 m SL management strategy with 100% derived from growing season initiated tillers. The number of secondary tillers between the 4 leaf stage and the 8 leaf stage remained at 31.3/$m^2$ during early and mid May and early June, increased to 62.7/$m^2$ in mid June and early July, increased to 78.3/$m^2$ in mid July and early August, decreased to 62.7/$m^2$ in late August, and increased to 94.0/$m^2$ in mid October (table 3).

Growing season mean total tiller density was 626.5/$m^2$ on the June 25% treatment of the 6.0 m SL management strategy. The number of total tillers between the 4 leaf stage and the flower stage increased from 156.6/$m^2$ in early May to 344.6/$m^2$ in early June and 407.2/$m^2$ in mid June, then decreased to 344.6/$m^2$ in mid July and 328.9/$m^2$ in early August, decreased to 297.6/$m^2$ in late August, and remained at 297.6/$m^2$ until mid October (table 3, figure 2).

Reproductive lead tillers composed 24% of the tiller population on the June 50% treatment of the 6.0 m SL management strategy with 100% derived from carry over tillers. The number of reproductive lead tillers between the 4 leaf stage and the flower stage increased from 47.0/$m^2$ in early May to 109.6/$m^2$ in mid May as tillers developed additional leaves, then decreased to 94.0/$m^2$ in early June, 62.7/$m^2$ in mid June, and 0.0/$m^2$ in early July as increasing numbers of tillers reached flower stages (table 3).

Vegetative lead tillers composed 54% of the tiller population on the June 50% treatment of the 6.0 m SL management strategy with 100% derived from carry over tillers. The number of vegetative lead tillers between the 4 leaf stage and the 10 leaf stage increased from 47.0/$m^2$ in early May to 250.6/$m^2$ in early June and 313.3/$m^2$ in mid June, then decreased slightly to 297.6/$m^2$ in early July, and remained at 297.6/$m^2$ until mid October (table 3).

Secondary tillers composed 22% of the tiller population on the June 50% treatment of the 6.0 m SL management strategy with 100% derived from growing season initiated tillers. The number of secondary tillers between the 4 leaf stage and the 8 leaf stage increased from 15.6/$m^2$ in early May to 31.3/$m^2$ during mid May and early and mid June, increased to 47.0/$m^2$ in early July, then decreased to 31.3/$m^2$ in mid July and 15.6/$m^2$ in early August, and increased to 31.3/$m^2$ in late August and 78.3/$m^2$ in mid October (table 3).

Growing season mean total tiller density was 657.9/$m^2$ on the June 50% treatment of the 6.0 m SL management strategy. The number of total tillers between the 4 leaf stage and the flower stage increased from 109.6/$m^2$ in early May to 375.9/$m^2$ in early June and 407.2/$m^2$ in mid June, then decreased to 328.9/$m^2$ in mid July and 313.3/$m^2$ in early August, and then increased to 328.9/$m^2$ in late August and 375.9/$m^2$ in mid October (table 3, figure 3).

Reproductive lead tillers composed 18% of the tiller population on the control treatment of the 4.5 m SL management strategy with 100% derived from carry over tillers. The number of reproductive lead tillers between the 4 leaf stage and the flower stage increased from 15.6/$m^2$ in early May to 47.0/$m^2$ in early June as tillers developed additional leaves, then decreased to 15.6/$m^2$ in early July and

$0.0/m^2$ in mid July as increasing numbers of tillers reached flower stages (table 4). The density of the reproductive lead tillers between the 4 leaf stage and the flower stage was the lowest on the control treatment of the 4.5 m SL management strategy.

Vegetative lead tillers composed 43% of the tiller population on the control treatment of the 4.5 m SL management strategy with 100% derived from carry over tillers. The number of vegetative lead tillers between the 4 leaf stage and the 10 leaf stage increased from $15.6/m^2$ in early May to $78.3/m^2$ in early June and $156.6/m^2$ in early July, and remained at $156.6/m^2$ until mid October (table 4). The density of the vegetative lead tillers between the 4 leaf stage and the 10 leaf stage was the lowest on the control treatment of the 4.5 m SL management strategy.

Secondary tillers composed 39% of the tiller population on the control treatment of the 4.5 m SL management strategy with 100% derived from growing season initiated tillers. The number of secondary tillers between the 4 leaf stage and the 8 leaf stage remained at $0.0/m^2$ during early and mid May and early June, increased to $15.6/m^2$ in mid June and early July, increased to $31.3/m^2$ in mid July, decreased to $15.6/m^2$ in early August, and increased to $47.0/m^2$ in late August and $78.3/m^2$ in mid October (table 4). The density of the secondary tillers between the 4 leaf stage and the 8 leaf stage was the lowest on the control treatment of the 4.5 m SL management strategy.

Growing season mean total tiller density was $422.9/m^2$ on the control treatment of the 4.5 m SL management strategy. The number of total tillers between the 4 leaf stage and the flower stage increased from $31.3/m^2$ in early May to $125.3/m^2$ in early June and $188.0/m^2$ in early and mid July, decreased to $172.3/m^2$ in early August, and increased to $203.6/m^2$ in late August and $235.0/m^2$ in mid October (table 4, figure 1). The density of the total tillers between the 4 leaf stage and the flower stage was the lowest on the control treatment of the 4.5 m SL management strategy.

Reproductive lead tillers composed 24% of the tiller population on the June 25% treatment of the 4.5 m SL management strategy with 100% derived from carry over tillers. The number of reproductive lead tillers between the 4 leaf stage and the flower stage increased from $15.6/m^2$ in early May to $62.7/m^2$ in early June as tillers developed additional leaves, then decreased to $31.3/m^2$ in early July and $0.0/m^2$ in mid July as increasing numbers of tillers reached flower stages (table 4).

Vegetative lead tillers composed 38% of the tiller population on the June 25% treatment of the 4.5 m SL management strategy with 100% derived from carry over tillers. The number of vegetative lead tillers between the 4 leaf stage and the 10 leaf stage increased from $47.0/m^2$ in early May to $141.0/m^2$ in early June and $156.6/m^2$ in mid June, remained at $156.6/m^2$ until early August, then decreased to $125.3/m^2$ in late August as some tillers progressed through senescence, and remained at $125.3/m^2$ until mid October (table 4).

Secondary tillers composed 38% of the tiller population on the June 25% treatment of the 4.5 m SL management strategy with 100% derived from growing season initiated tillers. The number of secondary tillers between the 4 leaf stage and the 8 leaf stage remained at $0.0/m^2$ during early May to mid June, increased to $31.3/m^2$ in early July, remained at $31.3/m^2$ until early August, then increased to $109.6/m^2$ in late August, and decreased to $94.0/m^2$ in mid October (table 4).

Growing season mean total tiller density was $454.3/m^2$ on the June 25% treatment of the 4.5 m SL management strategy. The number of total tillers between the 4 leaf stage and the flower stage increased from $62.7/m^2$ in early May to $203.6/m^2$ in early and mid June and $219.3/m^2$ in early July, then decreased to $188.0/m^2$ in mid July and early August, and increased to $219.3/m^2$ in mid October (table 4, figure 2).

Reproductive lead tillers composed 23% of the tiller population on the June 50% treatment of the 4.5 m SL management strategy with 100% derived from carry over tillers. The number of reproductive lead tillers between the 4 leaf stage and the flower stage increased from $0.0/m^2$ in early May to $78.3/m^2$ in early June as tillers developed additional leaves, then decreased to $15.6/m^2$ in early and mid July and $0.0/m^2$ in early August as increasing numbers of tillers reached flower stages (table 4).

Vegetative lead tillers composed 48% of the tiller population on the June 50% treatment of the 4.5 m SL management strategy with 100% derived from carry over tillers. The number of vegetative lead tillers between the 4 leaf stage and the 10 leaf stage increased from $15.6/m^2$ in early May to $47.0/m^2$ in early June, $141.0/m^2$ in mid June, and $172.3/m^2$ in early July, remained at $172.3/m^2$ until early August, and then decreased to $156.6/m^2$ in late August and $141.0/m^2$ in mid October as some tillers progressed through senescence (table 4).

Secondary tillers composed 29% of the tiller population on the June 50% treatment of the 4.5 m SL management strategy with 100% derived from growing season initiated tillers. The number of secondary tillers between the 4 leaf stage and the 8 leaf stage remained at 0.0/m$^2$ during early May to early June, increased to 15.6/m$^2$ in mid June and 47.0/m$^2$ in early July, remained at 47.0/m$^2$ until late August, and then decreased to 15.6/m$^2$ in mid October (table 4).

Growing season mean total tiller density was 438.6/m$^2$ on the June 50% treatment of the 4.5 m SL management strategy. The number of total tillers between the 4 leaf stage and the flower stage increased from 15.6/m$^2$ in early May to 125.3/m$^2$ in early June and 235.0/m$^2$ in early and mid July, then decreased to 219.3/m$^2$ in early August, and decreased to 203.6/m$^2$ in late August and 156.6/m$^2$ in mid October (table 4, figure 3).

Reproductive lead tillers composed 39% of the tiller population on the control treatment of the 4.5 m TOR management strategy with 100% derived from carry over tillers. The number of reproductive lead tillers between the 4 leaf stage and the flower stage increased from 125.3/m$^2$ in early May to 281.9/m$^2$ in early June as tillers developed additional leaves, then decreased to 156.6/m$^2$ in early July, 47.0/m$^2$ in mid July, and 0.0/m$^2$ in late August as increasing numbers of tillers reached flower stages (table 5). The density of the reproductive lead tillers between the 4 leaf stage and the flower stage was the greatest on the control treatment of the 4.5 m TOR management strategy.

Vegetative lead tillers composed 30% of the tiller population on the control treatment of the 4.5 m TOR management strategy with 90% derived from carry over tillers and 10% derived from early spring initiated tillers. The number of vegetative lead tillers between the 4 leaf stage and the 10 leaf stage increased from 47.0/m$^2$ in early May to 188.0/m$^2$ in early June and 266.3/m$^2$ in early and mid July, then decreased slightly to 235.0/m$^2$ in early August, and remained at 235.0/m$^2$ until mid October (table 5).

Secondary tillers composed 31% of the tiller population on the control treatment of the 4.5 m TOR management strategy with 100% derived from growing season initiated tillers. The number of secondary tillers between the 4 leaf stage and the 8 leaf stage increased from 31.3/m$^2$ in early May to 141.0/m$^2$ in mid May, decreased to 78.3/m$^2$ in early June and 62.7/m$^2$ in mid June, then increased to 109.6/m$^2$ in early July, 141.0/m$^2$ in mid July, and 172.3/m$^2$ in early August, and then decreased to 156.6/m$^2$ in mid October (table 5).

Growing season mean total tiller density was 1049.4/m$^2$ on the control treatment of the 4.5 m TOR management strategy. The number of total tillers between the 4 leaf stage and the flower stage increased from 203.6/m$^2$ in early May to 548.2/m$^2$ in early June and 595.2/m$^2$ in mid June, then decreased to 454.2/m$^2$ in mid July and 438.6/m$^2$ in early August, decreased to 360.3/m$^2$ in late August, and increased to 391.6/m$^2$ in mid October (table 5, figure 1).

Reproductive lead tillers composed 16% of the tiller population on the June 25% treatment of the 4.5 m TOR management strategy with 100% derived from carry over tillers. The number of reproductive lead tillers between the 4 leaf stage and the flower stage increased from 78.3/m$^2$ in early May to 172.3/m$^2$ in early June as tillers developed additional leaves, then decreased to 62.7/m$^2$ in early July, 15.6/m$^2$ in mid July, and 0.0/m$^2$ in early August as increasing numbers of tillers reached flower stages (table 5). The tiller population on the June 25% treatment of the 4.5 m TOR management strategy contained the lowest percentage of reproductive lead tillers.

Vegetative lead tillers composed 52% of the tiller population on the June 25% treatment of the 4.5 m TOR management strategy with 74% derived from carry over tillers and 26% derived from early spring initiated tillers. The number of vegetative lead tillers between the 4 leaf stage and the 10 leaf stage increased from 188.0/m$^2$ in early May to 532.5/m$^2$ in early June and 579.5/m$^2$ in mid June, decreased to 516.9/m$^2$ in early July, remained at 516.9/m$^2$ until mid August, then decreased to 485.6/m$^2$ in late August as some tillers progressed through senescence, and remained at 485.6/m$^2$ until mid October (table 5). The density of the vegetative lead tillers between the 4 leaf stage and the 10 leaf stage was significantly the greatest on the June 25% treatment of the 4.5 m TOR management strategy .

Secondary tillers composed 32% of the tiller population on the June 25% treatment of the 4.5 m TOR management strategy with 100% derived from growing season initiated tillers. The number of secondary tillers between the 4 leaf stage and the 8 leaf stage decreased from 15.6/m$^2$ in early May to 0.0/m$^2$ in mid May, increased from 15.6/m$^2$ in early June to 47.0/m$^2$ in mid June and 203.6/m$^2$ in early

July, then decreased to 141.0/m$^2$ in early and late August, and increased to 203.6/m$^2$ in mid October (table 5). The density of the secondary tillers between the 4 leaf stage and the 8 leaf stage was the greatest on the June 25% treatment of the 4.5 m TOR management strategy.

Growing season mean total tiller density was 1127.8/m$^2$ on the June 25% treatment of the 4.5 m TOR management strategy. The number of total tillers between the 4 leaf stage and the flower stage increased from 281.9/m$^2$ in early May to 720.5/m$^2$ in early June and 783.2/m$^2$ in early July, then decreased to 689.2/m$^2$ in mid July, 657.8/m$^2$ in early August, and 626.5/m$^2$ in late August, and then increased to 689.2/m$^2$ in mid October (table 5, figure 2). The density of the total tillers between the 4 leaf stage and the flower stage was significantly the greatest on the June 25% treatment of the 4.5 m TOR management strategy.

Reproductive lead tillers composed 30% of the tiller population on the June 50% treatment of the 4.5 m TOR management strategy with 100% derived from carry over tillers. The number of reproductive lead tillers between the 4 leaf stage and the flower stage increased from 109.6/m$^2$ in early May to 219.3/m$^2$ in early June as tillers developed additional leaves, then decreased to 62.7/m$^2$ in early July, 15.6/m$^2$ in mid July, and 0.0/m$^2$ in late August as increasing numbers of tillers reached flower stages (table 5).

Vegetative lead tillers composed 52% of the tiller population on the June 50% treatment of the 4.5 m TOR management strategy with 78% derived from carry over tillers and 22% derived from early spring initiated tillers. The number of vegetative lead tillers between the 4 leaf stage and the 10 leaf stage increased from 62.7/m$^2$ in early May to 328.9/m$^2$ in early June and 407.2/m$^2$ in mid June, decreased slightly to 391.6/m$^2$ in early July, remained at 391.6/m$^2$ until late August, and then decreased to 328.9/m$^2$ in mid October as some tillers progressed through senescence (table 5).

Secondary tillers composed 18% of the tiller population on the June 50% treatment of the 4.5 m TOR management strategy with 100% derived from growing season initiated tillers. The number of secondary tillers between the 4 leaf stage and the 8 leaf stage decreased from 15.6/m$^2$ in early May to 0.0/m$^2$ in mid May, increased from 15.6/m$^2$ in early June to 78.3/m$^2$ in mid June and 125.3/m$^2$ in early July, then decreased to 94.0/m$^2$ in mid July, increased to 109.6/m$^2$ in early and late August, and decreased to 78.3/m$^2$ in mid October (table 5).

Growing season mean total tiller density was 986.8/m$^2$ on the June 50% treatment of the 4.5 m TOR management strategy. The number of total tillers between the 4 leaf stage and the flower stage increased from 188.0/m$^2$ in early May to 563.9/m$^2$ in early June and 642.2/m$^2$ in mid June, then decreased to 579.5/m$^2$ in early July and 501.2/m$^2$ in mid July, increased slightly to 516.9/m$^2$ early August, and then decreased to 501.2/m$^2$ in late August and 407.2/m$^2$ in mid October (table 5, figure 3).

The primary period the reproductive lead tillers were forage tillers between the 4 leaf stage and the flower stage was from just prior to early June until mid July. The primary period the vegetative lead tillers were forage tillers between the 4 leaf stage and the 10 leaf stage was from early June until mid October. The primary period the secondary tillers were forage tillers between the 4 leaf stage and the 8 leaf stage was from early July until mid October.

Two Grazing Periods

The defoliation resistance mechanisms can be activated by partial defoliation by grazing when the lead tillers are at the vegetative phenological growth stages between the 3.5 new leaf stage and the flower stage. For native grasses, the first grazing period occurs for 45 days each year between early June and mid July. The benefits that result from the activated mechanisms happen during the 90 day second grazing period that occurs between mid July and mid October.

The degree of mechanism activation and the quantity of benefit development are greatly affected by the grazing management strategy. The number of forage tillers between the 4 leaf stage and the flower stage growing during the first and second grazing periods was greatest on the 4.5 m TOR management strategy, lowest on the 4.5 m SL management strategy, and intermediate on the 6.0 m SL management strategy (table 6).

The forage tiller densities were not significantly different among the three treatments of the 6.0 m SL management strategy and among the three treatments of the 4.5 m SL management strategy. The forage tiller densities on the three treatments of the 6.0 m SL management strategy were significantly greater than those on the three treatments of the 4.5 m SL management strategy (table 6).

Densities of the total forage tillers were not significantly different during the first and second grazing periods on the control, June 25%, and June 50% treatments of the 6.0 m SL and 4.5 m SL management strategies and on the June 25% and June 50% treatments of the 4.5 m TOR management strategy. On the control treatment of the 4.5 m TOR management strategy, the total forage tiller densities during the second grazing period were significantly lower than those during the first grazing period (table 6).

The forage tiller densities during the first and second grazing periods were not significantly different on the control and June 50% treatments of the 4.5 m TOR management strategy. The forage tiller densities during the first and second grazing periods on the June 25% treatment of the 4.5 m TOR management strategy were significantly greater than those on the control and June 50% treatments of the 4.5 m TOR management strategy and significantly greater than those on the control, June 25%, and June 50% treatments of the 6.0 m SL and 4.5 m SL management strategies (table 6).

The forage tillers are comprised of reproductive lead tillers, vegetative lead tillers, and secondary tillers. The density and percent composition of each tiller type changed between the first grazing period and the second grazing period.

The preflower reproductive lead tillers that are between the 4 leaf stage and the flower stage have greater densities during the first grazing period than during the second grazing period and the forage tillers have greater percent composition of preflower reproductive lead tillers during the first grazing period than during the second grazing period on all three treatments of each of the three management strategies (tables 7 and 8). The preflower reproductive lead tillers are forage tillers primarily from early June until mid July.

The tiller densities of vegetative lead tillers that are between the 4 leaf stage and the 10 leaf stage are dynamic during the growing season with only small differences in the mean forage tiller densities between the first and second grazing periods on all three treatments of each of the three management strategies. The number of leaves per forage tiller increased during the second grazing period. Most of the vegetative lead tillers that are forage tillers have 4 to 6 leaves during the first grazing period and have 5 to 9 leaves during the second grazing period on all three treatments of each of the three management strategies. The forage tillers have greater percent composition of vegetative lead tillers during the second grazing period than during the first grazing period on all three treatments of each of the three management strategies; except on the June 25% treatment of the 4.5 m SL management strategy, the forage tiller percent composition of vegetative lead tillers is slightly greater during the first grazing period than during the second grazing period (tables 7 and 8). The vegetative lead tillers are forage tillers primarily from early June until mid October.

The secondary tillers that are between the 4 leaf stage and the 8 leaf stage have greater densities during the second grazing period than during the first grazing period and the forage tillers have greater percent composition of secondary tillers during the second grazing period than during the first grazing period on all three treatments of each of the three management strategies (tables 7 and 8). The secondary tillers are forage tillers primarily from early July until mid October.

The forage tillers are comprised primarily of preflower reproductive lead tillers and vegetative lead tillers during the first grazing period and during the second grazing period, the forage tillers are comprised primarily of vegetative lead tillers and secondary tillers. The forage tiller densities are not different between the first and second grazing periods, except on the control treatment of the 4.5 m TOR management strategy, the forage tiller density was lower during the second grazing period than during the first grazing period. The total forage tiller densities were significantly greater on the June 25% treatment of the 4.5 m TOR management strategy than on the control and June 50% treatments of the 4.5 m TOR management strategy. The total forage tiller densities on the three treatments of the 4.5 m TOR management strategy were significantly greater than those on the three treatments of the 6.0 m SL and 4.5 m SL management strategies. The total forage tiller densities on the three treatments of the 6.0 m SL management strategy were significantly greater than those on the three treatments of the 4.5 m SL management strategy (tables 7 and 8).

The two partial defoliation treatments of the 6.0 m SL and the 4.5 m SL management strategies triggered the defoliation resistance mechanisms, however, the physiological, biological, and chemical processes did not occur or occurred at very low rates resulting in no improvement above the respective control treatments. The biogeochemical processes produced insignificant results because the rhizosphere volume was low and the quantity of available mineral nitrogen was below the threshold amount of 100 lbs/ac on both the 6.0 m SL and the 4.5 m SL management strategies. The tiller densities on the 4.5 m SL management strategy were lower than on the 6.0 m SL management strategy because the soil depth of the surface horizon was shallower on the 4.5 m SL management strategy.

The tiller densities on the three treatments of the 4.5 m TOR management strategy were greater than those on the three treatments of the 6.0 m SL and 4.5 m SL management strategies because the rhizosphere volume was greater and the quantity of available mineral nitrogen was above the threshold amount of 100 lbs/ac on the 4.5 m TOR management strategy. The results on the June 50% treatment were not different than those on the control treatment of the 4.5 m TOR management strategy, even though the defoliation treatment triggered the defoliation resistance mechanisms and the quantity of available mineral nitrogen was adequate, however, the quantity of fixed carbon energy was insufficient because 50% leaf material removal from grass tillers between the 3.5 new leaf stage and the flower stage leaves inadequate leaf area for the necessary photosynthetic activity.

The greatest number of tillers was produced and maintained on the June 25% treatment of the 4.5 m TOR management strategy. The quantity of available mineral nitrogen was above the threshold amount of 100 lbs/ac. Removal of 25% of the leaf material from grass tillers between the 3.5 new leaf stage and the flower stage also removed sufficient quantities of the growth-inhibiting hormone, auxin, permitting synthesis or utilization of the growth hormone, cytokinin, in the axillary buds, and activating the asexual process of vegetative production of tillers. The remaining 75% leaf material had sufficient leaf area to fix carbon energy at adequate quantities for growth and development of the tillers from the activated axillary buds.

**Discussion**

Tiller leaf stage development did not occur at the same rate for all tillers. Rate of leaf stage development was affected by tiller rank on an hierarchical continuum of dominance from most dominant to greatest subordinate and by the tillers' proportional access to essential elements. Grazing management strategy and partial defoliation treatments did not appear to directly affect tiller leaf stage development.

The dominant tillers had rapid or unimpeded leaf stage development. The reproductive lead tillers were nearly-independent carry over tillers that developed flower stalks and had the fastest rate of leaf development; after the flower stage, no additional leaves were produced. The vegetative lead tillers were nearly-independent carry over tillers and early spring initiated tillers that did not develop flower stalks and had the second fastest rate of leaf development; from mid July until the end of the growing season, leaf development continued at slower rates.

Subordinate tillers had slow or inhibited leaf stage development. Secondary tillers were totally dependent on lead tillers for access to carbohydrates and mineral nitrogen during early leaf stages through the 3 leaf stage and had the slowest rate of leaf development. After the reproductive lead tillers had completed the greatest amount of leaf development around mid July, several of the secondary tillers developed additional leaves at faster rates. With the development of leaves 4 and 5, secondary tillers seemed to transition toward greater independence.

The density of tillers and the number of tillers between the 4 leaf stage and the flower stage were greatly affected by the grazing management strategy because of the difference in the quantities of mineral nitrogen available in the grassland ecosystem. Soil of northern mixed grass prairie ecosystems generally contains about three to eight tons of organic nitrogen per acre. Conversion of organic nitrogen into inorganic (mineral) nitrogen requires active rhizosphere organisms. Rhizosphere organism biomass and activity are limited by access to simple carbon chains (Curl and Truelove 1986) because the microflora trophic levels lack chlorophyll and have low carbon (energy) content. Partial defoliation of grass plants at vegetative phenological growth stages between the 3.5 leaf stage and flower stage (Manske 2007) by large grazing herbivores causes greater quantities of exudates containing simple carbon compounds to be released from the grass plant through the roots into the rhizosphere (Hamilton and Frank 2001). With an increase of carbon compounds in the rhizosphere, the biomass and activity of the microorganisms increases (Anderson et al. 1981, Curl and Truelove 1986, Whipps 1990). The increase in rhizosphere organism biomass and activity results in greater quantities of organic nitrogen converted into inorganic nitrogen (Coleman et al. 1983, Klein et al. 1988, Burrows and Pfleger 2002, Rillig et al. 2002, Bird et al. 2002, Driver et al. 2005). Inorganic (mineral) nitrogen available in quantities of 100 lbs/ac or greater allows defoliated grass tillers full activation of the defoliation resistance mechanisms (Manske 2009). Full activation of the compensatory physiological processes within grass plants accelerates growth rates of replacement leaves and shoots and increases restoration of biological processes enabling rapid and complete recovery of defoliated tillers. Full activation of the asexual processes of vegetative reproduction of secondary tillers from axillary buds increases initiated tiller density during the grazing season (Manske 2007).

The tiller density and the number of tillers between the 4 leaf stage and the flower stage during the growing season were greatest on the 4.5 m TOR management strategy as a result of mineral nitrogen availability at quantities greater than 100 lbs/ac because the timing and severity of grass tiller defoliation was beneficial to rhizosphere organism activity. The tiller density and the number of tillers between the 4 leaf stage and the flower stage were intermediate on the 6.0 m SL management strategy as a result of mineral nitrogen availability at quantities less than 100 lbs/ac because the timing and severity of grass tiller defoliation was antagonistic to rhizosphere organism activity. The tiller density and the number of tillers between the 4 leaf stage and the flower stage were lowest on the 4.5 m SL management strategy as a result of mineral nitrogen availability at quantities less than 100 lbs/ac because the timing and severity of grass tiller defoliation was antagonistic to rhizosphere organism activity and because of the shallower surface soil horizon depth (Manske 2009).

Tillers on the June 25% treatment of the 4.5 m TOR management strategy produced: the greatest density of vegetative lead tillers; the greatest density of secondary tillers; the greatest density of total tillers; the lowest percent of the total tiller population comprised of reproductive lead tillers; the greatest number of vegetative lead tillers between the 4 leaf stage and the 10 leaf stage; the greatest number of secondary tillers between the 4 leaf stage and the 8 leaf stage; the greatest number of growing season initiated secondary tillers that developed into vegetative lead tillers; and the greatest number of total tillers between the 4 leaf stage and the flower stage during the grazing season.

Production of enormous number of healthy grass tillers requires all of the biogeochemical processes of the grassland ecosystem to be functioning at full activation. Full activation of the compensatory physiological processes within grass plants that enable rapid replacement of removed leaf material and full activation of the asexual processes of vegetative reproduction that produce secondary tillers from axillary buds require mineral nitrogen availability at 100 lbs/ac or greater (Manske 2009). Full activation of the processes associated with grass plant soil water use efficiency enables production of herbage per inch of precipitation to increase by about 102% requires mineral nitrogen availability at 100 lbs/ac or greater (Wight and Black 1979). Supplying ecosystem mineral nitrogen at 100 lbs/ac or greater requires the rhizosphere volume to be large and the biomass of microorganisms to actively mineralize large quantities of soil organic nitrogen. Full activation of the rhizosphere organisms can occur only when sufficient quantities of simple carbohydrates are exudated into the rhizosphere from grass tillers that have adequate remaining or replaced leaf area. The trigger that activates carbon exudation is partial defoliation by large grazing herbivores that removes around 25% of the aboveground foliage when reproductive lead tillers are at phenological growth stages between the 3.5 new leaf stage and the flower stage (early June to mid July). The 4.5 month twice-over rotation grazing system (4.5 m TOR) is the only known management strategy designed to meet the biological requirements of grassland plants and rhizosphere organisms, to facilitate operation of biogeochemical processes, to sustain healthy production on grassland ecosystems, and to provide nutritious forage for livestock and abundant habitat for grassland wildlife.

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Table 1. Precipitation in inches for growing-season months and the annual total precipitation for 2000-2001, DREC Ranch, Manning, North Dakota.

| | Apr | May | Jun | Jul | Aug | Sep | Oct | Growing Season | Annual Total |
|---|---|---|---|---|---|---|---|---|---|
| Long-term mean | | | | | | | | | |
| 1982-2009 | 1.40 | 2.40 | 3.27 | 2.46 | 1.70 | 1.36 | 1.35 | 13.94 | 16.73 |
| 2000 | 1.26 | 1.90 | 3.77 | 2.77 | 2.74 | 1.09 | 1.46 | 14.99 | 20.23 |
| % of LTM | 90.00 | 79.17 | 115.29 | 112.60 | 161.18 | 80.15 | 108.15 | 107.53 | 120.92 |
| 2001 | 2.70 | 0.53 | 6.36 | 4.87 | 0.00 | 1.94 | 0.00 | 16.40 | 18.03 |
| % of LTM | 192.86 | 22.08 | 194.50 | 197.97 | 0.00 | 142.65 | 0.00 | 117.65 | 107.77 |
| 2000-2001 | 1.98 | 1.22 | 5.07 | 3.82 | 1.37 | 1.52 | 0.73 | 15.70 | 19.13 |
| % of LTM | 141.43 | 50.83 | 155.05 | 155.28 | 80.59 | 111.76 | 54.07 | 112.63 | 114.35 |

Table 2a. Mean leaf stage of reproductive lead tillers during biweekly periods.

| Tiller Type<br>Management Strategy<br>Treatment | Biweekly Periods<br>E May | M May | E Jun | M Jun | E Jul | M Jul | E Aug |
|---|---|---|---|---|---|---|---|
| Reproductive | | | | | | | |
| 6.0 m SL | | | | | | | |
| Control | 3.4 | 4.1 | 4.9 | 8.8 | 11.7 | 12.0 | 12.0 |
| June 25% | 3.3 | 4.1 | 4.7 | 7.7 | 10.4 | 11.3 | 11.3 |
| June 50% | 3.2 | 3.9 | 4.4 | 8.9 | 12.0 | 12.0 | 12.0 |
| 4.5 m SL | | | | | | | |
| Control | 2.9 | 3.7 | 4.2 | 10.2 | 10.2 | 12.0 | 12.0 |
| June 25% | 3.2 | 3.5 | 3.8 | 8.2 | 10.0 | 12.0 | 12.0 |
| June 50% | 2.7 | 3.2 | 4.2 | 7.8 | 10.8 | 10.8 | 12.0 |
| 4.5 m TOR | | | | | | | |
| Control | 3.2 | 3.8 | 4.6 | 5.8 | 9.0 | 10.8 | 11.7 |
| June 25% | 3.5 | 4.1 | 4.7 | 6.4 | 9.9 | 11.5 | 12.0 |
| June 50% | 3.5 | 4.3 | 4.7 | 8.1 | 10.6 | 11.8 | 11.8 |
| Mean Tiller | 3.2 | 3.9 | 4.5 | 8.0 | 10.5 | 11.6 | 11.9 |

Table 2b. Mean leaf stage of vegetative lead tillers during biweekly periods.

| Tiller Type<br>Management Strategy<br>Treatment | Biweekly Periods<br>E May | <br>M May | <br>E Jun | <br>M Jun | <br>E Jul | <br>M Jul | <br>E Aug |
|---|---|---|---|---|---|---|---|
| Vegetative | | | | | | | |
| 6.0 m SL | | | | | | | |
| Control | 3.2 | 3.7 | 4.5 | 5.3 | 6.4 | 6.9 | 7.4 |
| June 25% | 2.9 | 3.6 | 4.1 | 4.8 | 5.6 | 6.0 | 6.7 |
| June 50% | 3.1 | 3.5 | 4.1 | 4.8 | 5.8 | 6.3 | 6.7 |
| 4.5 m SL | | | | | | | |
| Control | 2.6 | 3.3 | 3.8 | 4.1 | 4.9 | 5.2 | 5.9 |
| June 25% | 3.3 | 3.7 | 3.9 | 4.6 | 5.4 | 5.9 | 6.5 |
| June 50% | 2.9 | 3.0 | 3.0 | 4.1 | 5.0 | 5.5 | 5.9 |
| 4.5 m TOR | | | | | | | |
| Control | 2.8 | 3.3 | 3.9 | 4.6 | 5.2 | 5.6 | 6.1 |
| June 25% | 3.3 | 3.8 | 4.5 | 5.0 | 5.8 | 6.7 | 7.3 |
| June 50% | 2.9 | 3.4 | 4.2 | 4.7 | 5.4 | 6.0 | 6.6 |
| Mean Tiller | 3.0 | 3.5 | 4.0 | 4.7 | 5.5 | 6.0 | 6.6 |

Table 2c. Mean leaf stage of secondary tillers during biweekly periods.

| Tiller Type<br>Management Strategy<br>Treatment | Biweekly Periods<br>E May | <br>M May | <br>E Jun | <br>M Jun | <br>E Jul | <br>M Jul | <br>E Aug |
|---|---|---|---|---|---|---|---|
| Secondary | | | | | | | |
| 6.0 m SL | | | | | | | |
| Control | 2.2 | 2.5 | 2.8 | 2.9 | 3.3 | 3.3 | 3.9 |
| June 25% | 2.7 | 3.0 | 2.9 | 3.3 | 3.3 | 3.3 | 3.3 |
| June 50% | 2.2 | 2.2 | 2.4 | 2.4 | 2.7 | 2.6 | 2.4 |
| 4.5 m SL | | | | | | | |
| Control | 1.8 | 2.2 | 2.6 | 2.7 | 2.8 | 2.8 | 3.2 |
| June 25% | 2.1 | 2.3 | 2.6 | 2.7 | 2.9 | 2.7 | 2.9 |
| June 50% | 1.8 | 2.1 | 2.3 | 2.5 | 3.1 | 3.7 | 3.5 |
| 4.5 m TOR | | | | | | | |
| Control | 2.7 | 3.1 | 2.8 | 3.1 | 3.4 | 3.5 | 3.8 |
| June 25% | 2.0 | 2.3 | 2.5 | 2.6 | 3.4 | 3.4 | 3.5 |
| June 50% | 2.6 | 3.0 | 3.1 | 3.6 | 3.7 | 4.1 | 4.1 |
| Mean Tiller | 2.2 | 2.5 | 2.7 | 2.9 | 3.2 | 3.3 | 3.4 |

Table 3. Number of forage tillers per square meter between the 4 leaf stage and flower stage on three defoliation treatments of the 6.0 month seasonlong management strategy.

| Treatment<br>Tiller Type | E May | M May | E Jun | M Jun | E Jul | M Jul | E Aug | L Aug | M Oct |
|---|---|---|---|---|---|---|---|---|---|
| 6.0 m SL | | | | | | | | | |
| Control | | | | | | | | | |
| Reproductive | 78.3 | 172.3 | 188.0 | 94.0 | 15.6 | 0.0 | 0.0 | 0.0 | 0.0 |
| Vegetative | 47.0 | 172.3 | 235.0 | 235.0 | 219.3 | 219.3 | 203.6 | 188.0 | 172.3 |
| Secondary | 0.0 | 0.0 | 47.0 | 78.3 | 125.3 | 109.6 | 109.6 | 141.0 | 141.0 |
| Total | 125.3 | 344.6 | 469.9 | 407.2 | 360.3 | 328.9 | 313.3 | 328.9 | 313.3 |
| June 25% | | | | | | | | | |
| Reproductive | 78.3 | 109.6 | 125.3 | 94.0 | 47.0 | 15.6 | 15.6 | 0.0 | 0.0 |
| Vegetative | 47.0 | 94.0 | 188.0 | 250.6 | 250.6 | 250.6 | 235.0 | 235.0 | 203.6 |
| Secondary | 31.3 | 31.3 | 31.3 | 62.7 | 62.7 | 78.3 | 78.3 | 62.7 | 94.0 |
| Total | 156.6 | 235.0 | 344.6 | 407.2 | 360.3 | 344.6 | 328.9 | 297.7 | 297.7 |
| June 50% | | | | | | | | | |
| Reproductive | 47.0 | 109.6 | 94.0 | 62.7 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| Vegetative | 47.0 | 188.0 | 250.6 | 313.3 | 297.6 | 297.6 | 297.6 | 297.6 | 297.6 |
| Secondary | 15.6 | 31.3 | 31.3 | 31.3 | 47.0 | 31.3 | 15.6 | 31.3 | 78.3 |
| Total | 109.6 | 328.9 | 375.9 | 407.2 | 344.6 | 328.9 | 313.3 | 328.9 | 375.9 |

Table 4. Number of forage tillers per square meter between the 4 leaf stage and flower stage on three defoliation treatments of the 4.5 month seasonlong management strategy.

| Treatment<br>Tiller Type | E May | M May | E Jun | M Jun | E Jul | M Jul | E Aug | L Aug | M Oct |
|---|---|---|---|---|---|---|---|---|---|
| 4.5 m SL | | | | | | | | | |
| Control | | | | | | | | | |
| Reproductive | 15.6 | 31.3 | 47.0 | 15.6 | 15.6 | 0.0 | 0.0 | 0.0 | 0.0 |
| Vegetative | 15.6 | 47.0 | 78.3 | 109.6 | 156.6 | 156.6 | 156.6 | 156.6 | 156.6 |
| Secondary | 0.0 | 0.0 | 0.0 | 15.6 | 15.6 | 31.3 | 15.6 | 47.0 | 78.3 |
| Total | 31.3 | 78.3 | 125.3 | 141.0 | 188.0 | 188.0 | 172.3 | 203.6 | 235.0 |
| June 25% | | | | | | | | | |
| Reproductive | 15.6 | 47.0 | 62.7 | 47.0 | 31.3 | 0.0 | 0.0 | 0.0 | 0.0 |
| Vegetative | 47.0 | 94.0 | 141.0 | 156.6 | 156.6 | 156.6 | 156.6 | 125.3 | 125.3 |
| Secondary | 0.0 | 0.0 | 0.0 | 0.0 | 31.3 | 31.3 | 31.3 | 109.6 | 94.0 |
| Total | 62.7 | 141.0 | 203.6 | 203.6 | 219.3 | 188.0 | 188.0 | 234.9 | 219.3 |
| June 50% | | | | | | | | | |
| Reproductive | 0.0 | 15.6 | 78.3 | 47.0 | 15.6 | 15.6 | 0.0 | 0.0 | 0.0 |
| Vegetative | 15.6 | 15.6 | 47.0 | 141.0 | 172.3 | 172.3 | 172.3 | 156.6 | 141.0 |
| Secondary | 0.0 | 0.0 | 0.0 | 15.6 | 47.0 | 47.0 | 47.0 | 47.0 | 15.6 |
| Total | 15.6 | 31.3 | 125.3 | 203.6 | 235.0 | 235.0 | 219.3 | 203.6 | 156.6 |

Table 5. Number of forage tillers per square meter between the 4 leaf stage and flower stage on three defoliation treatments of the 4.5 month twice-over rotation management strategy.

| Treatment<br>Tiller Type | E May | M May | E Jun | M Jun | E Jul | M Jul | E Aug | L Aug | M Oct |
|---|---|---|---|---|---|---|---|---|---|
| 4.5 m TOR | | | | | | | | | |
| Control | | | | | | | | | |
| Reproductive | 125.3 | 203.6 | 281.9 | 281.9 | 156.6 | 47.0 | 31.3 | 0.0 | 0.0 |
| Vegetative | 47.0 | 78.3 | 188.0 | 250.6 | 266.3 | 266.3 | 235.0 | 235.0 | 235.0 |
| Secondary | 31.3 | 141.0 | 78.3 | 62.7 | 109.6 | 141.0 | 172.3 | 125.3 | 156.6 |
| Total | 203.6 | 422.9 | 548.2 | 595.2 | 532.5 | 454.2 | 438.6 | 360.3 | 391.6 |
| June 25% | | | | | | | | | |
| Reproductive | 78.3 | 141.0 | 172.3 | 141.0 | 62.7 | 15.6 | 0.0 | 0.0 | 0.0 |
| Vegetative | 188.0 | 375.9 | 532.5 | 579.5 | 516.9 | 516.9 | 516.9 | 485.6 | 485.6 |
| Secondary | 15.6 | 0.0 | 15.6 | 47.0 | 203.6 | 156.6 | 141.0 | 141.0 | 203.6 |
| Total | 281.9 | 516.9 | 720.5 | 767.5 | 783.2 | 689.2 | 657.8 | 626.6 | 689.2 |
| June 50% | | | | | | | | | |
| Reproductive | 109.6 | 188.0 | 219.3 | 156.6 | 62.7 | 15.6 | 15.6 | 0.0 | 0.0 |
| Vegetative | 62.7 | 203.6 | 328.9 | 407.2 | 391.6 | 391.6 | 391.6 | 391.6 | 328.9 |
| Secondary | 15.6 | 0.0 | 15.6 | 78.3 | 125.3 | 94.0 | 109.6 | 109.6 | 78.3 |
| Total | 188.0 | 391.6 | 563.9 | 642.2 | 579.5 | 501.2 | 516.9 | 501.2 | 407.2 |

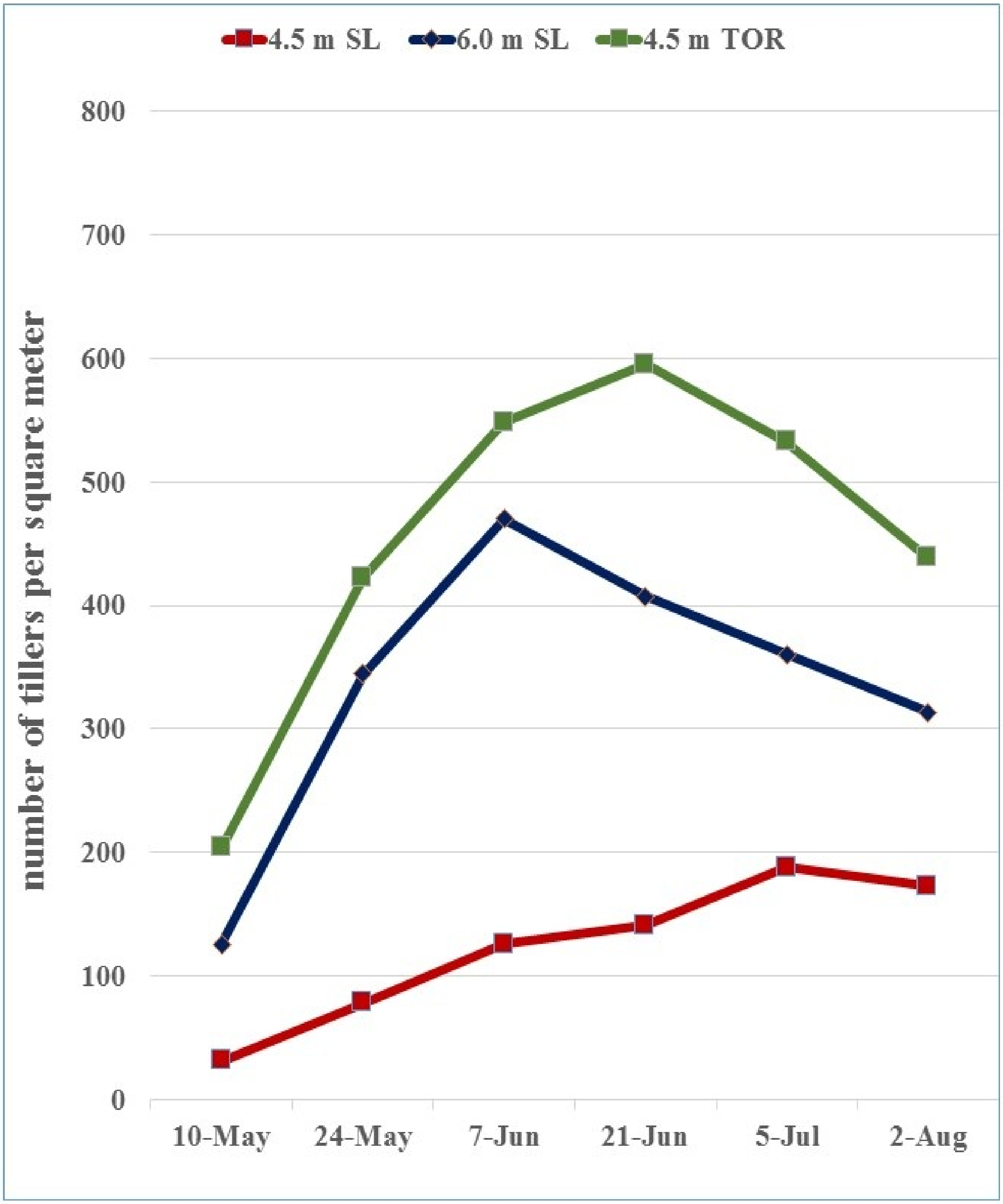


**Figure 1. Number of total tillers per square meter between the 4 leaf stage and flower stage on the control treatments of three management strategies.**

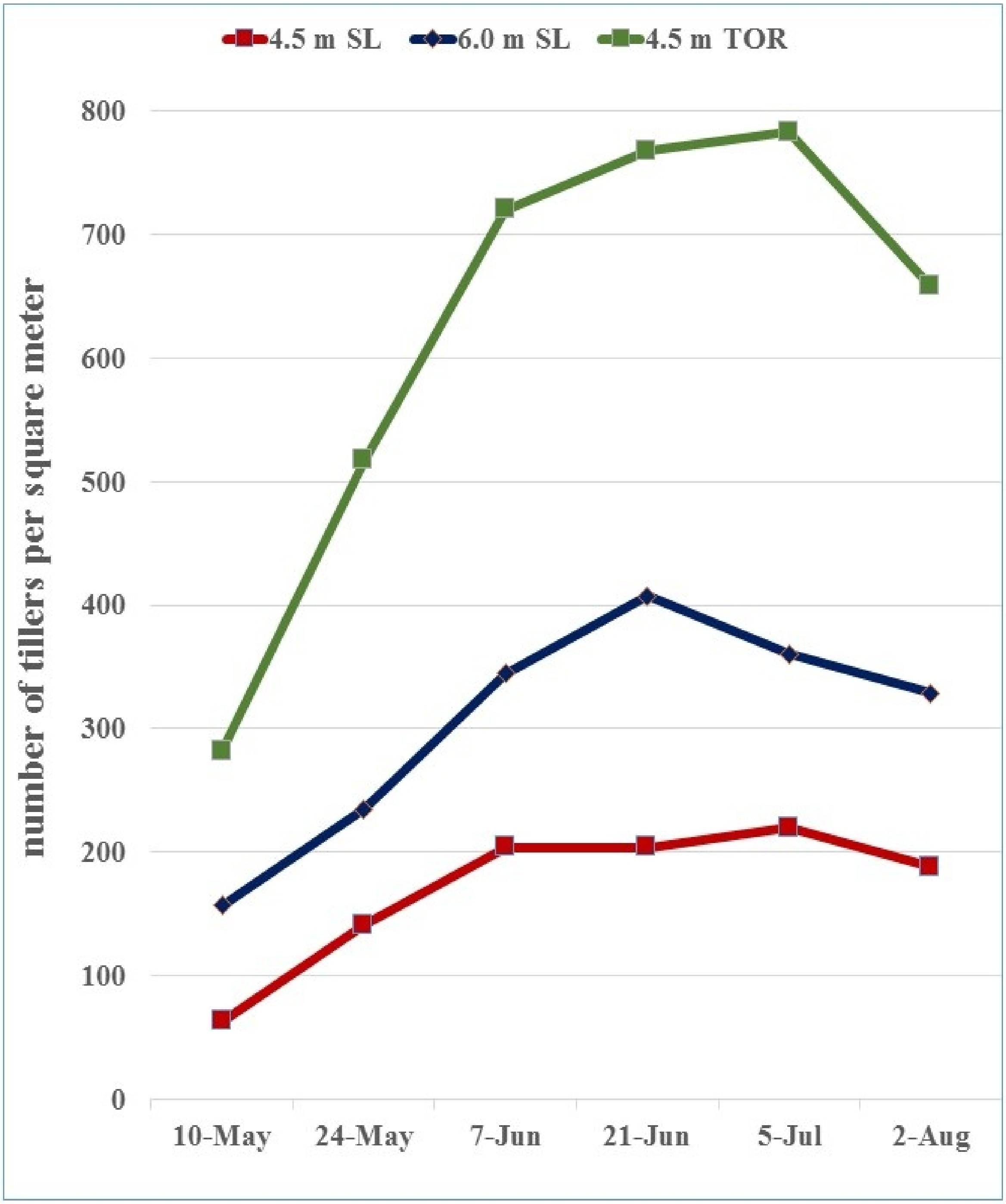


**Figure 2. Number of total tillers per square meter between the 4 leaf stage and flower stage on the June 25% defoliation treatments of three management strategies.**

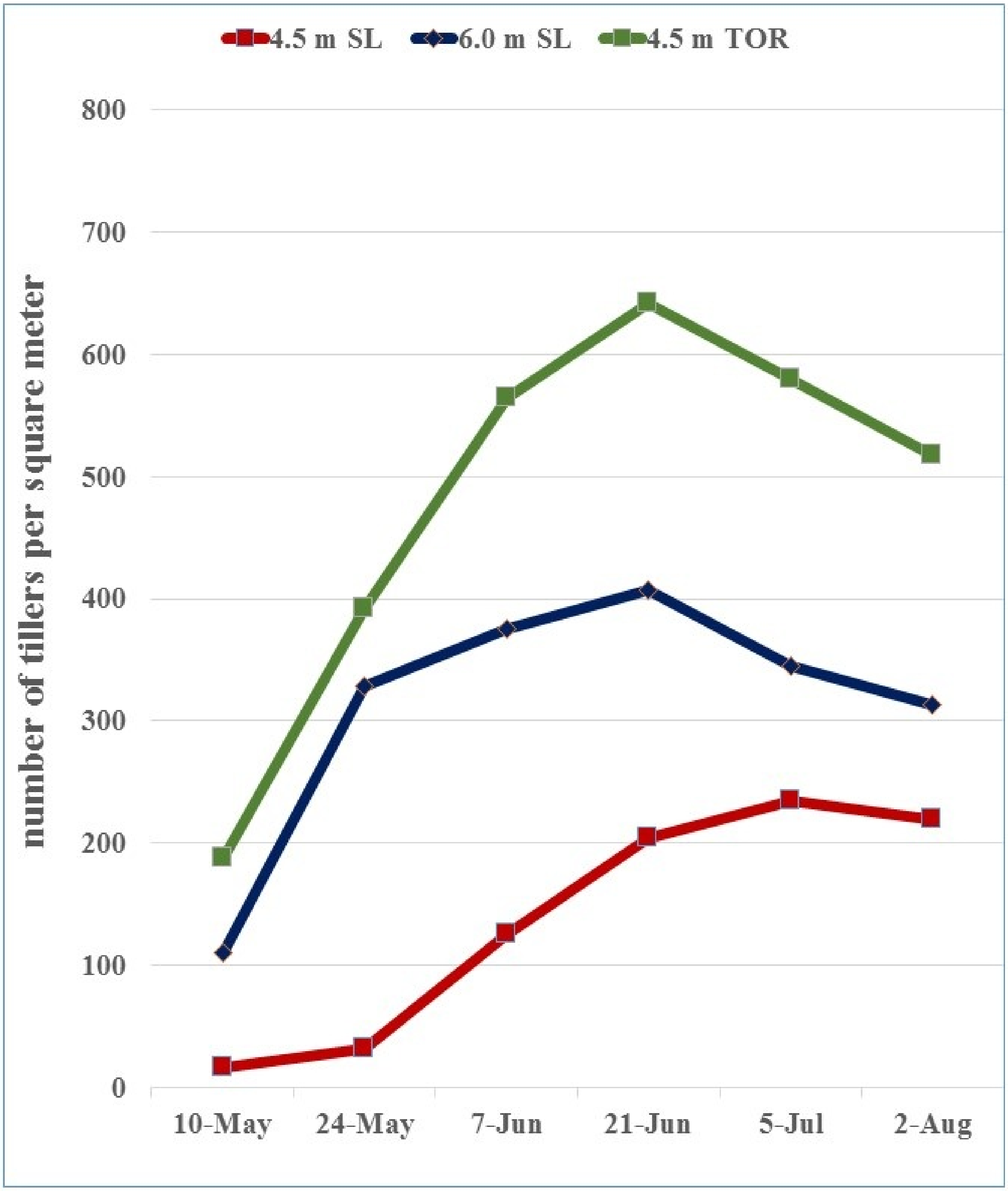


**Figure 3. Number of total tillers per square meter between the 4 leaf stage and flower stage on the June 50% defoliation treatments of three management strategies.**

Table 6. Mean tiller density per square meter of total forage tillers between the 4 leaf stage and the flower stage during the first and second grazing periods and the entire grazing season.

| Management Strategy Treatment | First Grazing Period Early June to Mid July | Second Grazing Period Mid July to Mid October | Grazing Season Early June to Mid October |
|---|---|---|---|
| 6.0 m SL | | | |
| Control | 391.6cde | 321.1e | 360.3xy |
| June 25% | 364.2de | 317.2e | 340.1y |
| June 50% | 364.2de | 336.8e | 353.5y |
| 4.5 m SL | | | |
| Control | 160.6f | 199.7f | 179.0z |
| June 25% | 203.6f | 207.6f | 208.1z |
| June 50% | 199.7f | 203.6f | 196.9z |
| 4.5 m TOR | | | |
| Control | 532.5b | 411.2cd | 474.4wx |
| June 25% | 740.4a | 665.7a | 704.8v |
| June 50% | 571.7b | 481.6bc | 530.3w |

Means followed by the same letter are not significantly different (P<0.05).

Table 7. Mean number of forage tillers per square meter between the 4 leaf stage and flower stage during the first and second grazing periods on three defoliation treatments of the three management strategies.

| Management strategy<br>Tiller Type | Control<br>Grazing Period | | June 25%<br>Grazing Period | | June 50%<br>Grazing Period | |
|---|---|---|---|---|---|---|
| | First | Second | First | Second | First | Second |
| 6.0 m SL | | | | | | |
| Reproductive | 74.4 | 0.0 | 70.5 | 7.8 | 39.2 | 0.0 |
| Vegetative | 227.2 | 195.8 | 235.0 | 231.1 | 289.8 | 297.6 |
| Secondary | 90.0 | 125.3 | 58.8 | 78.3 | 35.2 | 39.1 |
| Total | 391.6cd | 321.1d | 364.2d | 317.2d | 364.2d | 336.8d |
| 4.5 m SL | | | | | | |
| Reproductive | 19.6 | 0.0 | 35.3 | 0.0 | 39.1 | 3.9 |
| Vegetative | 125.3 | 156.6 | 152.7 | 141.0 | 133.2 | 160.6 |
| Secondary | 15.6 | 43.1 | 15.6 | 66.6 | 27.4 | 39.2 |
| Total | 160.6e | 199.7e | 203.6e | 207.6e | 199.7e | 203.6e |
| 4.5 m TOR | | | | | | |
| Reproductive | 191.9 | 19.6 | 97.9 | 3.9 | 113.6 | 7.8 |
| Vegetative | 242.8 | 242.8 | 536.5 | 501.3 | 379.8 | 375.9 |
| Secondary | 97.9 | 148.8 | 105.7 | 160.6 | 78.3 | 97.9 |
| Total | 532.5b | 411.2c | 740.1a | 665.7a | 571.7b | 481.6bc |

Means followed by the same letter are not significantly different ($P<0.05$).

Table 8. Percent tiller type composition of the total forage tillers between the 4 leaf stage and flower stage during the first and second grazing periods on three defoliation treatments of the three management strategies.

| Management strategy Tiller Type | | Control Grazing Period | | June 25% Grazing Period | | June 50% Grazing Period | |
|---|---|---|---|---|---|---|---|
| | | First | Second | First | Second | First | Second |
| 6.0 m SL | | | | | | | |
| Reproductive | % | 19.0 | 0.0 | 19.4 | 2.5 | 10.8 | 0.0 |
| Vegetative | % | 58.0 | 61.0 | 64.5 | 72.9 | 79.6 | 88.4 |
| Secondary | % | 23.0 | 39.0 | 16.1 | 24.7 | 9.7 | 11.6 |
| Total | #/m$^2$ | 391.6cd | 321.1d | 364.2d | 317.2d | 364.2d | 336.8d |
| 4.5 m SL | | | | | | | |
| Reproductive | % | 12.2 | 0.0 | 17.3 | 0.0 | 19.6 | 1.9 |
| Vegetative | % | 78.0 | 78.4 | 75.0 | 67.9 | 66.7 | 78.9 |
| Secondary | % | 9.7 | 21.6 | 7.7 | 32.1 | 13.7 | 19.2 |
| Total | #/m$^2$ | 160.6e | 199.7e | 203.6e | 207.6e | 199.7e | 203.6e |
| 4.5 m TOR | | | | | | | |
| Reproductive | % | 36.0 | 4.8 | 13.2 | 0.6 | 19.9 | 1.6 |
| Vegetative | % | 45.6 | 59.0 | 72.5 | 75.3 | 66.4 | 78.1 |
| Secondary | % | 18.4 | 36.2 | 14.3 | 24.1 | 13.7 | 20.3 |
| Total | #/m$^2$ | 532.5b | 411.2c | 740.1a | 665.7a | 571.7b | 481.6bc |

Means followed by the same letter are not significantly different (P<0.05).

## Literature Cited


**Anderson, R.V., D.C. Coleman, C.V. Cole, and E.T. Elliott. 1981.** Effect of nematodes *Acrobeloides sp.* and *Mesodiplogaster lheritieri* on substrate utilization and nitrogen and phosphorus mineralization. Ecology 62:549-555.

**Barker, W.T., and W.C. Whitman. 1988.** Vegetation of the Northern Great Plains. Rangelands 10:266-272.

**Bird, S.B., J.E. Herrick, M.M. Wander, and S.F. Wright. 2002.** Spatial heterogeneity of aggregate stability and soil carbon in semi-arid rangeland. Environmental Pollution 116:445-455.

**Burrows, R.L., and F.L. Pfleger. 2002.** Arbuscular mycorrhizal fungi respond to increasing plant diversity. Canadian Journal of Botany 80:120-130.

**Campbell, J.B. 1952.** Farming range pastures. Journal of Range Management 5:252-258.

**Coleman, D.C., C.P.P. Reid, and C.V. Cole. 1983.** Biological strategies of nutrient cycling in soil ecosystems. Advances in Ecological Research 13:1-55.

**Coyne, P.I., M.J. Trlica, and C.E. Owensby. 1995.** Carbon and nitrogen dynamics in range plants. p. 59-167. *in* D.J. Bedunah and R.E. Sosebee (eds.). Wildland plants: physiological ecology and developmental morphology. Society for Range Management, Denver, CO.

**Curl, E.A., and B. Truelove. 1986.** The rhizosphere. Springer-Verlag, New York, NY.

**Driver, J.D., W.E. Holben, and M.C. Rillig. 2005.** Characterization of glomalin as a hyphal wall component of arbuscular mycorrhizal fungi. Soil Biology and Biochemistry 37:101-106.

**Frank, A.B., J.D. Berdahl, and J.F. Karn. 1997.** Phyllochron development in cool-season grasses. XVIII International Grassland Congress Poster.

**Frank, A.B. 1996.** Evaluating grass development for grazing management. Rangelands 18:106-109.

**Goetz, H. 1963.** Growth and development of native range plants in the mixed prairie of western North Dakota. M. S. Thesis, North Dakota State University, Fargo, ND. 165p.

**Hamilton, E.W., and D.A. Frank. 2001.** Can plants stimulate soil microbes and their own nutrient supply? Evidence from a grazing tolerant grass. Ecology 82:2397-2402.

**Klein, D.A., B.A. Frederick, M. Biondini, and M.J. Trlica. 1988.** Rhizosphere microorganism effects on soluble amino acids, sugars, and organic acids in the root zone of *Agropyron cristatum, A. smithii,* and *Bouteloua gracilis*. Plant and Soil 110:19-25.

**Manske, L.L. 2000.** Grazing before grass is ready. NDSU Dickinson Research Extension Center. Range Management Report DREC 00-1032. Dickinson, ND. 6p.

**Manske, L.L. 2007.** Biology of defoliation by grazing. NDSU Dickinson Research Extension Center. Range Management Report DREC 07-1067. Dickinson, ND. 25p.

**Manske, L.L. 2008a.** Annual nutritional quality curves for graminoids in the Northern Plains. NDSU Dickinson Research Extension Center. Summary Range Management Report DREC 08-3014c. Dickinson, ND. 15p.

**Manske, L.L. 2008b.** Cow and calf performance as affected by grazing management. NDSU Dickinson Research Extension Center. Range Research Report DREC 08-1052b. Dickinson, ND. 28p.

**Manske, L.L. 2009.** Grass plant responses to defoliation. NDSU Dickinson Research Extension Center. Range Research Report DREC 09-1074. Dickinson, ND. 47p.

**Manske, L.L. 2010.** Ombrothermic interpretation of range plant water deficiency from temperature and precipitation data collected at the Ranch Headquarters of the Dickinson Research Extension Center in western North Dakota, 1982-2009. NDSU Dickinson Research Extension Center. Range Research Report DREC 10-1019m. Dickinson, ND. 17p.

**Mosteller, F., and R.E.K. Rourke. 1973.** Sturdy statistics. Addison-Wesley Publishing Co., MA. 395p.

**National Research Council. 1996.** Nutrient requirements of beef cattle. 7th rev. ed. National Academy Press, Washington, DC.

**Rillig, M.C., S.F. Wright, and V.T. Eviner. 2002.** The role of arbuscular mycorrhizal fungi and glomalin in soil aggregation: comparing effects of five plant species. Plant and Soil 238:325-333.

**Rogler, G.A., R.J. Lorenz, and H.M. Schaaf. 1962.** Progress with grass. North Dakota Agricultural Experiment Station. Bulletin 439. 15p.

**Shiflet, T.N. (ed.). 1994.** Rangeland cover types. Society for Range Management. Denver, CO. 152p.

**Whipps, J.M. 1990.** Carbon economy. p. 59-97. *in* J.M. Lynch (ed.). The rhizosphere. John Wiley and Sons, New York, NY.

**Whitman, W.C., D.W. Bolin, E.W. Klosterman, H.J. Klostermann, K.D. Ford, L. Moomaw, D.G. Hoag, and M.L. Buchanan. 1951.** Carotene, protein, and phosphorus in range and tame grasses of western North Dakota. North Dakota Agricultural Experiment Station. Bulletin 370. Fargo, ND. 55p.

**Wight, J.R., and A.L. Black. 1979.** Range fertilization: plant response and water use. Journal of Range Management 32:345-349.