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.

Acknowledgment

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

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 Management Strategy Treatment	Biweekly Periods 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 Management Strategy Treatment	Biweekly Periods E May	 M May	 E Jun	 M Jun	 E Jul	 M Jul	 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 Management Strategy Treatment	Biweekly Periods E May	M May	E Jun	M Jun	E Jul	M Jul	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 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 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 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

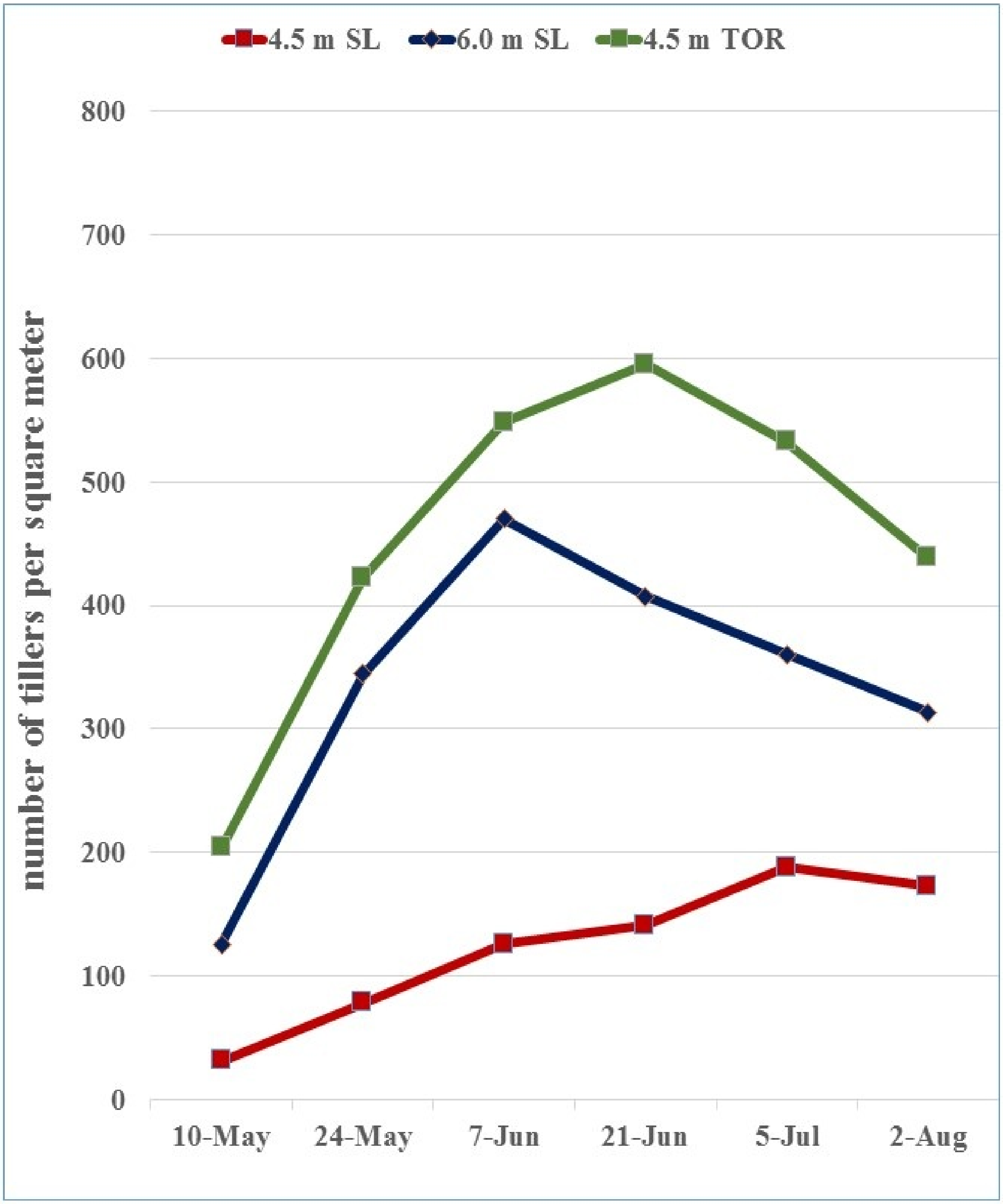

Figure 1. Number of total tillers per square meter between the 4 leaf stage and flower stage on the control treatments of three management strategies.

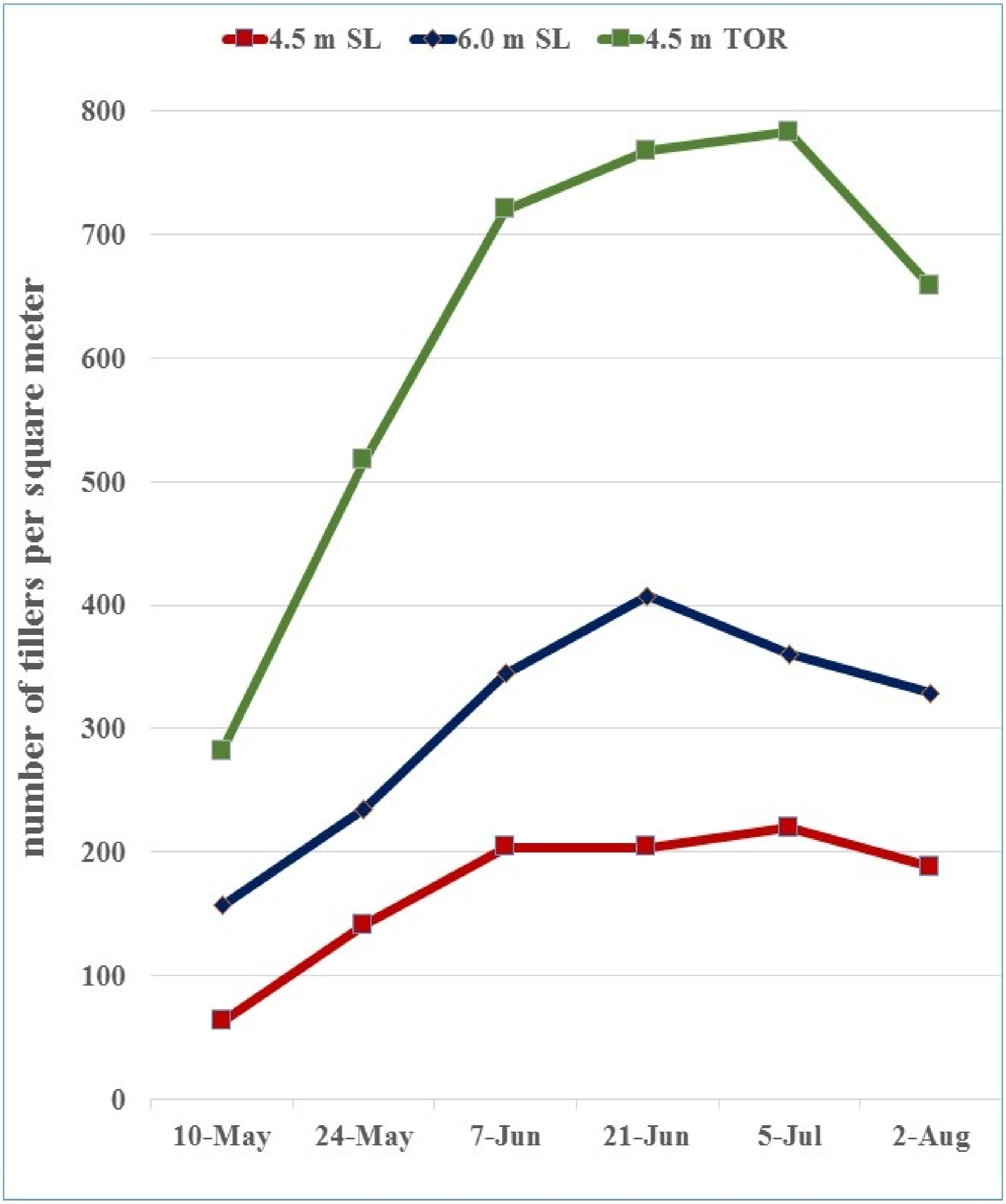

Figure 2. Number of total tillers per square meter between the 4 leaf stage and flower stage on the June 25% defoliation treatments of three management strategies.

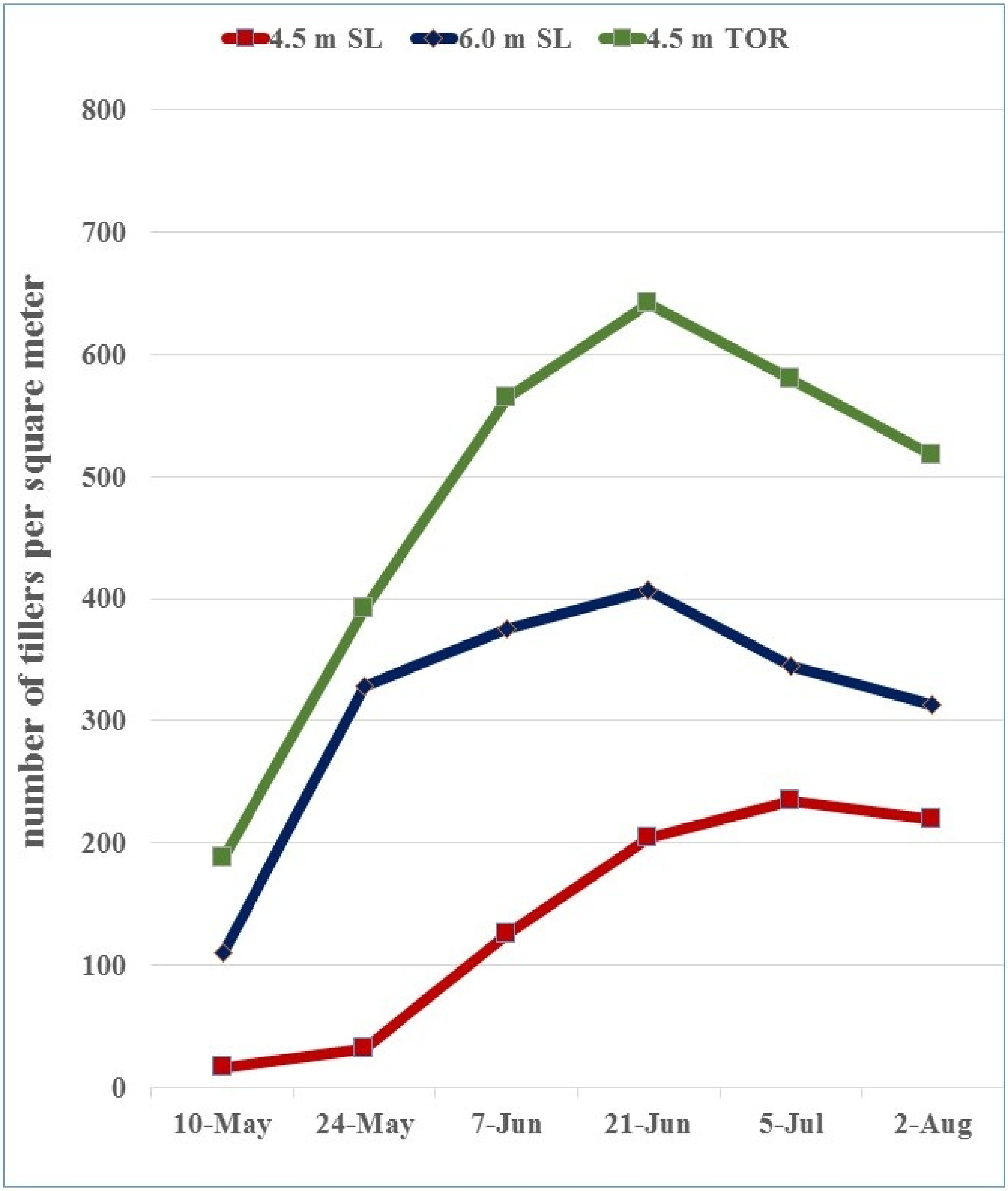

Figure 3. Number of total tillers per square meter between the 4 leaf stage and flower stage on the June 50% defoliation treatments of three management strategies.

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 Tiller Type	Control Grazing Period		June 25% Grazing Period		June 50% 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.