Grass Vegetative Tillering Responses to Partial Defoliation

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

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

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

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

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

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

Study Area

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

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

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

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

Procedures

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

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

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

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

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

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

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

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

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

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

Results

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

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

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

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

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

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

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

Tiller Dynamics

Control Treatment

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

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

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

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

Mid June 25% Treatment

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

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

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

Mid June 50% Treatment

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

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

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

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

Tiller Density

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

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

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

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

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

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

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

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

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

Tiller Initiation

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

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

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

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

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

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

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

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

Tiller Termination

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

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

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

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

Tiller Leaf Height

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

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

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

Tiller Growth and Development

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

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

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

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

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

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

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

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

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

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

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

Discussion

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

Summary

Northern Plains ranchers who implemented the biologically effective twice-over rotation management strategy found that it required three to five years before grass tiller density increased significantly. An intensive timing and severity defoliation treatment study was conducted with western wheatgrass to determine treatments that activated vegetative reproduction of tillers from axillary buds. Two defoliation treatments and a control with seven microplots each were established on silty range sites in 6.0 month seasonlong (6.0 m SL), 4.5 month seasonlong (4.5 m SL), and 4.5 month twice-over rotation (4.5 m TOR) management strategies. Mean annual tiller densities on the control treatments were 532.6 $/m^2$, 908.5 $/m^2$, and 1331.4 $/m^2$; on the June 25% treatments were 626.5 $/m^2$, 861.5 $/m^2$, and 1441.0 $/m^2$; and on the June 50% treatments

were 548.2 /m^2, 877.2 /m^2, and 1206.1 /m^2 of the 4.5 m SL, 6.0 m SL, and 4.5 m TOR management strategies, respectively. Fewer vegetative tillers were maintained on the control treatment than on the June 25% and June 50% treatments of the 4.5 m SL management strategy. Fewer vegetative tillers were produced on the June 25% and June 50% treatments than on the control treatment of the 6.0 m SL management strategy. Fewer vegetative tillers were maintained on the June 50% treatment than on the control treatment of the 4.5 m TOR management strategy and greater numbers of vegetative tillers were produced on the June 25% treatment than on the control treatment of the 4.5 m TOR management strategy. Removal of 25% of the leaf material from grass tillers between the three and a half new leaf stage and the flower stage produces the greatest number of vegetative tillers from axillary buds when soil mineral nitrogen is available at quantities greater than 100 lbs/ac. Twenty five percent removal of leaf weight during vegetative growth stages also removed sufficient quantities of the growth-inhibiting hormone, auxin, permitting synthesis or utilization of the growth hormone, cytokinin, in the axillary buds, and activating the asexual process of vegetative production of tillers. On the June 25% treatment of the 4.5 m TOR management strategy there was adequate quantities of available mineral nitrogen and the remaining 75% leaf weight had sufficient leaf area to fix carbon at adequate quantities for growth and development of the tillers from the activated axillary buds. On the June 25% treatments of the 6.0 m SL and 4.5 m SL management strategies, the process of vegetative tiller production was activated by the defoliation treatment, however, the required quantity of mineral nitrogen was not available for growth and development of the tillers. On the June 50% treatment of the 4.5 m TOR management strategy, the defoliation treatment activated the process of vegetative tillering, adequate quantities of mineral nitrogen was available, however, the remaining 50% leaf area could not supply adequate quantities of fixed carbon causing fewer tillers to develop. On the June 50% treatments of the 6.0 m SL and 4.5 m SL management strategies, the vegetative tillering process was activated, however, adequate quantities of mineral nitrogen and fixed carbon were not available. On the control treatments of the 6.0 m SL, 4.5 m SL and 4.5 m TOR management strategies, because there was no defoliation treatment, the process of vegetative tiller production was not activated, however, some vegetative tillers were produced; these processes do not stop instantaneously, the quantity of vegetative tillers would decrease at the rates the respective decrease in available mineral nitrogen and fixed carbon down to producing one vegetative tiller per lead tiller and then the number of lead tillers would soon be reduced. These processes do not start instantaneously either, it has been taking three to five years with annual removal of 25% of the leaf material during vegetative growth stages before the tiller numbers increase adequately. The soil rhizosphere organisms need to increase in biomass and activity before they can mineralize 100 lbs/ac of organic nitrogen. The increase in rhizosphere organisms requires an increase in the quantity of exudated short chain carbon energy from the grass plants, which requires annual removal of 25% of the leaf material during vegetative growth stages.

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

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

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

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

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

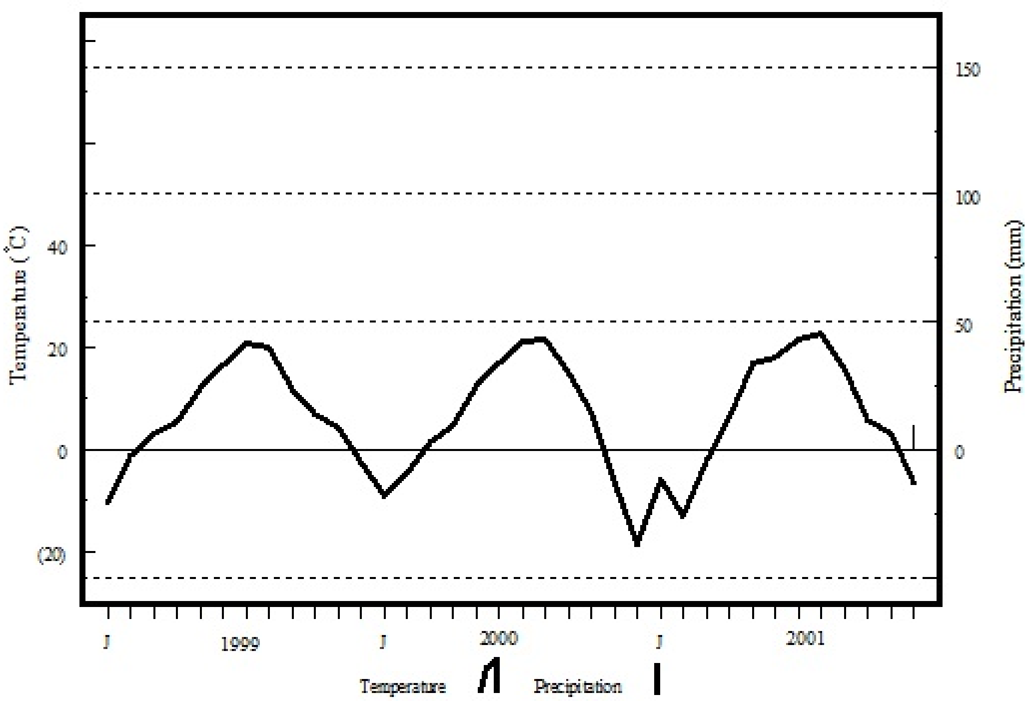

Fig. 1. Ombrothermic diagram of 1999-2001 mean monthly temperature and monthly precipitation at DREC Ranch, Manning, North Dakota.

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

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

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

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

Treatment Management Strategy	Live tillers early May #/m^2	New tillers first season #/m^2	Total first season tillers #/m^2	Tillers at flower stages #/m^2	Dead tillers first season #/m^2	Live tillers fall #/m^2	New fall tillers #/m^2	Total live tillers mid October #/m^2	Dead tillers winter period #/m^2
Control									
6.0 m SL	469.9b	0.0c	469.9b	219.3b	31.3c	219.3b	219.3b	438.6b	0.0c
4.5 m SL	281.9c	0.0c	281.9c	94.0b	62.7b	125.3c	94.0c	219.3c	0.0c
4.5 m TOR	877.1a	62.7b	939.8a	344.6a	250.6b	344.6b	250.6b	595.2b	31.3b
June 25%									
6.0 m SL	469.9b	62.7b	532.5b	94.0b	31.3c	407.2b	125.3b	532.5b	62.7b
4.5 m SL	438.6b	31.3b	469.9b	94.0b	156.6b	219.3b	125.3b	344.6b	0.0c
4.5 m TOR	971.1a	62.7b	1033.8a	156.6b	407.2a	469.9b	344.6b	814.5b	188.0b
June 50%									
6.0 m SL	563.9b	62.7b	626.5b	156.6b	62.7b	407.2b	188.0b	595.2b	156.6b
4.5 m SL	375.9c	0.0c	375.9c	62.7b	125.3b	188.0b	156.6b	344.6b	125.3b
4.5 m TOR	720.5a	62.7b	783.2b	219.3b	250.6b	313.3b	344.6b	657.8b	219.3b

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

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

Treatment Management Strategy	Carry over tillers #/m^2	New tillers early spring #/m^2	Live tillers early May #/m^2	New tillers second season #/m^2	Total second season tillers #/m^2	Tillers at flower stages #/m^2	Dead tillers second season #/m^2	Live tillers fall #/m^2	New fall tillers #/m^2	Total live tillers mid October #/m^2
Control										
6.0 m SL	438.6b	344.6b	783.2b	31.3c	814.5b	156.6b	250.6b	407.2b	313.3b	720.5b
4.5 m SL	219.3c	188.0b	407.2b	125.3b	532.5b	31.3c	188.0b	313.3b	156.6b	469.9b
4.5 m TOR	563.9b	469.9a	1033.8a	250.6a	1284.4a	375.9a	438.6a	469.9b	188.0b	657.8b
June 25%										
6.0 m SL	469.9b	31.3b	501.2b	94.0c	595.2b	188.0b	94.0b	313.3b	469.9a	783.2b
4.5 m SL	344.6b	0.0c	344.6c	188.0b	532.5b	125.3b	156.6b	250.6b	125.3c	375.9c
4.5 m TOR	626.5b	469.9a	1096.4a	188.0b	1284.4a	188.0b	281.9b	814.5a	219.3b	1033.8a
June 50%										
6.0 m SL	438.6b	31.3b	469.9b	156.6b	626.5b	125.3b	94.0b	407.2b	313.3b	720.5b
4.5 m SL	219.3c	31.3b	250.6c	94.0c	344.6c	94.0b	94.0b	156.6c	219.3b	375.9c
4.5 m TOR	438.6b	250.6b	689.2b	250.6a	939.8b	281.9a	156.6b	501.2b	344.6b	845.8b

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

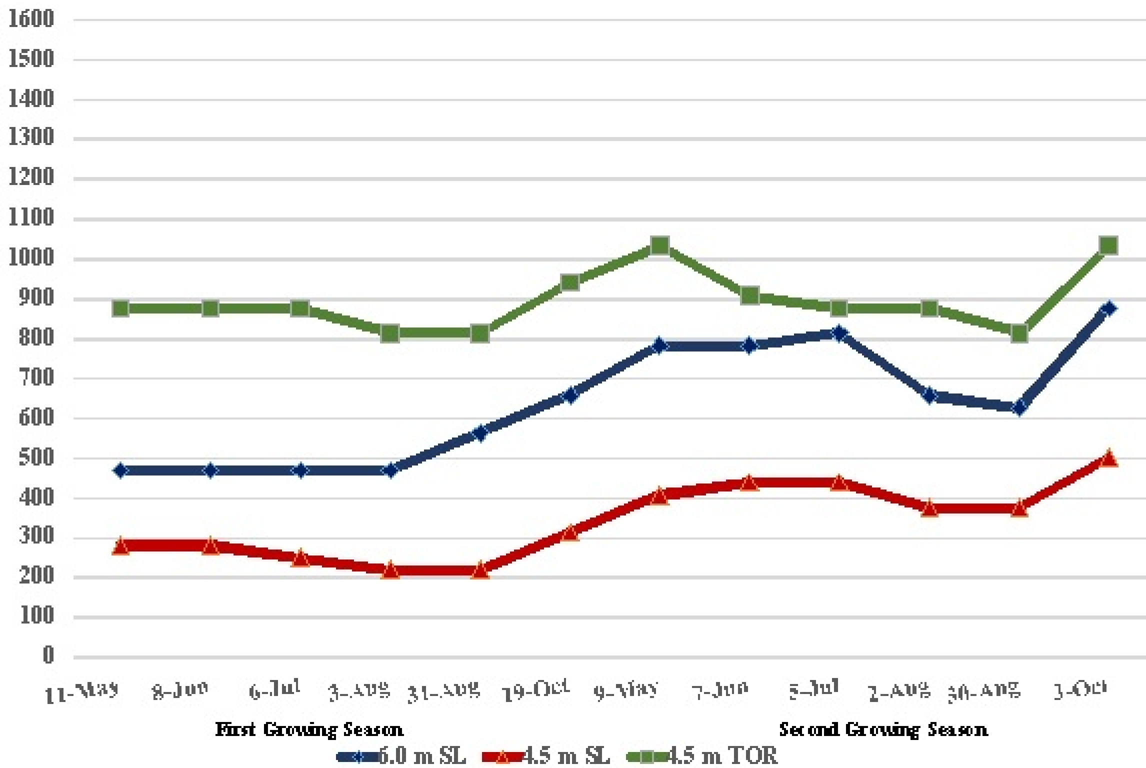

Figure 2. Monthly tiller density per square meter on the control treatments during the first and second growing seasons.

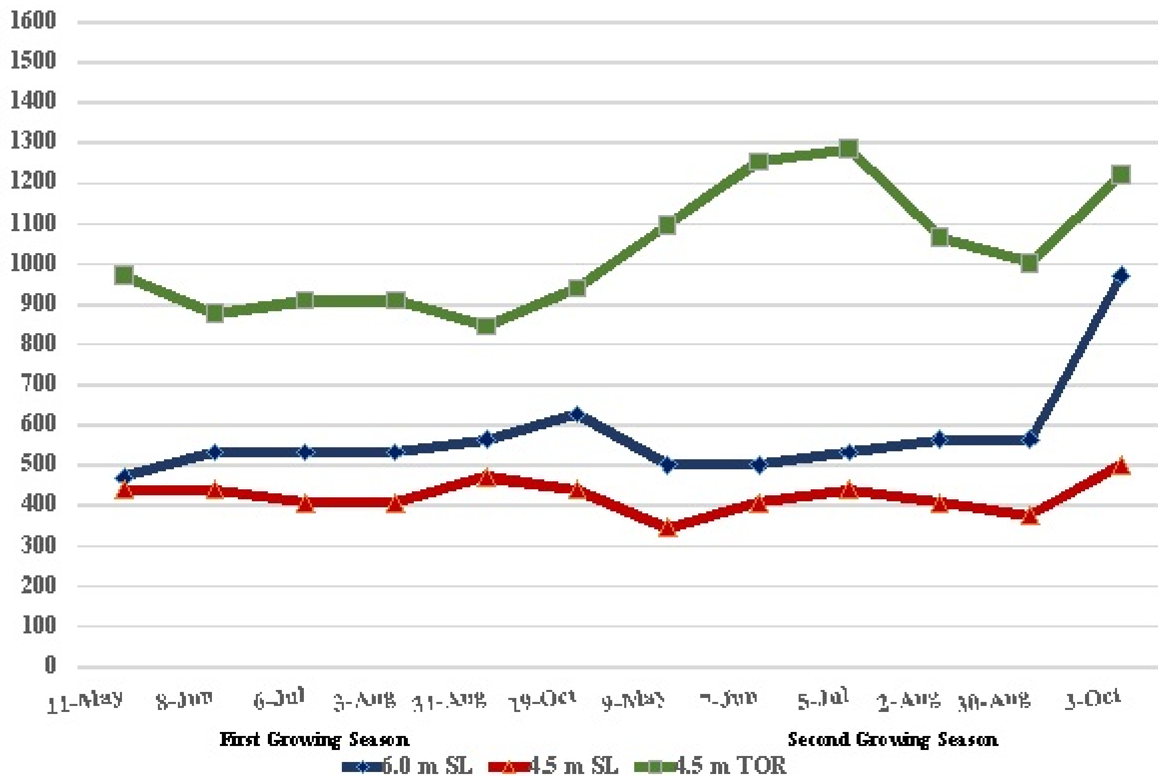

Figure 3. Monthly tiller density per square meter on the mid June 25% defoliation treatments during the first and second growing seasons.

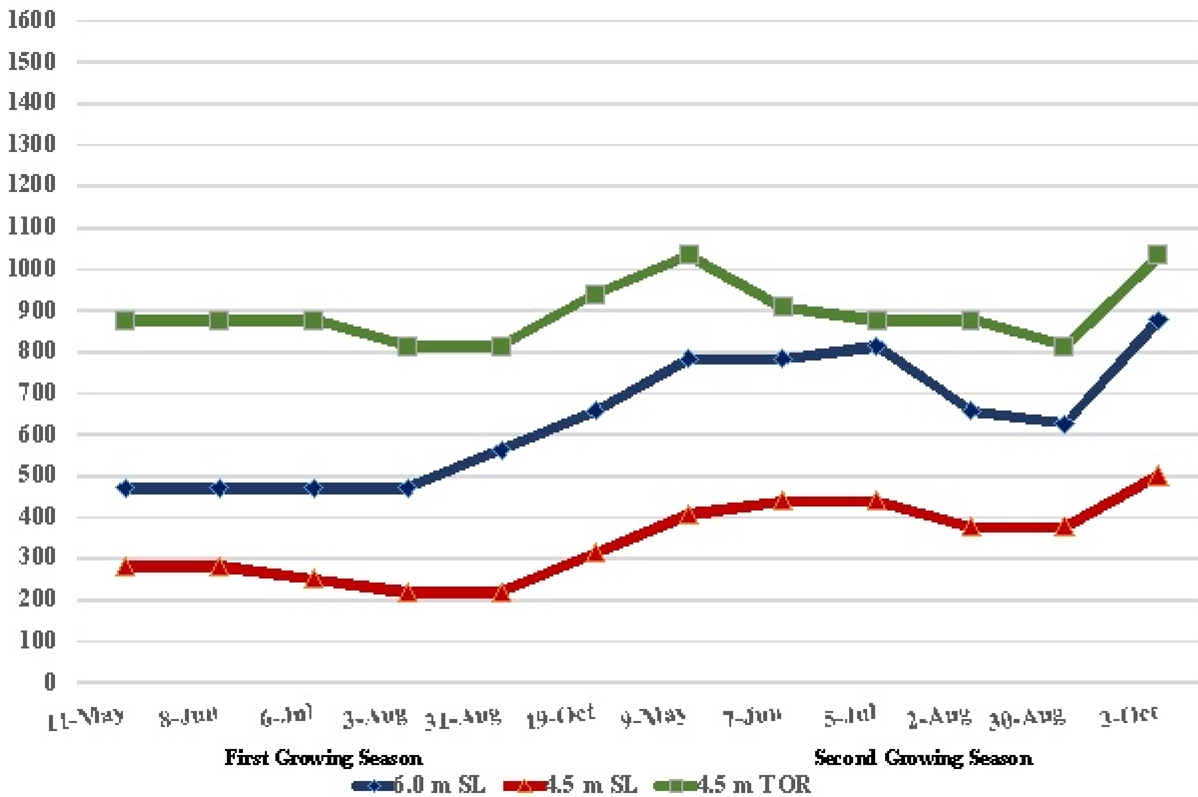

Figure 4. Monthly tiller density per square meter on the mid June 50% defoliation treatments during the first and second growing seasons.

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

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

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

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

Treatment Management Strategy	First Growing Season Tillers #/m^2	Fall Tillers First Year #/m^2	Total Tillers First Year #/m^2	Carry Over Tillers #/m^2	Second Growing Season Tillers #/m^2	Fall Tillers Second Year #/m^2	Total Tillers Second Year #/m^2	Two Year Total Tillers #/m^2
Control								
6.0 m SL	469.9b	219.3b	689.2b	438.6b	814.5b	313.3b	1127.7b	1378.3b
4.5 m SL	281.9c	94.0c	375.9c	219.3c	532.5b	156.6b	689.2c	845.8c
4.5 m TOR	939.8a	250.6b	1190.4b	563.9b	1284.4a	188.0b	1472.3b	2098.8b
June 25%								
6.0 m SL	532.5b	125.3b	657.8b	469.9b	595.2b	469.9a	1065.1b	1253.0b
4.5 m SL	469.9b	125.3b	595.2b	344.6b	532.5b	125.3c	657.8c	908.5c
4.5 m TOR	1033.8a	344.6b	1378.3a	626.5b	1284.4a	219.3b	1503.6b	2255.5a
June 50%								
6.0 m SL	626.5b	188.0b	814.5b	438.6b	626.5b	313.3b	939.8b	1315.7b
4.5 m SL	375.9c	156.6b	532.5c	219.3c	344.6c	219.3b	563.9c	877.1c
4.5 m TOR	783.2b	344.6b	1127.7b	438.6b	939.8b	344.6b	1284.4b	1973.5b

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

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

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

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

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

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

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

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

Treatment Management Strategy	Seasonal Periods				Total Terminated Tillers	Seasonal Periods			
	Early Season #/m²	Mid and Fall Season #/m²	Flowering Lead Tillers #/m²	Winter Period #/m²	#/m²	Early Season %	Mid and Fall Season %	Flowering Lead Tillers %	Winter Period %
Control									
6.0 m SL	0.0b	281.9b	375.9b	0.0c	657.8b	0.0b	42.9b	57.1a	0.0c
4.5 m SL	0.0b	250.6b	125.3c	0.0c	375.9c	0.0b	66.7a	33.3b	0.0c
4.5 m TOR	281.9a	407.2b	720.5a	31.3b	1441.0a	19.5a	28.3b	50.0b	2.2c
June 25%									
6.0 m SL	0.0b	125.3c	281.9b	62.7b	469.9b	0.0b	26.7c	60.0a	13.3b
4.5 m SL	0.0b	313.3b	219.3b	0.0c	532.5b	0.0b	58.8a	41.2b	0.0c
4.5 m TOR	125.3a	563.9b	344.6b	188.0b	1221.7b	10.3a	46.2b	28.2b	15.3b
June 50%									
6.0 m SL	0.0b	156.6b	281.9b	156.6b	595.2b	0.0b	26.3c	47.4b	26.3b
4.5 m SL	0.0b	219.3b	156.6c	125.3b	501.2b	0.0b	43.8b	31.2b	25.0b
4.5 m TOR	31.3b	375.9b	501.2a	219.3b	1127.7b	2.8b	33.3b	44.4b	19.5b

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

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