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

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Report DREC 10-1076

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

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

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

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

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

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

Study Area

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

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

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

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

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

Procedures

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

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

Results

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

Initiated Secondary Tillers

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

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

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

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

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

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

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

Densities of Tiller Types

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

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

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

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

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

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

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

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

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

Discussion

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

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

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

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

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

Acknowledgment

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

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

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

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

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

Data from Manske 2009.

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

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

Data from Manske 2009.

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

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

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

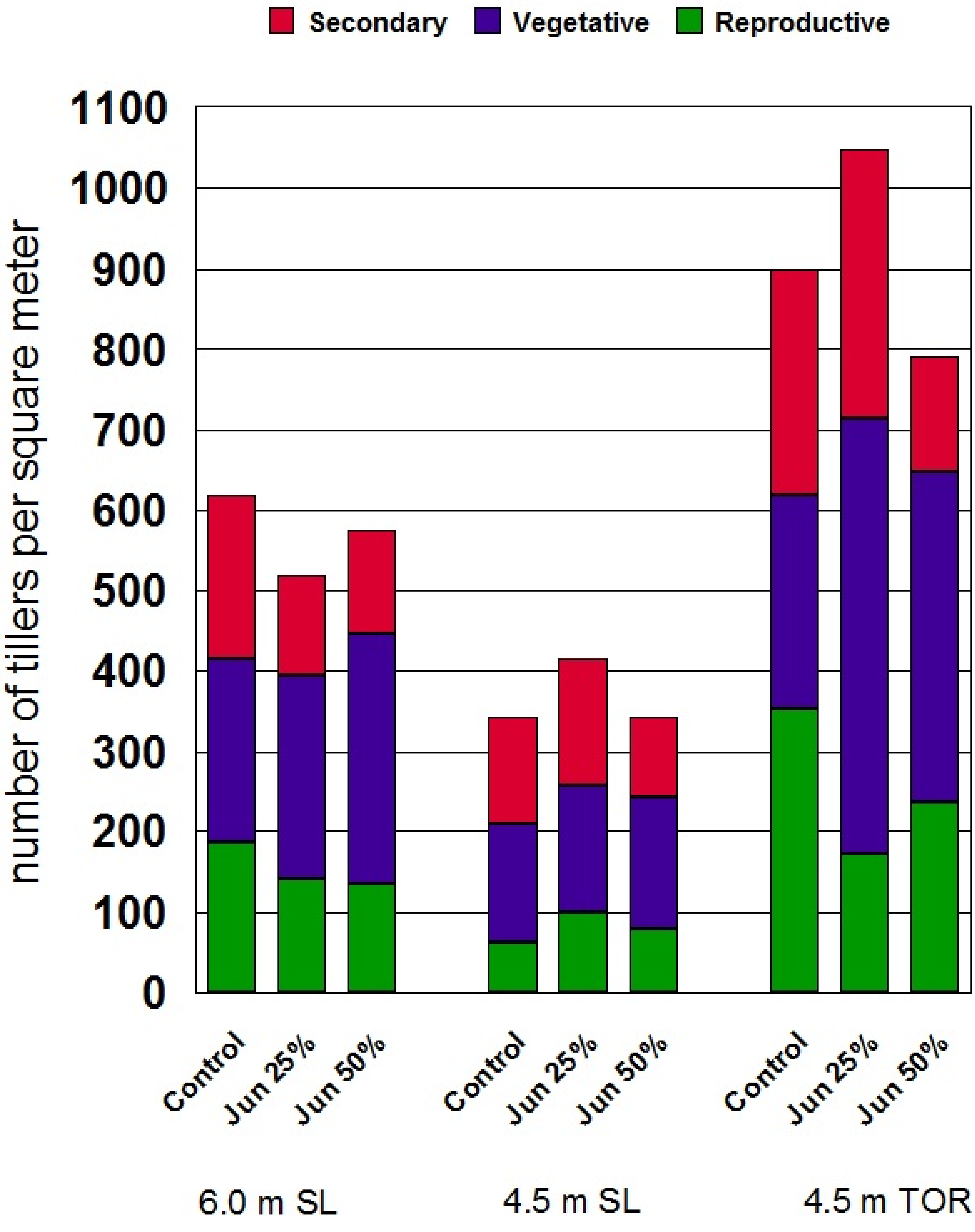

Figure 1. Seasonal mean tiller numbers per square meter on the three defoliation treatments of three management strategies.

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