

## Leaf Stage Development of Western Wheatgrass Tillers

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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).

This project was conducted to quantitatively describe the leaf stage development of western wheatgrass tillers during the early portion of the growing season (May, June, and July) and to determine the number of tillers between the three and a half new leaf stage and the flowering (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 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.

The volume of the rhizospheres on the 6.0 m SL and 4.5 m SL management strategies were low at 1142.2 cm<sup>3</sup>/m<sup>3</sup> and 1552.3 cm<sup>3</sup>/m<sup>3</sup>, 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<sup>3</sup>/m<sup>3</sup> (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).

## 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 phenological growth stage and number of leaves produced data 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 time line for phenological development of reproductive lead tillers, vegetative lead tillers, and secondary tillers during May, June, and July. A standard paired-plot t-test was used to analyze differences among means (Mosteller and Rourke 1973).

## Results

The three tiller types 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 Stage Phenology

During early May on the control treatment of the 6.0 m SL management strategy (table 2), 42% of the reproductive lead tillers were at the 4 leaf stage and 58% were at the 3 leaf stage; 20% of the vegetative lead tillers were at the 4 leaf stage and 80% were at the 3 leaf stage; and 46% of the secondary tillers were at the 3 leaf stage and 54% were at the 1 or 2 leaf stage. During mid May, 17% of the reproductive lead tillers were at the 5 leaf stage, 75% were at the 4 leaf stage, and 8% were at the 3 leaf stage; 73% of the vegetative lead tillers were at the 4 leaf stage and 27% were at the 3 leaf stage; and 69% of the secondary tillers were at the 3 leaf stage and 31% were at the 1 or 2 leaf stage. During early June, 17% of the reproductive lead tillers were at the 6 leaf stage, 58% were at the 5 leaf stage, and 25% were at the 4 leaf stage; 53% of the vegetative lead tillers were at the 5 leaf stage and 47% were at the 4 leaf stage; and 23% of the secondary tillers were at the 4 leaf stage, 46% were at the 3 leaf stage, and 31% were at the 1 or 2 leaf stage. During mid June, 50% of the reproductive lead tillers were at flower stages, 25% were at the 6 leaf stage, and 25% were at the 5 leaf stage; 40% of the vegetative lead tillers were at the 6 leaf stage, 53% were at the 5 leaf stage, and 7% were at the 4 leaf stage; and 38% of the secondary tillers were at the 4 leaf stage, 31% were at the 3 leaf stage, and 31% were at the 1 or 2 leaf stage. During early July, 92% of the reproductive lead tillers were at flower stages and 8% were at the 8 leaf stage; 43% of the vegetative lead tillers were at the 7 leaf stage and 57% were at the 6 leaf stage; and 20% of the secondary tillers were at the 5 leaf stage, 33% were at

the 4 leaf stage, 20% were at the 3 leaf stage, and 27% were at the 1 or 2 leaf stage. During mid July, 100% of the reproductive lead tillers were at flower stages; 21% of the vegetative lead tillers were at the 8 leaf stage, 50% were at the 7 leaf stage, and 29% were at the 6 leaf stage; and 14% of the secondary tillers were at the 6 leaf stage, 7% were at the 5 leaf stage, 29% were at the 4 leaf stage, 14% were at the 3 leaf stage, and 36% were at the 1 or 2 leaf stage. During early August, 8% of the vegetative lead tillers were at the 9 leaf stage, 46% were at the 8 leaf stage, 23% were at the 7 leaf stage, and 23% were at the 6 leaf stage; and 27% of the secondary tillers were at the 6 leaf stage, 9% were at the 5 leaf stage, 27% were at the 4 leaf stage, 9% were at the 3 leaf stage, and 27% were at the 1 or 2 leaf stage.

During early May on the June 25% treatment of the 6.0 m SL management strategy (table 3), 11% of the reproductive lead tillers were at the 5 leaf stage, 44% were at the 4 leaf stage, 22% were at the 3 leaf stage, and 22% were at the 1 or 2 leaf stage; 18% of the vegetative lead tillers were at the 4 leaf stage, 65% were at the 3 leaf stage, and 18% were at the 1 or 2 leaf stage; and 20% of the secondary tillers were at the 5 leaf stage, 20% were at the 4 leaf stage, and 60% were at the 1 or 2 leaf stage. During mid May, 11% of the reproductive lead tillers were at the 6 leaf stage, 11% were at the 5 leaf stage, 56% were at the 4 leaf stage, and 22% were at the 3 leaf stage; 6% of the vegetative lead tillers were at the 7 leaf stage, 6% were at the 5 leaf stage, 23% were at the 4 leaf stage, and 65% were at the 3 leaf stage; and 17% of the secondary tillers were at the 5 leaf stage, 17% were at the 4 leaf stage, 33% were at the 3 leaf stage, and 33% were at the 1 or 2 leaf stage. During early June, 11% of the reproductive lead tillers were at the 7 leaf stage, 45% were at the 5 leaf stage, 33% were at the 4 leaf stage, and 11% were at the 3 leaf stage; 6% of the vegetative lead tillers were at the 7 leaf stage, 6% were at the 6 leaf stage, 6% were at the 5 leaf stage, 56% were at the 4 leaf stage, and 25% were at the 3 leaf stage; and 25% of the secondary tillers were at the 5 leaf stage, 38% were at the 3 leaf stage, and 38% were at the 1 or 2 leaf stage. During mid June, 33% of the reproductive lead tillers were at flower stages, 11% were at the 8 leaf stage, 11% were at the 6 leaf stage, 33% were at the 5 leaf stage, and 11% were at the 4 leaf stage; 6% of the vegetative lead tillers were at the 7 leaf stage, 12% were at the 6 leaf stage, 31% were at the 5 leaf stage, and 50% were at the 4 leaf stage; and 22% of the secondary tillers were at the 5 leaf stage, 22% were at the 4 leaf stage, 33% were at the 3 leaf stage, and 22% were at the 1 or 2 leaf stage. During early July, 67% of the

reproductive lead tillers were at flower stages, 11% were at the 9 leaf stage, 11% were at the 7 leaf stage, and 11% were at the 6 leaf stage; 12% of the vegetative lead tillers were at the 7 leaf stage, 50% were at the 6 leaf stage, 25% were at the 5 leaf stage, and 13% were at the 4 leaf stage; and 22% of the secondary tillers were at the 5 leaf stage, 22% were at the 4 leaf stage, 33% were at the 3 leaf stage, and 22% were at the 1 or 2 leaf stage. During mid July, 89% of the reproductive lead tillers were at flower stages and 11% were at the 6 leaf stage; 19% of the vegetative lead tillers were at the 7 leaf stage, 62% were at the 6 leaf stage, and 19% were at the 5 leaf stage; and 11% of the secondary tillers were at the 5 leaf stage, 44% were at the 4 leaf stage, 22% were at the 3 leaf stage, and 22% were at the 1 or 2 leaf stage. During early August, 89% of the reproductive lead tillers were at flower stages and 11% were at the 6 leaf stage; 13% of the vegetative lead tillers were at the 8 leaf stage, 40% were at the 7 leaf stage, and 47% were at the 6 leaf stage; and 9% of the secondary tillers were at the 5 leaf stage, 36% were at the 4 leaf stage, 36% were at the 3 leaf stage, and 18% were at the 1 or 2 leaf stage.

During early May on the June 50% treatment of the 6.0 m SL management strategy (table 4), 43% of the reproductive lead tillers were at the 4 leaf stage, 43% were at the 3 leaf stage, and 14% were at the 1 or 2 leaf stage; 15% of the vegetative lead tillers were at the 4 leaf stage, 80% were at the 3 leaf stage, and 5% were at the 1 or 2 leaf stage; and 17% of the secondary tillers were at the 4 leaf stage, 17% were at the 3 leaf stage, and 66% were at the 1 or 2 leaf stage. During mid May, 33% of the reproductive lead tillers were at the 5 leaf stage, 45% were at the 4 leaf stage, 11% were at the 3 leaf stage, and 11% were at the 1 or 2 leaf stage; 57% of the vegetative lead tillers were at the 4 leaf stage, 38% were at the 3 leaf stage, and 5% were at the 1 or 2 leaf stage; and 29% of the secondary tillers were at the 4 leaf stage and 71% were at the 1 or 2 leaf stage. During early June, 22% of the reproductive lead tillers were at flower stages, 11% were at the 6 leaf stage, 22% were at the 5 leaf stage, 33% were at the 4 leaf stage, and 11% were at the 3 leaf stage; 30% of the vegetative lead tillers were at the 5 leaf stage, 50% were at the 4 leaf stage, and 20% were at the 3 leaf stage; and 22% of the secondary tillers were at the 4 leaf stage, 22% were at the 3 leaf stage, and 56% were at the 1 or 2 leaf stage. During mid June, 56% of the reproductive lead tillers were at flower stages, 11% were at the 6 leaf stage, 22% were at the 5 leaf stage, and 11% were at the 4 leaf stage; 15% of the vegetative lead tillers were at the 6 leaf stage,

45% were at the 5 leaf stage, and 40% were at the 4 leaf stage; and 22% of the secondary tillers were at the 4 leaf stage, 22% were at the 3 leaf stage, and 56% were at the 1 or 2 leaf stage. During early July, 100% of the reproductive lead tillers were at flower stages; 21% of the vegetative lead tillers were at the 7 leaf stage, 42% were at the 6 leaf stage, 32% were at the 5 leaf stage, and 5% were at the 4 leaf stage; and 30% of the secondary tillers were at the 4 leaf stage, 30% were at the 3 leaf stage, and 40% were at the 1 or 2 leaf stage. During mid July, 11% of the vegetative lead tillers were at the 8 leaf stage, 32% were at the 7 leaf stage, 37% were at the 6 leaf stage, and 21% were at the 5 leaf stage; and 22% of the secondary tillers were at the 4 leaf stage, 33% were at the 3 leaf stage, and 44% were at the 1 or 2 leaf stage. During early August, 10% of the vegetative lead tillers were at the 9 leaf stage, 16% were at the 8 leaf stage, 32% were at the 7 leaf stage, 21% were at the 6 leaf stage, and 21% were at the 5 leaf stage; and 13% of the secondary tillers were at the 4 leaf stage, 37% were at the 3 leaf stage, and 50% were at the 1 or 2 leaf stage.

During early May on the control treatment of the 4.5 m SL management strategy (table 5), 25% of the reproductive lead tillers were at the 4 leaf stage, 50% were at the 3 leaf stage, and 25% were at the 1 or 2 leaf stage; 11% of the vegetative lead tillers were at the 4 leaf stage, 56% were at the 3 leaf stage, and 33% were at the 1 or 2 leaf stage; and 22% of the secondary tillers were at the 3 leaf stage, and 78% were at the 1 or 2 leaf stage. During mid May, 25% of the reproductive lead tillers were at the 5 leaf stage, 25% were at the 4 leaf stage, and 50% were at the 3 leaf stage; 33% of the vegetative lead tillers were at the 4 leaf stage and 67% were at the 3 leaf stage; and 44% of the secondary tillers were at the 3 leaf stage and 56% were at the 1 or 2 leaf stage. During early June, 25% of the reproductive lead tillers were at the 6 leaf stage, 50% were at the 4 leaf stage, and 25% were at the 3 leaf stage; 22% of the vegetative lead tillers were at the 5 leaf stage, 33% were at the 4 leaf stage, and 44% were at the 3 leaf stage; and 70% of the secondary tillers were at the 3 leaf stage and 30% were at the 1 or 2 leaf stage. During mid June, 75% of the reproductive lead tillers were at flower stages and 25% were at the 5 leaf stage; 33% of the vegetative lead tillers were at the 5 leaf stage, 44% were at the 4 leaf stage, and 22% were at the 3 leaf stage; and 10% of the secondary tillers were at the 4 leaf stage, 60% were at the 3 leaf stage, and 30% were at the 1 or 2 leaf stage. During early July, 75% of the reproductive lead tillers were at flower stages and 25% were at the 5 leaf stage;

20% of the vegetative lead tillers were at the 6 leaf stage, 50% were at the 5 leaf stage, and 30% were at the 4 leaf stage; and 13% of the secondary tillers were at the 4 leaf stage, 62% were at the 3 leaf stage, and 25% were at the 1 or 2 leaf stage. During mid July, 100% of the reproductive lead tillers were at flower stages; 40% of the vegetative lead tillers were at the 6 leaf stage, 40% were at the 5 leaf stage, and 20% were at the 4 leaf stage; and 33% of the secondary tillers were at the 4 leaf stage, 33% were at the 3 leaf stage, and 33% were at the 1 or 2 leaf stage. During early August, 20% of the vegetative lead tillers were at the 7 leaf stage, 60% were at the 6 leaf stage, 10% were at the 5 leaf stage, and 10% were at the 4 leaf stage; and 20% of the secondary tillers were at the 4 leaf stage and 80% were at the 3 leaf stage.

During early May on the June 25% treatment of the 4.5 m SL management strategy (table 6), 17% of the reproductive lead tillers were at the 4 leaf stage and 83% were at the 3 leaf stage; 33% of the vegetative lead tillers were at the 4 leaf stage and 67% were at the 3 leaf stage; and 40% of the secondary tillers were at the 3 leaf stage and 60% were at the 1 or 2 leaf stage. During mid May, 50% of the reproductive lead tillers were at the 4 leaf stage and 50% were at the 3 leaf stage; 10% of the vegetative lead tillers were at the 5 leaf stage, 50% were at the 4 leaf stage, and 40% were at the 3 leaf stage; and 55% of the secondary tillers were at the 3 leaf stage and 45% were at the 1 or 2 leaf stage. During early June, 17% of the reproductive lead tillers were at the 5 leaf stage, 50% were at the 4 leaf stage, and 33% were at the 3 leaf stage; 9% of the vegetative lead tillers were at the 5 leaf stage, 73% were at the 4 leaf stage, and 18% were at the 3 leaf stage; and 70% of the secondary tillers were at the 3 leaf stage and 30% were at the 1 or 2 leaf stage. During mid June, 50% of the reproductive lead tillers were at flower stages, 17% were at the 5 leaf stage, and 33% were at the 4 leaf stage; 18% of the vegetative lead tillers were at the 6 leaf stage, 36% were at the 5 leaf stage, 36% were at the 4 leaf stage, and 9% were at the 3 leaf stage; and 80% of the secondary tillers were at the 3 leaf stage and 20% were at the 1 or 2 leaf stage. During early July, 71% of the reproductive lead tillers were at flower stages and 29% were at the 5 leaf stage; 40% of the vegetative lead tillers were at the 6 leaf stage and 60% were at the 5 leaf stage; and 20% of the secondary tillers were at the 4 leaf stage, 60% were at the 3 leaf stage, and 20% were at the 1 or 2 leaf stage. During mid July, 100% of the reproductive lead tillers were at flower stages; 40% of the vegetative

lead tillers were at the 7 leaf stage, 10% were at the 6 leaf stage, and 50% were at the 5 leaf stage; and 22% of the secondary tillers were at the 4 leaf stage, 44% were at the 3 leaf stage, and 33% were at the 1 or 2 leaf stage. During early August, 20% of the vegetative lead tillers were at the 8 leaf stage, 40% were at the 7 leaf stage, 10% were at the 6 leaf stage, and 30% were at the 5 leaf stage; and 22% of the secondary tillers were at the 4 leaf stage, 56% were at the 3 leaf stage, and 22% were at the 1 or 2 leaf stage.

During early May on the June 50% treatment of the 4.5 m SL management strategy (table 7), 80% of the reproductive lead tillers were at the 3 leaf stage and 20% were at the 1 or 2 leaf stage; 11% of the vegetative lead tillers were at the 4 leaf stage, 78% were at the 3 leaf stage, and 11% were at the 1 or 2 leaf stage; and 17% of the secondary tillers were at the 3 leaf stage and 83% were at the 1 or 2 leaf stage. During mid May, 20% of the reproductive lead tillers were at the 4 leaf stage and 80% were at the 3 leaf stage; 10% of the vegetative lead tillers were at the 4 leaf stage, 80% were at the 3 leaf stage, and 10% were at the 1 or 2 leaf stage; and 43% of the secondary tillers were at the 3 leaf stage and 57% were at the 1 or 2 leaf stage. During early June, 20% of the reproductive lead tillers were at the 5 leaf stage and 80% were at the 4 leaf stage; 27% of the vegetative lead tillers were at the 4 leaf stage, 55% were at the 3 leaf stage, and 18% were at the 1 or 2 leaf stage; and 50% of the secondary tillers were at the 3 leaf stage and 50% were at the 1 or 2 leaf stage. During mid June, 40% of the reproductive lead tillers were at flower stages and 60% were at the 5 leaf stage; 27% of the vegetative lead tillers were at the 5 leaf stage, 55% were at the 4 leaf stage, and 18% were at the 3 leaf stage; and 14% of the secondary tillers were at the 4 leaf stage, 43% were at the 3 leaf stage, and 43% were at the 1 or 2 leaf stage. During early July, 80% of the reproductive lead tillers were at flower stages and 20% were at the 6 leaf stage; 27% of the vegetative lead tillers were at the 6 leaf stage, 45% were at the 5 leaf stage, and 27% were at the 4 leaf stage; and 14% of the secondary tillers were at the 5 leaf stage, 29% were at the 4 leaf stage, 29% were at the 3 leaf stage, and 29% were at the 1 or 2 leaf stage. During mid July, 80% of the reproductive lead tillers were at flower stages and 20% were at the 6 leaf stage; 55% of the vegetative lead tillers were at the 6 leaf stage, 36% were at the 5 leaf stage, and 9% were at the 4 leaf stage; and 40% of the secondary tillers were at the 5 leaf stage, 20% were at the 4 leaf stage, 20% were at the 3 leaf stage, and 20% were at the 1 or 2 leaf stage. During early August, 100% of the reproductive lead tillers were at

flower stages; 18% of the vegetative lead tillers were at the 7 leaf stage, 55% were at the 6 leaf stage, and 27% were at the 5 leaf stage; and 20% of the secondary tillers were at the 5 leaf stage, 40% were at the 4 leaf stage, 20% were at the 3 leaf stage, and 20% were at the 1 or 2 leaf stage.

During early May on the control treatment of the 4.5 m TOR management strategy (table 8), 14% of the reproductive lead tillers were at the 5 leaf stage, 23% were at the 4 leaf stage, 41% were at the 3 leaf stage, and 23% were at the 1 or 2 leaf stage; 17% of the vegetative lead tillers were at the 4 leaf stage, 61% were at the 3 leaf stage, and 22% were at the 1 or 2 leaf stage; and 10% of the secondary tillers were at the 4 leaf stage, 62% were at the 3 leaf stage, and 29% were at the 1 or 2 leaf stage. During mid May, 5% of the reproductive lead tillers were at the 6 leaf stage, 23% were at the 5 leaf stage, 32% were at the 4 leaf stage, 32% were at the 3 leaf stage, and 9% were at the 1 or 2 leaf stage; 6% of the vegetative lead tillers were at the 5 leaf stage, 22% were at the 4 leaf stage, 67% were at the 3 leaf stage, and 6% were at the 1 or 2 leaf stage; and 5% of the secondary tillers were at the 5 leaf stage, 38% were at the 4 leaf stage, 29% were at the 3 leaf stage, and 29% were at the 1 or 2 leaf stage. During early June, 5% of the reproductive lead tillers were at the 7 leaf stage, 18% were at the 6 leaf stage, 32% were at the 5 leaf stage, 27% were at the 4 leaf stage, 14% were at the 3 leaf stage, and 5% were at the 1 or 2 leaf stage; 19% of the vegetative lead tillers were at the 5 leaf stage, 56% were at the 4 leaf stage, and 25% were at the 3 leaf stage; and 6% of the secondary tillers were at the 5 leaf stage, 22% were at the 4 leaf stage, 33% were at the 3 leaf stage, and 39% were at the 1 or 2 leaf stage. During mid June, 13% of the reproductive lead tillers were at flower stages, 22% were at the 6 leaf stage, 39% were at the 5 leaf stage, 17% were at the 4 leaf stage, and 9% were at the 3 leaf stage; 11% of the vegetative lead tillers were at the 6 leaf stage, 44% were at the 5 leaf stage, 33% were at the 4 leaf stage, and 11% were at the 3 leaf stage; and 13% of the secondary tillers were at the 5 leaf stage, 13% were at the 4 leaf stage, 53% were at the 3 leaf stage, and 20% were at the 1 or 2 leaf stage. During early July, 52% of the reproductive lead tillers were at flower stages, 13% were at the 7 leaf stage, 13% were at the 6 leaf stage, 17% were at the 5 leaf stage, and 4% were at the 3 leaf stage; 29% of the vegetative lead tillers were at the 6 leaf stage, 59% were at the 5 leaf stage, and 12% were at the 4 leaf stage; and 13% of the secondary tillers were at the 5 leaf stage, 31% were at the 4 leaf stage, 44% were at the 3 leaf stage, and 12% were at the 1 or 2 leaf stage. During mid

July, 78% of the reproductive lead tillers were at flower stages, 4% were at the 9 leaf stage, 4% were at the 8 leaf stage, 4% were at the 7 leaf stage, 4% were at the 6 leaf stage, and 4% were at the 3 leaf stage; 12% of the vegetative lead tillers were at the 7 leaf stage, 41% were at the 6 leaf stage, and 47% were at the 5 leaf stage; and 13% of the secondary tillers were at the 5 leaf stage, 44% were at the 4 leaf stage, 31% were at the 3 leaf stage, and 12% were at the 1 or 2 leaf stage. During early August, 91% of the reproductive lead tillers were at flower stages, 4% were at the 9 leaf stage, and 4% were at the 7 leaf stage; 7% of the vegetative lead tillers were at the 8 leaf stage, 27% were at the 7 leaf stage, 40% were at the 6 leaf stage, and 27% were at the 5 leaf stage; and 25% of the secondary tillers were at the 5 leaf stage, 44% were at the 4 leaf stage, 25% were at the 3 leaf stage, and 6% were at the 1 or 2 leaf stage.

During early May on the June 25% treatment of the 4.5 m TOR management strategy (table 9), 45% of the reproductive lead tillers were at the 4 leaf stage and 55% were at the 3 leaf stage; 34% of the vegetative lead tillers were at the 4 leaf stage and 66% were at the 3 leaf stage; and 5% of the secondary tillers were at the 4 leaf stage, 25% were at the 3 leaf stage, and 70% were at the 1 or 2 leaf stage. During mid May, 27% of the reproductive lead tillers were at the 5 leaf stage, 55% were at the 4 leaf stage, and 18% were at the 3 leaf stage; 14% of the vegetative lead tillers were at the 5 leaf stage, 53% were at the 4 leaf stage, and 33% were at the 3 leaf stage; and 50% of the secondary tillers were at the 3 leaf stage and 50% were at the 1 or 2 leaf stage. During early June, 73% of the reproductive lead tillers were at the 5 leaf stage and 27% were at the 4 leaf stage; 3% of the vegetative lead tillers were at the 6 leaf stage, 41% were at the 5 leaf stage, and 56% were at the 4 leaf stage; and 4% of the secondary tillers were at the 4 leaf stage, 61% were at the 3 leaf stage, and 35% were at the 1 or 2 leaf stage. During mid June, 18% of the reproductive lead tillers were at flower stages, 27% were at the 6 leaf stage, 36% were at the 5 leaf stage, and 18% were at the 4 leaf stage; 24% of the vegetative lead tillers were at the 6 leaf stage, 46% were at the 5 leaf stage, and 30% were at the 4 leaf stage; and 15% of the secondary tillers were at the 4 leaf stage, 50% were at the 3 leaf stage, and 35% were at the 1 or 2 leaf stage. During early July, 64% of the reproductive lead tillers were at flower stages, 18% were at the 7 leaf stage, 9% were at the 6 leaf stage, and 9% were at the 5 leaf stage; 15% of the vegetative lead tillers were at the 7 leaf stage, 52% were at the 6 leaf stage, and 33% were at the 5 leaf stage; and 4% of the secondary

tillers were at the 6 leaf stage, 15% were at the 5 leaf stage, 31% were at the 4 leaf stage, 31% were at the 3 leaf stage, and 19% were at the 1 or 2 leaf stage. During mid July, 91% of the reproductive lead tillers were at flower stages and 9% were at the 7 leaf stage; 21% of the vegetative lead tillers were at the 8 leaf stage, 36% were at the 7 leaf stage, 30% were at the 6 leaf stage, and 12% were at the 5 leaf stage; and 4% of the secondary tillers were at the 6 leaf stage, 9% were at the 5 leaf stage, 30% were at the 4 leaf stage, 43% were at the 3 leaf stage, and 13% were at the 1 or 2 leaf stage. During early August, 100% of the reproductive lead tillers were at flower stages; 15% of the vegetative lead tillers were at the 9 leaf stage; 30% were at the 8 leaf stage, 27% were at the 7 leaf stage, 21% were at the 6 leaf stage, and 6% were at the 5 leaf stage; and 5% of the secondary tillers were at the 6 leaf stage, 11% were at the 5 leaf stage, 32% were at the 4 leaf stage, 42% were at the 3 leaf stage, and 11% were at the 1 or 2 leaf stage.

During early May on the June 50% treatment of the 4.5 m TOR management strategy (table 10), 64% of the reproductive lead tillers were at the 4 leaf stage, 27% were at the 3 leaf stage, and 9% were at the 1 or 2 leaf stage; 4% of the vegetative lead tillers were at the 5 leaf stage, 12% were at the 4 leaf stage, 65% were at the 3 leaf stage, and 19% were at the 1 or 2 leaf stage; and 12% of the secondary tillers were at the 4 leaf stage, 50% were at the 3 leaf stage, and 38% were at the 1 or 2 leaf stage. During mid May, 53% of the reproductive lead tillers were at the 5 leaf stage, 27% were at the 4 leaf stage, and 20% were at the 3 leaf stage; 7% of the vegetative lead tillers were at the 5 leaf stage, 41% were at the 4 leaf stage, 44% were at the 3 leaf stage, and 7% were at the 1 or 2 leaf stage; and 100% of the secondary tillers were at the 3 leaf stage. During early June, 12% of the reproductive lead tillers were at the 6 leaf stage, 56% were at the 5 leaf stage, 19% were at the 4 leaf stage, 13% were at the 3 leaf stage; 37% of the vegetative lead tillers were at the 5 leaf stage, 41% were at the 4 leaf stage, and 22% were at the 3 leaf stage; and 13% of the secondary tillers were at the 4 leaf stage and 88% were at the 3 leaf stage. During mid June, 38% of the reproductive lead tillers were at flower stages, 12% were at the 7 leaf stage, 25% were at the 6 leaf stage, 19% were at the 5 leaf stage, and 6% were at the 4 leaf stage; 7% of the vegetative lead tillers were at the 6 leaf stage, 61% were at the 5 leaf stage, 25% were at the 4 leaf stage, and 7% were at the 3 leaf stage; and 56% of the secondary tillers were at the 4 leaf stage and 44% were at the 3 leaf stage. During early July, 75% of the reproductive lead tillers were at flower stages, 6%

were at the 8 leaf stage, 13% were at the 6 leaf stage, and 6% were at the 5 leaf stage; 52% of the vegetative lead tillers were at the 6 leaf stage, 40% were at the 5 leaf stage, and 8% were at the 4 leaf stage; and 67% of the secondary tillers were at the 4 leaf stage and 33% were at the 3 leaf stage. During mid July, 94% of the reproductive lead tillers were at flower stages and 6% were at the 9 leaf stage; 4% of the vegetative lead tillers were at the 8 leaf stage, 28% were at the 7 leaf stage, 36% were at the 6 leaf stage, 24% were at the 5 leaf stage, and 8% were at the 4 leaf stage; and 29% of the secondary tillers were at the 5 leaf stage, 57% were at the 4 leaf stage, and 14% were at the 3 leaf stage. During early August, 94% of the reproductive lead tillers were at flower stages and 6% were at the 9 leaf stage; 8% of the vegetative lead tillers were at the 9 leaf stage, 24% were at the 8 leaf stage, 12% were at the 7 leaf stage, 36% were at the 6 leaf stage, and 20% were at the 5 leaf stage; and 14% of the secondary tillers were at the 5 leaf stage and 86% were at the 4 leaf stage.

Grass tillers at the 3.5 leaf stage are physiologically capable of enduring defoliation that removes around 25% of the aboveground herbage. Grass tillers do not fully recover from defoliation occurring before the 3.5 leaf stage (Manske 2007), or from defoliation at the 4 and 5 leaf stages that removes 50% of the aboveground herbage (Manske 2009).

Results of leaf stage development by tillers on the control treatment of the 6.0 m SL management strategy showed that 188.0/m<sup>2</sup> (100%) reproductive lead tillers had produced 4 or more leaves by early June and 188.0/m<sup>2</sup> (100%) had produced flower stalks by mid July; 235.0/m<sup>2</sup> (100%) vegetative lead tillers had produced 4 or more leaves by early June; and 109.6/m<sup>2</sup> (50%) secondary tillers had produced 4 or more leaves by mid July.

Results of leaf stage development by tillers on the June 25% treatment of the 6.0 m SL management strategy showed that 125.3/m<sup>2</sup> (89%) reproductive lead tillers had produced 4 or more leaves by early June and 125.3/m<sup>2</sup> (89%) had produced flower stalks by mid July; 188.0/m<sup>2</sup> (75%) vegetative lead tillers had produced 4 or more leaves by early June; and 78.3/m<sup>2</sup> (55%) secondary tillers had produced 4 or more leaves by mid July.

Results of leaf stage development by tillers on the June 50% treatment of the 6.0 m SL management strategy showed that 125.3/m<sup>2</sup> (89%)

reproductive lead tillers had produced 4 or more leaves by early June and 141.0/m<sup>2</sup> (100%) had produced flower stalks by mid July; 250.6/m<sup>2</sup> (80%) vegetative lead tillers had produced 4 or more leaves by early June; and 31.3/m<sup>2</sup> (22%) secondary tillers had produced 4 or more leaves by mid July.

Results of leaf stage development by tillers on the control treatment of the 4.5 m SL management strategy showed that 47.0/m<sup>2</sup> (75%) reproductive lead tillers had produced 4 or more leaves by early June and 62.7/m<sup>2</sup> (100%) had produced flower stalks by mid July; 78.3/m<sup>2</sup> (56%) vegetative lead tillers had produced 4 or more leaves by early June; and 31.3/m<sup>2</sup> (33%) secondary tillers had produced 4 or more leaves by mid July.

Results of leaf stage development by tillers on the June 25% treatment of the 4.5 m SL management strategy showed that 62.7/m<sup>2</sup> (67%) reproductive lead tillers had produced 4 or more leaves by early June and 109.6/m<sup>2</sup> (100%) had produced flower stalks by mid July; 141.0/m<sup>2</sup> (82%) vegetative lead tillers had produced 4 or more leaves by early June; and 31.3/m<sup>2</sup> (22%) secondary tillers had produced 4 or more leaves by mid July.

Results of leaf stage development by tillers on the June 50% treatment of the 4.5 m SL management strategy showed that 78.3/m<sup>2</sup> (100%) reproductive lead tillers had produced 4 or more leaves by early June and 62.7/m<sup>2</sup> (80%) had produced flower stalks by mid July; 47.0/m<sup>2</sup> (27%) vegetative lead tillers had produced 4 or more leaves by early June; and 47.0/m<sup>2</sup> (60%) secondary tillers had produced 4 or more leaves by mid July.

Results of leaf stage development by tillers on the control treatment of the 4.5 m TOR management strategy showed that 281.9/m<sup>2</sup> (82%) reproductive lead tillers had produced 4 or more leaves by early June and 281.9/m<sup>2</sup> (78%) had produced flower stalks by mid July; 188.0/m<sup>2</sup> (75%) vegetative lead tillers had produced 4 or more leaves by early June; and 141.0/m<sup>2</sup> (57%) secondary tillers had produced 4 or more leaves by mid July.

Results of leaf stage development by tillers on the June 25% treatment of the 4.5 m TOR management strategy showed that 172.3/m<sup>2</sup> (100%) reproductive lead tillers had produced 4 or more leaves by early June and 156.6/m<sup>2</sup> (91%) had produced flower stalks by mid July; 532.5/m<sup>2</sup> (100%) vegetative lead tillers had produced 4 or more leaves

by early June; and 156.6/m<sup>2</sup> (43%) secondary tillers had produced 4 or more leaves by mid July.

Results of leaf stage development by tillers on the June 50% treatment of the 4.5 m TOR management strategy showed that 219.3/m<sup>2</sup> (88%) reproductive lead tillers had produced 4 or more leaves by early June and 235.0/m<sup>2</sup> (94%) had produced flower stalks by mid July; 328.9/m<sup>2</sup> (78%) vegetative lead tillers had produced 4 or more leaves by early June; and 94.0/m<sup>2</sup> (86%) secondary tillers had produced 4 or more leaves by mid July.

#### Leaf Development Rates

The reproductive lead tillers had the fastest rate of growth and development (table 11a). Usually 5 to 8 leaves had developed when reproductive lead tillers reached the flowering (anthesis) stage and no additional leaves were produced during development of flower stalk stages. Reproductive lead tillers that produced flower stalks early in the flowering period had 5 to 6 leaves and tillers that produced flower stalks late in the flowering period had 7 or 8 leaves. The reproductive lead tillers developed 1.27 leaves per tiller between early May and early June. The mean reproductive lead tiller was at the 4.47 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 between early June and early July, produced 1.71 leaves per tiller. The reproductive lead tillers that did not produce flower stalks between early July and early August, produced 2.31 leaves per tiller. During early August, the mean reproductive lead tiller that had not yet produced a flower stalk was at the 8.49 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 flowering 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 flowering period differed greatly on the three management strategies. The end of the flowering period occurred on the June 50% treatment of the 6.0 m SL management strategy during early July; 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 during 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 during early August; occurred on the June 25% treatment of the 6.0 m SL management strategy during mid August; and occurred on the control and June 50% treatments of the 4.5 m TOR management strategy during late August.

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 11b). The vegetative lead tillers developed 3.56 leaves in 3 months from the 3.01 leaf stage in early May to the 6.57 leaf stage in early August at an average rate of 0.59 leaves produced per biweekly period. An average of 0.98 leaves developed per tiller between early May and early June; an average of 1.51 leaves developed between early June and early July; and an average of 1.06 leaves developed between early July and early August. The mean vegetative lead tiller was at the 4.00 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 June 50% treatment 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 11c). The secondary tillers developed 1.18 leaves in 3 months from the 2.22 leaf stage in early May to the 3.40 leaf stage in early August at an average rate of 0.20 leaves produced per biweekly period. An average of 0.43 leaves developed per tiller between early May and early June; an average of 0.53 leaves developed between early June and early July; and an average of 0.22 leaves developed between early July and early August. The mean secondary tiller was at the 2.65 leaf stage during early June, and during mid July, was at the 3.07 leaf stage on the 6.0 m SL and 4.5 m SL management strategies and at the 3.68 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).

#### 4 Leaf to Flower Stage

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 flowering (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 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.

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<sup>2</sup> in early May to 188.0/m<sup>2</sup> in early June as tillers developed additional leaves, then decreased to 15.6/m<sup>2</sup> in early July and 0.0/m<sup>2</sup> in mid July as increasing numbers of tillers reached flower stages (table 12).

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<sup>2</sup> in early May to 125.3/m<sup>2</sup> in early June as tillers developed additional leaves, then decreased to 47.0/m<sup>2</sup> in early July, 15.6/m<sup>2</sup> in mid July (table 12), and 0.0/m<sup>2</sup> in mid August as increasing numbers of tillers reached flower stages.

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<sup>2</sup> in early May to 109.6/m<sup>2</sup> in mid May as tillers developed additional leaves, then decreased to 94.0/m<sup>2</sup> in early June, 62.7/m<sup>2</sup> in mid June, and 0.0/m<sup>2</sup> in early July as increasing numbers of tillers reached flower stages (table 12).

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<sup>2</sup> in early May to 47.0/m<sup>2</sup> in early June as tillers developed additional leaves, then decreased to 15.6/m<sup>2</sup> in early July and 0.0/m<sup>2</sup> in mid July as increasing numbers of tillers reached flower stages (table 12). 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.

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<sup>2</sup> in early May to 62.7/m<sup>2</sup> in early June as tillers developed additional leaves, then decreased to 31.3/m<sup>2</sup> in early July and 0.0/m<sup>2</sup> in mid July as increasing numbers of tillers reached flower stages (table 12).

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<sup>2</sup> in early May to 78.3/m<sup>2</sup>

in early June as tillers developed additional leaves, then decreased to 15.6/m<sup>2</sup> in early and mid July and 0.0/m<sup>2</sup> in early August as increasing numbers of tillers reached flower stages (table 12).

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<sup>2</sup> in early May to 281.9/m<sup>2</sup> in early June as tillers developed additional leaves, then decreased to 156.6/m<sup>2</sup> in early July, 47.0/m<sup>2</sup> in mid July (table 12), and 0.0/m<sup>2</sup> in late August as increasing numbers of tillers reached flower stages. 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.

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<sup>2</sup> in early May to 172.3/m<sup>2</sup> in early June as tillers developed additional leaves, then decreased to 62.7/m<sup>2</sup> in early July, 15.6/m<sup>2</sup> in mid July, and 0.0/m<sup>2</sup> in early August as increasing numbers of tillers reached flower stages (table 12). The tiller population on the June 25% treatment of the 4.5 m TOR management strategy contained the lowest percentage of reproductive lead tillers.

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<sup>2</sup> in early May to 219.3/m<sup>2</sup> in early June as tillers developed additional leaves, then decreased to 62.7/m<sup>2</sup> in early July, 15.6/m<sup>2</sup> in mid July (table 12), and 0.0/m<sup>2</sup> in late August as increasing numbers of tillers reached flower stages.

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<sup>2</sup> in early May to 235.0/m<sup>2</sup> in early and mid June as tillers developed additional

leaves, then decreased to 219.3/m<sup>2</sup> in mid July, 203.6/m<sup>2</sup> in early August (table 13), 188.0/m<sup>2</sup> in late August, and 172.3/m<sup>2</sup> in mid October as some tillers progressed through senescence.

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<sup>2</sup> in early May to 188.0/m<sup>2</sup> in early June and 250.6/m<sup>2</sup> in mid June and early and mid July as tillers developed additional leaves, then decreased to 235.0/m<sup>2</sup> in early and late August (table 13), and 203.6/m<sup>2</sup> in mid October as some tillers progressed through senescence.

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<sup>2</sup> in early May to 250.6/m<sup>2</sup> in early June and 313.3/m<sup>2</sup> in mid June, then decreased slightly to 297.6/m<sup>2</sup> in early July (table 13), and remained at 297.6/m<sup>2</sup> until mid October.

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<sup>2</sup> in early May to 78.3/m<sup>2</sup> in early June and 156.6/m<sup>2</sup> in early July (table 13), and remained at 156.6/m<sup>2</sup> until mid October. 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.

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<sup>2</sup> in early May to 141.0/m<sup>2</sup> in early June and 156.6/m<sup>2</sup> in mid June, remained at 156.6/m<sup>2</sup> until early August (table 13), then decreased to 125.3/m<sup>2</sup> in late August as some tillers progressed through senescence, and remained at 125.3/m<sup>2</sup> until mid October.

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<sup>2</sup> in early May to 47.0/m<sup>2</sup> in early June, 141.0/m<sup>2</sup> in mid June, and 172.3/m<sup>2</sup> in early July, remained at 172.3/m<sup>2</sup> until early August (table 13), and then decreased to 156.6/m<sup>2</sup> in late August and 141.0/m<sup>2</sup> in mid October as some tillers progressed through senescence.

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<sup>2</sup> in early May to 188.0/m<sup>2</sup> in early June and 266.3/m<sup>2</sup> in early and mid July, then decreased slightly to 235.0/m<sup>2</sup> in early August (table 13), and remained at 235.0/m<sup>2</sup> until mid October.

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<sup>2</sup> in early May to 532.5/m<sup>2</sup> in early June and 579.5/m<sup>2</sup> in mid June, decreased to 516.9/m<sup>2</sup> in early July, remained at 516.9/m<sup>2</sup> until mid August (table 13), then decreased to 485.6/m<sup>2</sup> in late August as some tillers progressed through senescence, and remained at 485.6/m<sup>2</sup> until mid October. 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.

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<sup>2</sup> in early May to 328.9/m<sup>2</sup> in early June and 407.2/m<sup>2</sup> in mid June, decreased slightly to 391.6/m<sup>2</sup> in early July (table 13), remained at 391.6/m<sup>2</sup> until late August, and then decreased to 328.9/m<sup>2</sup> in mid October as some tillers progressed through senescence.

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<sup>2</sup> during early and mid May, increased from 47.0/m<sup>2</sup> in early June to 78.3/m<sup>2</sup> in mid June and 125.3/m<sup>2</sup> in early July, then decreased slightly to 109.6/m<sup>2</sup> in mid July and early August (table 14), and increased to 141.0/m<sup>2</sup> in late August, and remained at 141.0/m<sup>2</sup> until mid October.

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<sup>2</sup> during early and mid May and early June, increased to 62.7/m<sup>2</sup> in mid June and early July, increased to 78.3/m<sup>2</sup> in mid July and early August (table 14), decreased to 62.7/m<sup>2</sup> in late August, and increased to 94.0/m<sup>2</sup> in mid October.

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<sup>2</sup> in early May to 31.3/m<sup>2</sup> during mid May and early and mid June, increased to 47.0/m<sup>2</sup> in early July, then decreased to 31.3/m<sup>2</sup> in mid July and 15.6/m<sup>2</sup> in early August (table 14), and increased to 31.3/m<sup>2</sup> in late August and 78.3/m<sup>2</sup> in mid October.

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<sup>2</sup> during early and mid May and early June, increased to 15.6/m<sup>2</sup> in mid June and early July, increased to 31.3/m<sup>2</sup> in mid July, decreased to 15.6/m<sup>2</sup> in early August (table 14), and increased to 47.0/m<sup>2</sup> in late August and 78.3/m<sup>2</sup> in mid October. 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.

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<sup>2</sup> during early May to mid June, increased to 31.3/m<sup>2</sup> in early July, remained at 31.3/m<sup>2</sup> until early August (table 14), then increased to 109.6/m<sup>2</sup> in late August, and decreased to 94.0/m<sup>2</sup> in mid October.

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<sup>2</sup> during early May to early June, increased to 15.6/m<sup>2</sup> in mid June and 47.0/m<sup>2</sup> in early July (table 14), remained at 47.0/m<sup>2</sup> until late August, and then decreased to 15.6/m<sup>2</sup> in mid October.

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<sup>2</sup> in early May to 141.0/m<sup>2</sup> in mid May, decreased to 78.3/m<sup>2</sup> in early June and 62.7/m<sup>2</sup> in mid June, then increased to 109.6/m<sup>2</sup> in early July, 141.0/m<sup>2</sup> in mid July, and 172.3/m<sup>2</sup> in early August (table 14), and then decreased to 109.6/m<sup>2</sup> in mid October.

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<sup>2</sup> in early May to 0.0/m<sup>2</sup> in mid May, increased from 15.6/m<sup>2</sup> in early June to 47.0/m<sup>2</sup> in mid June and 203.6/m<sup>2</sup> in early July, then decreased to 141.0/m<sup>2</sup> in early and late August (table 14), and increased to 203.6/m<sup>2</sup> in mid October. 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.

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<sup>2</sup> in early May to 0.0/m<sup>2</sup> in mid May, increased from 15.6/m<sup>2</sup> in early June to 78.3/m<sup>2</sup> in mid June and 125.3/m<sup>2</sup> in early July, then decreased to 94.0/m<sup>2</sup> in mid July, increased to 109.6/m<sup>2</sup> in early and late August (table 14), and decreased to 78.3/m<sup>2</sup> in mid October.

The primary period the reproductive lead tillers were 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 between the 4 leaf stage and the 10 leaf stage was

from early June until mid October. The primary period the secondary tillers were between the 4 leaf stage and the 8 leaf stage was from mid July until mid October.

Growing season mean total tiller density was 637.0/m<sup>2</sup> 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<sup>2</sup> in early May to 469.9/m<sup>2</sup> in early June, then decreased to 328.9/m<sup>2</sup> in mid July and 313.3/m<sup>2</sup> in early August (table 15, figure 1), and remained at 313.3/m<sup>2</sup> until mid October.

Growing season mean total tiller density was 574.3/m<sup>2</sup> 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<sup>2</sup> in early May to 344.6/m<sup>2</sup> in early June and 407.2/m<sup>2</sup> in mid June, then decreased to 344.6/m<sup>2</sup> in mid July and 328.9/m<sup>2</sup> in early August (table 15, figure 2), decreased to 297.6/m<sup>2</sup> in late August, and remained at 297.6/m<sup>2</sup> until mid October.

Growing season mean total tiller density was 608.3/m<sup>2</sup> 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<sup>2</sup> in early May to 375.9/m<sup>2</sup> in early June and 407.2/m<sup>2</sup> in mid June, then decreased to 328.9/m<sup>2</sup> in mid July and 313.3/m<sup>2</sup> in early August (table 15, figure 3), and then increased to 328.9/m<sup>2</sup> in late August and 375.9/m<sup>2</sup> in mid October.

Growing season mean total tiller density was 342.0/m<sup>2</sup> 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<sup>2</sup> in early May to 125.3/m<sup>2</sup> in early June and 188.0/m<sup>2</sup> in early and mid July, decreased to 172.3/m<sup>2</sup> in early August (table 15, figure 1), and increased to 203.6/m<sup>2</sup> in late August and 235.0/m<sup>2</sup> in mid October. 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.

Growing season mean total tiller density was 422.9/m<sup>2</sup> 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<sup>2</sup> in early May to 203.6/m<sup>2</sup> in early and mid June and 219.3/m<sup>2</sup> in early July, then decreased to 188.0/m<sup>2</sup> in mid July and early August

(table 15, figure 2), and increased to 219.3/m<sup>2</sup> in mid October.

Growing season mean total tiller density was 349.8/m<sup>2</sup> 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<sup>2</sup> in early May to 125.3/m<sup>2</sup> in early June and 235.0/m<sup>2</sup> in early and mid July, then decreased to 219.3/m<sup>2</sup> in early August (table 15, figure 3), and decreased to 203.6/m<sup>2</sup> in late August and 156.6/m<sup>2</sup> in mid October.

Growing season mean total tiller density was 895.4/m<sup>2</sup> 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<sup>2</sup> in early May to 548.2/m<sup>2</sup> in early June and 595.2/m<sup>2</sup> in mid June, then decreased to 454.2/m<sup>2</sup> in mid July and 438.6/m<sup>2</sup> in early August (table 15, figure 1), decreased to 360.3/m<sup>2</sup> in late August, and increased to 391.6/m<sup>2</sup> in mid October.

Growing season mean total tiller density was 1031.2/m<sup>2</sup> 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<sup>2</sup> in early May to 720.5/m<sup>2</sup> in early June and 783.2/m<sup>2</sup> in early July, then decreased to 689.2/m<sup>2</sup> in mid July, 657.8/m<sup>2</sup> in early August (table 15, figure 2), and 626.5/m<sup>2</sup> in late August, and then increased to 689.2/m<sup>2</sup> in mid October. 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.

Growing season mean total tiller density was 811.9/m<sup>2</sup> 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<sup>2</sup> in early May to 563.9/m<sup>2</sup> in early June and 642.2/m<sup>2</sup> in mid June, then decreased to 579.5/m<sup>2</sup> in early July and 501.2/m<sup>2</sup> in mid July, increased slightly to 516.9/m<sup>2</sup> early August (table 15, figure 3), and then decreased to 501.2/m<sup>2</sup> in late August and 407.2/m<sup>2</sup> in mid October.

The number of total tillers between the 4 leaf stage and the flower stage 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.

The tiller densities of total tillers between the 4 leaf stage and the flower stage that developed during the entire grazing season on the June 25% treatment of the 4.5 m TOR management strategy were significantly greater than those that developed on the control and June 50% treatments of the 4.5 m TOR management strategy and that developed on the control, June 25%, and June 50% treatments of the 6.0 m SL and 4.5 m SL management strategies (table 16).

The tiller densities of total tillers between the 4 leaf stage and the flower stage that developed during the entire grazing season on the June 50% treatment of the 4.5 m TOR management strategy were significantly greater than those that developed on the control, June 25%, and June 50% treatments of the 6.0 m SL and 4.5 m SL management strategies (table 16).

The tiller densities were not significantly different for the total tillers between the 4 leaf stage and the flower stage that developed during the entire grazing season on the control treatment and on the June 50% treatment of the 4.5 m TOR management strategy (table 16).

The tiller densities of total tillers between the 4 leaf stage and the flower stage that developed during the entire grazing season on the control treatment of the 4.5 m TOR management strategy were not significantly different from those that developed on the control treatment of the 6.0 m SL management strategy (table 16).

The tiller densities of total tillers between the 4 leaf stage and the flower stage that developed during the entire grazing season on the control, June 25%, and June 50% treatments of the 6.0 m SL management strategy were not significantly different (table 16). The total tiller densities that developed during the entire grazing season on the control, June 25%, and June 50% treatments of the 6.0 m SL management strategy were significantly greater than the total tiller densities that developed on the control, June 25%, and June 50% treatments of the 4.5 m SL management strategy (table 16).

The tiller densities of total tillers between the 4 leaf stage and the flower stage that developed during the entire grazing season on the control, June 25%, and June 50% treatments of the 4.5 m SL management strategy were not significantly different (table 16). The total tiller densities that developed during the entire grazing season on the control, June

25%, and June 50% treatments of the 4.5 m SL management strategy were significantly lower than the total tiller densities that developed on the control, June 25%, and June 50% treatments of the 6.0 m SL and 4.5 m TOR management strategies (table 16).

A significantly greater density of total tillers between the 4 leaf stage and the flower stage developed on the June 25% treatment of the 4.5 TOR management strategy during the first and second grazing periods than the respective densities of total tillers that developed on the control and June 50% treatments of the 4.5 m TOR management strategy and that developed on the control, June 25%, and June 50% treatments of the 6.0 m SL and 4.5 m SL management strategies (table 16).

The tiller densities were not significantly different for the total tillers between the 4 leaf stage and the flower stage that developed during the first and second grazing periods on the June 50% treatment and during the first grazing period on the control treatment of the 4.5 m TOR management strategy (table 16).

The tiller densities of total tillers between the 4 leaf stage and the flower stage that developed during the first grazing periods on the control and June 50% treatments of the 4.5 m TOR management strategy were significantly greater than the total tiller densities that developed 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 (table 16).

The tiller densities of total tillers between the 4 leaf stage and the flower stage that developed during the second grazing periods on the control and June 50% treatments of the 4.5 m TOR management strategy were not significantly different from the total tiller density that developed during the first grazing period on the control treatment of the 6.0 m SL management strategy. The total tiller densities that developed during the second grazing period on the control treatment of the 4.5 m TOR management strategy were not significantly different from the total tiller densities that developed during the first grazing period on the control, June 25%, and June 50% treatments of the 6.0 m SL management strategy (table 16).

The tiller densities were not significantly different for the total tillers between the 4 leaf stage and the flower stage that developed during the first and second grazing periods on the control, June 25%,

and June 50% treatments of the 6.0 m SL management strategy; and these total tiller densities on the three treatments of the 6.0 m SL management strategy were significantly greater than the respective total tiller densities on the three treatments of the 4.5 m SL management strategy (table 16).

The tillers densities were not significantly different for the total tillers between the 4 leaf stage and the flower stage that developed during the first and second grazing periods on the control, June 25%, and June 50% treatments of the 4.5 m SL management strategy; and these total tiller densities on the three treatments of the 4.5 m SL management strategy were significantly lower than the respective total tiller densities on the three treatments of the 6.0 m SL and 4.5 m TOR management strategies (table 16).

The grazing management strategy effected the quantity of available mineral nitrogen. Mineral nitrogen was available at greater than 100 lbs/ac on the 4.5 m TOR management strategy and available at less than 100 lbs/ac on the 6.0 m SL and 4.5 m SL management strategies. The quantity of soil mineral nitrogen effected the degree of activation of the defoliation resistance mechanisms. The processes of the defoliation resistance mechanisms were fully activated on the 4.5 m TOR management strategy and activated at levels much less than full on the 6.0 m SL management strategy and 4.5 m SL management strategies. The level of activation of the defoliation resistance mechanisms determines the extent that the compensatory physiological processes replace the leaf area removed by partial defoliation and determines the number of secondary tillers initiated through vegetative reproduction from axillary buds effecting the tiller density and the number of total tillers between the 4 leaf stage and flower stage during the grazing season (Manske 2009). The tiller density per square meter and the number of total tillers between the 4 leaf stage and flower stage 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. The June 25% treatment of the 4.5 m TOR management strategy had the significantly greatest tiller density and the significantly greatest number of total tillers between the 4 leaf stage and the flower stage during the grazing season.

## 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 Pflieger 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 exuded 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 2. Progression of leaf stage development of tiller types in numbers and percentage per square meter on the control treatment of the 6.0 month seasonlong management strategy.

Date Tiller Types	Tiller Numbers Leaf Stage				Tiller Density #/m <sup>2</sup>	Tiller Percentage Leaf Stage			
	1-3	4	5-10	Flower Stage		1-3	4	5-10	Flower Stage
10 May									
Reproductiv	109.6	78.3			188.0	58.3	41.7		
Vegetative	188.0	47.0			235.0	80.0	20.0		
Secondary	203.6				203.6	100.0			
					626.5				
24 May									
Reproductiv	15.6	141.0	31.3		188.0	8.3	75.0	16.7	
Vegetative	62.7	172.3			235.0	26.7	73.3		
Secondary	203.6				203.6	100.0			
					626.5				
7 June									
Reproductiv		47.0	141.0		188.0		25.0	75.0	
Vegetative		109.6	125.3		235.0		46.7	53.3	
Secondary	156.6	47.0			203.6	77.0	23.0		
					626.5				
21 June									
Reproductiv			94.0	94.0	188.0			50.0	50.0
Vegetative		15.6	219.3		235.0		6.7	93.3	
Secondary	125.3	78.3			203.6	61.6	38.4		
					626.5				
5 July									
Reproductiv			15.6	172.3	188.0			8.3	91.7
Vegetative			219.3		219.3			100.0	
Secondary	109.6	78.3	47.0		235.0	46.7	33.3	20.0	
					642.2				
2 August									
Reproductiv				188.0	188.0				100.0
Vegetative			203.6		203.6			100.0	
Secondary	62.7	47.0	62.7		172.3	36.4	27.3	36.4	
					563.9				

Table 3. Progression of leaf stage development of tiller types in numbers and percentage per square meter on the mid June 25% defoliation treatment of the 6.0 month seasonlong management strategy.

Date Tiller Types	Tiller Numbers				Tiller Density #/m <sup>2</sup>	Tiller Percentage			
	Leaf Stage			Flower Stage		Leaf Stage			Flower Stage
	1-3	4	5-10				1-3	4	
10 May									
Reproductiv	62.7	62.7	15.6		141.0	44.4	44.4	11.1	
Vegetative	219.3	47.0			266.3	82.3	17.7		
Secondary	47.0	15.6	15.6		78.3	60.0	20.0	20.0	
					485.6				
24 May									
Reproductiv	31.3	78.3	31.3		141.0	22.2	55.6	22.2	
Vegetative	172.3	62.7	31.3		266.3	64.7	23.5	11.8	
Secondary	62.7	15.6	15.6		94.0	66.6	16.7	16.7	
					501.2				
7 June									
Reproductiv	15.6	47.0	78.3		141.0	11.1	33.3	55.6	
Vegetative	62.7	141.0	47.0		250.6	25.0	56.2	18.8	
Secondary	94.0		31.3		125.3	75.0		25.0	
					516.9				
21 June									
Reproductiv		15.6	78.3	47.0	141.0		11.1	55.6	33.3
Vegetative		125.3	125.3		250.6		50.0	50.0	
Secondary	78.3	31.3	31.3		141.0	55.6	22.2	22.2	
					532.5				
5 July									
Reproductiv			47.0	94.0	141.0			33.3	66.7
Vegetative		31.3	219.3		250.6		12.5	87.5	
Secondary	78.3	31.3	31.3		141.0	55.6	22.2	22.2	
					532.5				
2 August									
Reproductiv			15.6	125.3	141.0			11.1	88.9
Vegetative			235.0		235.0			100.0	
Secondary	94.0	62.7	15.6		172.3	54.6	36.4	9.0	
					548.2				

Table 4. Progression of leaf stage development of tiller types in numbers and percentage per square meter on the mid June 50% defoliation treatment of the 6.0 month seasonlong management strategy.

Date Tiller Types	Tiller Numbers Leaf Stage				Tiller Density #/m <sup>2</sup>	Tiller Percentage Leaf Stage			
	1-3	4	5-10	Flower Stage		1-3	4	5-10	Flower Stage
10 May									
Reproductiv	62.7	47.0			109.6	57.1	42.9		
Vegetative	266.3	47.0			313.3	85.0	15.0		
Secondary	78.3	15.6			94.0	83.3	16.7		
					516.9				
24 May									
Reproductiv	31.3	62.7	47.0		141.0	22.2	44.5	33.3	
Vegetative	141.0	188.0			328.9	42.9	57.1		
Secondary	78.3	31.3			109.6	71.4	28.6		
					579.5				
7 June									
Reproductiv	15.6	47.0	47.0	31.3	141.0	11.1	33.3	33.3	22.2
Vegetative	62.7	156.6	94.0		313.3	20.0	50.0	30.0	
Secondary	109.6	31.3			141.0	77.8	22.2		
					595.2				
21 June									
Reproductiv		15.6	47.0	78.3	141.0		11.1	33.3	55.5
Vegetative		125.3	188.0		313.3		40.0	60.0	
Secondary	109.6	31.3			141.0	77.8	22.2		
					595.2				
5 July									
Reproductiv				141.0	141.0				100.0
Vegetative		15.6	281.9		297.6		5.3	94.7	
Secondary	109.6	47.0			156.6	70.0	30.0		
					595.2				
2 August									
Reproductiv				141.0	141.0				100.0
Vegetative			297.6		297.6			100.0	
Secondary	109.6	15.6			125.3	87.5	12.5		
					563.9				

Table 5. Progression of leaf stage development of tiller types in numbers and percentage per square meter on the control treatment of the 4.5 month seasonlong management strategy.

Date Tiller Types	Tiller Numbers Leaf Stage				Tiller Density #/m <sup>2</sup>	Tiller Percentage Leaf Stage			
	1-3	4	5-10	Flower Stage		1-3	4	5-10	Flower Stage
10 May									
Reproductiv	47.0	15.6			62.7	75.0	25.0		
Vegetative	125.3	15.6			141.0	88.9	11.1		
Secondary	141.0				141.0	100.0			
					344.6				
24 May									
Reproductiv	31.3	15.6	15.6		62.7	50.0	25.0	25.0	
Vegetative	94.0	47.0			141.0	66.7	33.3		
Secondary	141.0				141.0	100.0			
					344.6				
7 June									
Reproductiv	15.6	31.3	15.6		62.7	25.0	50.0	25.0	
Vegetative	62.7	47.0	31.3		141.0	44.4	33.3	22.2	
Secondary	156.6				156.6	100.0			
					360.3				
21 June									
Reproductiv			15.6	47.0	62.7			25.0	75.0
Vegetative	31.3	62.7	47.0		141.0	22.2	44.4	33.3	
Secondary	141.0	15.6			156.6	90.0	10.0		
					360.3				
5 July									
Reproductiv			15.6	47.0	62.7			25.0	75.0
Vegetative		47.0	109.6		156.6		30.0	70.0	
Secondary	109.6	15.6			125.3	87.5	12.5		
					344.6				
2 August									
Reproductiv				62.7	62.7				100.0
Vegetative		15.6	141.0		156.6		10.0	90.0	
Secondary	62.7	15.6			78.3	80.0	20.0		
					297.6				

Table 6. Progression of leaf stage development of tiller types in numbers and percentage per square meter on the mid June 25% defoliation treatment of the 4.5 month seasonlong management strategy.

Date Tiller Types	Tiller Numbers Leaf Stage				Tiller Density #/m <sup>2</sup>	Tiller Percentage Leaf Stage			
	1-3	4	5-10	Flower Stage		1-3	4	5-10	Flower Stage
10 May									
Reproductiv	78.3	15.6			94.0	83.3	16.7		
Vegetative	94.0	47.0			141.0	66.7	33.3		
Secondary	156.6				156.6	100.0			
					391.6				
24 May									
Reproductiv	47.0	47.0			94.0	50.0	50.0		
Vegetative	62.7	78.3	15.6		156.6	40.0	50.0	10.0	
Secondary	172.3				172.3	100.0			
					422.9				
7 June									
Reproductiv	31.3	47.0	15.6		94.0	33.3	50.0	16.7	
Vegetative	31.3	125.3	15.6		172.3	18.2	72.7	9.1	
Secondary	156.6				156.6	100.0			
					422.9				
21 June									
Reproductiv		31.3	15.6	47.0	94.0		33.3	16.7	50.0
Vegetative	15.6	62.7	94.0		172.3	9.0	36.4	54.6	
Secondary	156.6				156.6	100.0			
					422.9				
5 July									
Reproductiv			31.3	78.3	109.6			28.6	71.4
Vegetative			156.6		156.6			100.0	
Secondary	125.3	31.3			156.6	80.0	20.0		
					422.9				
2 August									
Reproductiv				109.6	109.6				100.0
Vegetative			156.6		156.6			100.0	
Secondary	109.6	31.3			141.0	77.8	22.2		
					407.2				

Table 7. Progression of leaf stage development of tiller types in numbers and percentage per square meter on the mid June 50% defoliation treatment of the 4.5 month seasonlong management strategy.

Date Tiller Types	Tiller Numbers Leaf Stage				Tiller Density #/m <sup>2</sup>	Tiller Percentage Leaf Stage			
	1-3	4	5-10	Flower Stage		1-3	4	5-10	Flower Stage
10 May									
Reproductiv	78.3				78.3	100.0			
Vegetative	125.3	15.6			141.0	88.9	11.1		
Secondary	94.0				94.0	100.0			
					313.3				
24 May									
Reproductiv	62.7	15.6			78.3	80.0	20.0		
Vegetative	141.0	15.6			156.6	90.0	10.0		
Secondary	109.6				109.6	100.0			
					344.6				
7 June									
Reproductiv		62.7	15.6		78.3		80.0	20.0	
Vegetative	125.3	47.0			172.3	72.7	27.3		
Secondary	94.0				94.0	100.0			
					344.6				
21 June									
Reproductiv			47.0	31.3	78.3			60.0	40.0
Vegetative	31.3	94.0	47.0		172.3	18.2	54.5	27.3	
Secondary	94.0	15.6			109.6	85.6	14.4		
					360.3				
5 July									
Reproductiv			15.6	62.7	78.3			20.0	80.0
Vegetative		47.0	125.3		172.3		27.3	72.7	
Secondary	62.7	31.3	15.6		109.6	57.2	28.6	14.2	
					360.3				
2 August									
Reproductiv				78.3	78.3				100.0
Vegetative			172.3		172.3			100.0	
Secondary	31.3	31.3	15.6		78.3	40.0	40.0	20.0	
					328.9				

Table 8. Progression of leaf stage development of tiller types in numbers and percentage per square meter on the control treatment of the 4.5 month twice-over rotation management strategy.

Date Tiller Types	Tiller Numbers				Tiller Density #/m <sup>2</sup>	Tiller Percentage			
	Leaf Stage			Flower Stage		Leaf Stage			Flower Stage
	1-3	4	5-10			1-3	4	5-10	
10 May									
Reproductiv	219.3	78.3	47.0		344.6	63.6	22.7	13.7	
Vegetative	235.0	47.0			281.9	83.3	16.7		
Secondary	297.6	31.3			328.9	90.5	9.5		
					955.4				
24 May									
Reproductiv	141.0	109.6	94.0		344.6	40.9	31.8	27.2	
Vegetative	203.6	62.7	15.6		281.9	72.2	22.2	5.6	
Secondary	188.0	125.3	15.6		328.9	57.2	38.0	4.8	
					955.4				
7 June									
Reproductiv	62.7	94.0	188.0		344.6	18.2	27.3	54.5	
Vegetative	62.7	141.0	47.0		250.6	25.0	56.3	18.7	
Secondary	203.6	62.7	15.6		281.9	72.2	22.2	5.6	
					877.1				
21 June									
Reproductiv	31.3	62.7	219.3	47.0	360.3	8.7	17.4	60.8	13.1
Vegetative	31.3	94.0	156.6		281.9	11.1	33.3	55.5	
Secondary	172.3	31.3	31.3		235.0	73.3	13.3	13.3	
					877.1				
5 July									
Reproductiv	15.6		156.6	188.0	360.3	4.3		43.5	52.2
Vegetative		31.3	235.0		266.3		11.8	88.2	
Secondary	141.0	78.3	31.3		250.6	56.3	31.2	12.5	
					877.1				
2 August									
Reproductiv			31.3	328.9	360.3			8.7	91.3
Vegetative			235.0		235.0			100.0	
Secondary	78.3	109.6	62.7		250.6	31.3	43.7	25.0	
					845.8				



Table 9. Progression of leaf stage development of tiller types in numbers and percentage per square meter on the mid June 25% defoliation treatment of the 4.5 month twice-over rotation management strategy.

Date Tiller Types	Tiller Numbers Leaf Stage				Tiller Density #/m <sup>2</sup>	Tiller Percentage Leaf Stage			
	1-3	4	5-10	Flower Stage		1-3	4	5-10	Flower Stage
10 May									
Reproductiv	94.0	78.3			172.3	54.6	45.4		
Vegetative	360.3	188.0			548.2	65.7	34.3		
Secondary	297.6	15.6			313.3	95.0	5.0		
					1033.8				
24 May									
Reproductiv	31.3	94.0	47.0		172.3	18.2	54.5	27.3	
Vegetative	188.0	297.6	78.3		563.9	33.3	52.8	13.9	
Secondary	313.3				313.3	100.0			
					1049.4				
7 June									
Reproductiv		47.0	125.3		172.3		27.3	72.7	
Vegetative		297.6	235.0		532.5		55.9	44.1	
Secondary	344.6	15.6			360.3	95.7	4.3		
					1065.1				
21 June									
Reproductiv		31.3	109.6	31.3	172.3		18.2	63.6	18.2
Vegetative		172.3	407.2		579.5		29.7	70.3	
Secondary	266.3	47.0			313.3	85.0	15.0		
					1065.1				
5 July									
Reproductiv			62.7	109.6	172.3			36.4	63.6
Vegetative			516.9		516.9			100.0	
Secondary	203.6	125.3	78.3		407.2	50.0	30.8	19.2	
					1096.4				
2 August									
Reproductiv				172.3	172.3				100.0
Vegetative			516.9		516.9			100.0	
Secondary	156.6	94.0	47.0		297.6	52.6	31.6	15.8	
					986.8				

Table 10. Progression of leaf stage development of tiller types in numbers and percentage per square meter on the mid June 50% defoliation treatment of the 4.5 month twice-over rotation management strategy.

Date Tiller Types	Tiller Numbers Leaf Stage				Tiller Density #/m <sup>2</sup>	Tiller Percentage Leaf Stage			
	1-3	4	5-10	Flower Stage		1-3	4	5-10	Flower Stage
10 May									
Reproductiv	62.7	109.6			172.3	36.4	63.6		
Vegetative	344.6	47.0	15.6		407.2	84.6	11.6	3.8	
Secondary	109.6	15.6			125.3	87.5	12.5		
					704.8				
24 May									
Reproductiv	47.0	62.7	125.3		235.0	20.0	26.7	53.3	
Vegetative	219.3	172.3	31.3		422.9	51.8	40.8	7.4	
Secondary	172.3				172.3	100.0			
					830.1				
7 June									
Reproductiv	31.3	47.0	172.3		250.6	12.5	18.8	68.7	
Vegetative	94.0	172.3	156.6		422.9	22.2	40.8	37.0	
Secondary	109.6	15.6			125.3	87.5	12.5		
					798.8				
21 June									
Reproductiv		15.6	141.0	94.0	250.6		6.2	56.3	37.5
Vegetative	31.3	109.6	297.6		438.6	7.2	25.0	67.8	
Secondary	62.7	78.3			141.0	44.4	55.6		
					830.1				
5 July									
Reproductiv			62.7	188.0	250.6			25.0	75.0
Vegetative		31.3	360.3		391.6		8.0	92.0	
Secondary	62.7	125.3			188.0	33.3	66.7		
					830.1				
2 August									
Reproductiv			15.6	235.0	250.6			6.2	93.8
Vegetative			391.6		391.6			100.0	
Secondary		94.0	15.6		109.6		85.7	14.3	
					751.8				

Table 11a. Prorated mean leaf stage of reproductive lead tillers during biweekly periods.

Tiller Type Management Strategy Treatment	Biweekly Periods						
	10 May	24 May	7 Jun	21 Jun	5 Jul	20 Jul	2 Aug
Reproductive							
6.0 m SL							
Control	3.41	4.08	4.91	8.75	11.66	12.00	12.00
June 25%	3.33	4.10	4.66	7.66	10.43	11.33	11.33
June 50%	3.22	3.94	4.42	8.88	12.00	12.00	12.00
4.5 m SL							
Control	2.87	3.74	4.24	10.24	10.24	12.00	12.00
June 25%	3.16	3.50	3.83	8.16	10.00	12.00	12.00
June 50%	2.70	3.20	4.20	7.80	10.80	10.80	12.00
4.5 m TOR							
Control	3.16	3.77	4.57	5.78	8.96	10.82	11.65
June 25%	3.45	4.09	4.73	6.36	9.90	11.54	12.00
June 50%	3.50	4.33	4.69	8.06	10.56	11.81	11.81
Mean Tiller	3.20	3.86	4.47	7.97	10.51	11.59	11.87

Table 11b. Prorated mean leaf stage of vegetative lead tillers during biweekly periods.

Tiller Type Management Strategy Treatment	Biweekly Periods						
	10 May	24 May	7 Jun	21 Jun	5 Jul	20 Jul	2 Aug
Vegetative							
6.0 m SL							
Control	3.20	3.73	4.53	5.33	6.43	6.93	7.38
June 25%	2.91	3.59	4.12	4.75	5.62	6.00	6.66
June 50%	3.07	3.50	4.10	4.75	5.79	6.32	6.74
4.5 m SL							
Control	2.61	3.33	3.78	4.11	4.90	5.20	5.90
June 25%	3.33	3.70	3.91	4.64	5.40	5.90	6.50
June 50%	2.94	2.95	3.00	4.09	5.00	5.46	5.91
4.5 m TOR							
Control	2.83	3.25	3.94	4.56	5.17	5.64	6.13
June 25%	3.34	3.81	4.47	4.95	5.82	6.67	7.27
June 50%	2.90	3.44	4.15	4.68	5.44	5.96	6.64
Mean Tiller	3.01	3.48	4.00	4.65	5.51	6.01	6.57

Table 11c. Prorated mean leaf stage of secondary tillers during biweekly periods.

Tiller Type Management Strategy Treatment	Biweekly Periods						
	10 May	24 May	7 Jun	21 Jun	5 Jul	20 Jul	2 Aug
Secondary							
6.0 m SL							
Control	2.19	2.54	2.77	2.92	3.33	3.32	3.86
June 25%	2.69	2.99	2.94	3.33	3.33	3.33	3.27
June 50%	2.16	2.21	2.39	2.39	2.70	2.55	2.37
4.5 m SL							
Control	1.83	2.17	2.55	2.65	2.75	2.83	3.20
June 25%	2.10	2.32	2.55	2.70	2.90	2.72	2.89
June 50%	1.75	2.14	2.25	2.50	3.14	3.69	3.49
4.5 m TOR							
Control	2.67	3.05	2.75	3.10	3.37	3.50	3.84
June 25%	2.00	2.25	2.52	2.62	3.44	3.41	3.52
June 50%	2.56	3.00	3.12	3.56	3.67	4.14	4.14
Mean Tiller	2.22	2.52	2.65	2.86	3.18	3.28	3.40

Table 12. Growing season changes in the numbers and percentages per square meter of reproductive lead tillers between the 4 leaf stage and flower stage on three defoliation treatments of three management strategies.

Date Management Strategy	Control Treatment		June 25% Treatment		June 50% Treatment	
	Tiller Numbers	Tiller Percentage	Tiller Numbers	Tiller Percentage	Tiller Numbers	Tiller Percentage
10 May						
6.0 m SL	78.3	41.7	78.3	55.5	47.0	42.9
4.5 m SL	15.6	25.0	15.6	16.7	0.0	0.0
4.5 m TOR	125.3	36.4	78.3	45.4	109.6	63.6
24 May						
6.0 m SL	172.3	91.7	109.6	77.8	109.6	77.8
4.5 m SL	31.3	50.0	47.0	50.0	15.6	20.0
4.5 m TOR	203.6	59.0	141.0	81.8	188.0	80.0
7 June						
6.0 m SL	188.0	100.0	125.3	88.8	94.0	66.6
4.5 m SL	47.0	75.0	62.7	66.7	78.3	100.0
4.5 m TOR	281.9	81.8	172.3	100.0	219.3	87.5
21 June						
6.0 m SL	94.0	50.0	94.0	66.6	62.7	44.4
4.5 m SL	15.6	25.0	47.0	50.0	47.0	60.0
4.5 m TOR	281.9	78.2	141.0	81.8	156.6	62.5
5 July						
6.0 m SL	15.6	8.3	47.0	33.3	0.0	0.0
4.5 m SL	15.6	25.0	31.3	28.6	15.6	20.0
4.5 m TOR	156.6	43.5	62.7	36.4	62.7	25.0
20 July						
6.0 m SL	0.0	0.0	15.6	11.1	0.0	0.0
4.5 m SL	0.0	0.0	0.0	0.0	15.6	20.0
4.5 m TOR	47.0	21.7	15.6	9.1	15.6	6.2
2 August						
6.0 m SL	0.0	0.0	15.6	11.1	0.0	0.0
4.5 m SL	0.0	0.0	0.0	0.0	0.0	0.0
4.5 m TOR	31.3	8.7	0.0	0.0	15.6	6.2

Table 13. Growing season changes in the numbers and percentages per square meter of vegetative lead tillers between the 4 leaf stage and 10 leaf stage on three defoliation treatments of three management strategies.

Date Management Strategy	Control Treatment		June 25% Treatment		June 50% Treatment	
	Tiller Numbers	Tiller Percentage	Tiller Numbers	Tiller Percentage	Tiller Numbers	Tiller Percentage
10 May						
6.0 m SL	47.0	20.0	47.0	17.6	47.0	15.0
4.5 m SL	15.6	11.1	47.0	33.3	15.6	11.1
4.5 m TOR	47.0	16.7	188.0	34.3	62.7	15.4
24 May						
6.0 m SL	172.3	73.3	94.0	35.3	188.0	57.2
4.5 m SL	47.0	33.3	94.0	60.0	15.6	10.0
4.5 m TOR	78.3	27.8	375.9	66.7	203.6	48.1
7 June						
6.0 m SL	235.0	100.0	188.0	75.0	250.6	80.0
4.5 m SL	78.3	55.5	141.0	81.8	47.0	27.3
4.5 m TOR	188.0	75.0	532.5	100.0	328.9	77.8
21 June						
6.0 m SL	235.0	100.0	250.6	100.0	313.3	100.0
4.5 m SL	109.6	77.7	156.6	90.9	141.0	81.8
4.5 m TOR	250.6	88.9	579.5	100.0	407.2	92.8
5 July						
6.0 m SL	219.3	100.0	250.6	100.0	297.6	100.0
4.5 m SL	156.6	100.0	156.6	100.0	172.3	100.0
4.5 m TOR	266.3	100.0	516.9	100.0	391.6	100.0
20 July						
6.0 m SL	219.3	100.0	250.6	100.0	297.6	100.0
4.5 m SL	156.6	100.0	156.6	100.0	172.3	100.0
4.5 m TOR	266.3	100.0	516.9	100.0	391.6	100.0
2 August						
6.0 m SL	203.6	100.0	235.0	100.0	297.6	100.0
4.5 m SL	156.6	100.0	156.6	100.0	172.3	100.0
4.5 m TOR	235.0	100.0	516.9	100.0	391.6	100.0

Table 14. Growing season changes in the numbers and percentages per square meter of secondary tillers between the 4 leaf stage and 8 leaf stage on three defoliation treatments of three management strategies.

Date Management Strategy	Control Treatment		June 25% Treatment		June 50% Treatment	
	Tiller Numbers	Tiller Percentage	Tiller Numbers	Tiller Percentage	Tiller Numbers	Tiller Percentage
10 May						
6.0 m SL	0.0	0.0	31.3	40.0	15.6	16.7
4.5 m SL	0.0	0.0	0.0	0.0	0.0	0.0
4.5 m TOR	31.3	9.5	15.6	5.0	15.6	12.5
24 May						
6.0 m SL	0.0	0.0	31.3	33.3	31.3	28.6
4.5 m SL	0.0	0.0	0.0	0.0	0.0	0.0
4.5 m TOR	141.0	42.8	0.0	0.0	0.0	0.0
7 June						
6.0 m SL	47.0	23.0	31.3	25.0	31.3	22.2
4.5 m SL	0.0	0.0	0.0	0.0	0.0	0.0
4.5 m TOR	78.3	27.8	15.6	4.3	15.6	12.5
21 June						
6.0 m SL	78.3	38.4	62.7	44.4	31.3	22.2
4.5 m SL	15.6	10.0	0.0	0.0	15.6	14.4
4.5 m TOR	62.7	26.6	47.0	15.0	78.3	55.6
5 July						
6.0 m SL	125.3	53.3	62.7	44.4	47.0	30.0
4.5 m SL	15.6	12.5	31.3	20.0	47.0	42.8
4.5 m TOR	109.6	43.7	203.6	50.0	125.3	66.7
20 July						
6.0 m SL	109.6	50.0	78.3	55.5	31.3	22.2
4.5 m SL	31.3	33.3	31.3	22.2	47.0	60.0
4.5 m TOR	141.0	56.3	156.6	43.5	94.0	85.8
2 August						
6.0 m SL	109.6	63.7	78.3	45.4	15.6	12.5
4.5 m SL	15.6	20.0	31.3	22.2	47.0	60.0
4.5 m TOR	172.3	68.7	141.0	47.4	109.6	100.0



Table 15. Growing season changes in the numbers and percentages per square meter of total tillers between the 4 leaf stage and flower stage on three defoliation treatments of three management strategies.

Date Management Strategy	Control Treatment		June 25% Treatment		June 50% Treatment	
	Tiller Numbers	Tiller Percentage	Tiller Numbers	Tiller Percentage	Tiller Numbers	Tiller Percentage
10 May						
6.0 m SL	125.3	20.0	156.6	32.2	109.6	21.2
4.5 m SL	31.3	9.1	62.7	16.0	15.6	5.0
4.5 m TOR	203.6	21.3	281.9	27.3	188.0	26.6
24 May						
6.0 m SL	344.6	55.0	235.0	46.8	328.9	56.7
4.5 m SL	78.3	22.7	141.0	33.3	31.3	9.1
4.5 m TOR	422.9	44.2	516.9	49.2	391.6	47.2
7 June						
6.0 m SL	469.9	75.0	344.6	66.7	375.9	63.2
4.5 m SL	125.3	34.7	203.6	48.1	125.3	36.3
4.5 m TOR	548.2	62.4	720.5	67.7	563.9	70.6
21 June						
6.0 m SL	407.2	65.0	407.2	76.5	407.2	68.4
4.5 m SL	141.0	39.1	203.6	48.1	203.6	56.5
4.5 m TOR	595.2	67.8	767.5	72.1	642.2	77.3
5 July						
6.0 m SL	360.3	56.1	360.3	67.6	344.6	57.9
4.5 m SL	188.0	54.6	219.3	51.8	235.0	65.2
4.5 m TOR	532.5	60.7	783.2	71.4	579.5	69.9
20 July						
6.0 m SL	328.9	52.5	344.6	64.7	328.9	56.8
4.5 m SL	188.0	60.0	188.0	46.1	235.0	71.5
4.5 m TOR	454.2	53.6	689.2	65.7	501.2	66.7
2 August						
6.0 m SL	313.3	55.5	328.9	59.9	313.3	55.6
4.5 m SL	172.3	57.8	188.0	46.1	219.3	66.7
4.5 m TOR	438.6	51.9	657.8	66.7	516.9	68.7

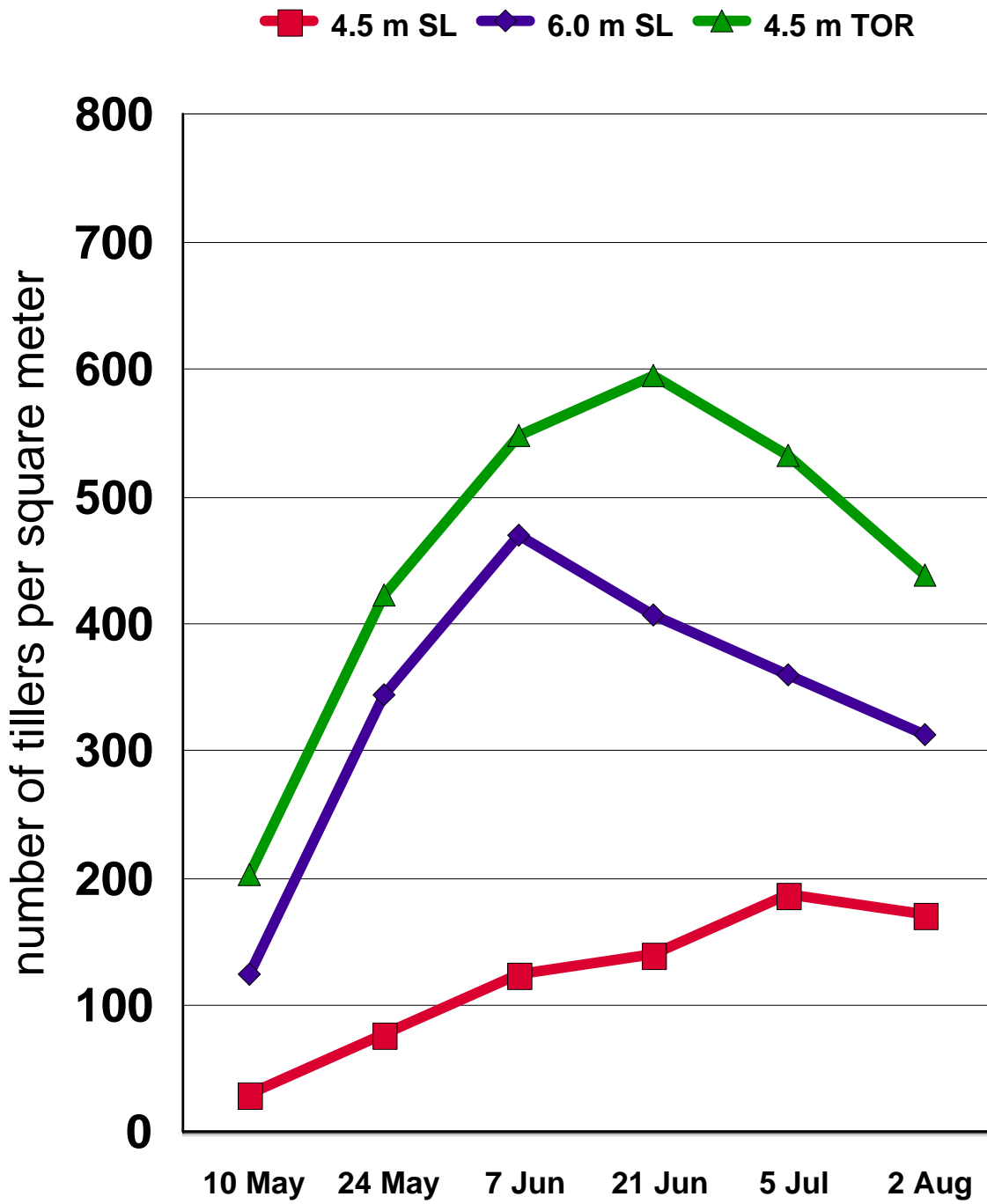


Figure 1. Number of total tillers per square meter between the 4 leaf stage and flower stage on the control treatments of three management strategies.

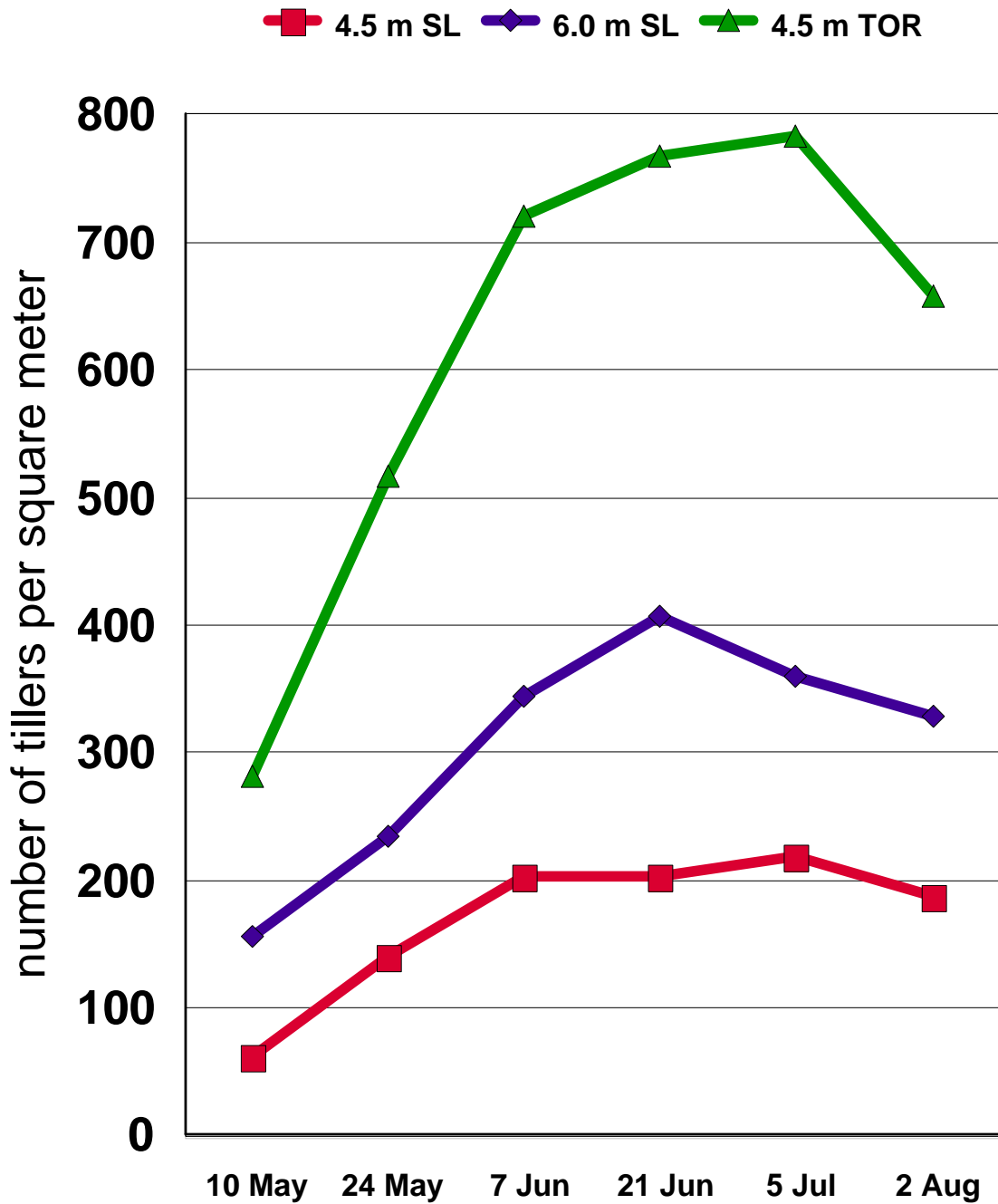


Figure 2. Number of total tillers per square meter between the 4 leaf stage and flower stage on the June 25% defoliation treatments of three management strategies.

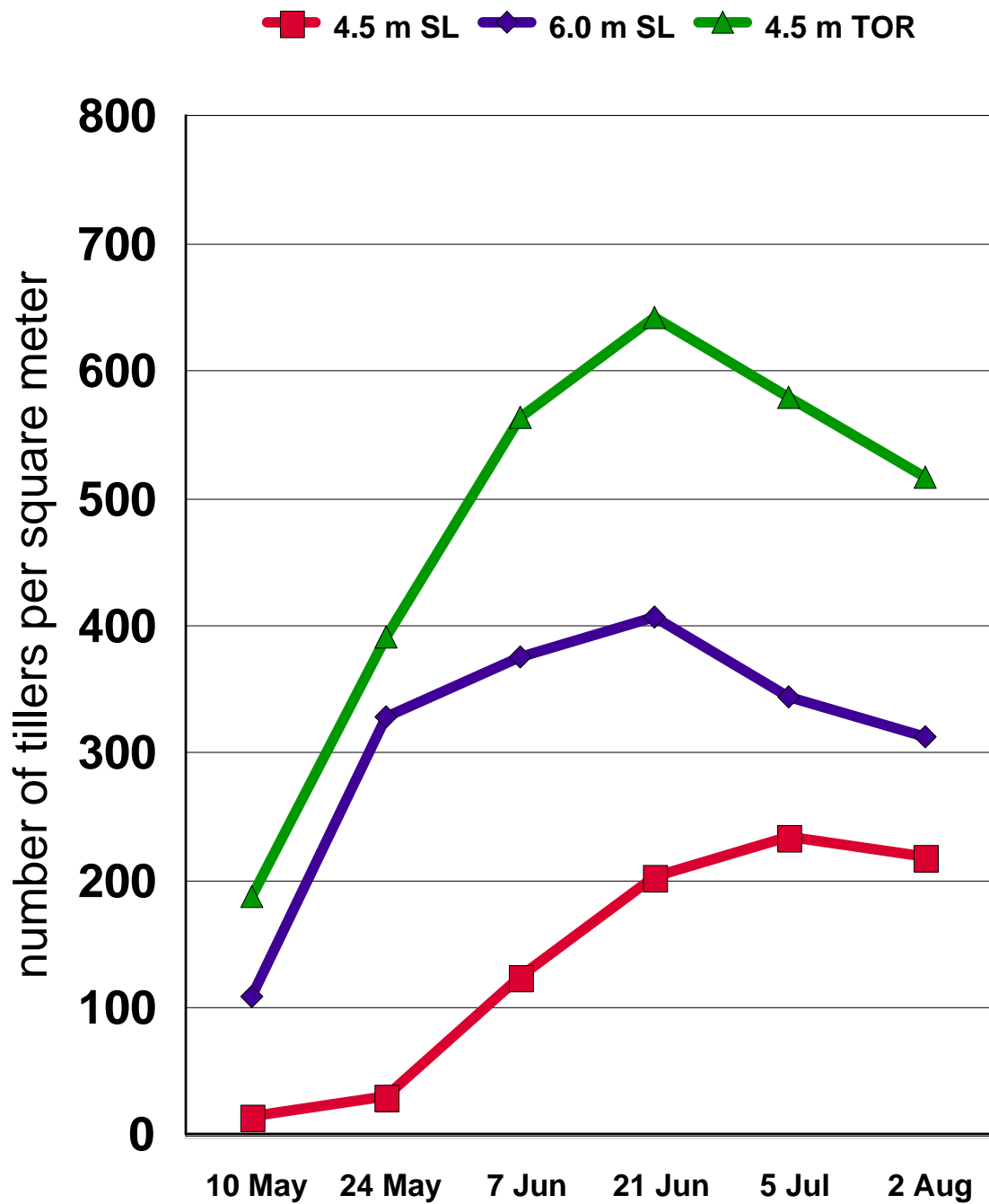


Figure 3. Number of total tillers per square meter between the 4 leaf stage and flower stage on the June 50% defoliation treatments of three management strategies.

Table 16. Mean tiller density per square meter of total 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).

## Literature Cited

- Anderson, R.V., D.C. Coleman, C.V. Cole, and E.T. Elliott. 1981.** Effect of nematodes *Acroboloides 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. Pflieger. 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. 7<sup>th</sup> 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.